Ecology and movements of the Australian Bustard *Ardeotis australis* in a dynamic landscape

Mark Ziembicki

School of Earth & Environmental Sciences
University of Adelaide

Thesis submitted for the degree
of Doctor of Philosophy

August 2009

Chapter 1

Talking Turkey: Introduction

Steve Wilson

The Bustard is an exquisite fowl
With minimal reason to growl
It escapes what would be
Illegitimacy
By the grace of a fortunate vowel.

Elizabeth Livingston

Chapter 1

Talking Turkey: Introduction

GENERAL INTRODUCTION

The Australian continent is unique. Among the world's major landmasses Australia is isolated, is of comparatively limited area and is characterised by some of the greatest extremes of climatic and environmental variability of any region on the planet (Stafford Smith and Morton 1990). More than 70% (6 million km^2) of the continent is classified as rangelands, which include the low and highly variable rainfall regions of the arid and semi-arid interior, and the markedly seasonal and comparatively high rainfall areas of the northern tropical savannas. These characteristics are among the primary factors that drive Australia's unique ecology, and the many and varied adaptations of its flora and fauna (Stafford Smith and Morton 1990; Woinarski *et al.* 2005).

Australia's birds are adapted to cope with the environment's variability and extreme conditions through a variety of strategies. Species or populations may exhibit boom-bust population fluctuations, switch diets to exploit available resources opportunistically, be able to tolerate lean periods, change activity rates, or move to more productive regions as required (Dawson 1981; Dean 2004; Maclean 1996; Ward 2008). While these strategies synergise in different ways to determine an organism's ultimate response to its environment, for birds in particular, among the most important mechanisms for coping with change is their mobility. Australia's birds exhibit a variety of movement strategies that differ fundamentally from many of their northern hemisphere counterparts. A defining feature is their flexibility. There are comparatively few 'traditional' migrants, instead a significant proportion of the avifauna is characterised by nomadic, irruptive or partial movements, with movements across the landscape often occurring to exploit favourable conditions opportunistically (Chan 2001; Gilmore *et al.* 2007; Griffioen and Clarke 2002; Kingsford and Norman 2002; Nix 1976; Roshier *et al.* 2001a). However, despite (or in part because of) the apparent prevalence of such strategies, these movements and the population dynamics of the majority of Australia's birds are poorly understood.

Recent advances in satellite telemetry and spatial information systems have provided biologists with unprecedented opportunities for examining the movement patterns of fauna over broad spatial and temporal scales (Grigg *et al.* 1995; Jiguet and Villarubias 2004; Meyburg and Meyburg 1998; Roshier *et al.* 2006; Stokes and Boersma 1998; Verlinden and Gavor 1998), and have allowed such movements to be assessed in relation to potential environmental drivers (Boone *et al.* 2006; Roshier *et al.* 2008a). Largely as a consequence of the dominant research focus developed in the temperate northern hemisphere, many avian tracking studies have focussed on the long distance, regular seasonal migratory movements of species in relation to pronounced seasonal conditions. Indeed, many of the dominant theoretical paradigms explaining the evolution and mechanics of avian movement strategies (and many other fields within behavioural ecology and ornithology for that matter (see Stutchbury and Morton 2001)) are based on northern temperate zone systems. Considerably less attention has been directed towards other systems, including the dispersive movement strategies that appear to be the norm for austral birds, despite their potential for offering new perspectives and insights regarding our understanding of the ecology, physiology and evolution of faunal movements generally (Berthold 1991; Chan 2001; Dingle 2008).

The Australian Bustard *Ardeotis australis* is representative of a suite of terrestrial, generally poorly known, Australian birds that reportedly exhibit widespread dispersive movements in response to variable habitat conditions (Downes 1982a; Marchant and Higgins 1993). Based largely on anecdotal information, Australian Bustards are thought to move readily in relation to fire and rainfall events, tracking areas of higher productivity and concentrations of food availability opportunistically across the landscape (Downes 1982a; Marchant and Higgins 1993). The species may be an amenable model for examining distribution and movement patterns in relation to environmental variability because of its ranging habits and widespread distribution, its large size (enabling long term satellite tracking), and its conspicuousness and iconic status across outback Australia (making it readily recognisable to rangeland users thereby facilitating community-based monitoring efforts). However, underlying these notional advantages are also specific challenges. For example, whereas the widely distributed and ephemeral wetland habitats used by nomadic waterbirds (Kingsford and Norman 2002; Roshier *et al.* 2001a), or the discrete rainforest patches used by frugivorous animals in monsoonal Australia (Palmer and Woinarski 1999; Price *et al.* 1999), are circumscribed habitats that are relatively easily mapped (Roshier *et al.* 2001b; Russell-Smith 1991), defining the availability or quality of less circumscribed habitats used by bustards, and the majority of other terrestrial birds, is arguably more difficult. Nevertheless, emerging technologies may provide novel opportunities for assessing such habitat remotely over broad scales and in near-real time (Berry *et al.* 2007; Osborne *et al.* 2001).

The general premise of this study then was to examine the movements and ecology of the Australian Bustard, and to use the species as a model for examining movements and their drivers among Australian terrestrial birds. However, any such attempts that aim to examine movement dynamics in response to environmental conditions rely on basic knowledge of a focal species' biology and habitat requirements. For many of Australia's birds such knowledge is inadequate, presenting an elementary challenge. Recognising the paucity of knowledge concerning the biology of the bustard, a major focus of the study was to examine aspects of its ecology, particularly those elements that may interact to influence its movement patterns. Accordingly, the study sought to integrate broad-scale analyses of bustard distribution and movement patterns, with in depth, *in situ* studies of the bustard's ecology at two representative sites in Australia's northern savannas. Primary elements of the autecological study included assessment of food resource and habitat availability, bustard population dynamics, local home range and habitat use, diet and activity patterns, and aspects of the species' mating system and breeding behaviour.

This introductory chapter begins then with a review outlining the mechanics of avian movement strategies, with a particular focus on the Australian context. Given the ambiguity associated with defining movement strategies across, and even within disciplines, the section necessarily begins with a review of terminology and concepts used to define faunal movements. To help contextualise movements it draws on a framework for classifying movements in dynamic landscapes. The focus then shifts to the study's subject by providing a brief introduction to the Australian Bustard. The third part of the chapter provides a general introduction to the study region, the tropical savannas of northern Australia. This biome is regarded as a stronghold of the bustard in Australia and is accordingly the location for the in-depth studies of the species ecology. The chapter concludes with an outline of the scope and primary objectives of the thesis and includes a brief synopsis of its structure and content.

AVIAN MOVEMENT STRATEGIES

In this section I primarily address avian movement strategies. However, mobility is an almost universal and defining trait of animals, therefore, a broader perspective that transcends taxa, forms of movements and environments, provides a more informative, holistic context for understanding faunal movements in general (Dingle 2006; Dingle and Drake 2007). Accordingly, I draw on concepts and insights across disciplines. Nevertheless, the principal aim here is to define and distinguish between the various types of movement strategies that birds employ and to examine the principal regulatory mechanisms that underpin them.

Terminology and general concepts

The literature concerning faunal movements comprises a complex and at times confusing array of terms and concepts describing the various movement strategies animals employ and the mechanisms that underpin them. As research has progressed, more and increasingly complex movement strategies have been recognised, adding to the nomenclature and further complicating the discourse. The variable and often imprecise and ambiguous application of terms hampers effective communication and comparisons between studies (Terrill and Able 1988). The problem is highlighted, for example, by the often random and interchangeable use of terms such as resident and sedentary and, in an Australian context, the frequent and often indiscriminate use of the term nomadism to describe complex movements – which may simply be more reflective of a lack of knowledge (Higgins *et al.* 2001, and see below). In many cases the conceptual boundaries between these movement types are indistinct and overlap leading to difficulties over their definition and application. Recognising the need for greater precision and consistency, various authors have proposed the use of specific definitions and conceptual frameworks (e.g. Dingle and Drake 2007; Drake *et al.* 1995; Gauthreaux 1982; Roshier and Reid 2003; Terrill and Able 1988). Here I define these terms and review general concepts that subsequently serve to define and conceptualise the movement patterns of the Australian Bustard observed in this study.

Maintenance and dispersive movements

Birds exhibit a variety of movement strategies at a range of scales that have evolved as adaptations to the particular temporal and spatial vagaries of their environments. The reasons for movement may be varied, but most are primarily made in relation to the exploitation of resources, be they food, mates, shelter, or other requirements. Movements may be classified into two general categories: those that are largely restricted to a circumscribed home range and those that venture beyond it (Dingle and Drake 2007; Roshier and Reid 2003). Home range restricted movements are primarily associated with the general up-keep of an individual and have been variously termed “maintenance” (Rosher and Reid 2003) or “station keeping” movements (Dingle 1996). Hereafter, I refer to these specifically as ‘maintenance movements’, and use the term *dispersive* movements (following Recher 2007, and references in same volume) to refer to movements outside the home range. Dispersive movements as defined here are equivalent to Roshier and Reid’s ‘non-sedentariness’ and Dingle and Drake’s broad use of the word ‘migration’.

Maintenance movements are made to satisfy the daily requirements of individuals and are generally characterised by repetitive meandering over relatively short spatial and temporal scales. However, Dingle and Drake (2007) also define an extended form they term “commuting”. Commuting movements may be longer to-and-fro or round trip (loop) movements made regularly to resource patches or localities where other specific activities (e.g. roosting) occur. In this sense it is notable that not all mobile organisms necessarily have home ranges as traditionally defined (see below for definition). An extreme example is the round-trip foraging movements albatross make between nesting islands and foraging areas that may cover several thousand kilometres and extend over several days (Dingle and Drake 2007). A defining feature is fidelity to a central site.

Dispersive movements that extend outside of a home range may be regarded as occurring in a continuum from regular seasonal migration to increasingly complex movements such as nomadism and irruptions. Characteristic of these movements is that they are “notably persistent, undistracted and straightened out” and involve the relocation of an individual on a scale that is significantly greater than those arising from maintenance movements (Dingle and Drake 2007). Intuitively, the distinctions between these main types of movements (maintenance, nomadic and migratory) are most readily apparent when a home range is discrete and easily identified. Consequently, the movements of annual migrants or sedentary individuals with circumscribed ranges in time and space may be clearly defined. Less easily recognised are the home ranges and movements of nomadic individuals that may vary substantially and unpredictably in time and space. Nevertheless, these movements may be distinguished by the patterns of relocations of individuals or populations (Dingle and Drake 2007, and see conceptual framework below).

Organisational level

At the base of much of the confusion concerning the definition of movement strategies is a failure to precisely identify the organisational level at which movements occur. Specifically, whether movements should be defined for individuals or for populations. The notion of individual versus population based frameworks has been part of a general debate regarding the nature of movements (Dingle and Drake 2007; Gatehouse 1987). In essence, a focus on the individual entails a behaviour-based approach, whereas a population focus is essentially an ecological function-based perspective.

Considering movements at an individual level is consistent with how natural selection operates, that is, that it acts on variations in the movement behaviour of individuals. Furthermore, an individual, behaviour-based viewpoint is useful because it allows for defining specific characteristics that enable distinctions to be made between different movement types. For example, during migratory movements individuals may be focussed or undistracted (that is they move directly without stopping over extended periods), they may move at high altitude, or they may exhibit specific temporary morphological differences compared to other times (e.g. greater fat reserves to increase energy and gut shrinkage to reduce weight) (Dingle 1996; Piersma and Lindstrom 1997). Such characteristics may be readily distinguishable from characteristics associated with localised maintenance movements. In general, while such characteristics are reasonably well defined for migratory individuals/species, similar characteristics for nomadic or irruptive birds are less well known (but see Dean 1997; Woinarski 2006).

An emphasis on the behavioural has also been used to explain the marked variability evident in the movement strategies employed between individuals within a population. Grey Teal *Anas gracilis* in the highly dynamic environments of central Australia exhibit notable variability in movement patterns between individuals within the same population (Roshier *et al.* 2008a; Roshier *et al.* 2008b). This behavioural complexity is likely a consequence of individual decisions or responses to resource distributions. These choices may depend on various factors, including an individual's breeding status, experience, energy reserves and exposure to competition or predation risk. Any given movement pattern is therefore a complex, condition-dependent strategy (Doerr and Doerr 2005; Roshier *et al.* 2008b). Furthermore, just as such factors vary between individuals, so too are their relative influences likely to vary for an individual over its life time, potentially leading to different responses to environmental influences at different times. Therefore, not only should movements be primarily described for individuals, but a conscious regard for how adoption strategies may vary for an individual should also be considered.

Types of dispersive movements

Migration

Migration in the traditional sense may be defined as the regular, repeatable movements of animals between different geographical areas, often from a breeding location to a non-breeding location and back, over a regular time period (usually a single year) (Gauthreaux 1982). These breeding and non-breeding locations are geographically disjunct and are often used repeatedly. Migratory movements may follow the same pathway or occur in more circuitous return journeys, and relative to the time spent at non-breeding and breeding locations, they occur over a short period of time. Migration tends to occur between areas with regular, seasonally predictable availability of resources.

Nomadism

Nomadism in its extreme form contrasts diametrically to seasonally driven annual migration. As Roshier and Reid (2003) point out pure nomadism departs from all the characteristics that define migration. That is, breeding and non-breeding areas may overlap extensively, there is no return journey, timing of movements is irregular and subject to longer than seasonal cycles of climatic variability, movements may occur in any direction, and movements occur over an extended duration, possibly occupying a large proportion of the individual's lifespan. However, whether nomadism exists in such an extreme form is debatable (see below).

Here I distinguish between three general types of nomadic movements which differ primarily on the basis of motivation for movement and environmental drivers (Table 1.1).

i) Exploratory nomadism: exploratory ranging movements made when conditions are favourable over broad areas allowing an individual to effectively roam with limited energy expenditure and risk. Such movements may aid in knowledge collation of an individual's environment.

ii) Deterministic nomadism: deterministic or prescient movements made to locations on the basis of prior knowledge and spatial memory or as a result of detection of environmental cues (e.g. rainfall or fire events).

iii) Obligate nomadism: forced movements made when conditions in an area deteriorate to the point that movement is obligatory. Movements may subsequently be based on prior knowledge or random chance.

Table 1.1: Types of nomadic movements in relation to prevailing local environmental conditions and knowledge of movement destination or direction.

		Conditions at starting point	
Knowledge of movement direction?		Good	Poor
	Yes	Deterministic	Deterministic Obligate
	No	Exploratory	Obligate

Irruptive movements

Irruptions are triggered by high population levels as a consequence of prolonged or sequentially highly productive periods whereby numbers build up in an area followed by a substantial reduction in food resources which force *en masse* movements of large numbers of individuals into other areas (Gauthreaux 1982). Among birds, irruptive movements mostly occur irregularly at intervals of a few years or decades, and in Australia may occur in apparently random directions with frequent underlying movements towards the coast from the inland (Higgins *et al.* 2001).

Natal dispersal

Post-breeding or natal dispersal may be interpreted as a process or an outcome. This dichotomy has inevitably led to confusion and ambiguous uses of the term. As a process, natal dispersal is the one-way, one-off movement of an individual away from its birth area. Such movements are often in random directions and continue until an appropriate new unoccupied patch is found at which to settle and breed. Such a specific definition distinguishes it from broader definitions that have defined dispersal for the entire or part of a breeding population (e.g. Gauthreaux 1982), and definitions that have referred to repetitive breeding events by the same individual whereby each movement from a breeding area is deemed ‘dispersal’ (e.g. Greenwood 1984).

As an outcome, dispersal is the relocation of the individual away from its birthplace and may be considered an adaptation to avoid inbreeding and competition (Greenwood 1984). Whether dispersal as an outcome is successful or not depends on the vagility of the organism, the availability of suitable unoccupied habitat and whether it subsequently breeds.

Modifying terms

Within the lexicon describing faunal movements are several modifying terms used to further define movement types. In the literature their use has been largely restricted to defining types of migratory movements, but they may also be applied to other movement types, including nomadism.

Total, partial and differential movements

At the population level movements may be described according to the relative proportions and demographics of the population that move. Accordingly, *total* movements involve the relocation of the entire population. *Partial* movements describe the syndrome whereby some individuals in a population move while others are sedentary or resident, without regard to the component of the population that moves. Movements that are made by a specific component of the population (e.g. sex or age) are known as *differential* movements (Terrill and Able 1988). The term ‘partial’ has often been used as a general term to describe such proportional movements, even though many studies have now demonstrated that there is often a specific component of the population demographic that moves. In general, the majority of moving birds are often young and/or female (Gauthreaux 1982), although a bias towards males moving may also occur for some species (e.g. Alonso and Alonso 1992; Morales *et al.* 2000). More often than not, the term partial has been used as a default reflecting a lack of knowledge of the demographics of moving individuals.

The definitions of ‘partial’ and ‘differential’ I employ here also differs from some previous applications. For example, ‘differential’ has been used to describe movements whereby a whole population moves but the distance travelled by different elements of the population (sex, age) varies (e.g. Ketterson and Nolan 1983). At an individual level ‘partial’ has also been used to describe an individual that may have moved in one year but not in another (e.g. Roshier and Reid 2003). These examples are equally valid and notable movement strategies in themselves but again emphasise the need to be explicit and consistent in defining such terms.

Obligate and facultative movements

Movements may also be classified according to whether they are *obligate* or *facultative*. Obligate movements are those that are always made or must be made by necessity. Facultative movements, in contrast, are not compulsory and are made in response to proximate environmental cues. Intuitively, obligate movements are more characteristic of tightly, genetically controlled regular migration, whereas facultative movements are more characteristic of flexible or opportunistic, dispersive movements. Nevertheless, both terms may equally apply to opposite ends of the movement spectrum. For example, some annual migrants exhibit facultative phases to their movements whereby stages of migration are responses to external, stochastic stimuli such as extreme weather conditions or a failure in food supplies (Terrill and Able 1988). Similarly, obligate nomadic movements may occur when individuals are forced to move as a result of deteriorating environmental conditions.

Classification of movements

Several authors have attempted to classify Australian bird species according to specific types of movements. Ambiguity in defining movement strategies and a lack of information about the movements of birds generally has led to variable outcomes. This is reflected by the debate over the relative proportions of birds that exhibit different movement strategies. For example, Keast (1959) estimated that 23% of the entire Australian avifauna could be classed as nomadic and only 8% as 'true' north-south migrants. Rowley (1975) by comparison, classified 15% of Australian species as migrants, with less than 5% of all land birds being migratory. Following an extensive review of partial migration in Australian birds, Chan (2001) estimated that up to 40% undertake regular seasonal movements or exhibit consistent seasonal fluctuations in numbers in an area. More recently, Gilmore *et al.* (2007) categorised 51% of land and freshwater bird species as exhibiting some type of dispersive movement. Such classifications may be useful generalizations at the species level and while most authors highlight that a variety of movement strategies are employed within a species, such general classifications cannot account for variability between and within populations and individuals in the adoption of different strategies.

The problem with classifying according to movement strategies is highlighted by the significant overlap between migration and nomadism. While these strategies may be regarded as at opposite ends of a spectrum, and species or populations are commonly categorised according to these categories, in practice there are likely to be few individuals, let alone populations or species, that fit neatly into these categories. An increasing number of studies that have focussed on movements in more detail suggest that movements previously considered nomadic, upon more detailed investigation, have been shown to exhibit underlying patterns (e.g . Griffioen and Clarke 2002; Ward 1971; Wyndham 1983)). Wyndham's (1983) study of the budgerigar *Melopsittacus undulatus* illustrates the point. This species has been labelled highly nomadic (Serventy 1971; Storr 1967), but Wyndham demonstrated that there are underlying north-south seasonal patterns to the movements and breeding patterns of the species. Furthermore, he speculates that when food becomes short budgerigars not only start to move, but experienced birds move towards traditional locations determined by previous experience and naïve birds either follow experienced birds or move at random. The notion that birds return to favourable sites is contrary to the extreme end of the nomadism definition that implies that animals undertake movements haphazardly. This may be true on rare occasions but it is unlikely that such extreme strategies are common. Instead it is more likely that movements are deterministic or prescient to an extent and that specific areas are used and returned to at least more than once. Defining this ‘middle ground’ whereby varying degrees of migration and nomadism are employed between and within individuals and populations is the challenge.

A conceptual framework for classifying movements

A useful way of conceptualising patterns of movements, particularly in the dynamic landscapes characteristic of much of Australia, is through a simple conceptual framework presented by Roshier and Reid (2003). Home range has been defined as “the extent of area with a defined probability of occurrence of an animal during a specified time period” (Kernohan *et al.* 2001). The geographic range of a species or population may be regarded as the sum of all the individual home ranges that comprise the assemblage (Gaston 1991; Roshier and Reid 2003). These concepts are inherently fluid and require an explicitly defined time scale. Recognising the inherent plasticity of home and geographic ranges, Roshier and Reid’s (2003) framework attempts to integrate an individual’s movement patterns with its home and geographic ranges. Underlying the framework is the idea of life-time range, defined by Baker (1978) as “the total area of space perceived by an individual between birth and death”. It is the interactions between these range units that may be used to classify movement types, and to consequently assess the implications of movements of individuals and populations. Based on the characteristics of these range types in relation to each other Roshier and Reid (2003) developed two indices as follows:

$$\text{Range Stability Index} = \text{Home range}/\text{Life-time Range}$$

$$\text{Realised Mobility Index} = \text{Life-time Range}/\text{Geographic Range}$$

The range stability index (RSI) describes the relationship between home range (maintenance movements) and the area used by an individual over its life-time. For sedentary individuals home range and life time range are similar and the index approaches one. For a nomadic individual, home range and life-time range differ markedly and the RSI is low. The realised mobility index (RMI) describes the extent of individual dispersive movements in relation to the geographic range of the species. Among sedentary individuals, or animals with limited mobility, RMI is low. For highly mobile animals, life-time range approaches the geographic range and the RMI approaches one.

Among migratory individuals that use distinct breeding and non-breeding geographic ranges that do not overlap, it is possible to refer to “life-time breeding range” and “life-time non-breeding range” and use the indices to define breeding and non-breeding ranges. For individuals that exhibit strong breeding (or lekking) site philopatry the breeding range index will be similar to that of sedentary individuals. As

Roshier and Reid (2003) explain if consideration of breeding dispersal is of primary interest then the index describing breeding range is used, whereas for highly mobile, nomadic individuals that move between breeding locations, consideration of both sets of indices and the differences between them may be insightful.

These indices are summarised in Figure 1.1 and Table 1.2. In subsequent chapters that address the movement patterns of bustards, I refer back to this framework to contextualise the variable movements bustards make in different parts of the species' range.

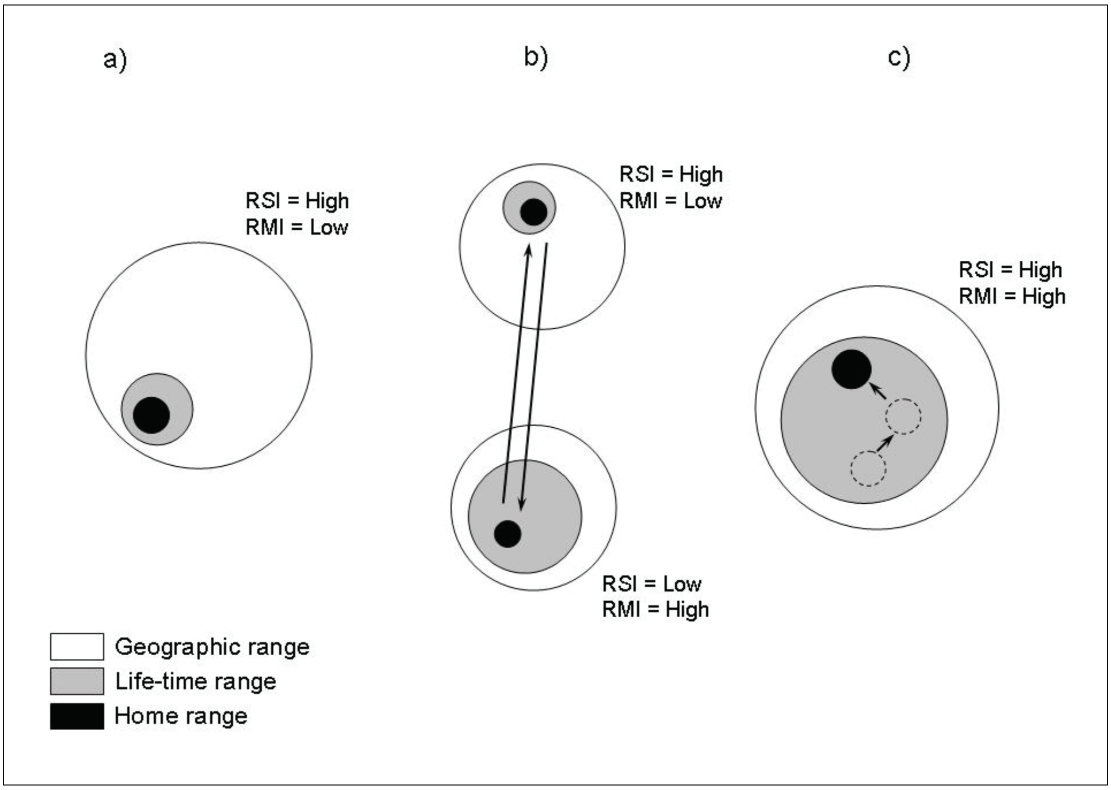

Figure 1.1: Geographic, life-time and home range in (a) sedentary, (b) migratory species (individuals or populations) with different life-time range in its breeding and non-breeding ranges and (c) nomadic species (individuals or populations). Indicative values for range stability index (RSI) and range mobility index (RMI) within each range are shown. (reproduced with permission from Roshier and Reid 2003).

Table 1.2: Indicative values for range stability (RSI) and realised mobility index (RMI) for individuals across a wide range of movement strategies following natal dispersal. Indices for the geographic and breeding range are contrasted (reproduced with permission from Roshier and Reid 2003).

		Sedentary	Migrant		Nomad	
			Strict	Partial	Wide-ranging	Local
Within geographic range	RSI	High	low	low	low	low
	RMI	Low	mid-high	mid-high	high	low-mid
Within breeding range	RSI	High	high	low-high	low	low
	RMI	Low	low	low-high	high	low-mid

As Roshier and Reid (2003) explain “If an individual has a low or high value for RSI its value will be opposite for RMI; so a partial migrant which always breeds in the same territory, and winters elsewhere in some years but not others, will have a high RSI and a low RMI within its breeding range; whereas a species which breeds in a variety of locations but generally winters elsewhere will have a low RSI and a high RMI within its breeding range”.

Table 1.3: Summary of movement terminology employed in this study and as used by others in the literature.

Term	As defined here	As used by others
Movement types		
Maintenance	Daily, routine movements generally restricted to a circumscribed home range	Also termed 'station keeping movements' (Dingle and Drake 2007)
Dispersive	Any long distance movement that is not a maintenance movement	-Used synonymously with 'nomadism' (e.g. Higgins *et al.* 2001) and 'natal dispersal' (e.g. Gauthreaux 1982). -Termed 'non-sedentariness' by Roshier and Reid (2003)
Migration	Regular, seasonally or annually repeated movements between two geographical areas, usually breeding and non-breeding sites	Any movement that is not a maintenance movement (Dingle and Drake 2007)
Nomadism	Irregular movement in timing, direction and destination	Several species with complex movement patterns labelled nomadic though more a reflection of lack of knowledge (Higgins *et al.* 2001)
Irruption	*En masse* movements away from an area following a substantial population increase, often due to decline in resources following prolonged favourable conditions	
Natal dispersal	One-way, one off movement of an individual away from its birth area	-movement by a breeding individual away from its breeding area (e.g. Greenwood 1984)
Sedentariness	Range restricted to a circumscribed area or home range with no longer distance movements	-most individuals usually not moving more than 50 km (Higgins et al. 2001)
Modifying terms		
Total	Entire population moves	
Partial	Some individuals in a population move while others remain sedentary with no particular component of the population moving	-often used in place of 'differential' -movement by an individual in one year but not in another (Roshier and Reid 2003)
Differential	Individuals of a specific component of a population (e.g. age, sex) move while others remain sedentary	Movements by whole population but distance travelled by different elements of population (e.g. sex, age) varies (e.g. Ketterson and Nolan 1983)
Obligate	Movements that are always made or must be made by necessity, often underpinned by a genetic control	
Facultative	Movements that are not compulsory and made in response to proximate environmental cues	
Deterministic	Prescient movements made to known locations or as a result of detection of environmental cues	
Exploratory	Opportunistic ranging movements usually made when conditions are favourable over broad areas	

Regulatory mechanisms and drivers of extensive movements

Underlying all movements are regulatory mechanisms and environmental drivers. A large part of the variability evident between movement strategies may be based on differences in the relative importance of mechanisms or cues that drive these movements. In general, these regulatory mechanisms remain poorly understood. Only for a relatively small proportion of species is there much information, particularly for the Australian fauna.

Just as migratory and nomadic movements may be regarded as opposite ends of a continuum so too can the drivers of movements be regarded as ranging from endogenous controls largely based on genetic programming to exogenous, proximate environmental factors. However, once again a middle ground is the norm with most movements likely a result of varying degrees of influence between these factors. In general, obligate annual migratory movements are regarded as primarily genetically programmed and underpinned by endogenous controls (Berthold 1999). In northern temperate environments, for example, where annual north-south migrations are made in relation to pronounced seasons, temperature and day length trigger hormonal changes that stimulate the initiation of migratory movements (Berthold 1991). However, even among annual migrants, movements may not be entirely the result of an endogenous motivation (Terrill and Able 1988). Evidence for a range of migratory passerines suggests that many exhibit a delayed or facultative phase of migratory behaviour that can only occur in response to external stimuli, such as high intra-specific competition or a failure in food supply (Terrill and Able 1988).

Partial migrants, at least in the northern hemisphere, also appear to have a strong genetic basis for migration (Berthold 1991), but their movements may be more facultative and increasingly influenced by environmental cues. Much less is known of the regulatory mechanisms governing the movements of southern hemisphere species that experience less predictable conditions. In the highly variable, stochastic environments that characterize much of continental Australia, it is unlikely that many movements are stimulated by tight endogenous controls (Roshier *et al.* 2008a; Whitehead 1998). Nomadism and partial migration may rely on individuals being able to detect and respond to the sudden and ephemeral presence of favourable conditions, often rapidly and over vast scales. The ability to detect or predict where favourable habitat conditions occur confers a significant selective advantage for populations that have well developed abilities to do so. Rainfall is a particularly important influence on movement strategies among Australia's birds, particularly in drier areas where it tends to be more erratically distributed in time and space (Davies 1984; Ford 1989; Keast and Marshall 1954). Movements may also be made in relation to other events, for example, fire or outbreaks of particular food types (e.g. grasshoppers). The mechanisms for detection of such factors are poorly known and largely speculative. Some have suggested that visual cues or detection of changes in pressure or temperature gradients may be important (Simmons *et al.* 1998), while olfactory cues may also play a role (Roshier *et al.* 2006; Wallraff 2004).

Nomadic movements may also occur under different scenarios. For example, exploratory facultative, movements may be made during periods of high resource availability over broad-scales. At such times movements may be energetically inexpensive because of widespread resources and the risk associated with moving without finding required resources is low. Such movements allow an individual to learn about its landscape, collating knowledge about locations that may be subsequently re-visited during leaner times. Spatial memory is apparently well developed among birds and may be subsequently used in navigation and to orient movements (Healy and Hurly 2004). The detection of proximate cues and use of spatial memory is likely to be a function of distance and landscape variability, with both likely to decline with distance or increasing spatial and temporal resource variation (Roshier *et al.* 2008a). Nevertheless, recent satellite tracking studies of the Grey Teal *Anas gracilis* have suggested that spatial memory plays a role in the movements of this species, even over broad scales (Roshier *et al.* 2008a; Roshier *et al.* 2008b).

In contrast to the above, obligate nomadic or irruptive movements may be forced. For example, when a threshold of food resource availability is reached a movement is required or else the individual would perish. In this case, the initiation of the move may also depend on exhausting other possible ways of coping with environmental stresses such as diet switching, or going into torpor. Ultimately, it is the interaction of these factors, and the condition status of an individual, that may determine an individual’s response and whether it moves or not.

Evolution of movement strategies

Dispersive movement strategies have evolved independently among many faunal groups, including birds, mammals, fish, reptiles, amphibians, insects and marine invertebrates. Movements are an adaptive response to variable environments, allowing animals to use resources as they fluctuate in time and space, minimise competition and to avoid predators and parasites.

As previously noted, the majority of research and the dominant paradigms concerning the dynamics and evolution of movement strategies, particularly among birds, are based on temperate zone systems. Consequently, the discussion has overwhelmingly focussed on migration (Alerstam and Hedenstrom 1998; Alerstam *et al.* 2003; Fretwell 1980; Lack 1968; Pulido 2007; Rappole 1995; Zink 2003), even though annual migration is likely an exception rather than the rule among avian movement strategies (Dingle and Drake 2007).

Ultimate causes for the evolution of dispersive movements

Modern developments concerning the evolution of bird migration largely began with an emphasis on the ecological circumstances that favour such a strategy whereby movements occur primarily in relation to competition and seasonal availability of food resources (Lack 1954). Referring to regular north-south migrants in the northern hemisphere Lack suggested that movements away from breeding grounds are advantageous if there are substantial shortcomings in food resources later in winter. During spring and summer more food becomes available at the breeding grounds to raise young than at crowded winter areas hence a return to the breeding areas occurs. The roles of inter- and intra-specific competition over food resources were further emphasised by Cox (1968) who asserted that movements into adjacent favourable areas would evolve among residents when gains in survival and reproduction, because of reduced competition, outweigh the costs of movement. He showed that morphological variation in feeding apparatus of many migrants is significantly less than that found in tropical resident species of the same group, implying that migrants have opted to change space rather than morphology in solving problems of interspecific competition.

These ideas are the basis for explaining the selective advantage of differential and partial migration, and why all individuals of some species migrate while only certain individuals in other species move. The basis of these explanations rests on the notion of behavioural dominance. Dominant, resident birds attain the benefits of site dominance by sacrificing their chance to move to a better habitat (Fretwell 1980). In this case, site dominance is correlated with the location where the species is limited. If the species is limited on the wintering grounds, then site dominance should provide an individual with the best wintering site, and if the species is limited on the breeding grounds, then site dominance should provide an individual with the best breeding site. However, Gauthreaux (1982) suggested that residents do not necessarily sacrifice their chance to move to a better habitat, instead have greater resource-holding abilities to allow them to remain in their present habitat. Less competitive or less dominant individuals, mostly younger or of the ‘inferior’ sex, must leave an area when resources become limiting for a more favourable environment. According to Gauthreaux’s model, individuals of all ages and sexes are able to remain in the breeding location when conditions are optimal or highly favourable, however, when favourable conditions decrease, uncompetitive individuals must move or face mortality. These individuals then face a trade-off between the ultimate advantages of moving to a more favourable location and the risks of the journey. Conversely, for more dominant individuals, the trade-off is between the benefits of access to optimal breeding sites and the risks of remaining at the breeding locality during the non-breeding season. This model is also applicable to short and long distance migration except that no individuals are able to remain on the breeding grounds during the non-breeding season due to unfavourable conditions. In this case dominance status is related to the distance travelled or the quality of the non-breeding habitat so that dominant individuals travel a shorter distance or occupy the best areas. In both cases, dominant individuals are able to arrive on breeding grounds first when these areas once again become suitable, either because they are closer to them or because they are energetically more capable of starting their return journeys sooner because they have occupied better habitats over the non-breeding season.

Dispersive movements such as nomadism are considered an adaptation to environments that are unpredictable and patchy in the timing and location of highly productive areas allowing animals to exploit favourable resources by tracking them across the landscape opportunistically (Sinclair 1984). Individuals that are able to move quickly and efficiently between these patches can exploit abundant food and shelter resources and a lack of intense competition, so that selection would favour such movements by birds (Dean 1997). Nomadism is regarded as an evolutionary stable strategy among individual species or populations only when extremes in environmental conditions occur sufficiently frequently and unpredictably enough, to maintain movements to high resource patches or to maintain dispersal away from low resource patches (Dean 1997). Nomadism would not be maintained as a movement strategy if high rainfall years are too regular or infrequent, or peaks in fluctuations of resources in the environment too low. If environmental fluctuations are too frequent and regular (i.e. predictable), the predictability of events would impose regularity on the movements of individuals and thus result in migratory rather than nomadic movements.

Rapid evolution

Dispersive movement behaviour, and the various traits associated with it, are believed to have, and continue to rapidly evolve in many different lineages (Berthold and Pulido 1994; Pulido 2007). Some studies have suggested that novel migratory habits can evolve in less than 25 years, and that it is this ability for rapid evolution that has been responsible for changes already observed in migration patterns among birds due to climate change (Nilsson *et al.* 2006). Flexibility and rapid evolution of migratory behaviour may be particularly important in the Australian context where such a great variety of movement strategies abound (Griffioen and Clarke 2002). The expansion of ranges of some species, for example Galahs *Cacatua roseicapilla*, and the Australian Bustard itself, into recently cleared areas may be examples that illustrate the advantage of such flexibility.

The Australian avifauna

State of knowledge

Studies of the movements of Australia's terrestrial birds are inherently difficult because of the complex movement patterns much of the avifauna employ in response to a highly variable environment. This innate challenge is compounded by the demographics of Australia's human population, notably a low number of amateur and professional ornithologists, a very low overall population density and the concentration of Australia's population along southern and eastern coasts. Consequently, continental-scale monitoring is a considerable challenge and there have been very few systematic and detailed studies of marked individuals at biologically useful scales. The recent compilation of the most comprehensive synthesis of knowledge of the birds of the Australasian region through the HANZAB series (e.g. Higgins and Davies 1996; Higgins *et al.* 2001; Marchant and Higgins 1993), has illustrated how very little information exists regarding the movement strategies of the continent's birds. So poor is our knowledge that even a general overview by the authors has proven difficult, let alone a detailed analysis for each species (Higgins *et al.* 2001).

As a first step in understanding large-scale patterns of distribution and movements of mobile species in relation to erratically available resources, several studies have attempted to relate avian responses to general patterns of plant and resource productivity. Among the first general studies of bird movements in Australia was an examination of the ecological significance of seasonal movements by Australian honeyeaters (Keast 1968). Drawing on what at that stage was a very limited knowledge base, Keast (1968) proposed general relationships between movements in different areas and some of the ecological factors thought to influence them. Nix (1976) presented a generalised theoretical model relating climate variables to plant growth rates, and therefore production of food resources, which he then related to the general patterns of movements employed by Australia's birds on a continental scale. His general aim was to illuminate the apparent movement chaos described among Australian birds by relating movements to deterministic and predictable patterns of regular climate-driven pulses of productivity. Accordingly, Nix predicted that movements in the more seasonally influenced or climatically predictable regions of Australia would be more regular and predictable. In the seasonally influenced tropics and temperate regions along the east coast movements would be largely regular or migratory with predominantly north-south patterns. In contrast, the unpredictability of climate and primary productivity in the interior arid and semi-arid regions of the country leads to movements that are predominantly dispersive in response to episodic rainfall and resource availability, though here too it is suggested that there may be underlying north-south patterns in response to the influence of tropical and temperate weather systems (Nix 1976).

The initiation of national atlas and bird counts has greatly increased our knowledge of Australia's birds. Griffioen and Clarke's (2002) analyses of national count data combined presence/absence data from several databases across eastern Australia to detect and describe broad-scale bird movement patterns. For 407 species they pooled several years of atlas data into quarters in a single 'theoretical year'. They then compared reporting rates between quarters within grid-squares they assigned across the study region enabling them to define broad shifts in distributions of numerous species over an annual cycle. The study provides valuable information regarding seasonally shifting distribution patterns over large areas and the potential for testing hypotheses regarding the determinants of movement patterns, including Nix's (1976) theoretical scheme. Griffioen and Clarke (2002) demonstrated an underlying north-south alignment for many species consistent with previous descriptions (e.g. Fullager *et al.* 1986; Keast 1968; Nix 1976;

Rowley 1975). However, the most salient finding from the study was the number of different movement strategies that birds employ. They identified 19 distinctive patterns of movement among the birds of eastern Australia, including evidence of broad-scale movements for 101 out of 407 species. Furthermore, their analyses were limited to species and regions for which there were adequate data such that for vast areas of outback Northern Territory, Western Australia and South Australia too few surveys prohibited detailed temporal analyses. Consequently, variable irregular movements that are made over climatic, as opposed to annual cycles, could not be detected, nor was there information regarding the population demographic of moving individuals. It is likely then that many other distinctive strategies may be defined once our knowledge base improves.

Examples of Australian avian movement patterns

Migration among Australian birds

Owing to its climatic patterning and isolation Australia has relatively few typical north-south migrants and most of those that do migrate are distinguishable from those of other regions by the commonality of overlapping wintering and breeding grounds (Chan 2001). By comparison, partial (or differential) migration is common among austral birds (Chan 2001; Rappole 1995). Recent estimates suggest that more than one third (36%) of Australian terrestrial birds have both migratory and sedentary populations (Chan 2001). According to Chan (2001) partial migration is particularly common among non-passerine land birds, especially of the orders Falconiformes, Psittaciformes, Columbiformes, and Cuculiformes.

While typical, long range intercontinental migrants are proportionally few in Australia those that do come make among the longest annual migrations of all birds. During the austral summer Australia supports a number of these migrants (predominantly shorebirds and seabirds) that breed mostly in northern Asia, Alaska and the North Pacific and spend their non-breeding months here. Highlighting the geological isolation of Australasia from Asia is the very low number of land birds that migrate between the two continents and significantly there are no trans-equatorial land bird migrants that breed in Australia (Dingle 2008). More common are intra-continental and short-range migrations. Numerous species undertake shorter, predictable north-south local migrations either within Australia or to countries nearby and relatively few of them winter further than 1000 km from their breeding grounds. Australia also has several altitudinal migrants.

Nomadic and irruptive movements among Australian birds

The ‘nomad’ label has been applied to a wide range of birds from numerous ecosystems that exhibit complex, unpredictable or otherwise poorly understood movements. In fact, the phenomenon has been so widely reported among Australia’s avifauna that it has become somewhat of an overriding paradigm for understanding Australian bird movements (Higgins *et al.* 2001). Many of these examples are likely to be more a function of inadequate knowledge in light of the complex movement strategies birds employ. Notwithstanding these issues, the phenomenon is nevertheless most developed and exhibited by more species in Australia than anywhere else (Serventy 1971). Nomadism has been reported from a wide range of avifaunal groups. Perhaps the best studied are Australia's waterbirds (Kingsford *et al.* 1999; Maher and Braithwaite 1992). The irregular movements of these birds coincide with the temporary and erratic availability of the wetlands they depend on. Among the better studied waterfowl species is the Grey Teal which has been shown to adopt variable and complex movement strategies (Frith 1962; Roshier *et al.* 2008a).

Notable among Australia's vegetation is the prominence of nectar-producing plants that are the basis for the ecology of a large suite of vertebrate nectarivores, including birds (Ford and Paton 1982; Ford 1989; Keast 1968; Woinarski *et al.* 2000) and mammals (Palmer and Woinarski 1999). Characteristic of nectar producing plants is the marked seasonal and spatial variability in nectar production which nectarivores may track nomadically across the regional or local landscape (Keast 1968; Palmer and Woinarski 1999; Woinarski *et al.* 2000). A recent re-analysis of predictors of nomadism in a Mediterranean-climate ecosystem of southern Australia by (Woinarski 2006) suggested that of the factors considered diet was the best predictor of nomadism, with it being most prevalent among nectarivores.

Cited as among the most typically nomadic, and irruptive boom-bust bird species is the Flock Bronzewing Pigeon *Phaps histrionica* (Dostine 2009; Frith 1982; Higgins and Davies 1996). The species' core distribution occurs on the Barkly Tableland in the Northern Territory and the Mitchell Grass Downs region of Queensland from where it irrupts throughout most of inland Australia. The grasslands within its range are subject to highly variable productivity with high variation in seed availability in response to irregular rainfall which the birds may track over vast distances (Dostine 2009; Higgins and Davies 1996). Other examples of groups of birds that include a high number of reportedly nomadic species include quail, crakes and rails, cuckoos, pardalotes, chats, trillers, and woodswallows (Higgins and Davies 1996; Higgins and Peter 2002; Higgins *et al.* 2001; Pizzey and Knight 1997).

Irruptive movements that generally occur at irregularly intervals following periods of prolonged high productivity are also a feature of the Australian biota. A well known Australian avian example is the Black-tailed Native Hen *Gallinula ventralis* which often irrupt in large numbers into the southern parts of Australia following periods of high productivity after rains in the arid zones (Matheson 1978). Other non-avian examples of irruptive taxa include Long-haired Rats *Rattus villosissimus* (Carstairs 1974; 1976) and locusts (Farrow 1979). In response to such mass population fluctuations in their prey species, populations of Letter-winged Kites *Elanus scriptus* (Hall 1969) and Barn Owls *Tyto alba* (Heywood and Pavey), among other species (Szabo *et al.* 2003), similarly increase leading to irruptive movements.

Future directions

Our current knowledge of the dynamics of faunal movements and their environmental drivers, particularly in Australia, is poor. Clearly many questions remain. For example, to what degree are different movement strategies employed between individuals in a population? What are the factors that drive some individuals to move differently to others? How might the adoption of movement strategies vary for an individual over the course of its lifetime? To what extent are other coping strategies employed to deal with environmental stress and how do they interact with movement strategies to determine individual responses? To what extent are Australian avian movements truly migratory or nomadic? What are the potential implications of faunal movements for the conservation of species and ecological processes?

Impeding our understanding and effective communication among researchers has been a failure to consistently and precisely define the terms and concepts used to describe and discuss faunal movement patterns. Framing our discourse in a consistent manner is a primary imperative. Significant advances in our knowledge of movement strategies and their regulatory drivers are likely to come only through enquiry at the scales that resource dynamism and bird movements operate at (Woinarski 2006). With the advent of new technologies, including advances in satellite telemetry, spatial information systems and genetics (Webster *et al.* 2002), we stand on the verge of a Kuhnian-like revolution in biological field science whereby such studies will become possible for an increasing range of species. Such detailed studies of exemplar dispersive species, whereby new technologies coupled with systematic and detailed ecological studies over the sort of biologically meaningful scales required, may yield the insights we require. This study aims to employ such techniques, albeit within the temporal and logistical constraints of a PhD dissertation, to examine such questions for the Australian Bustard.

BIOLOGY OF THE AUSTRALIAN BUSTARD

The Otididae Family

The Australian Bustard *Ardeotis australis* (Gray, 1829) is the only Australasian representative of the Otididae family, a group of medium to large, terrestrial birds that include the heaviest birds that fly. The family is confined to the Old World and consists of 25 species in 11 genera, most of which are found in Africa, although the distribution of some extends to Asia, Europe and Australasia (Collar 1996). Traditionally, and supported recently by DNA work (Sibley and Ahlquist 1990), the group is included among the Order Gruiformes, which includes among other families the rails, crakes and cranes. However, the bustards are grouped apart in their own infraorder, estimated to have been established over 70 million years ago (Collar 1996).

There are three species in the *Ardeotis* genus; the Indian Bustard *A. nigriceps* (confined to India); the Kori Bustard *A. kori* of Africa, and the Australian Bustard. In addition, the Arabian Bustard *A. arabs* is considered a superspecies with *A. kori* (Collar 1996).

Colloquially, the Australian Bustard is often referred to in outback Australia as the Plains, Bush or Wild Turkey. Hereafter, I use the common names Australian Bustard or simply ‘bustard’ interchangeably. When other bustard species are referred to I give their full common name followed by the species scientific name upon first use. On some occasions I refer to the Otididae collectively as bustards, when this occurs the meaning is self-evident.

Description

The Australian Bustard exhibits extreme sexual size dimorphism with males weighing on average approximately three times more than females. Mature males may stand up to over a metre tall and may vary significantly in weight depending on age, season and condition. Weights presented in HANZAB are based largely on captive birds and vary from 4.1 to 9.9 kg for males, and 2.0 to 4.0 kg for females (Marchant and Higgins 1993). The heaviest recorded male specimen recorded was from the wild and weighed 14.5 kg (Marchant and Higgins 1993; Serventy and Whittell 1976).

Bustards are a distinctive, ground-dwelling species with a characteristic shape, long legs and neck and stately erect posture. Males have a black crown with white eyebrow and neck and distinctive black breast band. Their back, wings and tail are brown, marked finely with buff and black. Upperwing coverts are black and white and underparts white to grey. Legs and feet are pale yellow to olive. Females, apart from a generally smaller shape, are distinguished by a narrow brown crown, narrower breast band that is often not visible, less black and white on wings and a more off-white to grey neck and breast.

Status and Distribution

The Australian Bustard is widely distributed across continental Australia, with a population also found in the savanna regions of southern New Guinea (Barrett *et al.* 2003; Marchant and Higgins 1993). The species' current strongholds are mostly in northern Australia, with most reports from the Great Sandy, Victoria and Tanami deserts, Daly River and Victoria River Districts, the Barkly Tableland, the east Kimberley and across Queensland (Barrett *et al.* 2003; Blakers *et al.* 1984; Downes 1982a; Grice *et al.* 1986; Marchant and Higgins 1993). In the south and south-east of the continent bustards have undergone large historical population declines, and are now largely absent from areas were they were formerly found (Garnett and Crowley 2000; Marchant and Higgins 1993). Declines have been variously attributed to altered fire regimes, pastoralism, hunting, disturbance, habitat alteration, pesticides and predation (particularly by the introduced fox). These factors assume varying importance in different parts of the bustard's range and combine in different ways to affect local populations. Other declines that have occurred patchily in some of the species's strongholds have been partially offset by localised increases in bustard populations, particularly in some recently cleared areas such as the Brigalow Belt in Queensland. In areas such as the horticultural developments on the Ord River in Western Australian and the Daly River in the Northern Territry, populations may be significantly greater than in surrounding 'natural' habitats (pers.obs).

Reflecting the bustard's variable contemporary distribution across Australia, and partly owing to different classification criteria, the species conservation status differs between jurisdictions. At present, the Australian Bustard is not listed under the Environment Protection and Biodiversity Conservation Act 1999, but is considered Near Threatened on a national scale by Garnett and Crowley (2000). More locally, the bustard is considered Critically Endangered in Victoria (DSE 2003), Endangered in New South Wales (NSW Threatened Species Conservation Act 1995) and Vulnerable in South Australia and the Northern Territory (S.A. National Parks and Wildlife Act 1972; Territory Parks and Wildlife Conservation Act 2000).

Habitat preferences

Bustards have a broad preference for open habitats, ranging from open grassland plains to low shrublands, grassy open woodlands and similar but artificial habitats including croplands, golf courses and airfields (Berney 1936; Boehm 1947; Downes and Speedie 1982). They may also be associated with watercourses, particularly in more arid regions, and are attracted to fires, often being found at fire fronts and in recently burnt areas. At such times they may venture into more wooded habitats that fires have opened up (Berney 1936; Boehm 1947). They tend to avoid densely vegetated areas and generally favour flat terrain, avoiding hilly areas. Although there have been no detailed studies of the species biology and habitat requirements, general classifications of bustard habitat associations in the Northern Territory and South Australia suggest the best quality habitat are at the margins between tussock grass plains and semi-desert scrub (Downes 1982a; Downes and Speedie 1982). Such ecotones between open plains and open woodlands are also regarded as preferred nesting areas (Downes 1982a; Downes and Speedie 1982; Marchant and Higgins 1993). Downes (1982a) also suggests that bustards may move across the savanna landscape to exploit areas of 'greener' grassland opportunistically.

Feeding ecology and diet

Although there have been no detailed studies of the feeding ecology of the bustard the range of food items reported for the species is extensive. Bustards have a broad omnivorous diet consisting of small animals (molluscs, centipedes, insects, small vertebrates) and seeds, fruits and leaves (Barker and Vestjens 1989). Foraging behaviour is said to be diurnal although other bustard species also forage at night (Combreau and Launay 1996). They feed on the ground, walking slowly and stopping to pick off parts of plants or seeds and fruits from the ground or to stab at prey. They readily congregate in larger numbers at bushfires to feed on animals killed or exposed by fire (Berney 1936; Boehm 1947) or in food resource rich areas following rain, and may track these events across the landscape (Downes and Speedie 1982). Though they reportedly move to water in the morning and afternoon to drink (Badman 1979) they are well adapted to waterless conditions and can apparently survive for extended periods without directly drinking (Marchant and Higgins 1993). In monsoonal Australia during the wet season they forage on plains with long grass, and in low shrub-covered plains during the dry (Downes 1982a). To aid with breakdown of food in the gizzard they readily ingest small stones and pebbles (Marchant and Higgins 1993). No information exists regarding seasonal dietary preferences, although they are likely to exploit abundant food opportunistically.

Social structure and breeding biology

Australian Bustards, like all other larger bustard species, are at least loosely gregarious. They most commonly occur in small groups of 2 – 6 individuals, although may often be solitary or in small family groups (i.e.female with young). They may also sometimes be observed in larger flocks, particularly at abundant food sources or in recently burnt areas (Marchant and Higgins 1993). Flocks in the hundreds (Serventy and Whittell 1976) and even up to a 1000 individuals (Boehm 1947) have been recorded, although such observations are likely to be very rare now given the overall decline in the species abundance. In the non-breeding groups segregation of sexes has been reported (Boehm 1947).

In the northern parts of its range, and in other areas characterised by consistently favourable conditions, the Australian Bustard exhibits what is known as an exploded lek mating system (Fitzherbert 1978; Morales *et al.* 2001). Leks are aggregations of displaying males that females visit solely to choose a mate

(Hoglund and Alatalo 1995). At traditional leks, males congregate on a patch or arena within close (usually at least visually close) proximity of each other. Lekking is a specialised mating system that generally favours a select few, particularly fit individuals. The females choose the male they judge as the best and fittest on the basis of characteristics such as the vigour of their display, their plumage and size and their position in the lek (Hoglund and Alatalo 1995). Following mating, females nest and raise the young themselves, with no further input from the male. The system is referred to as ‘exploded’ when individual males are separated by relatively large distances (up to 1 km or so), and it is only when displaying males are mapped over larger scales that such aggregations (leks) are apparent. These lekking areas act as foci for local populations with females and subordinate males aggregating within the vicinity of lekking sites.

In these northern regions, the timing of bustard breeding is generally predictable, commencing prior to the onset of monsoonal rains in the late dry season. Contrary to general reports that suggest breeding occurs at any time of the year in the north (Downes 1982a), breeding commences in the late dry season (September) and lasts through to the mid-late wet season (Feb. – March) (Chapter 7). In the more arid and semi-arid parts of the bustard’s range, breeding is likely to be more opportunistic, following rain and occuring at any time of the year. It is not known whether bustards form leks in these more climatically unpredictable regions, or revert to some other mating strategy. Patchy and unpredictable resource distribution and low population densities of bustards are a feature of these more arid parts of Australia. In these areas it is unlikely that large numbers of bustards aggregate on lekking grounds (at least not on a regular seasonal basis), rather they may be more opportunistic in their breeding strategies, adopting other systems, possibly even monogamy (Marchant and Higgins 1993). In southern Australia breeding has been reported at various times between July and December. Clutch size varies between one or two eggs, occasionally three. Incubation in captivity has been recorded at 24 days. The young are precocial and nidifugous, and parental care is restricted to females (Marchant and Higgins 1993).

Movements and ranging habits

The most comprehensive synthesis of information regarding the biology of the Australian Bustard appears in the HANZAB series which describes the bustard’s movements as dispersive, making “irregular widespread movements apparently over long distances” (Marchant and Higgins 1993). Movements are made “in response to condition of habitat: from areas affected by drought or dry season, to where vegetation is abundant, or large numbers of mice, grasshoppers or locusts occur” (Marchant and Higgins (1993) and references therein). On the Barkly Tableland, in the tropical savannas region of the Northern Territory, Downes (1982a) describes the species as nomadic, opportunistically moving over long distances during the non-breeding season after sporadic rains. Such movements in this region may be particularly pronounced following the first significant rainfall events in the wet season, whereby individuals gather in areas of rainfall and move rapidly between productive areas of grassland (Downes 1982a; Downes and Speedie 1982). In addition to these apparently nomadic movements, it has been suggested that the abundance of bustards peaks in southern regions seasonally. For example, several anecdotal observations suggest that numbers peak during the summer in Victoria, implying possible movements southwards from inland regions at this time (Berney 1907). This implies an element of migratory movement. In contrast to these examples of high mobility, are observations of apparently sedentary populations in areas such as Atherton in Queensland (Bravery 1970), and possibly in other artificial habitats that provide consistent resources year round, such as in areas cleared for horticulture (Blakers *et al.* 1984; Marchant and Higgins 1993). The underlying points are that the movement patterns of the Australian Bustard are poorly defined and understood. The species appears to exhibit a variety of movement strategies across its range. However, it is primarily regarded as undertaking dispersive movements.

The bustard's daily patterns of ranging behaviour or maintenance movements are similarly poorly known. Downes (1982a) suggests that bustards have daily rhythms of movement, moving between open plains, where they feed in the morning and evening, and scrub areas for shelter during the day. Studies of closely related species elsewhere have demonstrated bimodal peaks in activity in the morning and late afternoon, with daily patterns of movement or ranging behaviour varying between species (Allan 1994; Alonso *et al.* 1995; Combreau *et al.* 2000; Combreau and Launay 1996).

A BRIEF OVERVIEW OF TROPICAL SAVANNAS

Practically all bustard species share similar habitat preferences for open grassland systems. Tropical savannas are therefore important biomes for many species worldwide. In Australia, the northern tropical savannas represent a stronghold for the Australian Bustard. Detailed ecological investigations of the bustard were conducted here at two representative sites in the Northern Territory. In addition, satellite tracking included an individual originating and using the Channel County of south-western Queensland. A brief description of this region is included.

Tropical savannas are characterised by a continuous grass layer with a more or less discontinuous tree and/or shrub layer (Bourliere 1983; Cole 1986). Savannas occupy a large proportion of the world's tropics occurring across significant areas of Africa, South America, Australia and parts of Asia. In many of these places savannas span the region between tropical rainforests and deserts (Cole 1986). Characteristic features of these environments are a distinctive monsoonal wet-dry climate and frequent fire (Johnson and Tothill 1985). However, the onset and extent of rainfall may be variable over the geographic range of savanna systems, leading to variation in the types of vegetation communities that occur.

Australia's tropical savannas

Australia's savannas are the dominant ecosystem of Australia's tropics occupying about one quarter of the continent (1.9 million km^2), and extending from the south-west Kimberley to mid-eastern Queensland (Fox *et al.* 2001; Woinarski 2008). Owing in part to a very low human population, and in contrast to savannas in other parts of the world, Australia's savannas are regarded as relatively intact. However, the region is under increasing pressure from development, the spread of introduced weeds and feral animals, widespread pastoralism, broad-scale changes to fire regimes and other human induced impacts (Woinarski 2008). These impacts combine to affect the integrity of the savanna ecosystem, and are regarded as largely responsible for changes in the status of significant elements of the region's biota (Franklin 1999; Woinarski *et al.* 2007).

Climate

The savannas are dominated by a distinct wet-dry monsoonal climate with a distinct gradient in the extent and seasonality of rainfall from north to south. Annual rainfall and rainfall predictability is highest in the north, and declines steadily to the south (Figs. 1.2 & 1.3), with associated effects on many aspects of savanna dynamics (Ridpath 1985). Most of the rainfall occurs during a relatively short wet season (December to March) and is followed by a prolonged dry season with little or no rainfall. The seasonality of rainfall is a primary driver of savanna productivity. In general, this translates to a glut of many resources available to much of the biota in the late wet season which then gradually decline over the extended dry season leading to resource lows by the end of the year (Woinarski *et al.* 2005). Temperatures are relatively high throughout the year with highest humidity and temperatures towards the end of the dry season and during the wet season.

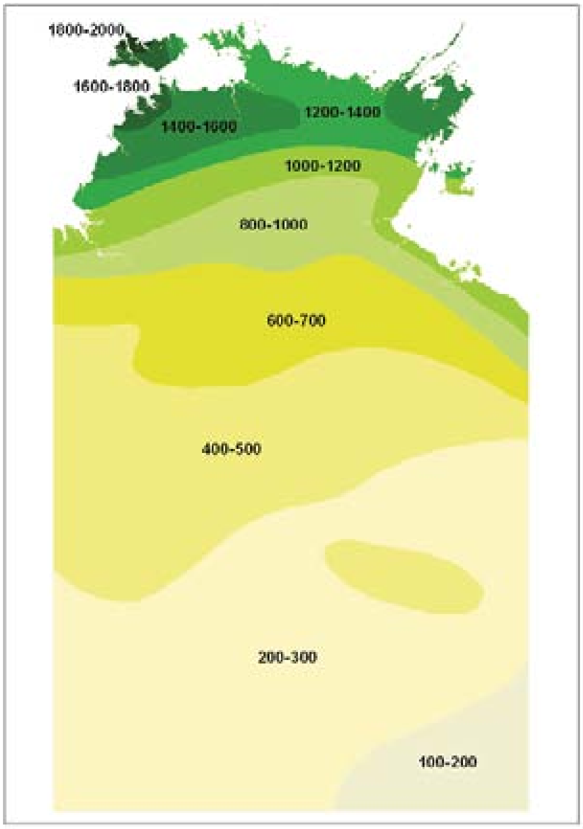

Figure 1.2: Average rainfall (mm) in the Northern Territory demonstrating the distinct gradient from north to south.

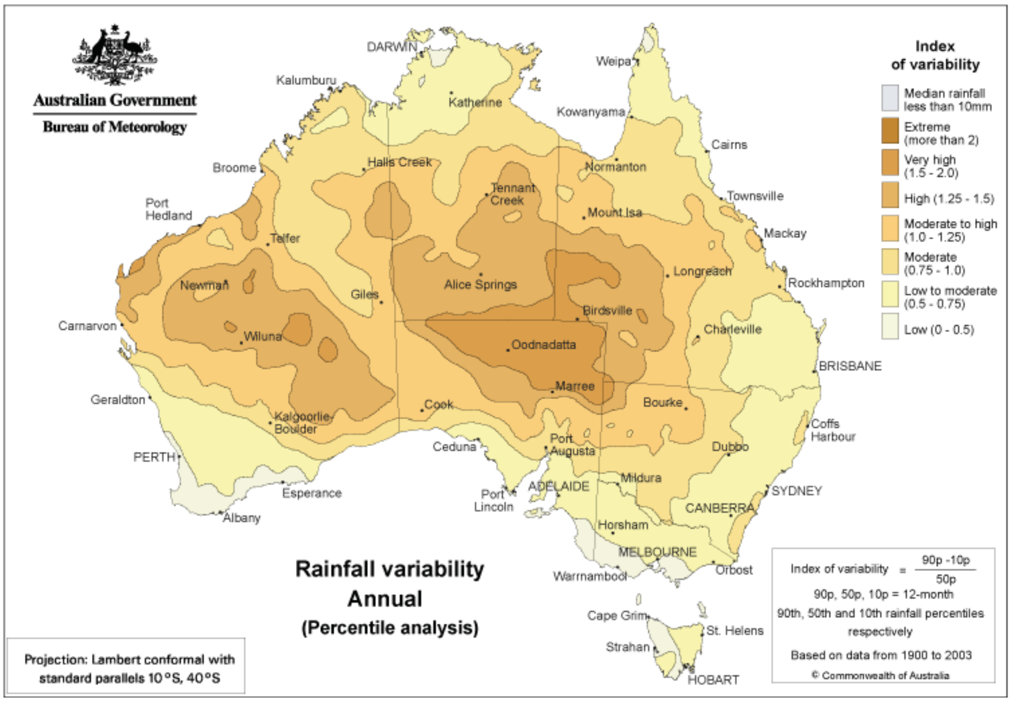

Figure 1.3: Annual rainfall variability across Australia with variability increasing from the coastal regions of northern Australia to the arid centre.

Fire

Along with the distinctive wet-dry climate, fire is the other fundamental driver of savanna landscape dynamics. Indeed, it is the alternation between the highly productive wet season, that stimulates extensive grass growth, followed by a prolonged dry period during which grasses senesce, that primes the landscape for regular burning. Fires in this biome are the most extensive and frequent of any in Australia (Dyer *et al.* 2001). In the higher rainfall areas of the savannas up to 50% of the entire landscape is burnt either every year or every second year, usually in the late dry season (Fig. 1.4) (Dyer *et al.* 2001; Russell-Smith *et al.* 1997).

The effects of fire on the flora and fauna are many and depend largely on particular fire scenarios. Having reached a relative equilibrium following human colonisation of Australia, the region's biota is generally well adapted to the fire regimes that prevailed under traditional Aboriginal land management (Bowman 1998). Fire was used as a tool by Aboriginal people for millennia to attract game (including bustards), to clear the country, for ceremonial purposes and to protect sacred sites (Bowman 1998; Bowman and Prior 2004). These fire regimes were largely characterised by low intensity early dry season (May-June) fires over relatively small scales leading to a mosaic of burnt and unburnt patches over the savanna landscape (Bowman 1998; Williams *et al.* 2002). Following European settlement, and the consequent cessation of traditional Aboriginal burning practices, fire regimes changed in northern Australia. Fires are now more frequent, particularly in more settled parts (Fig. 1.5), and occur late in the dry season, leading to larger and more intense fires (Russell-Smith *et al.* 1997).

The impact of contemporary fire regimes on Australia's savannas has received increasing attention in recent decades. Recent evidence suggests that fires regimes have detrimental impacts on vegetation communities, particularly fire sensitive species such as cypress pine *Callitris intratropica* (Price and Bowman 1994), monsoon rainforests (Russell-Smith and Bowman 1992) and escarpment vegetation communities (Russell-Smith *et al.* 1998). Fires may also significantly alter the structural composition of habitats, including promoting woody weed infestation of open habitats preferred by the bustard (Bowman *et al.* 2001; Lewis 2002; Sharp and Bowman 2004). Altered fire regimes have also been implicated as a contributing factor in the decline of several faunal assemblages (Woinarski *et al.* 2007), including ground nesting and foraging birds (Franklin 1999; Fraser *et al.* 2003).

NOTE:
This figure is included on page 32
of the print copy of the thesis held in
the University of Adelaide Library.

Figure 1.4: Timing and extent of fires within the tropical savannas during 2003. (Data sourced from DOLA, WA on behalf of the Bushfires Council of the Northern Territory).

NOTE:
This figure is included on page 32
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Figure 1.5: Fire frequency between 1997-2002 in northern Australia. (Data sourced from DOLA, WA on behalf of the Bushfires Council of the Northern Territory).

Vegetation

The pronounced north-south rainfall gradient and distribution patterns of soil types are primarily responsible for the structure and composition of vegetation communities across the savannas (Williams *et al.* 1996). In general, the tropical savannas are characterised by broad, homogeneous areas of vegetation, much of which, by Australian and international standards, remains extensive and intact (Woinarski *et al.*

2005). In the north, where rainfall is highest, woodlands and open forests dominate, while open shrublands and grasslands are a feature of areas with lower rainfall. Eucalypts dominate the tree layer, but other common tree and shrub genera include *Acacia, Terminalia,* and *Melaleuca*. However, defining the savanna biome, and the primary habitats favoured by bustards, is the grassy understorey which may vary in species and life forms from site to site. Hummock grasses (e.g. *Triodia* sp.) tend to dominate rocky and arid sandy soils. Perennial tussock grasses are common and widespread, but have also been replaced in many parts by annual grasses promoted by heavy grazing and altered fire regimes (Dyer 2001).

The marked seasonality of rainfall also drives significant seasonal variation in primary productivity (particularly of the grass layer) with peaks in the late wet and early dry season. Flowering and fruiting phenology is similarly periodic though often with wider, more idiosyncratic peaks. Grass seed resources are important to a range of species in the savannas, with seed availability generally peaking in the late wet and early dry months before declining throughout the dry season until there is a general paucity in the early wet season (Crowley and Garnett 1999; Dostine *et al.* 2001).

Other notable vegetation communities in monsoonal Australia include monsoonal rainforests, which occur in small pockets in areas of permanent water that are generally protected from fire (Russell-Smith and Bowman 1992), and mangrove communities found along coastlines and intertidal areas. However, the density of trees in these habitats makes them generally unsuitable for bustards. By comparison, larger rivers, particularly closer to the coast, are often bordered by extensive open floodplains, which although typically inundated in the wet season, may be of particular importance to bustards given their preferences for open habitats.

Land uses

A characteristic of Australian savannas that distinguish them from many of the world's savanna environments is that they remain largely intact and have not been as affected by human activities (Woinarski *et al.* 2007). Human occupation of the region is low supporting about 1% of the entire Australian population. A high proportion of the population is indigenous, reflected in the Northern Territory by a notable proportion of land under Aboriginal control (Fig 1.6). Pastoralism is the most widespread and dominant land use accounting for approximately 46% of the NT (Hosking 2002). Other uses include tourism, mining and military land, while approximately 9% of the Northern Territory is assigned for conservation if N.T. National Parks and Reseves, Indigenous Protected Areas and private conservation estates (e.g. Australian Wildlife Conservancy properties) are included (J.C.Z. Woinarski, pers. comm.).

NOTE:
This figure is included on page 34
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Figure 1.6: Major land tenures of the Northern Territory. (Sourced from the NT Dept. of Environment, Natural Resources, Arts and Sports).

Land clearing

Across much of the world, land clearing is recognised as a principal threat to biodiversity through habitat loss and fragmentation (Hobbs and Hopkins 1990). While clearing has been extensive in many parts of Australia, in the north it has been limited, restricted to approximately 4.6% of the savannas primarily in south-eastern Queensland (Fox *et al.* 2001) (Fig. 1.7). Most clearing in the savannas has occurred for pastoralism and horticulture. However, agricultural efforts have met with limited success to date (Fox *et al.* 2001), although with recent increasing interest in developing northern Australia, clearing and subsequent impacts are likely to increase (Price *et al.* 2003).

NOTE:
This figure is included on page 34
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Figure 1.7: Land clearing in Australia's northern savannas (from Fox *et al.* 2001)

Channel Country

The Channel Country bioregion spans several Australian jurisdictions including an area of the Northern Territory, a large part of south-west Queensland, the north-east corner of South Australia and a small section of far north-western New South Wales (Fig.1.8). The region's climate is considered arid with highly variable but generally very low rainfall with averages across the region below 200 mm (Morgan and Terrey 1992). Temperatures range from average maxima between 35 – 37°C to minima around 5°C. A characteristic feature of this bioregion is the multiple river channels, very wide floodplains and large waterholes that crisscross a landscape of gibber plain, low stony rises and dunefields. These extensive waterways are often dry, however, infrequent flooding, often as a consequence of rainfall far upstream, leads to widespread flooding of the river and floodplain systems. This leads to highly productive flushes of primary productivity along channels and floodplains, leading to highly favourable conditions for much of the region's biota even though rainfall is absent. Consequently, the area is regarded as an ecological refuge (Morton *et al.* 2001). Vegetation in the Channel Country is typical of arid zones with low shrubland and open grassy plains dominant. Riparian corridors are fringed with larger trees and shrubs including Coolabah *Eucalyptus microtheca*, River Red Gum *Eucalyptus camaldulensis* and Gidgee *Acacia cambagei*.

NOTE:
This figure is included on page 35
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Figure 1.8: The Channel Country bioregion straddles several jurisdictions. Map sourced from The Wilderness Society website http://www.wilderness.org.au/articles/channel-country-rivers

OBJECTIVES AND SCOPE OF THE STUDY

Scope and objectives

The general objective of the study was to use the Australian Bustard as a model species to examine the movements of a purportedly 'exemplar' highly mobile, terrestrial Australian bird. Recognising that any attempts to do so requires knowledge of a species' ecology the project aimed to examine specific aspects of the bustard's biology. In doing so, it took a multi-scaled view and sought to integrate broad-scale analyses of bustard distribution and movement patterns, with investigations of the bustard's ecology at two sites in Australia's tropical savannas. Broad-scale approaches included examining continental scale patterns of distribution and movements, while detailed ecological studies aimed to assess the effects of environmental variation on local population dynamics, seasonal habitat use and home ranges, activity budgets, diet and aspects of the bustard's mating system.

Synopsis and general aims of chapters

Chapter 2 takes a big picture approach. A primary challenge for studying broad-scale movements and large population fluctuations over vast and remote regions is acquiring adequate data regarding the distribution and status of such species. In this chapter, a large-scale mail survey of rangeland users and landowners across most of Australia aimed to characterise and describe the status, distribution and movement patterns of bustards and some of the factors that may influence these patterns at a near continental scale.

Complementing this broad-scale approach was a detailed *in situ* study of the bustard's ecology at two representative sites in northern Australia. ***Chapter 3*** describes and discusses the habitat characteristics and variability in key resources to bustards at these two sites. Consequently, it forms the basis for detailed studies of key features of the ecology of the bustard addressed in chapters 4 to 7.

Population dynamics and demographics of bustards at the two main study sites in northern Australia are addressed in ***Chapter 4***. Methods are developed for systematically surveying bustards in relation to the dynamic habitats they occur in. Seasonal population fluctuations are related to the variability of the bustard's main food resources as described in Chapter 3.

Chapter 5 considers habitat use and home ranges of bustards with particular emphasis on the breeding season. It also details the ranging and habitat use patterns of two female bustards over several seasons using information derived from satellite tracking.

An assessment of bustard diet in the northern savannas in the mid-late dry season and analyses of daily and seasonal activity patterns of bustards form the basis of ***Chapter 6***.

The breeding system of bustards is addressed in ***Chapter 7***. This chapter begins with a classification of display sites compared with a random set of sites to determine whether there are particular habitat features associated with preferred display areas. Fidelity of displaying males to preferred sites is assessed in relation to variability in habitat conditions. Detailed information is presented over an entire year for a mature male tracked by satellite that was captured at its display site. A general assessment of the bustard against a set of criteria used to define lekking behaviour is made.

Emerging technologies are allowing biologists to track the movements of fauna across broad temporal and spatial scales, and relating such movements to potential environmental drivers. Complementing the bigger picture approach in Chapter 2 and detailed *in situ* investigations of the bustard's ecology, ***Chapter 8*** presents an exploratory investigation of the movement patterns of bustards as determined by satellite telemetry in regions of contrasting climatic variability.

Chapter 9 synthesises the salient findings and conclusions of the study. It also discusses the management and conservation implications of the key findings in light of the perceived threats facing the bustard and dispersive species in general. The thesis concludes with a discussion of conservation strategies for dispersive species and requirements and opportunities for further research.

Limitations and caveats

This study was constrained by several factors that limit the interpretation and generalisation of some of the results. Specific issues will be addressed in greater detail in later chapters, however, here I present the salient limitations to note at the outset. Firstly, the study is unavoidably limited in its time frame and spatial scope. An argument made in this thesis is that much of the Australian fauna operates on climatic cycles that may extend over many seasons. In order to investigate faunal responses to Australia's climatic and environmental variability such studies must necessarily operate over extended periods which are often beyond the scope of current funding cycles let alone postgraduate research projects. Nevertheless, whenever possible this study considered aspects of the bustard's biology at various geographical scales, while the extended period over which satellite tracking data were collated allowed for analyses over several years that are unprecedented for a terrestrial Australian bird. Secondly, there were nonetheless relatively few individual birds subject to specific investigations of movement using satellite telemetry. This was partly due to expense, logistics and welfare issues that arose during the early stages of the study that altered the focus of the study. Additionally, an objective of the study was to examine movements in relation to environmental drivers. However, limited information on landscape-scale resource dynamics was available.

Chapter 2

Monitoring continental movement patterns of the Australian Bustard through community-based surveys and remote sensing

Bruce Doran

> *"The whole secret of life in arid regions is movement,*
> *a readiness and a freedom to migrate"*
>
> F. Debenham

Chapter 2

Monitoring continental movement patterns of the Australian Bustard through community-based surveys and remote sensing

This chapter has been published as cited below. A copy of the original publication appears in Appendix 2 (omitted in electronic version for copyright reasons). It is presented here with slight modifications and with larger and colour-formatted figures for greater clarity. Note that because it is presented largely as published there is some repetition with other parts of the thesis.

Ziembicki, M. and Woinarski, J.C.Z. (2007). Monitoring continental movement patterns of the Australian Bustard *Ardeotis australis* through community-based surveys and remote sensing. *Pacific Conservation. Biology.* **13**: 128-142

INTRODUCTION

Highly mobile species are difficult to conserve and manage since their conservation depends on ensuring the maintenance of suitable habitat in geographically distant and disconnected locations over broad time periods (Price *et al.* 1999; Webster *et al.* 2002; Woinarski *et al.* 1992). These difficulties are magnified for nomadic and irruptive species that move opportunistically and seemingly unpredictably across landscapes or undergo marked ‘boom-bust’ population fluctuations in response to variable and erratic climatic conditions and resource availability. Assessing the distribution, movements and population fluctuations of such fauna is inherently difficult because of the spatial and temporal scales involved and the complexities associated with movements and population dynamics in highly variable and unpredictable environments. In Australia, these difficulties are compounded by the characteristics of its human population, namely, a low number of amateur and professional ornithologists, a very low overall population density and the concentration of the population along southern and eastern coasts. Consequently, for mobile or irruptive species in remote regions, monitoring and conservation planning is a considerable challenge and many years may pass before significant and potentially catastrophic declines in population levels are detected, or critical areas identified.

The initiation of national atlas and bird counts has greatly increased our knowledge of Australia’s birds and demonstrated the utility of using the public in large-scale monitoring programs. Such schemes have facilitated broad-scale spatial and temporal analyses of Australian bird distributions (Barrett *et al.* 2003) and propagated the development of analytical tools to describe large-scale movement patterns (Griffioen and Clarke 2002). However, analyses of such atlas data are presently limited to species and regions for which there are adequate records. This largely excludes vast areas of outback Northern Territory, Western Australia and South Australia. Similarly, for species in eastern Australia that undergo marked population fluctuations or make nomadic movements, analyses are problematic because much of the complexity is lost in analyses that require data pooling across periods largely out of synchrony with the temporal patterning of bird movements. Consequently, such analyses make it difficult to detect variable, irregular movements and population fluctuations that are responses to climatic variation over longer and/or less regular periods than seasonal or annual cycles. Such limitations highlight the difficulties associated with collating data over biologically meaningful scales and may only be overcome by greater survey effort by atlas volunteers or the development of alternate or complementary survey methods (Mac Nally *et al.* 2004).

Collection of information from landholders and other rangeland users may provide a means for detecting patterns over broad spatial and temporal scales. Surveys involving landholders and the public have been widely used to document distribution and population status of numerous taxa (Lunney *et al.* 1997; Maroney 2005; Mawson and Long 1996; Parker and Bucher 2000; Saunders 1993) and are used to assess wildlife population trends for harvested species (Forsyth 1999; Frawley *et al.* 2004). In inland Australia, two previous studies have used mail surveys of rangeland residents to assess the distribution patterns, movements and population dynamics of the Long-haired Rat *Rattus villosissimus* (Carstairs 1974) and the Budgerigar *Melopsittacus undulatus* (Wyndham 1983) over near continental scales.

This chapter reports on a mail survey of rangeland users that aimed to provide information on variation in the distribution and abundance of the Australian Bustard, with such information sought to retrospectively cover a 12 year period (1990-2002). The bustard is particularly amenable to such a study because it is conspicuous, easily identifiable and an iconic species across outback Australia. The study aims to collate and characterise distributional patterns from this mail survey, and to report on factors given by the respondents as associated with the temporal variation in bustard distribution and abundance. I further aim to relate this reported variation in bustard distribution to factors that have been considered to underlie the shifting distributions in highly mobile Australian birds. Across much of the Australian continent, the principal factor driving such movement is rainfall and the consequential response of vegetation and food resources (Gilmore *et al.* 2007; Nix 1976; Roshier *et al.* 2001a).

Nix (1976) proposed that bird movements are broadly related to pulses in plant productivity that occur over seasonal and climatic cycles across Australia. This model, and limited previous information on bustard movement patterns (Downes 1984; Marchant and Higgins 1993) suggest, that bustards may respond to climatic variability in several ways. In regions influenced by marked, but predictable seasonal conditions, bustard numbers should fluctuate in a regular predictable manner as a proportion of the population migrates seasonally between regions. Accordingly, in northern, monsoon-influenced regions bustard abundance may peak over the summer wet season and diminish in the dry, while in southern areas dominated by more consistent winter rainfall, peaks over the winter months are more likely. In some districts characterised by suitable conditions throughout the year, especially regions dominated by crop agriculture, the majority of the population may be sedentary. As climatic conditions and associated resource availability become increasingly erratic in more arid regions, patterns of abundance and breeding should become less seasonally distinct. In such regions bustards may be expected to occur and breed at any time of the year with limited or no seasonal patterns to their occurrence. In these regions, the occurrence of bustards is likely related to significant rainfall events and I test for this by considering the relationship between bustard occurrence and rainfall patterns over several years. The influence of climatic conditions on the prevalence of highly mobile fauna in a region may be affected by prevailing conditions not only in that region itself but also by relative conditions in adjacent areas. For example, in times of extensive drought, movements outside of normal ranges, often towards wetter coastal districts, are common for many species (Keast 1968; Ford 1978; Blakers *et al.* 1984; Storr 1984; Marchant & Higgins 1993). This relationship is examined by comparing reporting rates in regions in relation to prevailing rainfall patterns in surrounding areas.

To link bustard movement patterns with the shifting patterns of resource availability requires not only reliable information on bustard abundance and distribution, but also comparably-scaled information on resource abundance. At the opposite technological extreme to simple mail-out surveys of landholders, advances in spatial information systems and satellite telemetry now make it possible to document changes in resource availability and to track mobile fauna over broad spatial and temporal scales. Accordingly, there is a growing body of research concerned with tracking variation in rainfall, vegetation greenness and primary productivity using satellite imagery (Berry *et al.* 2007; Paruelo and Lauenroth 1995; Pickup 1995; Pickup *et al.* 1994; Pickup *et al.* 1993), which is increasingly being applied to model the distribution of biodiversity and individual species on large scales (Fisher 1999; Oindo and Skidmore 2002; Osborne *et al.* 2001; Osborne *et al.* 1998; Serneels and Lambin 2001; Suarez-Seoane *et al.* 2002). Osborne *et al.* (2001) modelled the landscape-scale distribution of the Great Bustard *Otis tarda* in relation to remotely-derived plant productivity indices in agricultural regions of Spain. Such techniques have potential for assessing and predicting the opportunistic responses of highly mobile, nomadic birds to patterns of climate-driven pulses of productivity over large scales. However, they have been seldom used in an Australian context. A notable exception is a recent effort to map the distribution of temporary and permanent wetlands in arid Australia using satellite imagery in an attempt to assess the responses of waterbirds to habitat availability (Roshier *et al.* 2001a; Roshier *et al.* 2001b; Roshier *et al.* 2002). Here, I examine whether relationships exist between bustard abundance and vegetation greenness within regions characterised by relatively homogeneous and simple landscapes in central Queensland that part of the bustard's distribution for which I have the most data.

METHODS

Study Area

The study covered most of the rangeland areas of continental Australia, excluding Victoria (a total area of more than 4.6 million km^2). To facilitate data summaries and analyses, mail survey responses were grouped into regions based on aggregations of Interim Biogeographic Regionalisation of Australia (IBRA) bioregions Environment Australia (2000) and survey responses (Table 2.1; see also Figure 2.1). The rationale was to aggregate sufficient responses on a regional basis to allow comparisons between regions that differed broadly in climate, vegetation associations, landform and land use. Thirteen groups were defined but ‘South-west WA’ and ‘Central NSW’ regions were excluded from subsequent analyses because of the low number of survey responses for these regions.

Mail survey of rangeland users

The extent of mail survey coverage differed between regions and largely depended on the presence and density of pastoral properties per region. For example, central Queensland received comprehensive coverage owing to the large number of relatively small pastoral properties whereas the more sparsely inhabited adjacent areas of far south-west Queensland received limited coverage. Large, but sparsely populated areas of central-western Australia and most Aboriginal reserves of the Northern Territory and South Australia were not surveyed on this occasion.

A total of 5 012 survey forms were distributed to pastoral properties and rangeland users across the study region. The survey was designed to be simple and concise in order to maximise return rates. It included a cover letter, black and white identification diagrams and descriptions of the focal species, a reply paid envelope and 20 questions concerning the occurrence of bustards and Flock Bronzewing Pigeons *Phaps histrionica* (see Appendix 2). Information on the latter species is not addressed in this chapter. Logistical difficulties required that the survey be conducted in stages resulting in three different methods of survey distribution. Initial surveys were sent directly to pastoralists and rangeland users in Western Australia, South Australia and the Northern Territory in October 2002. Queensland Government restrictions over access to pastoral addresses delayed the distribution of surveys in the state until February 2003 when AgForce Queensland (a large, member-based organisation representing many of Queensland’s primary producers) posted surveys to its members across rural and remote Queensland on behalf of the study. Similar restrictions in New South Wales resulted in the distribution of surveys as a leaflet in NSW Agriculture’s ‘Western Division Newsletter’ in August 2003 with an accompanying short article in the newsletter regarding the project, including identification notes.

The geographical locations of survey respondents were collated using the ‘Gazetteer of Australia’ sourced from Geoscience Australia http://www.ga.gov.au/map/names. Each property’s homestead was taken as the geographical location for each survey response.

Table 2.1: Characteristics of regional groupings

Region	Characteristics of region
Barkly/ NW Qld	Dry monsoonal ranging to arid in south with pasture growth in summer and autumn. Dominated by tussock grass plains, ranges of the Mt Isa outlier and open woodland in north. Cattle grazing
Brigalow	Semi-arid to sub-humid climate. Alluvial plains and rugged ranges. Many areas developed for cropping and improved pasture. Rainfall and plant growth in summer, rainfall decreasing north-south and with distance from coast.
Cape York	Tropical monsoonal, strongly seasonal with wet summers and dry winters. Variety of landforms, extensive alluvial and coastal plains. Eucalypt and Melaleuca woodlands dominant.
Central Australia	Arid including tropical-temperate transition zone with highly variable, low and often summer rainfall. Dunefields, ranges, floodplains, alluvial plains and gibber. Vegetation dominated by hummock grassland, acacia shrublands and low eucalypt woodlands. Cattle grazing.
Central NSW	Temperate climate with moderate rainfall mostly in summer in north grading to winter rainfall in south. Undulating plains to mountain ranges. Highly developed and fragmented for crop agriculture and to a lesser degree pastoralism.
Central Qld	Dry monsoonal to arid climate with mostly summer rainfall. Treeless, Mitchell Grass plains predominate. Extensive cattle grazing.
Central South Qld	Arid to semi-arid. Summer dominant rainfall which is variable and unreliable. Flat, undulating plains dominated by mulga and low woodland. Sheep and cattle grazing.
Central-west WA	Arid to semi-arid with winter rainfall. Alluvial and colluvium plains dominated by hummock grasslands and mulga with low hills and mesas in north grading to shrublands and eucalypt woodlands. Important sheep and cattle grazing region.
Pilbara/ Gascoyne	Arid, hot climate with low and highly variable rainfall. Includes inland ranges and vast coastal and inland plains. Hummock and tussock grasses and shrubs dominant, but vegetation communities variable depending on landform. Cattle grazing.
Southern SA	Semi-arid to arid climate with pronounced rainfall gradient, erratic further north. Mountain ranges and wide flat plains. Eucalypt open forests, mulga woodlands and shrublands. Extensive clearing for crops in south, sheep and cattle grazing dominate.
South-west WA	Temperate with wet winters. Eucalypt woodlands and forests. Extensively cleared and fragmented for agriculture.
Top End/ Kimberley	Wet-dry tropical monsoonal climate with wet summers and winter dry season. Extensive savanna grasslands and open woodlands and forests. Mainly pastoral leasehold and Aboriginal lands.
Western NSW	Arid to semi-arid with highly variable rainfall, tendency towards summer dominant rainfall in north and winter in south. Undulating and extensive plains dominated by mulga, grassland, shrublands and open woodland. Sheep grazing is the main land use.

Data analyses

Data summaries

Summary data are presented for several survey questions based on regional groupings. These included: seasonal patterns of bustard abundance and evidence of breeding (measured as the proportion of respondents within each region that listed a particular month as favourable for sightings of bustards or breeding activities); geographical distribution of estimated numbers of bustards on each property in the 12 months preceding the survey; proportions of respondents that indicated the length of time they believed bustards remained on their properties; and, proportions of properties by region that listed particular factors as associated with above average bustard numbers.

Bustards and rainfall

For each region, the relationship between variation in rainfall and bustard abundance between years was investigated by generalized linear modelling in Statistica (Statsoft 2003). For any year, bustard abundance was defined as the proportion of properties in a region that recorded bustard numbers that were greater than the 1990-2002 average. The arcsine transformed values for these data were used as the dependent variable in the model. Only surveys where respondents had been in the region for more than 12 years were used resulting in a lower overall number of surveys than used for other data summaries.

Two predictor variables were used: i) % difference from average rainfall in survey year by region, and ii) % difference from average rainfall in the previous year by region. Rainfall data were obtained from the Australian Bureau of Meteorology as extrapolated surface coverages of annual rainfall for every year since 1972 calculated from 4785 rainfall gauges across Australia. The mean rainfall for each region was calculated from these data. For each year since 1990 the deviation from mean rainfall was then calculated for each region. A normal error distribution and log link function were used for this analysis, and the modelling employed a backward stepwise approach that successively excluded variables with $p>0.05$, until only significant variables remained in a minimum adequate model. The goodness of fit of this resultant model is measured by the % of deviance explained.

The potential influence on bustard abundance within a region of rainfall patterns in surrounding regions was also assessed. The dependent variable was again the proportion of properties in a region that recorded higher than average bustard numbers (arcsine transformed). The model's two predictor variables were the % deviance from average rainfall in the present year, and the % deviance from average rainfall in the past year, in all directly adjacent regions. A normal error distribution and log link function were assumed for this analysis, and the modeling procedure is as described above.

Bustards and NDVI

While rainfall is often an effective proxy for primary productivity in rangeland regions, measures of rainfall rely on information from weather stations that are sparsely distributed and which do not necessarily account for the very patchy nature of rainfall events. Additionally, variations in topography, substrate type, vegetation associations and the timing, intensity and duration of rainfall events may lead to localised variations in primary productivity. Advances in remote sensing and satellite imagery circumvent these limitations by allowing the assessment of vegetation greenness and primary productivity at high resolution over vast scales. Here I use a relatively coarse measure of vegetation greenness, the

Normalised Differential Vegetation Index (NDVI) derived from AVHRR data at a resolution of 1.1 km (sourced from the Environmental Resources Information Network, Department of Environment and Heritage), to examine the relationships between bustard abundance and greenness at intra-regional scales. Two regions were chosen for this exercise (‘Central Qld’ and ‘Central Sth Qld’) because of their high survey response rates and their relatively homogeneous and simple landscapes. The number of bustards seen on a property in the 12 months preceding the survey was estimated by respondents according to five abundance categories. For the purposes of this analysis these categorical scores were converted to median values (i.e., None = 0; <5 = 2.5; 5-10 = 7.5; 10-50 = 35; >50 = 75), and used as the dependent variable. A Poisson distribution and log-link function were assumed in the models. Imagery data consisted of maximum and minimum (positive) NDVI values for the 12 months preceding the survey using maximum and minimum value composites produced from all images for that period. These data were re-sampled using ArcInfo Version 9.0 (ESRI Redlands, California) to attain an average maximum and minimum NDVI value within a 2.5 km radius of each respondent’s homestead. A flush value (max. – min.), which acts as a surrogate for the response of vegetation to seasonal rainfall, was then calculated for each of these areas. Values for maximum, minimum and flush NDVI were used as predictor variables along with two vegetation structure characteristics: the growth form of the tallest stratum and density of foliage cover of the tallest stratum (Table 2.2), derived from Geoscience Australia’s 1:5 million scale map of vegetation structure and floristic type Geoscience Australia (2004). Property size was included in the models as an explanatory term to test for its potential influence on reporting of property-level assessment of abundance of bustards. The modelling procedure otherwise followed that described above.

Table 2.2: A list of the original set of explanatory variables used in the GLM analysis to assess Australian Bustard occurrence in relation to primary productivity at intra-regional scales, for two Queensland regions.

Variable	Description
Max NDVI	Mean maximum NDVI value
Min NDVI	Mean minimum NDVI value
Flush NDVI	Difference between mean maximum and minimum NDVI value
Area	Area of respondent’s property Log (area) km^2
Cover	Foliage cover of tallest stratum (<10%, 10-30%, 30-70%, >70%)
Form	Growth form of tallest stratum: 1 = grasses, 2 = low trees or shrubs <10m, 3 = medium trees 10-30m

RESULTS

Survey responses

A total of 755 survey responses were received across Australia representing an overall response rate of 15.1%. Response rates varied between states and the overall proportion of replies was significantly affected by the very low response rate from NSW (Table 2.3), probably because of the less personalised and direct delivery of these questionnaires. Excluding NSW, the total response rate for the remainder of the country was 34%, a relatively high proportion for this type of survey (cf. Carstairs 1974; Lunney *et al.* 1997). Of the total responses received, 10% (n = 76) did not include a property name or specify location details, leaving 679 surveys usable for analyses (Table 2.4). Appendix 1 lists the station names and geographic locations from where these responses were derived. Of these, 96% (n = 655) indicated they had seen bustards on their property at some time in the past. It should be noted however that there is a potential for bias in that respondents from properties without bustards may have been less motivated to reply.

Table 2.3: Survey response rates by State and Territory.

State	Surveys sent	Surveys received	Response rate (%)
Western Australia	487	140	28.7
South Australia	321	94	29.3
Northern Territory	218	59	27.1
Queensland	986	388	39.4
New South Wales	~3000	74	2.5
Total	5012	755	15.1

Table 2.4: Number of useable survey responses for data summaries and modelling analyses for Australian Bustards by region (* indicates that these regions were not considered in modelling analyses)

Region	Useable responses (data summaries)	Useable responses (modelling)
Barkly/ NW Qld	22	14
Brigalow	116	98
Cape York	17	10
Central Aust.	36	22
Central NSW	10	6*
Central Qld	110	96
Central South Qld	85	73
Central-west WA	63	40
Pilbara/ Gasc.	39	25
Southern SA	70	50
South-west WA	6	4*
Top End/ Kimberley	49	18
Western NSW	56	41
TOTAL	679	497

Summary of mail survey data

Peak seasonal abundance by region

In the northern, monsoon-influenced regions, respondents reported that bustard numbers generally peaked over the summer wet season months (December to April); while in the south and west, numbers tended to peak over the winter and early spring (Fig. 2.1). ‘Central-west WA’ and ‘Central South Qld’ exhibited the greatest seasonal variation in bustard numbers, although their highest and lowest periods were directly opposed to each other with numbers peaking in late winter/early spring in Western Australia in contrast to peaks in summer for the southern Queensland region. Variation in best months for bustards was low in some regions, most notably for the ‘Brigalow’ and ‘Western NSW’ regions.

Breeding season

The responses of landholders regarding the occurrence of breeding observations on their properties generally corresponded to best months for bustards (Fig. 2.2). In northern, monsoon-influenced regions breeding peaked in the wet season while in the west, central and south-eastern regions signs of breeding were largely observed in winter or spring. The ‘Pilbara/Gasc.’, ‘Top End/Kimberley’ and ‘Central Qld’ regions reported signs of breeding from all months.

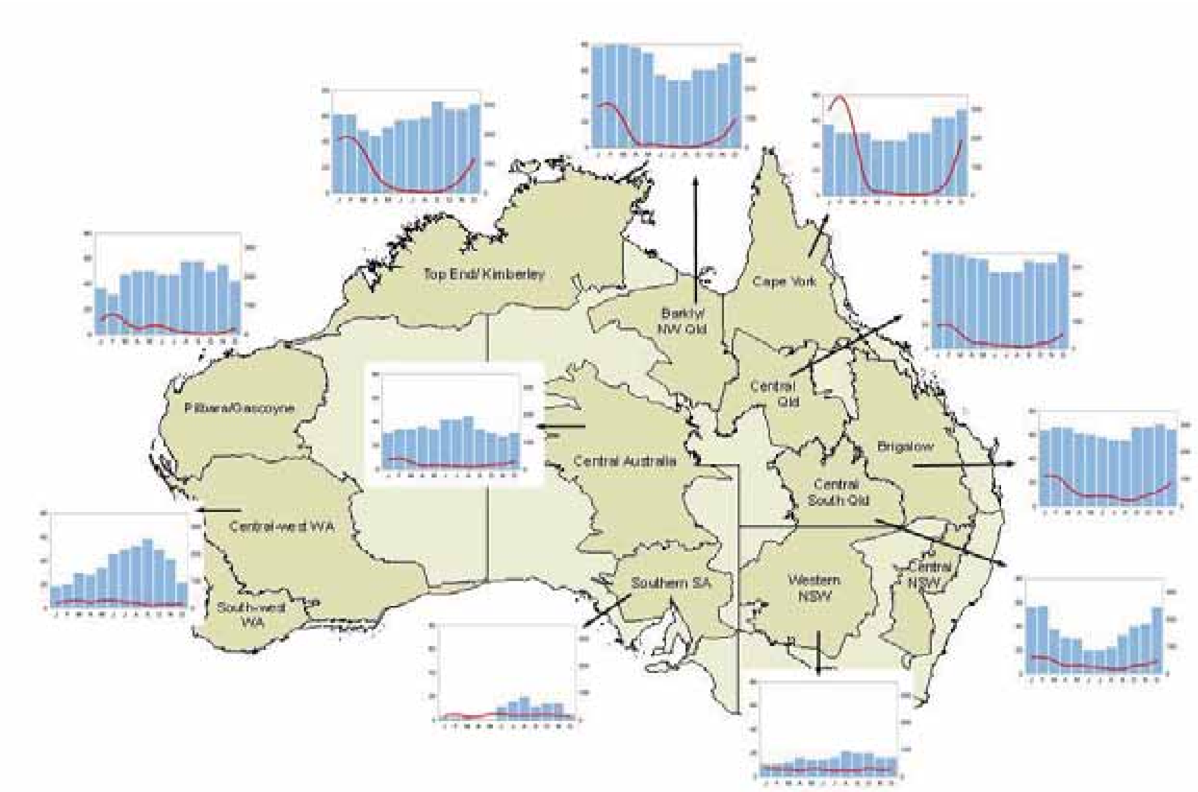

Figure 2.1: Patterns of Australian Bustard prevalence by month for each region, measured as the percentage of responses indicating favourable months for bustards in a region (bars). Scale on left y-axis ranges from 0 -80%. Mean monthly rainfall is included for each region (line) (scale on right y-axis ranges from 0 -300 mm).

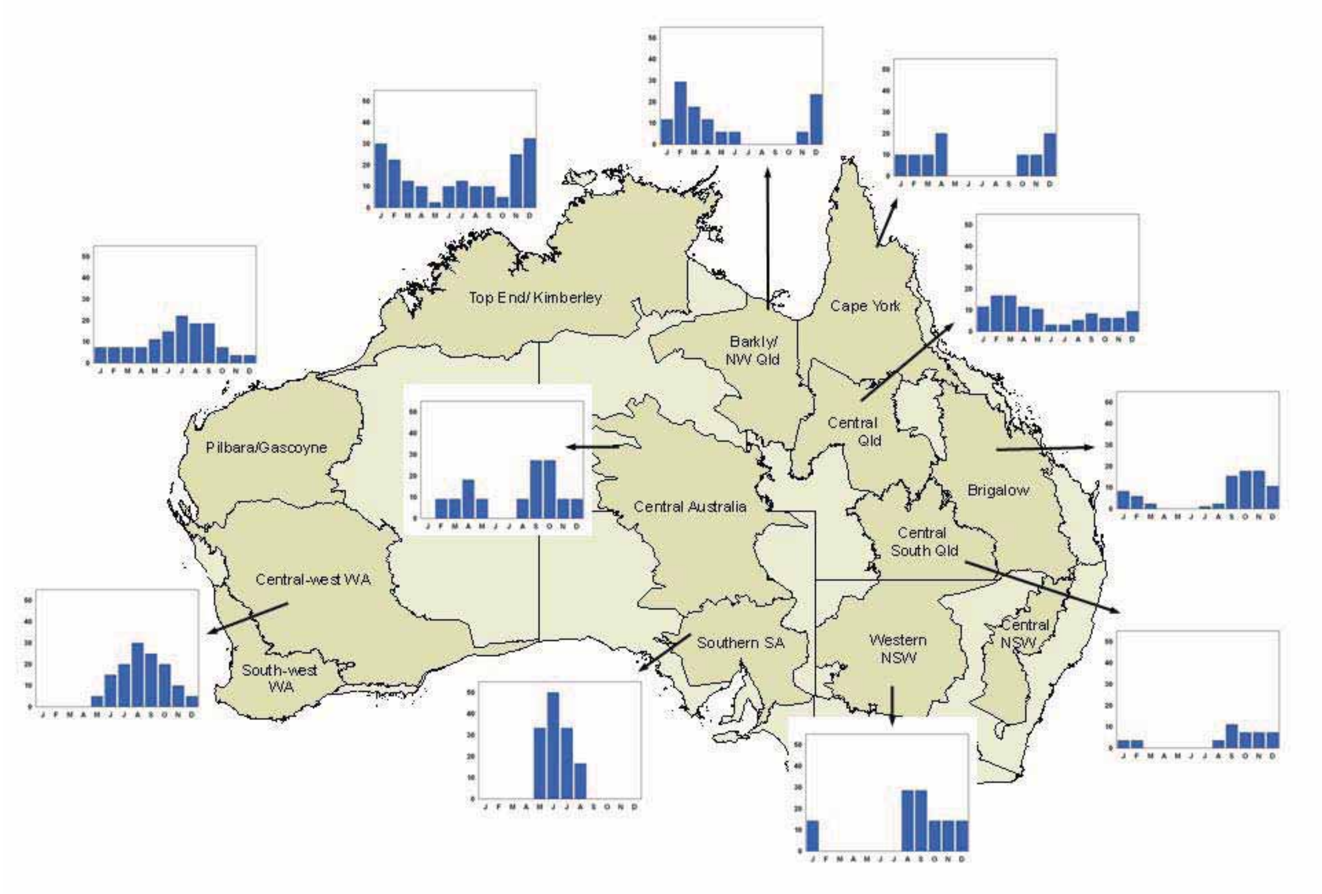

Figure 2.2: Patterns of Australian Bustard breeding by month for each region, measured as the percentage of responses indicating months in which breeding observations are made (breeding observations defined as the sighting of eggs, young or displaying males).

Estimated number in preceding 12 months

Bustard numbers in the 12 months preceding the distribution of surveys generally decreased with increasing latitude (Fig. 2.3). Regions including the ‘Top End/ Kimberley’, Barkly/ NW Qld’, ‘Central Qld’, ‘Brigalow’ and ‘Pilbara/ Gasc.’ recorded the greatest numbers of bustards, while ‘Central Australia’, ‘Central Sth Qld’ and “Central-west WA’ exhibited moderate numbers. In contrast, a majority of respondents in ‘Western NSW’, ‘Central NSW’ and ‘Southern SA’ regions, reported no bustards from their properties.

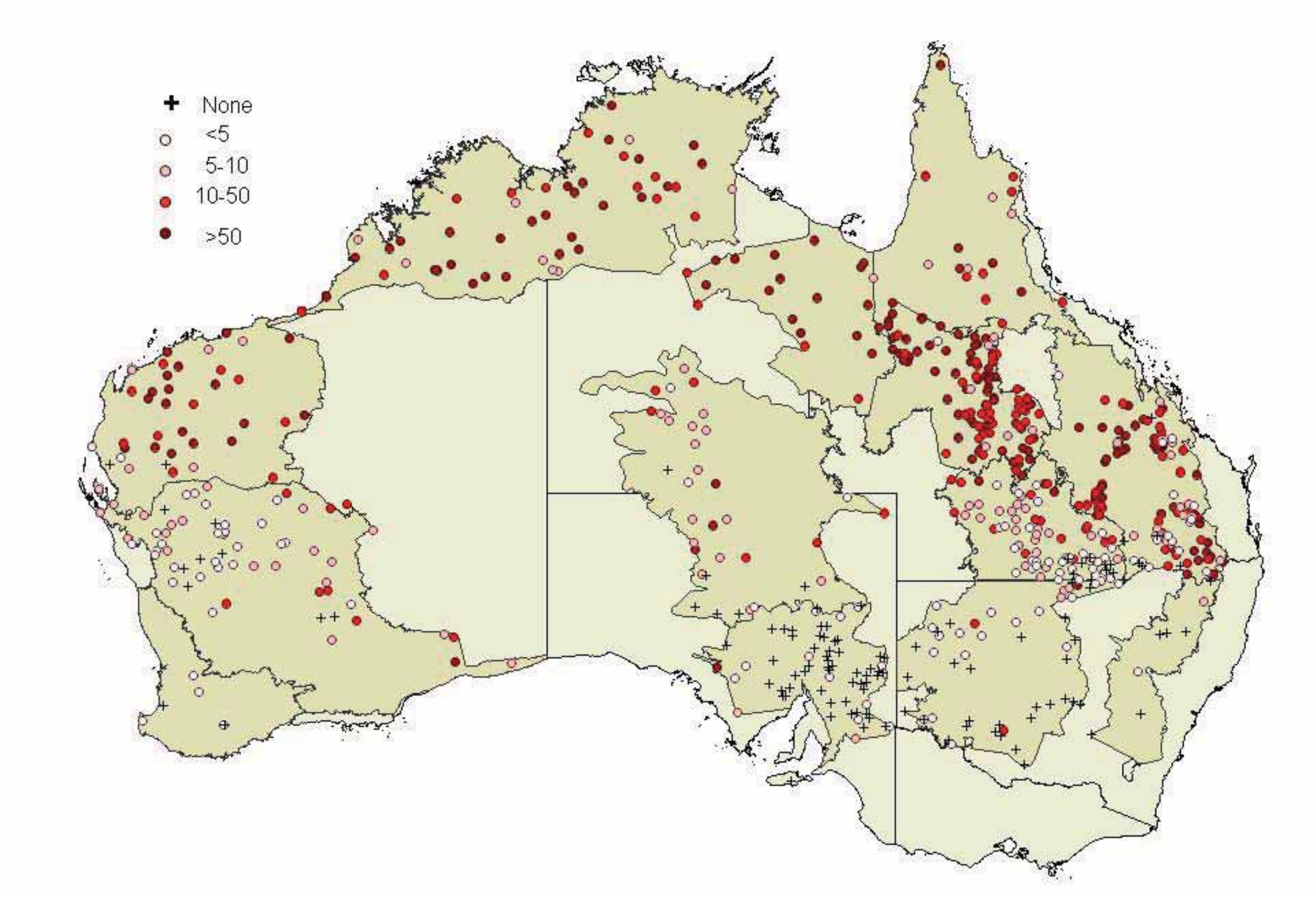

Figure 2.3: Estimated number of bustards seen on each property in the 12 months preceding the survey according to five categories of abundance.

Length of stay

The proportions of respondents that regarded bustards as permanent residents or visitors to their properties differed substantially between northern and southern regions (Fig. 2.4). Notably, a clear majority of respondents from the north including the 'Top End/Kimberley', Barkly Tableland/NW Qld', 'Cape York', 'Central Qld' and 'Brigalow' regions regarded bustards as largely permanent residents on their properties. In the 'Pilbara/Gascoyne' region just over half of all respondents regarded bustards as short or mid-term visitors while in the regions of 'Central-west WA', Central Australia' and 'Central South Qld', bustards were primarily short or medium term visitors. When bustards did occur in the regions of 'Southern SA', 'Western NSW' and 'Central NSW', they were almost always short term visitors. It should be noted that no explicit allowance was made in the questionnaire for respondents to distinguish between short-term seasonal visitors and short-term, aseasonal visitors. However, the low number of respondents from the southern regions that indicated that bustards occur on their properties seasonally, and information from other sources, suggests most short-term visitors occur in these regions irregularly.

Factors reported to be associated with higher than average abundance

Respondents considered above average rainfall as the most important factor associated with above average bustard numbers for all regions (Fig. 2.5). Noteworthy in the northern regions, including the 'Pilbara/Gasc.', 'Top End/ Kimberley', 'Barkly/ NW Qld', 'Cape York' and to a slightly lesser degree 'Central Qld', 'Brigalow' and 'Central Aust.' regions, fire was also regarded as an important factor. Many respondents in most regions identified the presence of high numbers of grasshoppers as an important determinant of bustard presence on their properties. The association of bustards with crops in the 'Brigalow' was greater than other regions though several respondents in the 'Top End/ Kimberley' and 'Central South Qld' regions also listed crops as important. Drought was considered a factor associated with bustard numbers in most southern and central regions.

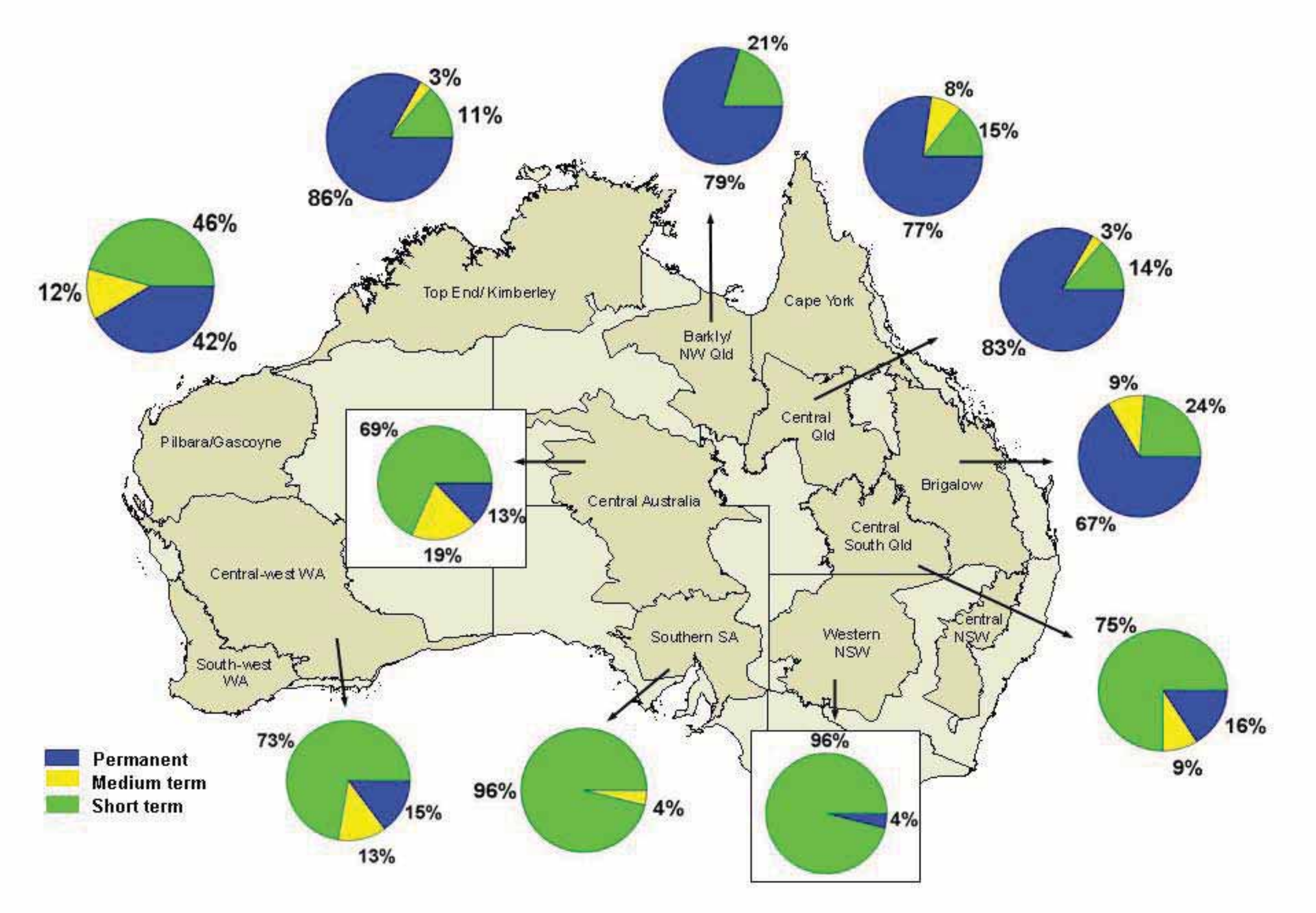

Figure 2.4: Percentage of properties by region recording bustards as permanent residents or medium or short-term visitors.

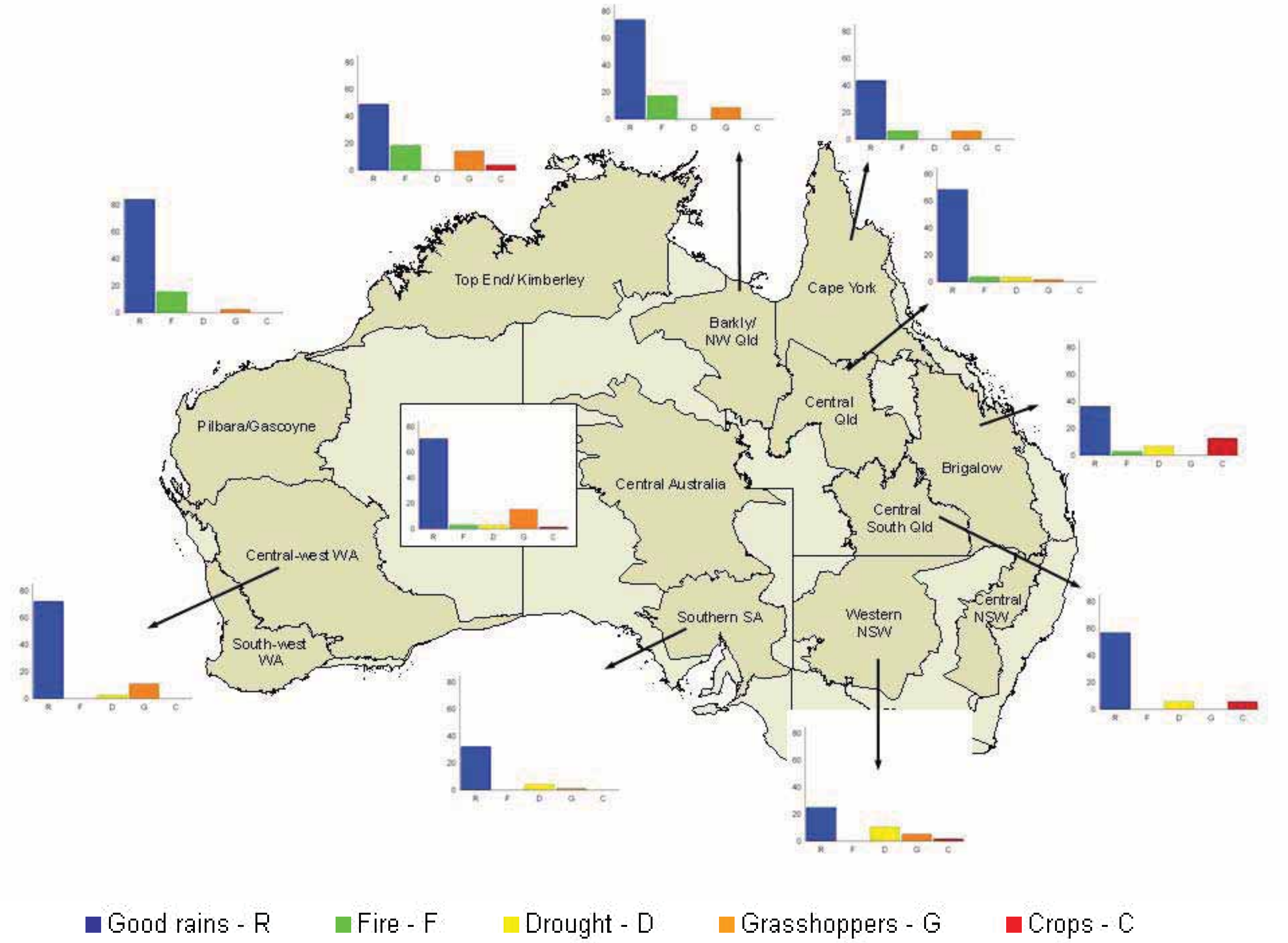

Figure 2.5: Factors respondents associated with above average numbers of bustards expressed as a percentage of responses per region (R = good rains; F = fire; D = drought; G = grasshoppers; C = crops).

Bustard abundance and rainfall

Relationship between regional abundance and rainfall

Of the eleven regions considered in the modelling of rainfall and bustard abundance, seven exhibited a significant relationship between bustard abundance and rainfall for the region in either, or both, the present or previous year (Table 2.5; Figs. 2.6 & 2.7). Except for ‘Western NSW’ these relationships were all positive, suggesting that bustards generally responded favourably to higher than average rainfall in these regions. The predictive performance of the models was strong with moderate to high percentage of deviance explained. With the exception of the ‘Barkly/ NW Qld’ region, which is on the interface between the monsoonal, semi-arid and arid zone, all significant ‘rain this year’ models were for regions that are largely arid, with confidence strongest for Western Australian regions and ‘Western NSW’ ($p < 0.001$). The effect of above average rainfall in the previous year on bustards between regions was significant for both monsoon-influenced and arid regions with confidence strongest ($p < 0.001$) for monsoon-influenced areas in the tropical savannas.

Relationship between bustard abundance in a region and rainfall in adjacent regions

Of the 26 model combinations that were tested to assess the influence of rainfall in adjacent areas, 16 exhibited a significant result for either the past or present year (Table 2.6). The majority of these were for regions in central Queensland and Western Australia, however, overall no clear or consistent patterns emerged. Bustard numbers in the 'Barkly/ NW Qld' and 'Central Qld' regions were positively correlated with above average rainfall in all surrounding regions, with the exception of no effect of conditions in the 'Barkly/ NW Qld' on 'Central Qld' bustard numbers. Bustard numbers in Western Australian regions were significantly correlated with rainfall in adjacent WA regions and for the 'Pilbara/Gascoyne' by rainfall towards the north. There was a significant ($p < 0.05$), moderately good model (34% deviance explained), that bustard numbers were higher in NSW when rainfall was below average in Southern SA. This represents the only result in which an increased reporting rate of bustards for a given region was associated with below average rainfall in adjacent regions.

Table 2.5: Generalized Linear Modelling of bustard abundance against rainfall in regions in years since 1990. Dependent variable is ArcSin (percentage of respondents by region reporting above average bustard numbers per year). Predictor variables are: (1) % deviance from average rainfall in current year, and (2) % deviance from average rainfall in previous year. (* = p<0.05, ** = p<0.01; *** = p<0.001)

Region	% deviance explained	Intercept	Rainfall this year			Rainfall previous year		
			Wald	p	estimate	Wald	p	estimate
Barkly/NW Qld	65 (df=2)	146.7	4.7	*	0.005	14.9	***	0.011
Brigalow	No sig model							
Cape York	No sig model							
Central Aust.	57 (df=2)	120.0	6.0	*	0.008	5.5	*	0.008
Central Qld	83 (df=1)	947.4				48.7	***	0.011
Central Sth Qld	No sig model							
Central-west WA	86 (df=1)	749.3	39.3	***	0.012			
Pilbara/Gasc.	79 (df=2)	224.7	20.9	***	0.007	5.8	*	0.004
Southern SA	No sig model							
Top End/ Kimb.	73 (df=1)	340.0				11.8	***	0.009
Western NSW	61 (df=2)	119.8	11.9	***	-0.022	5.9	*	-0.022

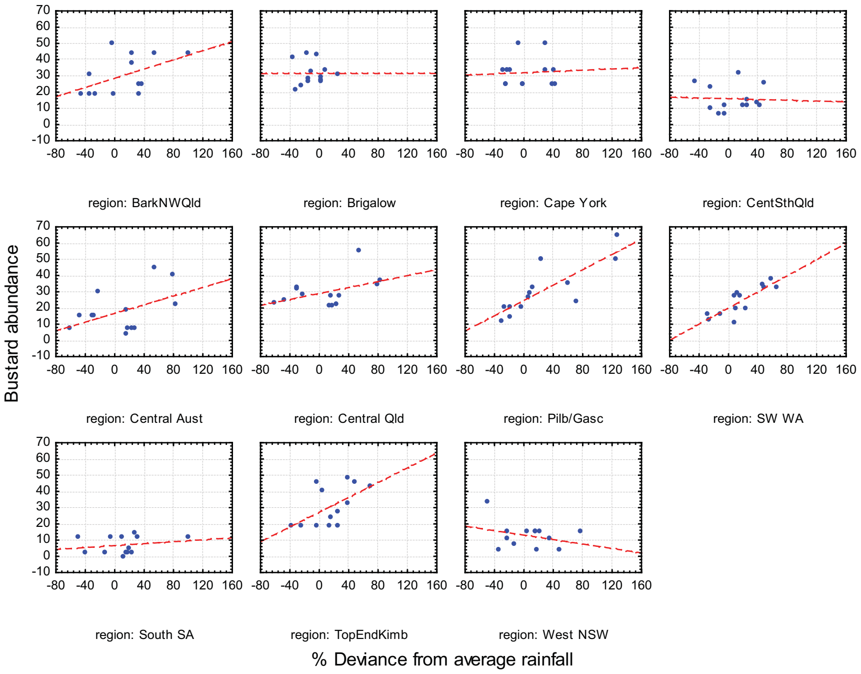

Figure 2.6: Generalized Linear Modelling of bustard abundance against rainfall in regions in years since 1990. Dependent variable is ArcSin (percentage of respondents by region reporting above average bustard numbers per year). Predictor variable is % deviance from average rainfall in current year.

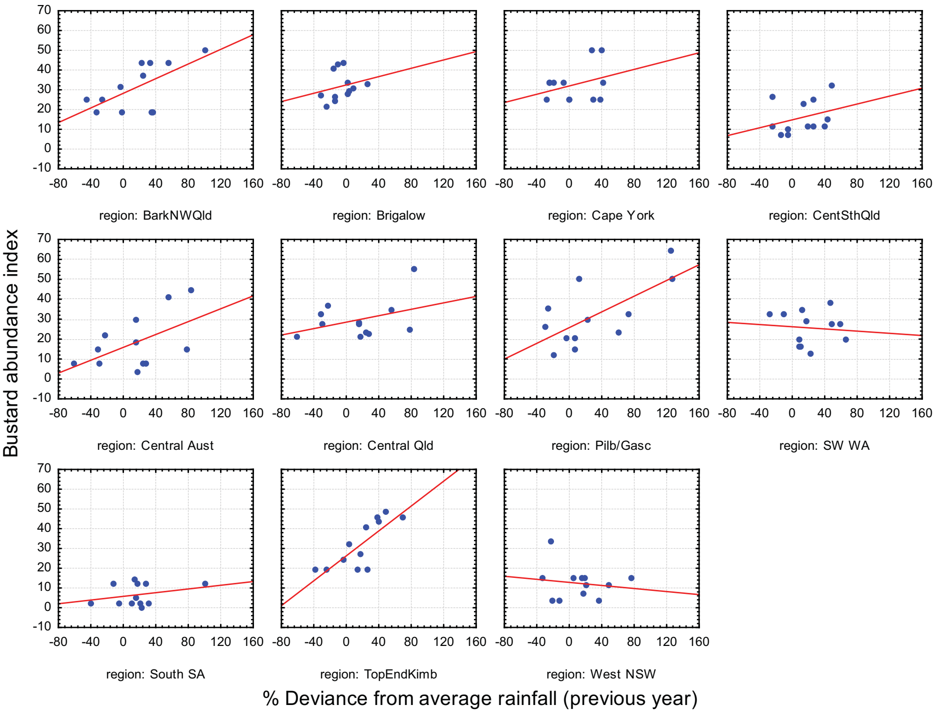

Figure 2.7: Generalized Linear Modelling of bustard abundance against rainfall in regions in years since 1990. Dependent variable is ArcSin (percentage of respondents by region reporting above average bustard numbers per year). Predictor variable is % deviance from average rainfall in previous year.

Table 2.6: GLM of bustard numbers within a region in relation to rainfall in adjacent regions. Acronyms are as follows; BNQ = Barkly/NW Qld, BR = Brigalow, CYP = Cape York Peninsula, CA = Central Australia, CQ = Central Qld., CSQ = Central South Qld., CWWA = Central-west WA, PG = Pilbara/Gascoyne, SSA = Southern SA, TEK = Top End/ Kimberley, WNSW = Western NSW. (* = p<0.05, ** = p<0.01; *** = p<0.001).

Region	% deviance explained	intercept	RAIN_THIS			RAIN_LAST		
(#bust vs %rain)			Wald	p	estimate	Wald	p	estimate
BNQ vs TEK	60 (df=2)	141	4.4	*	0.006	4.6	*	0.006
BNQ vs CQ	51 (df=1)	135				8.6	**	0.011
BNQ vs CA	58 (df=2)	168	8.6	**	0.005	4.8	*	0.004
BNQ vs CYP	55 (df=1)	167				3.9	*	0.007
BR vs CSQ	ns							
BR vs CQ	42 (df=1)	326				8.0	**	0.007
CYP vs CQ	45 (df=1)	214				8.8	**	0.009
CYP vs BNQ	ns							
CSQ vs WNSW	ns							
CSQ vs CQ	27 (df=1)	111				4.1	*	0.013
CSQ vs BR	45 (df=2)	159	6.9	**	0.006	4.9	*	0.006
CQ vsBNQ	ns							
CQ vs CSQ	53 (df=1)	215				12.2	***	0.011
CQ vs BR	82 (df =2)	604	45.3	***	0.006	14.8	***	0.004
CQ vs CYP	34 (df=1)	234				5.3	*	0.007
PG vs TEK	30 (df =1)	100	18.7	***	0.016			
PG vs CWWA	60 (df=2)	62	14.1	***	0.01	6.2	**	0.008
CWWA vs PG	59 (df=1)	391	18.5	***	0.004			
CA vs BNQ	ns							
CA vs SSA	ns							
SSA vs CA	ns							
SSA vs WNSW	ns							
TEK vs PG	42 (df=1)	117				7.7	**	0.004
TEK vs BNQ	ns							
WNSW vs CSQ	ns							
WNSW vs SSA	34 (df=1)	145	6.5	*	-0.013			

Bustard abundance and NDVI within regions

In both the ‘Central Qld’ and ‘Central Sth Qld’ regions, the occurrence of bustards was negatively related to maximum NDVI scores but positively related to minimum NDVI (Tables 2.7 and 2.8). Otherwise, models for the two regions showed some marked contrasts. In ‘Central Qld’, bustards were closely associated with open grassland and sparse tree cover. In this region, the number of bustards reported from a property was positively associated with property size. In contrast, in ‘Central Sth Qld’ region, the frequency of bustards was negatively associated with grasslands and with property size. Notwithstanding some highly significant associations of bustards with these factors, the models for both regions were relatively weak (explaining <25% of deviance).

Table 2.7: GLM of bustard numbers against NDVI and vegetation structural characteristics in ‘Central Qld’. (Explained deviance = 19.7%, * = $p<0.05$, ** = $p<0.01$; *** = $p<0.001$)

Factor	Estimate	SE	Wald	p
Intercept	3.57	0.15	592	***
Form (grasses)	0.62	0.06	110	***
Form (med. tree)	-0.50	0.05	104	***
Cover (<10%)	0.45	0.06	55	***
Cover (10-30%)	-0.36	0.04	101	***
Max NDVI	-0.005	0.001	20	***
Min NDVI	0.007	0.002	11	***
Log Area	0.06	0.01	19	***

Table 2.8: GLM of bustard numbers against NDVI and vegetation structural characteristics in ‘Central Sth Qld’. (Explained deviance = 23.1%, * = $p<0.05$, ** = $p<0.01$; *** = $p<0.001$)

Factor	Estimate	SE	Wald	p
Intercept	7.53	0.73	105	***
Form (grasses)	-0.29	0.07	17	***
Max NDVI	-0.25	0.08	9	***
Min NDVI	0.18	0.08	4	*
Flush NDVI	0.31	0.08	13	***
Log Area	-0.26	0.04	37	***

DISCUSSION

Data quality: caveats and interpretation issues

Before I further discuss and attempt to interpret the results of this study, I explicitly recognise some inherent limitations and assumptions in the procedures adopted. Our mail survey data rely on retrospective questions and information that may be inherently susceptible to errors as a result of fading memories, mistakes and biases. Nonetheless, because the bustard is such a recognisable, conspicuous and noteworthy bird, I consider that the mail survey data suffer no errors through misidentification.

I also acknowledge that the regional groupings for which generalisations are made are variable in size and traverse a range of environmental conditions. Inevitably, several geographical groupings, such as ‘Central Australia’ span a significant latitudinal gradient wherein a transition occurs in several environmental characteristics (e.g. summer rainfall in the north to predominantly winter rainfall in the south). In such regions, patterns in bustard occurrence may be masked as responses in parts of the region cancel out contradictory responses in other parts. The large size of these regional groupings also precludes examining movement patterns, and the environmental cues that govern them, that occur at smaller localised scales. Further, our consideration of bustard occurrence in relation to climate variation was based on a 12 year period, possibly insufficient to account for longer term variation in rainfall (Vines *et al.* 2004). These points emphasise the need for considering multiple spatial and temporal scales when monitoring such systems.

Bustard distribution and movement patterns

The mail survey data provided a record of distribution for bustards that was largely consistent with the generally less comprehensive descriptions in previous accounts (Barrett *et al.* 2003; Blakers *et al.* 1984; Grice *et al.* 1986). Bustards were most numerous in a swath across the savannas of northern Australia from the Pilbara in Western Australia to the Brigalow belt in Queensland, with localised concentrations in some other regions. However, there were some disparities from previous distributional accounts. For example, there were few reports of bustards in either the first or second Atlas of Australian Birds from NSW, far SE Queensland and south-central South Australia (Barrett *et al.* 2003; Blakers *et al.* 1984; Grice *et al.* 1986), whereas in our study, many landholders recorded bustards from these regions.

The inherent irregularities of Australia’s climate are reflected by the complexity of responses exhibited by Australia’s fauna and are exemplified by the plasticity of movement strategies employed by the bustard across its continental range. The patterns in seasonal occurrence and breeding periods of bustards varied across the continent in a partly systematic manner with the timing and amplitude of this variability differing between regions. Both our modelling exercise and landholder perceptions suggest that much of this temporal variability in bustard occurrence can be explained by intra-regional temporal variability in rainfall patterning.

In northern Australia and central Queensland, where bustard numbers peak in the late dry and wet season, the perceptions of landholders are concordant with expectations and findings reported previously (Downes 1982a; b; Downes and Speedie 1982; Nix 1976). The contrasting increase in reporting rates over the winter in central Australia and in western regions suggests there may be underlying north-south migration patterns between these regions in relation to the wet-dry seasons. Systematic, seasonal ground surveys of bustards in the Victoria River District of the Northern Territory have also noted lower bustard abundance in the early dry season before numbers again increase in the mid-late dry (M.Ziembicki, unpubl. data).

Somewhat unexpectedly, our results suggest that there were underlying seasonal patterns in the occurrence of bustards in several regions characterised by relatively low and irregular rainfall. This seems to challenge the notion that bustards in the arid zone undertake predominantly irregular, widespread movements over most of their range (Downes 1982a; Marchant and Higgins 1993). Particularly notable were the significant summer peaks in ‘Central South Qld’, winter/spring peaks in ‘Central-west WA’ and apparent peaks in winter for ‘Central Australia’ and ‘Southern SA’. The notable asynchrony in peaks in abundance between these regions suggests that a significant proportion of bustards in these regions may undertake some seasonal broad-scale movement.

The suggestion that many bustard movements in arid or semi-arid Australia may have an underlying seasonal component is consistent with previous rebuttals of the idea of largely irregular movements in species once considered highly nomadic. For example, when considering the species over its entire range, the movement patterns of Red-billed Quelea *Quelea quelea* in Africa appeared to occur randomly in all directions. However, once it was recognised that there are several different populations it became apparent that each population makes regular, predictable movements between specific regions (Ward 1971). The Black Honeyeater *Myzomela nigra*, once labelled an ultra-nomad (Keast 1968), exhibits a regular range expansion to the south in the spring before returning to mid-latitudes at other times (Ford 1978). Similarly, the Budgerigar has been regarded as highly nomadic, yet subsequent studies have concluded that there are underlying north-south seasonal patterns to movements that are highly influenced by rainfall (Wyndham 1983; Griffieon & Clarke 2002). While underlying seasonal patterns in movements exist in these regions they are also overlaid by more idiosyncratic movements. Such movements are likely to be more pronounced in more erratically variable regions whereby the number and demographics of individuals that move and the directions and distances they traverse differ significantly depending on prevailing conditions. For example, the movements and breeding seasons of Budgerigars may deviate from underlying north-south patterns opportunistically as a result of atypical seasonal conditions (Wyndham 1983). Similarly, the Namaqua Sandgrouse *Pterocles namaqua* undergoes partial migration to varying degrees at larger scales between two regions of southern Africa with more localised regional patterns of nomadism (Lloyd *et al.* 2001; Malan and Little 1994). Bustards seem to display similarly complex movement strategies exhibiting varying degrees of partial migration and nomadism.

In some regions, temporal variation in bustard abundance is far more muted. This may be because of either a higher proportion of resident individuals or a tendency for bustards to occur in a region opportunistically as a result of nomadic or irregular movements. The ‘Brigalow’ region is probably an example of the former. Here, the limited seasonal variation in abundance data and the high proportion of landholders who rated bustards as permanent residents, suggests that populations in this area may be largely sedentary with limited seasonal input from other regions. The large areas of recently cleared land in the Brigalow Belt are preferred habitats for bustards and may now provide resources for the species year round. Similarly cleared and irrigated regions in the Daly River region in the Northern Territory also support more constant populations at higher densities than adjacent savanna habitats (Chapter 4).

In contrast, the limited seasonal variation and high proportion of short-term visitors in ‘Western NSW’ suggests that bustards in this region may visit irregularly. Our data and analysis of abundance in this region suggest that the incidence of bustards here may increase with below-average rainfall in neighbouring regions. Such a pattern, of movements away from drought-affected areas towards the periphery of, or beyond, normal ranges, has previously been reported for many other species (Blakers *et al.* 1984; Marchant and Higgins 1993; Storr 1984). However, I acknowledge that the information base for such largely peripheral regions is relatively weak. A more general conclusion from our analyses was that inter-regional irregularities in rainfall events were not particularly important for shaping the movements or distribution patterns of bustards. This suggests that the bulk of the idiosyncratic, nomadic movements that bustards make, at least over the period of this study, are at intra-regional rather than continental scales.

Analyses that attempted to relate the occurrence of bustards to greenness of the vegetation at intra-regional scales (for two regions in Queensland) produced relatively ambiguous results. These models may be compromised by the scales considered and the complexity of accounting for variation in NDVI across different habitat types. The contrast between the two regions considered in terms of direction of association of bustards with growth form (grasses) and property size may be related to differences in the age and intensity of land use patterns between these regions, whereby smaller, older and more intensively used properties in central-south Queensland have become less favourable for bustards, as has been suggested for other regions elsewhere (Grice *et al.* 1986; Isakov 1974). Nonetheless, both regions exhibited a negative relationship between bustard abundance and maximum greenness and a positive relationship with minimum NDVI values. This suggests there may be a minimum threshold in greenness that bustards prefer rather than attraction to the greenest or possibly most productive regions *per se*. Although opportunistic in their diets, bustards may favour food resources (e.g. insects, small mammals and reptiles) that are more available at times of lower greenness as grasses senesce (Chapter 6). That is, there may be notable lags between periods of peak primary productivity and the responses of key food resources. This highlights the need to differentiate between levels of greenness and productivity according to the availability of food resources to dispersive species and requires knowledge of the species' foraging ecology and habitat requirements.

To a lesser degree and differently across regions, factors other than rainfall and vegetation cover (in particular, fire, grasshopper "plagues" and cleared vegetation) were perceived by respondents to influence the occurrence and movements of bustards. In northern and central Australia, bustards are often associated with fires, which provide ready access to favoured food resources both during the event and in the first few days that follow. Consequently, bustards track fire events across the landscape (Chapters 4 & 8) and large flocks often congregate in recently burnt areas (Marchant and Higgins 1993; Chapter 4). Movements directly in response to fire events depend on the ability of bustards to detect them. Therefore, most of these movements occur at intra-regional scales. The importance of grasshoppers in the diet of bustards and their readiness to track grasshopper outbreaks across the landscape have been noted previously (Boehm 1947; Brown 1950). Irruptions of grasshoppers are highly dependent on rainfall and the subsequent response of grasses (Hunter 1989) and are most pronounced following the occurrence of drought-breaking rains (Farrow 1979). Following outbreaks in regions of central Queensland and western NSW, grasshoppers undergo long range movements in a generally southwards direction (Farrow 1979), which bustards may follow opportunistically. The affinity of Australian Bustards, and several other bustard species, for agricultural areas is widely documented (Marchant and Higgins 1993; Martinez 1994; Suarez-Seoane *et al.* 2002). These associations are particularly strong in recently cleared and less populated regions where bustards have access to year round food resources with limited disturbance and has probably resulted in net immigration of bustards to areas such as the Brigalow in the recent past (Blakers *et al.* 1984). However, as such areas become more intensively used or affected by introduced predators, they may become less favourable (Grice *et al.* 1986; Isakov 1974).

Utility of mail surveys and further research

The protection of dispersive fauna has been regarded as one of the most problematic challenges for conservation biology because conventional monitoring, representative reservation and conservation practices cannot adequately cater for such species (Dean 2004; Soule *et al.* 2004; Woinarski *et al.* 1992). A primary challenge is acquiring adequate data regarding population dynamics and movements for dispersive species. The present study focuses on a particularly amenable focal species, and hence may have provided an unusually reliable and productive return. Nonetheless, broad-scale participation of landholders, combined with existing atlas survey techniques, may more generally provide an unusually spatially representative and cost-effective mechanism for monitoring programs (e.g. Carstairs 1974; Saunders 1993; Mawson & Long 1996; Barrett & Davidson 1999; MacNally *et al.* 2004). The engagement of rangeland users in such surveys may also serve to raise awareness of conservation issues and to stimulate the involvement of local communities in conservation and management programs (Barrett and Davidson 1999; Saunders 1993).

The collection of data from different sources (rangeland users, atlas volunteers and trained survey teams) may be validated against each other to assess their reliability. Furthermore, such community-based monitoring may be complemented and refined further through the employment of increasingly sophisticated technologies including genetic analyses, stable isotope chemistry, satellite telemetry and spatial information systems (Webster *et al.* 2002). For example, strategically planned survey efforts, combining the resources of these different contributors, could aim to test specific predictions regarding the distribution of certain exemplar species in specific areas, at specific times based on predictions from modelling remotely-derived indices of habitat quality and climate data. If the locations and preferred habitats of targeted species at particular times can be known or predicted, then such sites can be prioritised for protection at critical times. Such knowledge would effectively facilitate predictive or pre-emptive conservation planning (i.e., by developing mobile or shifting conservation zones in time and space) thereby overcoming the limitations of current static reserve design and conservation strategies. For example, favourable refugia required during drought, or breeding habitats and lekking areas used by bustards, could be protected at key times by controlling introduced predators, managing for appropriate fire regimes, minimising stocking rates for livestock or implementing moratoria for hunting. Current strategies for the conservation of dispersive fauna are largely inadequate highlighting the need for lateral and creative approaches for protecting bustards and other similarly mobile fauna.

Chapter 3

Habitat characteristics and food resource availability in relation to season, fire and land use at two contrasting sites in the tropical savannas

Bruce Doran

"A land... Of droughts and flooding rains"

Dorothea Mackellar – 'My Country'

Chapter 3

Habitat characteristics and food resource availability in relation to season, fire and land use at two contrasting sites in the tropical savannas

INTRODUCTION

The marked seasonality of rainfall characteristic of Australia's northern tropical savannas results in substantial seasonal fluctuations in primary productivity, particularly of the herbaceous ground layer. The resulting large, dry fuel loads drive a range of fire regimes that further shape the landscape. Overlaying these primary natural factors that shape the environment are human-induced influences that may be localized and acute (e.g. land clearing) or broad-scaled and more diffuse (e.g. widespread pastoralism). Combined with differences in soil types, moisture, topography and other environmental features, the structure and productivity of contemporary Australian savanna landscapes are consequences of many such factors acting together in a virtually intractable array of permutations. Consequently, while there are overall seasonal patterns in those characteristics that influence the ecology of the Australian Bustard in the north, there are also idiosyncratic and asynchronous responses in time and space of habitat and resources that may affect bustards differently.

Seasonal variation in the herbaceous ground layer is the most dynamic feature of bustard habitat, as a short period of significant growth in the wet and early dry season is followed by a prolonged period of steady decline in biomass as grasses senesce or are removed by fire and grazing. This variation directly affects cover and shelter for bustards and influences the availability and accessibility of food resources. The bustard's broad diet, ranging from various seeds and fruits to invertebrates and small vertebrates, means that these various components, with their varied ecological requirements, exhibit a great variety of potential responses to environmental changes. In general, the abundance and richness of arthropod assemblages in the northern savannas are strongly driven by rainfall patterns with highest numbers following the first rains in the early wet season and peaks often lasting through to the early dry season (Churchill 1994; Noske and Franklin 1999; Woinarski and Tidemann 1991). Nevertheless, there may be notable differences in the responses of specific elements of the arthropod fauna in relation to variation in the timing and spatial patterning of rainfall events.

The phenology of most flowering and fruiting trees and shrubs is similarly periodic though often with wider, more idiosyncratic peaks. There may be high variability in time and space and between species, particularly in the mid-dry or late dry season (Williams *et al.* 1999; Woinarski *et al.* 2000). Such contrasts are exemplified by the fruiting patterns of plants that are particularly important to bustards. For example, *Cassytha* species fruit year round, while fruiting peaks for *Cucumis melo* occur from the early to mid dry season, but may exhibit notable spatial and inter-seasonal variation (Cowie in prep; Crase in prep; Kerrigan and Dixon unpublished). Grass seeds, although they appear to make up a small proportion of the bustard's diet (Chapter 6), are critically important to other biota. Seed resource availability peaks in the late wet and early dry months and declines throughout the dry season until there is a general paucity in the early wet season (Crowley and Garnett 1999; Dostine *et al.* 2001).

Superimposed over the marked seasonal variability of rainfall in the savannas is the influence of fire. The tropical savannas are generally highly resilient to fire (Andersen *et al.* 2003; Andersen and Müller 2000; Williams *et al.* 2002; Woinarski *et al.* 2007). Most plant species regenerate vigorously while many animals rapidly recolonise recently burnt areas (Andersen and Müller 2000; Gillon 1983; Vigilante and Bowman 2004; Woinarski 1990; Woinarski *et al.* 1999). Indeed many plants and animals rely on fires (Vigilante and Bowman 2004; Woinarski 1990). Fires influence the habitat and food resources of bustards both in the short and long term, and directly and indirectly. Bustards may respond immediately to fires by aggregating at fire fronts or in recently burnt areas to exploit food resources exposed or killed by fires. Fires also 'open up' habitat which benefit bustards by providing open areas for display and foraging. Conversely, some late dry season fires may be detrimental if they destroy nests. Other impacts of fire may be indirect or operate over the longer term by influencing food resources, floristics, nutrient availability and habitat structure.

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Habitat clearing is a key threatening process to biodiversity globally (Brooks *et al.* 2002). To date, clearing of natural savanna woodland for agriculture and development in the northern savannas has been restricted to specific and relatively small regions (Price 2003; Woinarski *et al.* 2007) (see also Fig.1.7). While the effects of clearing are overtly detrimental to most species, some species, including the Australian Bustard, are benefited by open habitats (Barrett *et al.* 2003; Grice *et al.* 1986; Price 2003). Nevertheless, largely due to the relatively recent and limited areas cleared in the Australian tropical savannas, there have been few studies of the effects of clearing on much of the biota and practically no information on arthropods which are a major component of the bustard's diet.

The major land use across the northern savannas is pastoralism, with approximately 75% of the region directed largely towards improving the suitability of habitat for cattle (Woinarski *et al.* 2007). Grazing has the potential for directly affecting habitat structure and the food resources of bustards by altering understorey plant composition and phenology and changing fire regimes by reducing fuel loads (Hoffman 2000; 2003; Martin *et al.* 2005; Martin and Possingham 2005; Woinarski *et al.* 2002; Woinarski *et al.* 2007). Trampling of ground-based nests may also be a direct source of mortality. Indirect effects, through management practices, may include provision of artificial water sources, vegetation clearance and change in the composition of grass layer by favouring or introducing palatable pasture varieties. The pervasiveness of grazing in the north is such that it is now difficult to separate grazing from non-grazing impacts (Woinarski *et al.* 2002). The impact of grazing was not explicitly addressed in this study, although references to implied impacts are made in subsequent chapters.

A central part of this thesis is an in-depth study of the ecology of the Australian Bustard at two contrasting sites in northern Australia. These sites were chosen because of their robust bustard populations and to facilitate a comparison between a representative intact, natural savanna habitat with a decidedly more artificial site that was cleared of savanna woodland for crop agriculture and from where fire is excluded. Logistics and 'reality' prevented replication and use of paired sites that were identical except for land-use (i.e. there are geographical, environmental and other contrasts between the two main study sites other than only land-use). Nevertheless, the main objectives of this chapter are to describe the climatic and physical attributes of these two field sites and to document there the seasonal variation in food resource availability and habitat characteristics, including their relationships to fire regimes and land use. In the chapters that follow I use and refer back to the information presented here.

METHODS

Study sites

Site-specific investigations of the bustard's ecology, and associated assessment of habitat characteristics and food resource availability presented in this chapter, were conducted at two sites in the Northern Territory: Kidman Springs (also known as the Victoria River Research Station) and the Douglas-Daly Research Farm (DDRF), situated almost 250 kilometres to the north (Fig. 3.1). Both sites are within Australia's northern tropical savannas but differ in their land use, habitat types and climate. During this study, access to Kidman Springs was constrained by inaccessibility during the wet season months, restricting field work to the months of April to late November. The DDRF was accessible regardless of seasonal conditions, allowing an additional sampling period in the wet season (February).

Location

Kidman Springs is located in the Ord-Victoria bioregion (Baker *et. al* 2005) at 16º 6.900' S and 130º 57.250 E. It is part of the Victoria River District (VRD) situated 220 km south-west of Katherine and 410 km directly south of Darwin. The core study area is approximately 310 km^2 (Fig. 3.1).

The Douglas-Daly Research Farm is located at 13º 50.270 S and 131º 11.335 E, approximately 160 kilometres south of Darwin in the Daly Basin Region. The farm and parts of adjacent properties comprising the core study area is approximately 60 km^2 in size (Fig. 3.1).

NOTE:
This figure is included on page 67
of the print copy of the thesis held in
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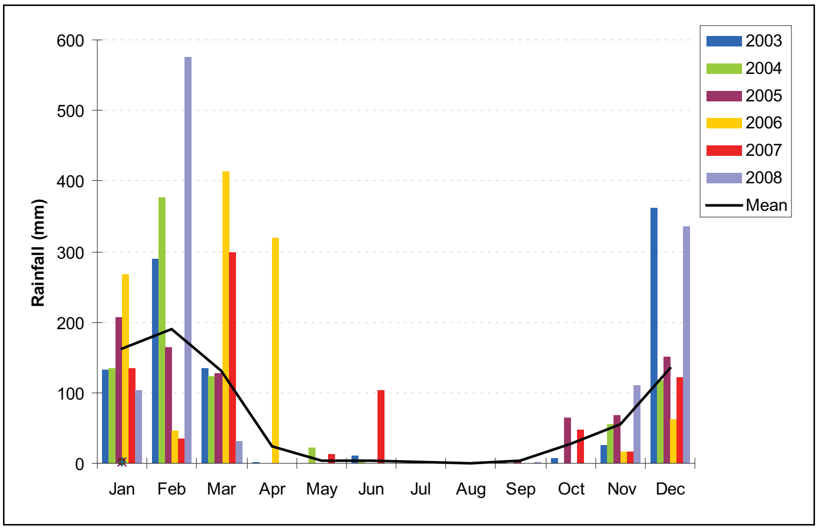
Figure 3.1: Locations of the two main study sites in the Northern Territory. Yellow boundaries denote core study areas at each site. Shaded areas on the NT map (at right) illustrate the bioregions within which the study sites occur (Baker *et al.* 2005).

Climate

The climate of Kidman Springs is regarded as semi-arid, monsoonal. Variability in rainfall here is low by Australian standards and the climate is dominated by strongly seasonal climatic patterns with a hot and wet summer wet season and an extended dry period from April to October. Mean annual rainfall at Kidman Springs is 743 mm, most of which falls between the months of November to March (Fig. 3.2). During this study rainfall was above the mean in both 2003 (969 mm) and 2004 (832 mm). Temperatures are generally high all year, with peaks in the 'build-up' period late in the year, and are lowest around June and July (Fig. 3.3). The DDRF is situated further to the north on the rainfall gradient and has a mean yearly rainfall of 1206 mm. Rainfall is also strongly seasonal falling predominantly during the wet season from November to March. During this study rainfall at the DDRF was above the mean. Variations in mean minimum and maximum temperatures are similar to those of Kidman Springs (Fig. 3.3).



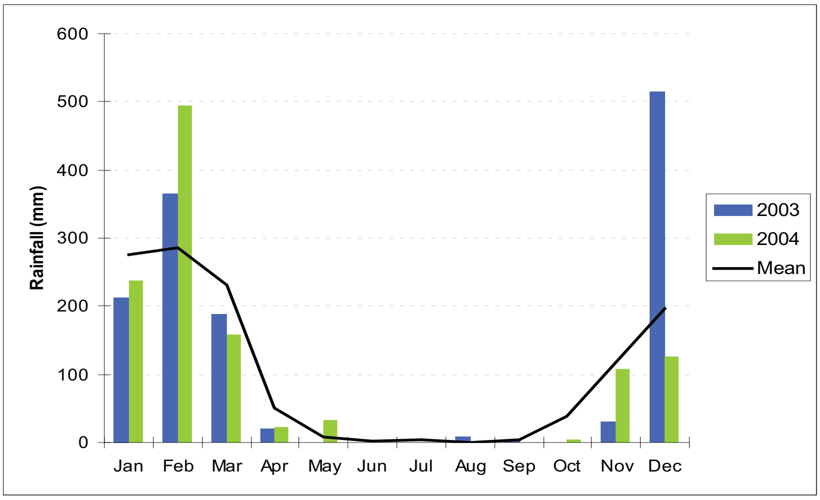


Figure 3.2: Rainfall during the study period and mean rainfall at Kidman Springs (top) and the DDRF (bottom). Rainfall values for Kidman Springs extend from 2003-2008 to include the main study period (2003-2004) and subsequent years during which satellite telemetry data were collated in the region. Mean rainfall values are based on records for each site over the past 38 years. (Source: Bureau of Meteorology)

NOTE:
This figure is included on page 69
of the print copy of the thesis held in
the University of Adelaide Library.

Figure 3.3: Mean maximum and minimum temperatures at Kidman Springs (left) and the Douglas-Daly Research Farm (right) (sourced from the Bureau of Meteorology).

Land uses

Kidman Springs is a pastoral research station that is subject to light to moderate levels of grazing (5 to 7 head km^{-2}) within an essentially unmodified natural landscape. It has a prescribed, paddock-scale fire regime, whereby most parts of the property are burnt on a 3 to 4 year basis. Burning primarily occurs in the late dry season and is dependent on weather and pasture conditions. The rationale behind fire management at Kidman Springs is to promote new growth for cattle fodder and to limit woody weed infestation.

The Douglas-Daly Research Farm was cleared in the 1960s and established as a mixed farming research and demonstration farm. It comprises 3,100 hectares of farm facilities, including pasture and cattle research areas, hay and crops, and centre pivot irrigation infrastructure. Crops include irrigated peanuts, dryland sorghum, mung bean, sesame and pasture seeds. The location and proportion of area dedicated to each crop type varies from year to year but is usually only a small proportion of the overall area of the site. Fire is excluded from the property. The farm is at the centre of the Douglas-Daly District which is a hub for cropping, horticulture, irrigated agriculture and pastoral production, with beef cattle production from improved pasture the dominant activity. An estimated 2070 km^2 of native vegetation in the Daly Basin (representing 9.3% of the region) had been cleared for these purposes by 2002 (Hosking 2002). Between 2003 and 2007 a further 175 km^2 had been approved for clearing by the Northern Territory Government, although the overall figure may be higher when unapproved, illegal clearing is considered (Blanch 2007).

Vegetation

The vegetation of Kidman Springs is typical of the Victoria River District comprising a mix of open woodland and grassland habitats. Its structure and composition is closely related to soil type and rainfall. Two dominant substrate types occur in the core study region on Kidman Springs, a limestone-derived red earth loam and an alluvial 'black soil' cracking clay. The former supports open woodland dominated primarily by *Eucalyptus pruinosa*, *E. terminalis*, *Carissa lanceolata* and *Hakea arborescens* with an understorey of grasses that include *Chrysopogon fallax*, *Heteropogon contortus*, *Sehima nervosum*, *Themeda triandra*, *Brachyachne convergens* and *Sarga* species. Habitats based on black (alluvial) soils grade between open treeless grasslands to open woodland of *Terminalia volucris*, *T. arostrata* and *Bauhinia cunninghamii* over a grassy understorey dominated by *Chrysopogon fallax* and various species of *Astrebla*, *Iseilema*, *Aristida* and *Dicanthium*. Subsequent analyses presented in this chapter are based on classification of habitats at Kidman Springs into three categories according to soil type and dominant vegetation community: i) open woodland on red loam earth soils (denoted as 'ROW' in subsequent reporting); ii) open woodland on alluvial black soils ('BOW') and, iii) open treeless grassland plains on alluvial black soils ('BOP'). Grass growth is strongly influenced by the amount and distribution of rainfall. The average start to the growing season at Kidman Springs is from early January and lasts for approximately 15 weeks (Dyer 2001). Relatively dense riparian vegetation occurs in narrow bands along watercourses. "Woody weed" infestation is identified as a significant issue in the VRD and appears particularly pronounced on alluvial soils (Fig. 3.4).

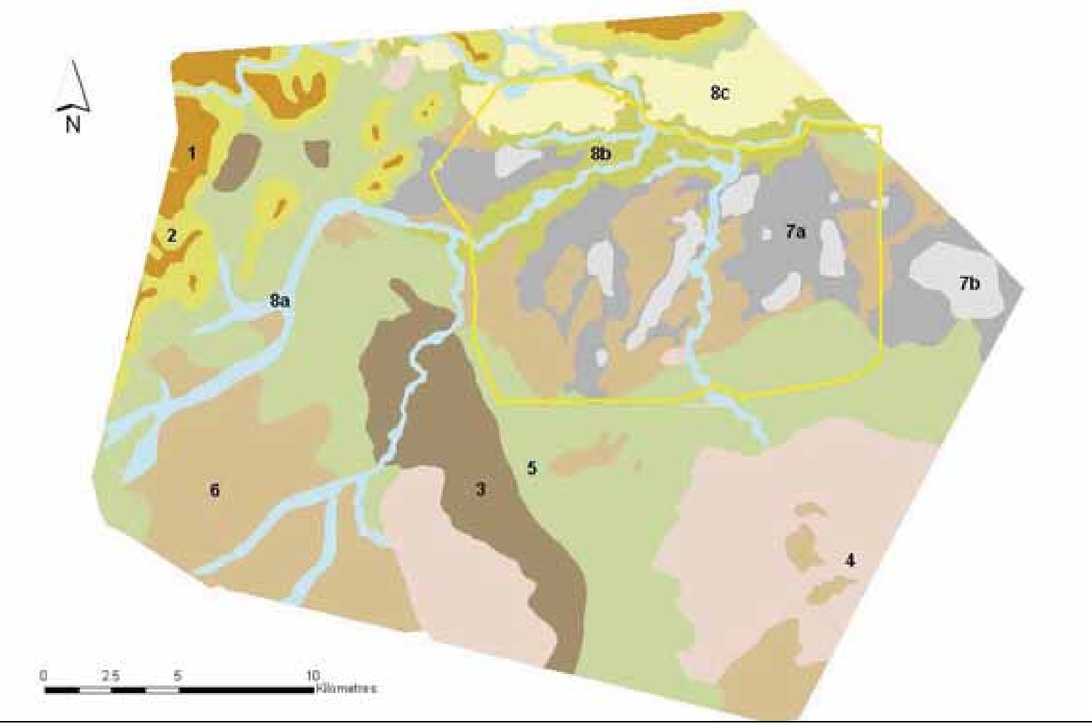
Vegetation associations at Kidman Springs have been represented by a land unit map developed by McLeod and Van Cuylenburg (in prep.) (Fig. 3.5). Land unit data for this map was prepared at a scale of 1:16500 from aerial photography and field collection of data describing the soil, landform and native vegetation along transects. This map was further modified in the present study to differentiate between open woodland and treeless open grassland on alluvial black soils because of the potential importance of open grasslands to bustards. The land unit information was subsequently used to determine sampling locations in the current chapter and formed the basis of habitat use analyses presented in chapter 5.

The DDRF site is relatively homogeneous in habitat structure predominantly comprising pasture used for cattle grazing (a mixture of legume and grass pastures dominated by perennial exotics including Buffel grass *Cenchrus ciliaris*, Sabi grass *Urochloa mosambicensis* and Jarrah grass *Digitaria milanjiana*). These grasses generally grow in monocultures at paddock scales across the site and are interspersed with hay and crop research areas (crops including sesame, soybeans, mungbean, sorghum and cavalcade *Centrosema pascuorum*). An irrigated, centre-pivot cropping area of peanut and maize is cultivated during the mid-dry season (June to September) in the centre of the research farm and represents an area of lush green vegetation in an otherwise dry landscape. There are isolated trees and small pockets of trees and shrubs on the farm but most of the site is generally devoid of woody vegetation. The farm is bordered to the east and north-west by adjacent areas of cleared land used for cattle grazing. To the north, west and south of the farm are extensive and dense riparian areas of mixed tree and shrub vegetation including monsoonal vine thickets. The remainder of the study site is surrounded by mixed woodlands dominated by *Eucalyptus tetrodonta* and *E. miniata*.

Figures 3.6 a-l illustrate the variety of habitat types found at Kidman Springs and the DDRF, including examples of seasonal differences and fire impacts that typically affect the tropical savannas.

NOTE:
These photographs are included on page 71 of the print copy of the thesis held in the University of Adelaide Library.

Figure 3.4: Progressive 'woody weed' infestation (primarily by native *Terminalia* spp.) of open plains at Kidman Springs; 1968 (top), 1979 (middle) and 1998 (bottom).



🟧	1	PLATEAU SURFACES Sandstone, basalt or limestone plateau; shallow soils, earths & duplex soils or cracking clays; Open woodland of Bloodwood, Rusty Bloodwood, Nutwood, Bauhinia, Silver Box & Inland Bloodwood over Spinifex, White Grass, White Spear Grass & Speargrass; surface gravel, stone & rock
🟨	2	ESCARPMENT &/or STEEP SIDESLOPES Sandstone, basalt or limestone scarps & slideslopes; shallow & duplex soils; Open woodland of Ironwood, Inland Bloodwood, Northern Grey Box, Emu Apple, Snappy Gum and Silver Box, over Spinifex, Golden Beard Grass & Speargrass; surface stone
🟫	3	ROLLING TO STEEP HILLS Sandstone, basalt or limestone hills; shallow soils; Open woodland of Snappy Gum, Rusty Bloodwood & Inland Bloodwood over Spinifex, Limestone Grass, White Grass & Speargrass; surface stone & rock
🟥	4	UNDULATING TO ROLLING HILLS Sandstone, basalt or limestone low hills; shallow soils; Open woodland of Inland Bloodwood, Snappy Gum and Lancewood, over Spinifex & White Spear Grass; surface gravel, stone & rock.
🟩	5	GENTLY UNDULATING TO ROLLING HILLS Sandstone, basalt, limestone or colluvial rises; shallow to structured earths & duplex soils; Open woodland of Snappy Gum, Nutwood, Inland Bloodwood, Northern Grey Box over White Grass, Spinifex, White Spear Grass, Black Spear Grass, Kangaroo Grass; surface gravel & stone
🟫	6	LEVEL TO UNDULATING PLAINS Sandstone, basalt, limestone or colluvial plains; alkaline soils; Open woodland of Inland Bloodwood, Silver Box, Nutwood, Bauhinia & Stinkwood over Limestone Grass, Black Spear Grass, White Spear Grass, White Grass, Curly Blue Grass & Native Couch; surface gravel & stone. **This habitat was sampled during the study and is denoted as ROW in analyses**.
⬛	7a	LEVEL TO UNDULATING ALLUVIAL PLAINS Alluivial (black soil) plains; cracking clays; Open woodland of Bauhinia and Nutwood over Grassland of Native Couch, Golden Beard Grass, Mitchell Grasses & Native Millet; surface gravel and stone. **This habitat was sampled during the study and is denoted as BOW in analyses.**
⬜	7b	Alluivial (black soil) plains; cracking clays; Grassland of Native Couch, Golden Beard Grass, Mitchell Grasses & Native Millet with very sparse isolated trees; surface gravel. **This habitat was sampled and is denoted as BOP in analyses.**
🟦	8a	RIVER SYSTEMS, DRAINAGE AREAS & BACKPLAINS River systems; cracking clays, alkaline soils & duplex soils; Open woodland to woodland or grassland of Wild Plum, Ghost Gum, River Red Gum, Paperbarks & Coolibah over Native Couch, Golden Beard, Curly Blue & Black Spear Grass; surface gravel & stone
🟩	8b	River systems (severely eroded areas associated with river systems); cracking clays, earths & alkaline soils; Open woodland of Coolibah, Gutta-Percha & Bauhinia over Golden Beard Grass, Native Couch, White Spear Grass, Limestone Grasses & Sedges
⬜	8c	River systems (levees & terraces); cracking clays, earths & duplex soils; Open woodland of Coolibah, Inland Bloodwood, Ghost Gum, & River Red Gum over Native Couch, Fairy Grass, White Grass & Mitchell Grasses; surface gravel & stone

Figure 3.5: Major land units of Kidman Springs (modified from McLeod & Van Cuylenburg, in prep.). Yellow outline denotes core study region. Note that habitats '6 - ROW', '7a - BOW' and '7b - BOP' were the focal habitats sampled for habitat characteristics and food resources in this chapter. They were also surveyed for bustard abundance (Chap. 4) and were considered in detail in home range and habitat use analyses (Chap. 5).

Figure 3.6 a-l: Photographs depicting the variety of habitats and conditions at the two main study sites

(a) Open grassland plain on alluvial black soil (BOP) at Kidman Springs in the early dry season.

(b) Open woodland on 'red' loam earth soils (ROW) at Kidman Springs in the early dry season. The trees are *Eucalytpus pruinosa*. The grass layer is mainly *Heteropogon contortus*.

(c) Open woodland on alluvial black soil cracking clays (BOW) at Kidman Springs in the early dry season. The trees are *Bauhinia cunninghamii.*

(d) Dense open woodland on loam earth soils (ROW) at Kidman Springs. The trees in the foreground are *Acacia* sp.

(e) An open area within a contiguous area of open woodland on loam earth soils at Kidman Springs towards the end of the dry season. The area pictured is significantly affected by grazing and was a commonly used display site for a male bustard during the breeding season.

(f) Open woodland on loam earth soils at Kidman Springs in a small fire exclusion area. This site had a thick grass layer consisting mostly of *Heteropogon contortus*

(g) A female Australian Bustard foraging in recently burnt (less than 24 hours) open woodland on loam earth soils at Kidman Springs.

(h) Northern savanna open woodland landscape following a recent fire.

(i) Sparse open woodland savanna in the late dry season demonstrating the relative difference in grass understorey following a fire earlier in the dry season (right) compared with no fire (left)

(j) Open grassland dominated by Sabi grass *Urochloa mosambicensis* at the DDRF during the mid to late wet season (*ca* February).

(k) Open grassland dominated by Sabi grass *Urochloa mosambicensis* at the DDRF during the mid to late dry season (*ca* August).

(l) Centre-pivot irrigated peanut cropping in the mid dry season (*ca* July) at the Douglas-Daly Research Farm.

Sampling design

Sampling was conducted at the DDRF at intervals of 2-3 months between February 2003 and September 2004 and at Kidman Springs between November 2002 and September 2004. However, no sampling was conducted at Kidman Springs over the wet season between December to April because of restricted access. Furthermore, due to logistical constraints not all features were sampled during every sampling period (see Table 3.1). Sampling periods were assigned to 5 periods of the year at DRRF and 4 periods of the year at Kidman Springs. Note that the names given to these periods are indicative in so far as they represent times of the year rather than specifically referring to sampling during the months listed. However, as far as possible sampling occurred in these months and as close as practical in time between sites. Surveys at Kidman Springs aimed to examine seasonal differences between habitat types and fire regimes in herbaceous cover and food resource availability. Sampling at the DDRF aimed for seasonal comparisons of herbaceous cover and food resource availability only. No attempt was made to compare between habitat types, in part due to the exclusion of fire from the property and the structural homogeneity of the site. Seasonal comparisons of arthropod food availability were made between the DDRF and Kidman Springs at the property scale.

Table 3.1: Summary of habitat characteristics and food resources sampled according to sampling period at Kidman Springs and the Douglas-Daly Research Farm during 2003 and 2004.

Site	Sampling period	Herb cover	Shrub - tree cover	Basal area	Floristics	Fruit phenology	Ground arthropods	Grass arthropods
Kidman Springs	Nov 02	X						X
	May 03	X				X	X	X
	Jul 03	X				X	X	X
	Sep 03	X				X	X	X
	Nov 03	X				X	X	X
	May 04	X	X	X	X	X		X
	Jul 04	X				X		X
	Sep 04	X				X		X
DDRF	Feb 03	X					X	X
	May 03	X					X	X
	Jul 03	X					X	X
	Sep 03	X					X	X
	Nov 03	X					X	X
	Feb 04							X
	May 04							X
	Jul 04							X
	Sep 04							X

Sampling at each site was conducted in one hectare plots. At Kidman Springs sampling was conducted in each of the three main habitat types within the core study area (Fig. 3.5). Within each of these habitat types sampling occurred according to three fire regimes that differed in the time since last fire. At the commencement of the study in early 2003 this equated to 0.5 years since fire, 2.5 years since fire and 4.5

years since fire. In effect, this represented 1, 3 and 5 growing (wet) seasons respectively. However, it should be noted that it was not possible to account for different fire histories between plots. That is, plots may have differed in fire frequency over a longer period prior to sampling efforts undertaken here. This unavoidably qualifies the results with respect to the potential effects of fire.

At the DDRF, sixteen plots were established with three plots designated to each of the five main pasture types (Sabi grass *Urochloa mosambicensis;* Buffel grass *Cenchrus ciliaris;* Jarrah grass *Digitaria milanjiana;* Round-leaf (Wynn) Cassia *Chamaecrista rotundifolia* and Cavalcade *Centrosema pascuorum*). One additional site was established in the irrigated peanut crop area.

Herbaceous cover

On each visit the ground layer was sampled using 16 1m^2 quadrats arranged within a 4 x 4 grid, with 15 metre spacing, at each plot at both Kidman Springs and the DDRF. The total ground layer and cover of perennial grasses, forbs, rocks, litter, bare ground and green foliage was estimated according to a cover scale with eight classes (0, 0-1%, 1-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-100%). Height of the grass layer was measured in centimetres in each of the 16 quadrats and a mean value derived for the site.

Shrub and tree cover

Canopy cover of three height size classes of shrubs and trees (1-3 m; 3-5 m; >5 m) was measured at the Kidman Springs plots during May 2004 from four points around the margin of each quadrat using a variable radius measure (Friedel and Chewings 1988). Woody plant density was measured as basal area of all shrub and tree species using a Bitterlich wedge (Friedel and Chewings 1988). Mean canopy height was estimated visually for each site.

Floristics

A complete floristics assessment was undertaken at Kidman Springs during May 2004 at each of the 27 plots. The assessment was timed to coincide with the peak occurrence and flowering and fruiting periods of herbaceous annual grasses and forbs following the wet season. The presence of herbaceous species was noted in each of 16 quadrats at each plot. Additionally, a search of each plot was conducted to record any other species not noted in quadrats. All shrub and tree species within the 1 hectare plot were also noted.

Food resources

An emphasis was placed on assessing the main food resources of bustards determined following a preliminary assessment of bustard diet (Chapter 6) and a review of the literature (Barker and Vestjens 1989; Marchant and Higgins 1993). Accordingly, there was a focus on ground and grass layer arthropods and the seeds and fruits of selected plant species as noted below.

Arthropod availability

Two methods were used to measure the relative abundance of arthropod prey availability. Ground-dwelling, small invertebrates (<30 mm in length) were sampled using 8 pitfall traps measuring 7 cm diameter by 5 cm deep arranged in a grid at each plot. Each trap was partly filled with a mixture of 70% ethanol and ethylene glycol. Pits were placed level with the ground and were collected after two days. These were sampled at both Kidman Springs and the DDRF at the same time as bustard surveys were conducted during the 2003 sampling periods only. All pitfalls were pooled for each sampling plot during each survey period and sorted, identified and counted in the laboratory to ordinal-level.

Larger, predominantly grass-layer dwelling taxa, including grasshoppers, mantids, phasmids, lepidopterans (and larvae), were counted by slowly walking five 60 metre transects at each site counting all observed individuals of each taxon. The rationale here was to employ a rapid assessment method that could be readily and consistently used that notionally mimicked the foraging strategy of bustards. However, a likely bias of the method is the likely comparative under-representation of phasmids and mantids compared with grasshoppers and lepidoterans because of the tendency for the latter taxa to flush when disturbed making them more easily observed. Nevertheless, the taxa were pooled for subsequent analyses. These counts were undertaken at both Kidman Springs and the DDRF during all sampling periods. Note also that, while abundance is used here as a measure of resource availability, arthropod biomass is a better overall measure of amount of food available to bustards. It could not be used in this instance given that sampling was based on sightings.

Fruiting phenology

The presence/absence of fruits of *Grewia retusifolia, Carrissa lanceolata, Cassytha* sp. and *Cucumis melo* were noted during each sampling period on each plot at Kidman Springs. These are the main fruiting plants bustards are believed to utilise in the region (see Chapter 6). The number of plots at which ripe fruits of each species were present during each sampling period represented a general measure of relative abundance. This measure is descriptive and simply serves to illustrate the seasonal patterns of relative availability of this resource. A thorough assessment of the fruiting phenology, availability and importance of potential food plants to bustards was beyond the logistical capacity of the study. Such an attempt would require taking into account differences in nutritional content, size, palatability and accessibility of each fruit type to bustards.

Data analyses

Changes in the abundance of arthropods at Kidman Springs and at the DDRF were examined using generalised linear modelling. The dependent variables (treated separately) were the abundance of grass-layer (pooled between years) and total ground layer arthropods at each site. Analyses for Kidman Springs included several explanatory variables, namely, time since fire (denoted as ‘FIRE” and equal to 1, 3 and 5 growing seasons), habitat type according to three pre-defined habitats (denoted as ‘HABITAT’ and including ‘ROW’, ‘BOW’ and ‘BOP’ as previously defined) and season (denoted as ‘PERIOD’ and equal to May, July, Sept. and Nov.). A set of candidate models were developed using single variables, additive models and models with interactions of the different variables. At the DDRF comparisons were made between seasons only and included the additional sampling period of February. Comparisons were also made for grass and ground layer arthropod abundance across sites (i.e. between Kidman Springs and the DDRF), and combined across sites to assess the influence of sampling periods.

Model analyses used the ‘Maximum Likelihood’ estimation method and Kullback-Leibler (K-L) information was used to assign relative strengths of evidence to the different component models (Burnham and Anderson 2002). Best models in a set were selected by the Akaike Information Criterion (AIC), corrected for small sample size (AIC_c) by the use of an additional bias-correction term. This method involves identifying the most parsimonious models from a candidate set of models given maximised log-likelihood of the fitted model. The relative values (ΔAIC_c) of each model over the set of models being considered were taken as the relative level of empirical support for each model. Models with ΔAIC_c values within 2 were considered to be plausible models. Models with ΔAIC_c values between 3-7 were considered less plausible and those >10 not plausible (Burnham and Anderson 2002). Given AIC_c differences for each model, the relative likelihood of a set of candidate models was calculated using Akaike weights (w_i). Akaike weights are a measure of evidence in favour of a model being the best approximating model from a candidate set given the data, and varies from 0 (i.e. no support) to 1 (complete support). Count data of arthropod abundance were assumed to fit a Poisson distribution and global models were tested for lack of fit using a Chi-squared goodness-of-fit test. Where global models did not fit the data ($P<0.001$) other models (quasi-poisson and negative binomial distributions) were trialled (Zeileis *et al.* 2008). Where overdispersion of count data was still present a correction for overdispersion was made by estimating the variance inflation factor (c) by dividing observed deviance of the global model by the mean deviance of the simulated data set. Model selection was then based on comparisons of the quasi-likelihood AIC_c ($QAIC_c$) (Burnham and Anderson 2002). These analyses were conducted using Program R (Team 2003).

Floristics at Kidman Springs

Similarity in vegetation assemblages at Kidman Springs was assessed using a multi-dimensional scaling ordination (MDS) based on the relative abundance of species according to their occurrence in 16 quadrats at each sampling plot. Abundance data were 4^{th} root transformed in order to account for rarer species and downplay the influence of dominant species. ANOSIM analyses were conducted to test whether there were significant differences in species composition of the herbaceous layer between the three main habitats and according to time since fire. All multivariate analyses were conducted using PRIMER v.6.

RESULTS

Habitat characteristics

Variation in ground-layer vegetation

Grass height and cover varied typically according to rainfall seasonality at both sites. General patterns in variation in the grass layer were apparent between the three main pre-defined habitats at Kidman Springs, although there were differences in the amplitude of variation between the habitats. Peaks in grass height and cover at Kidman Springs were noted in the early dry season (May) (Fig. 3.7) (but note that no sampling was conducted here during the late wet season). Grass height and cover were more variable between seasons at the alluvial soil habitats than at the ROW habitat. For example, grass heights varied between a mean low of 11.7 cm (Nov.'03) and high of 44.0 cm (May '04) (276% change) on alluvial open grassland compared with a mean low of 30.3 cm and maximum of 51.1 cm (69 % change) on loam open woodland. This difference may be due to the persistence of perennial grasses (e.g. *Heteropogon. contortus*) on ROW sites which may be less palatable to cattle therefore less likely to be removed.

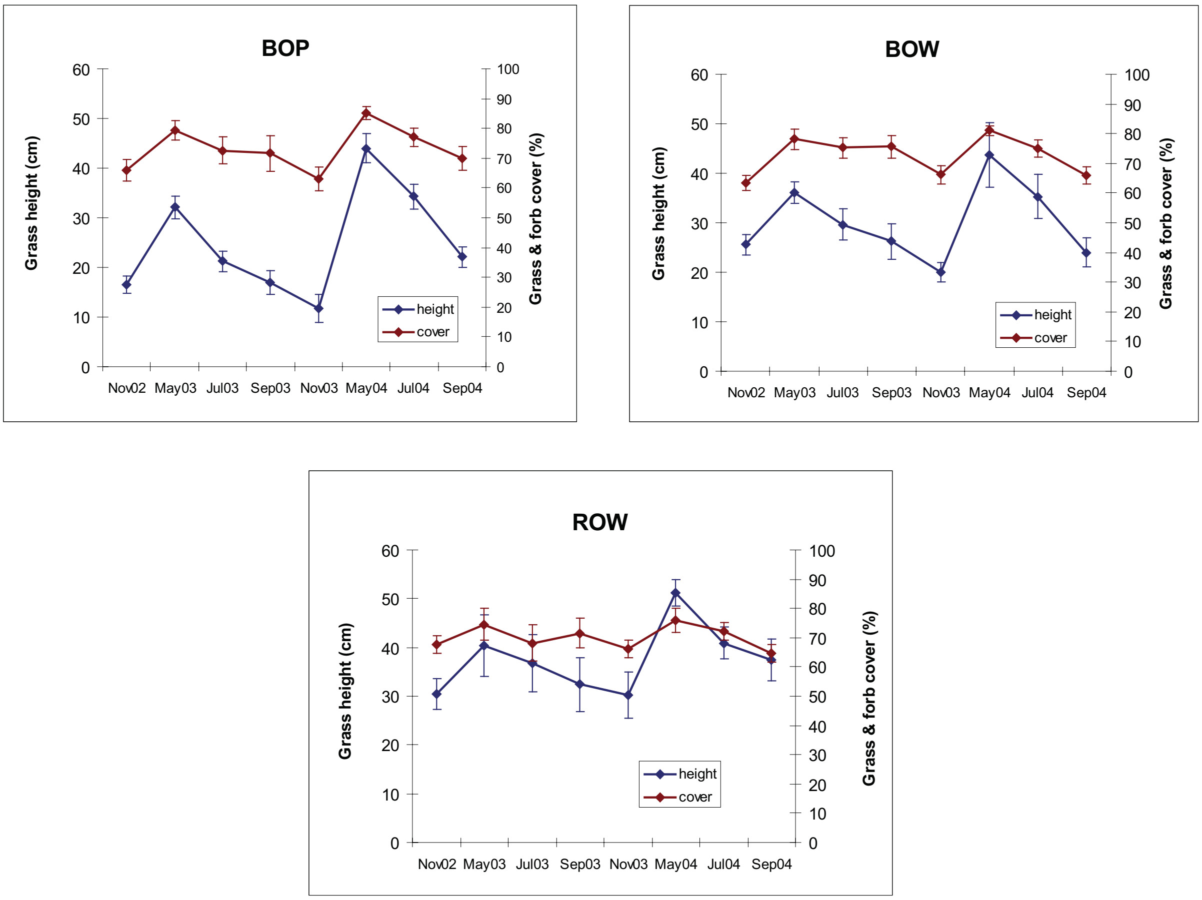


Figure 3.7: Seasonal variation in grass height and cover at Kidman Springs according to three habitat types (BOP = black soil open grassland plain; BOW = black soil open woodland; ROW = loam soil open woodland).

Grass cover was consistently high at the DDRF owing to the predominance of perennial pasture grasses, absence of fire and relatively low stocking rates (Fig. 3.8). Grass height was more variable but exhibited a typical pattern peaking in the late wet and early dry season before steadily declining to a low in the late dry season (Fig. 3.8). Of the five main pasture types at the DDRF, Jarrah grass *Digitaria milanjiana* accounted for much of this difference having ranged from a high of approximately 80 cm in Feb.'03 to a low of 16.6 cm in Nov.'03. The change in grass height over the dry season is due to senescence, 'knocking down' by winds and herbivore grazing.

Tree and shrub cover and density

The structural characteristics of woody vegetation were measured at Kidman Springs in each of the three main habitat types (Table 3.2). Cover, basal density and canopy height were all greatest in the red loam open woodland habitat followed by open woodland on black soil. Although not measured in this study it is worth noting that many of the woody plants present at Kidman Springs (particularly the common species such as *Terminalia volucris*) are partly or wholly deciduous during the mid to late dry season so that cover is lower at these times in those habitats where these deciduous species occur.

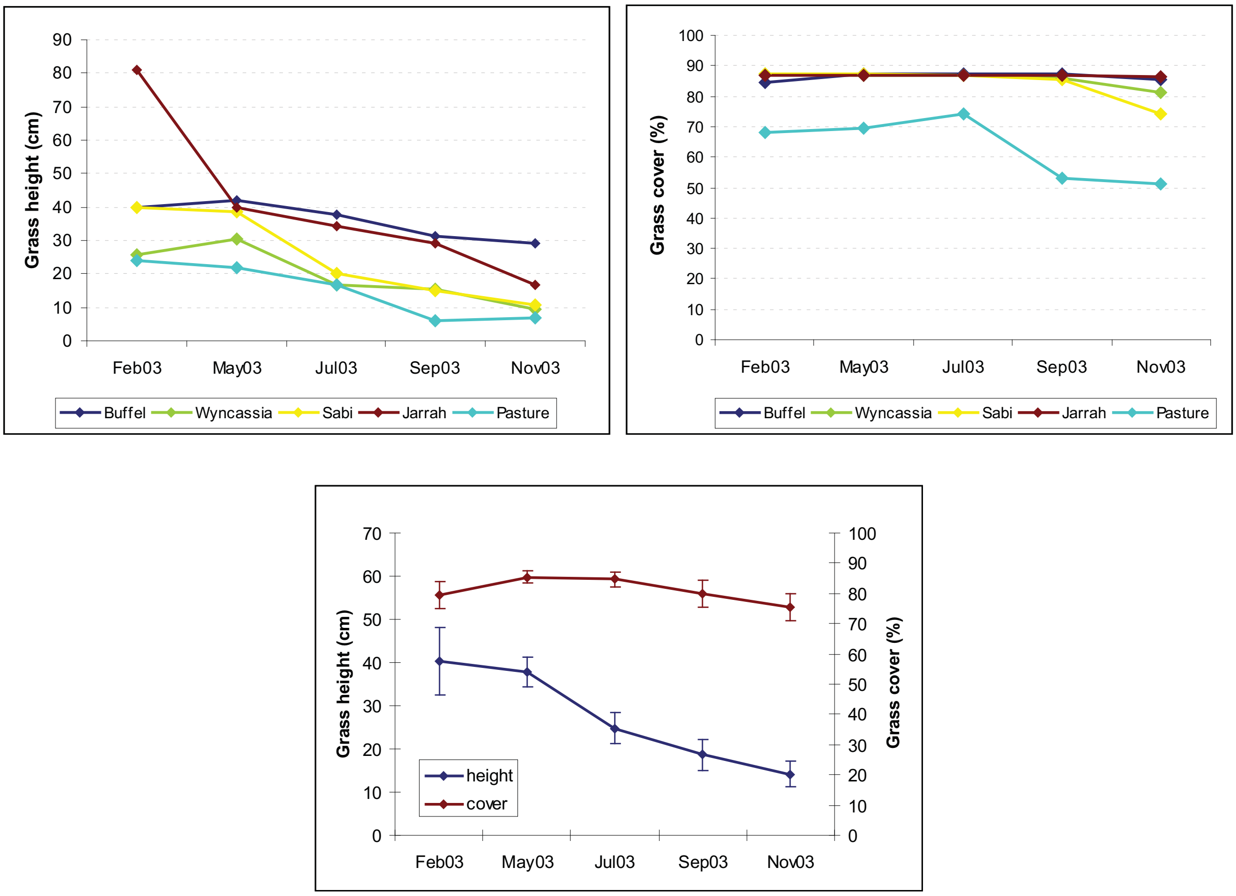


Figure 3.8: Seasonal variation in grass height (top left), proportional grass cover for five of the main grass/pasture associations (top right), and grass height and cover for all grass types combined (bottom) at the DDRF during 2003.

Table 3.2: Mean cover (of three height size classes), density and mean canopy height of woody vegetation (±SE) in three pre-defined habitats at Kidman Springs.

Habitat	% cover 1-3 m	% cover 3-5 m	% cover 5-10 m	% total cover	Basal area (m^2 / ha)	Mean canopy height (m)
ROW	7.6 (+1.1)	6.0 (+0.8)	8.3 (+1.4)	21.9 (+2.9)	5.2 (+0.5)	7.0 (+0.2)
BOW	4.6 (+0.7)	4.5 (+0.6)	3.7 (+1.0)	12.9 (+1.4)	3.4 (+0.4)	6.2 (+0.3)
BOP	0	0	0	0	0	0

Floristics

A total of 197 vascular plants were recorded at Kidman Springs in May 2004. There were substantial differences between each of the three main habitat types in floristic composition as demonstrated by an MDS ordination of all plots based on all plant species (Fig. 3.9). Excluding tree and shrub species, using only ground-layer vegetation, yielded similar results. An ANOSIM comparing habitats demonstrated that all habitats were significantly different from each other on the basis of floristics (Table 3.3) with fewest differences between the two black soil habitats (BOP and BOW). In contrast, there were no significant effects of fire regime as measured in this study on overall floristic composition.. Open woodland on loam earth (ROW) habitat had notably more heterogeneity in species composition than the two black soil habitats. A complete list of all plant species recorded at Kidman Springs in May 2004 including relative abundance based on occurrence within 27 plots across the site is presented in Table 3.4.

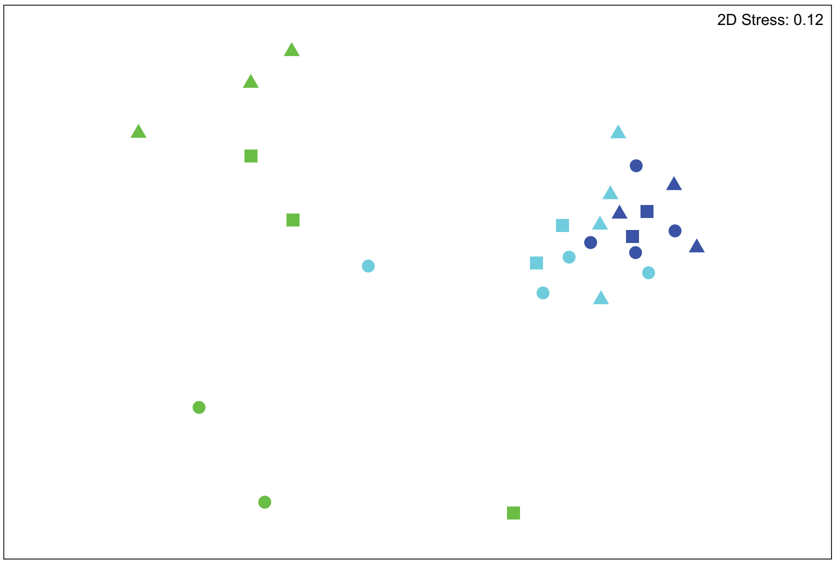


Figure 3.9: Ordination of plots at Kidman Springs according to floristic composition based on habitat (green = open woodland on loam earth soils; light blue = open woodland on alluvial soils; blue = open grassland on alluvial soils) and time since fire (triangle = 1 growing season; square = 3 seasons; circle = 5 seasons).

Table 3.3: Summary of ANOSIM results. Habitats (global R = 0.51, P = 0.001); open woodland on loam earth soil (ROW); open woodland on alluvial soil (BOW);and open treeless grassland plain on alluvial soil (BOP). Fire (global R = -0.042, P = 0.65); figures repesent number of growing (wet) seasons since fire.

	Group	R-statistic	P
Habitat	row, bop	0.868	**0.002**
	row, bow	0.748	**0.001**
	bop, bow	0.182	**0.04**
Fire history	1, 5	0.145	0.097
	1, 3	-0.125	0.762
	3, 5	-0.187	0.833

Table 3.4: List of plant species recorded at Kidman Springs in the early dry season (May 2004), including frequency of occurrence among 29 sampling plots at the site.

Family	Species	Sites
ACANTHACEAE	*Dicliptera armata*	1
	Rostellularia adscendens adscendens	19
AMARANTHACEAE	*Achyranthes aspera*	2
	Alternanthera nana	1
	Gomphrena affinis subsp. affinis	3
	Gomphrena canescens subsp. canescens	3
	Ptilotus exaltatus var. exaltatus	2
	Ptilotus fusiformis var. fusiformis	4
	Ptilotus spicatus subsp. burbidgeanus	6
APOCYNACEAE	*Carissa lanceolata*	10
ASCLEPIADACEAE	*Marsdenia sp.*	1
ASTERACEAE	*Bidens bipinnata*	5
	Blumea axillaris	1
	Blumea sp.	1
	Blumea tenella	22
	Flaveria australasica	2
	Pterocaulon serrulatum var. indeterminate	9
	Pterocaulon sphacelatum	3
	Streptoglossa bubakii	5
	Wedelia asperrima	1
BIGNONIACEAE	*Dolichandrone filiformis*	1
	Dolichandrone heterophylla	2
BIXACEAE	*Cochlospermum fraseri subsp. fraseri*	1
BORAGINACEAE	*Ehretia saligna var. indeterminate*	3
	Heliotropium foliatum	1
	Heliotropium plumosum	1
	Heliotropium sp.	3
	Trichodesma zeylanicum var. grandiflorum	24
CAESALPINIACEAE	*Bauhinia cunninghamii*	16
	Senna obtusifolia	1
	Senna occidentalis	1
	Senna planitiicola	3
CAPPARACEAE	*Cleome viscosa*	1
CARYOPHYLLACEAE	*Polycarpaea corymbosa*	1
	Polycarpaea spirostylis	1
COMBRETACEAE	*Terminalia canescens*	3
	Terminalia arosrtata	2
	Terminalia platyphylla	2
	Terminalia pterocarya	1
	Terminalia volucris	16
COMMELINACEAE	*Commelina ciliata*	12
	Commelina ensifolia	4
CONVOLVULACEAE	*Bonamia brevifolia*	1
	Bonamia media var. media	7
	Bonamia pannosa	3
	Evolvulus alsinoides var. alsinoides	9
	Polymeria ambigua	22
	Polymeria longifolia	10
CUCURBITACEAE	*Cucumis melo subsp. agrestis*	17
CYPERACEAE	*Bulbostylis barbata*	2
	Cyperus bifax	4
	Cyperus difformis	1
	Fimbristylis acuminata	1
	Fimbristylis complanata	2
	Fimbristylis schultzii	13
	Fimbristylis sp. Beverley Springs	15
	Fimbristylis sp. Howard River	4
	Fimbristylis sp. Timber Creek	1
	Rhynchosia minima	21
CYPERACEAE	*Rhynchospora corymbosa*	2
ELATINACEAE	*Bergia pedicellaris*	9
EUPHORBIACEAE	*Euphorbia alsiniflora*	1
	Euphorbia sp.	4
	Flueggea virosa subsp. Melanthesoides	8
	Leptopus decaisnei	9
	Phyllanthus maderaspatensis var. angustifolius	26
	Sauropus trachyspermus	12
FABACEAE	*Aeschynomene indica*	1
	Alysicarpus muelleri	3
	Cajanus acutifolius	1
	Cajanus sp.	1
	Crotalaria medicaginea var. indeterminate	8
	Crotalaria rostra var. angustifolia	11
	Cullen badocanum	2
	Desmodium muelleri	12
	Flemingia pauciflora	16
	Galactia tenuiflora	5
	Glycine falcata	5
	Indigofera linifolia	5
	Indigofera linnaei	3
	Indigofera trita	12
	Sesbania simpliciuscula	8
	Stylosanthes hamata	3
	Tephrosia rosea var. indeterminate	2
	Tephrosia supina	1
	Vigna lanceolata var. indeterminate	2
	Vigna lanceolata var. lanceolata	1
	Zornia muriculata subsp. Angustata	1
	Zornia rostrate var. indeterminate	1
GOODENIACEAE	*Goodenia byrnesii*	17
	Goodenia sepalosa var. sepalosa	3
	Goodenia strangfordii	1
LAURACEAE	*Cassytha capillaris*	7
LILIACEAE	*Crinum angustifolium*	3
LYTHRACEAE	*Ammannia multiflora*	17
	Rotala diandra	3
MALVACEAE	*Abelmoschus ficulneus*	19
	Abutilon otocarpum	1
	Abutilon sp.	5
	Gossypium australe	11
	Hibiscus panduriformis	7
	Hibiscus pentaphyllus	1
MALVACEAE	*Malvastrum americanum*	3
	Sida acuta	1
	Sida fibulifera	5
	Sida spinosa	15
MENISPERMACEAE	*Tinospora smilacina*	5
MIMOSACEAE	*Acacia holosericea*	4
	Acacia sp. Krichauff Range	2
	Acacia validinervia	1
	Neptunia dimorphantha	3
	Neptunia gracilis f. gracilis	17
	Neptunia monosperma	5
	Neptunia sp.	1
MORACEAE	*Ficus aculeata var. aculeata*	1
MYRTACEAE	*Calytrix exstipulata*	1
	Corymbia terminalis	8
	Eucalyptus pruinosa subsp. Indeter.	10
	Eucalyptus microtheca	3

Family	Species	Sites
NYCTAGINACEAE	*Boerhavia burbidgeana*	2
OLEACEAE	*Jasminum aemulum*	1
	Jasminum molle	4
ONAGRACEAE	*Ludwigia perennis*	15
PASSIFLORACEAE	*Passiflora foetida*	1
POACEAE	*Aristida holathera var. holathera*	1
	Aristida latifolia	25
	Aristida pruinosa	2
	Astrebla pectinata	1
	Brachyachne convergens	17
	Cenchrus ciliaris	1
	Chionachne hubbardiana	5
	Chloris sp	8
	Chrysopogon fallax	25
	Dichanthium fecundum	22
	Dichanthium sericeum subsp. humilius	18
	Echinochloa colonum	1
	Elytrophorus spicatus	3
	Enneapogon purpurascens	5
	Enneapogon sp	2
	Eragrostis cumingii	2
	Eragrostis tenellula	25
	Eriachne ciliata	1
	Eriachne glauca var. barbinodis	2
	Eriachne obtusa	4
	Eulalia annua	2
	Eulalia aurea	6
	Heteropogon contortus	12
	Iseilema fragile	22
	Iseilema vaginiflorum	6
	Iseilema macratherum	3
	Iseilema ciliatum	2
	Schizachyrium crinizonatum	1
	Schizachyrium sp.	2
	Sehima nervosum	10
	Setaria apiculata	1
	Sorghum timo	7
POACEAE	*Sporobolus australasicus*	9
	Sporobolus sp.	1
	Sporobolus australasicus	9
	Sporobolus sp.	1
	Themeda sp.	1
	Urochloa subquadripara	1
POLYGALACEAE	*Polygala rhinanthoides var. minor*	4
PORTULACACEAE	*Calandrinia uniflora*	1
PROTEACEAE	*Grevillea striata*	2
	Hakea arborescens	7
RHAMNACEAE	*Ventilago viminalis*	4
	Ziziphus sp.	1
RUBIACEAE	*Oldenlandia argillacea*	12
	Oldenlandia mitrasacmoides subsp.	1
	Spermacoce auriculata	3
	Spermacoce dolichosperma	5
	Spermacoce sp.	1
SAPINDACEAE	*Atalaya hemiglauca*	3
SCROPHULARIACEAE	*Bacopa floribunda*	1
	Buchnera asperata	7
	Stemodia glabella	3
	Stemodia tephropelina	18
	Striga curviflora	3
STERCULIACEAE	*Brachychiton diversifolius*	3
	Melhania oblongifolia	2
	Melochia pyramidata	10
	Waltheria indica	11
THYMELAEACEAE	*Thecanthes punicea*	1
TILIACEAE	*Corchorus aestuans*	12
	Corchorus fascicularis	4
	Corchorus sidoides subsp. Indeter.	6
	Corchorus tridens	4
	Grewia retusifolia	7
VERBENACEAE	*Clerodendrum floribundum var. indeter.*	2
	Premna acuminata	2
VIOLACEAE	*Hybanthus aurantiacus*	6
	Hybanthus enneaspermus subsp. enneaspermus	1
VITACEAE	*Cayratia trifolia*	3

Availability of food resources

Fruit availability

Fruit availability of each of the main food plants of bustards at Kidman Springs was generally highest during the early dry season (May) and then gradually declined during the year (Fig. 3.10). Native melons *Cucumis melo* were most abundant in the early dry season, and mainly on plots in the black soil habitats (Table 3.5). Fruits of *Cassytha* sp. were consistently present throughout the survey period and restricted to woodland sites. Fruits of *Grewia retusifolia* were present during all but one sampling period, although their occurrence was lower later in the dry season. *Carissa lanceolata* fruits were most abundant in woodland sites in the early and mid dry season. While no direct measures of fruit availability was made at the DDRF because of the absence of the main fruiting plants, the site is notable for a small but important irrigated peanut crop that is grown during the mid dry season that bustards utilize intensively.

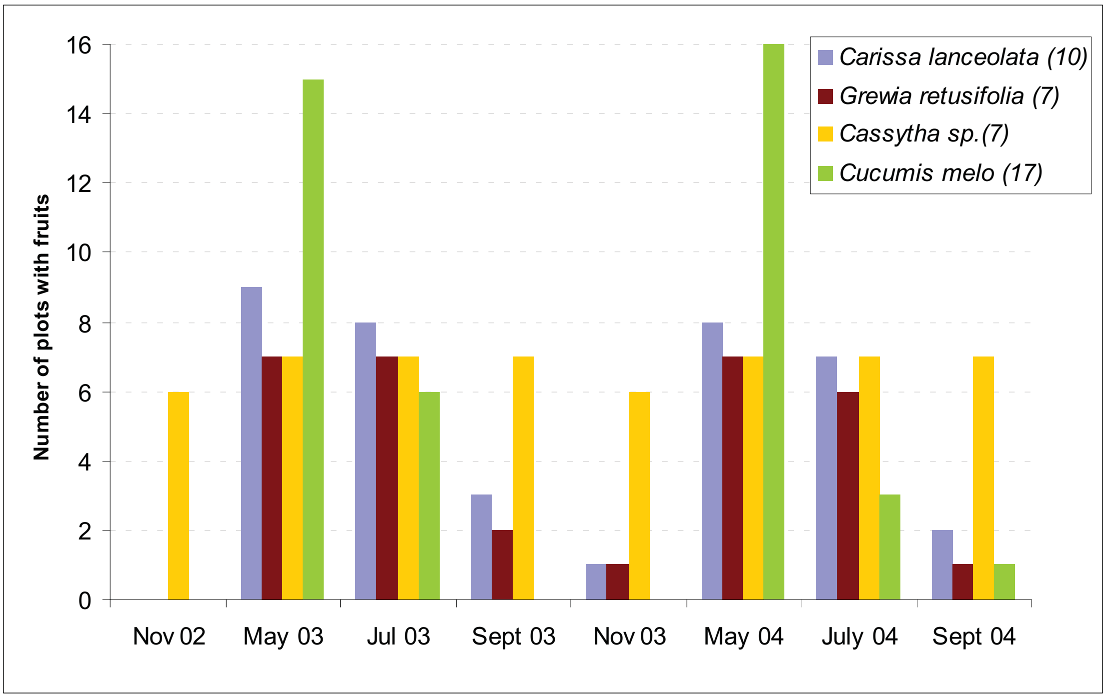


Figure 3.10: Number of plots at Kidman Springs (total n = 27) where ripe fruits from four plant species favoured by bustards where recorded as present during each sampling period. Number in brackets indicates number of plots at which each plant species occurred during a floristics survey in May 2004.

Table 3.5: Number of plots (n=9 per habitat) with ripe fruits of main food plants at Kidman Springs within three habitats in May 2004.

	ROW	BOW	BOP
Carissa lanceolata	4	6	0
Cucumis melo	4	5	7
Grewia retusifolia	3	3	1
Cassytha spp.	4	3	0

Arthropod availability

Grass layer arthropods

At both sites the dominant grass-layer taxa recorded were Orthoptera, Mantida, Phasmida and Lepidoptera. Of these the Orthoptera made up more than 80% of observations for almost all survey periods. Variation in the abundance of these arthropods at both Kidman Springs and the DDRF was highly seasonal, with marked peaks in the early dry season (May). At Kidman Springs, this variation was best explained by the model representing the parameters 'habitat' and 'period' (Table 3.6). This model had similar support to the model that incorporated all three explanatory variables but was the simpler of the two, therefore, based on parsimony was the preferred model. Inspection of coefficients for this model showed that the abundance of grass-layer arthropods was highest in open grasslands on black soil habitat than in other habitats, and in the early dry season compared to all other seasons (Table 3.7; Fig. 3.11).

Table 3.6: Generalized linear modeling statistics of grass-layer arthropod abundance sampled at four different times of the year in three habitats that varied in fire history at Kidman Springs.

(Log *L* is the maximised log-likelihood of the model, k is the number of estimated parameters,QAIC*c* is the selection criterion, ΔQ.AIC*c* is the difference between the model's QAIC*c* value and the minimum QAIC*c* value, and $QAIC_c$ weight is the Akaike weight. Shading denotes most parsimonious model with a significant level of support.)

Model	-Log likelihood	k	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	% deviance explained
FIRE+HABITAT+PERIOD	-259.00	10	251.28	0.00	0.56	70.9
HABITAT+PERIOD	-265.18	8	251.92	0.64	0.41	69.5
PERIOD*HABITAT	-254.48	14	257.56	6.28	0.02	71.9
PERIOD*FIRE	-259.54	14	262.03	10.75	0.00	70.8
PERIOD	-286.06	6	265.75	14.47	0.00	64.8
FIRE+PERIOD	-280.96	8	265.87	14.59	0.00	65.9
PERIOD*HABITAT*FIRE	-211.29	38	306.40	55.12	0.00	81.7
HABITAT*FIRE	-531.12	11	494.36	243.08	0.00	9.1
FIRE+HABITAT	-542.74	7	494.99	243.70	0.00	6.4
HABITAT	-548.31	5	495.37	244.09	0.00	5.2
Null model	-571.02	3	511.09	259.81	0.00	0
FIRE	-566.27	5	511.25	259.97	0.00	1.1

Table 3.7: Model parameters for the preferred model (HABITAT+PERIOD) of grass-layer arthropod abundance.

	Estimate	Std. Error	z-value	Pr(>|z|)	Sig.
(Intercept)	3.004	0.068	43.91	<0.0001	***
HABITAT bow	-0.613	0.102	-5.97	<0.0001	***
HABITAT row	-0.487	0.105	-4.60	<0.0001	***
PERIOD (July)	-1.923	0.141	-13.56	<0.0001	***
PERIOD (Sept)	-1.571	0.122	-12.87	<0.0001	***
PERIOD (Nov)	-3.273	0.272	-12.03	<0.0001	***

*p < 0.05. **p < 0.01, ***p < 0.001

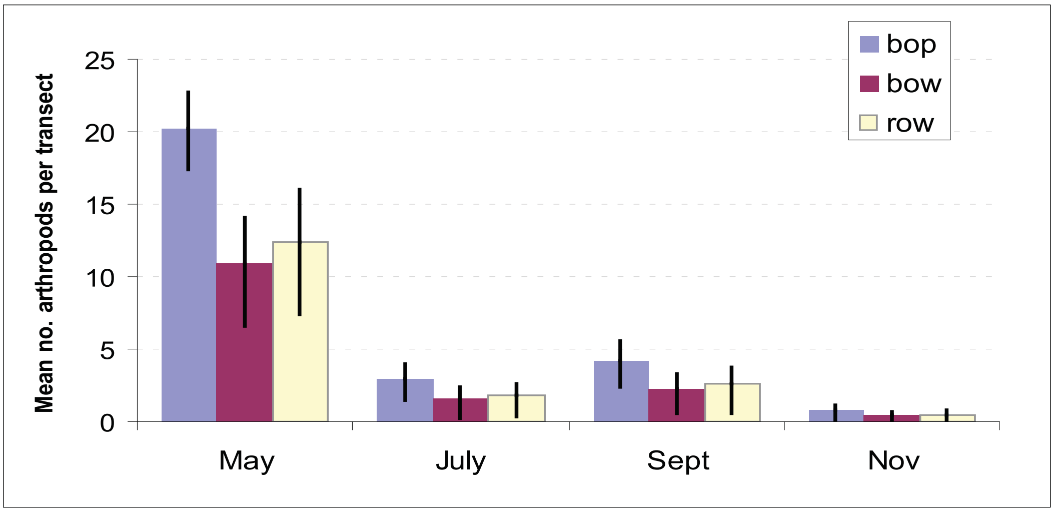


Figure 3.11: Mean abundance (with 95% confidence intervals) of grass-layer arthropods per transect in three pre-defined habitat types compared between sampling periods. Data were pooled from two years into each sampling period. (BOP = black soil open grassland plain; BOW = black soil open woodland; ROW = loam soil open woodland).

There were significant differences in grass layer arthropod abundance between the DDRF and Kidman Springs and between periods of the year (Table 3.8). Abundance was appreciably higher at the DDRF than at Kidman Springs. Indeed, for every individual survey period grass layer arthropods were at least twice as abundant at the DDRF (Fig. 3.12). Abundance was also higher in the early dry season (May) than in any other period, and in the mid-dry season (July) compared to the late dry season (November) (Table 3.9). In both seasons at both sites, peak abundance in the early dry season was followed by marked declines during the remainder of the year (Fig. 3.12).

Table 3.8: Two-way ANOVA results assessing grass layer arthropod abundance between the two main study sites and four periods of the year. (P = * <0.05, ** <0.01, *** <0.001)

Effect	d.f.	F	p
SITE	1	77.9	***
PERIOD	3	47.5	***
SITE*PERIOD	3	2.1	0.097

Table 3.9: Tukey HSD post-hoc tests results. (DD = DDRF, KS = Kidman Springs) (P = * <0.05, ** <0.01, *** <0.001)

PERIOD	May	July	Sept
May			
July	***		
Sept	***	0.967	
Nov	***	*	0.068

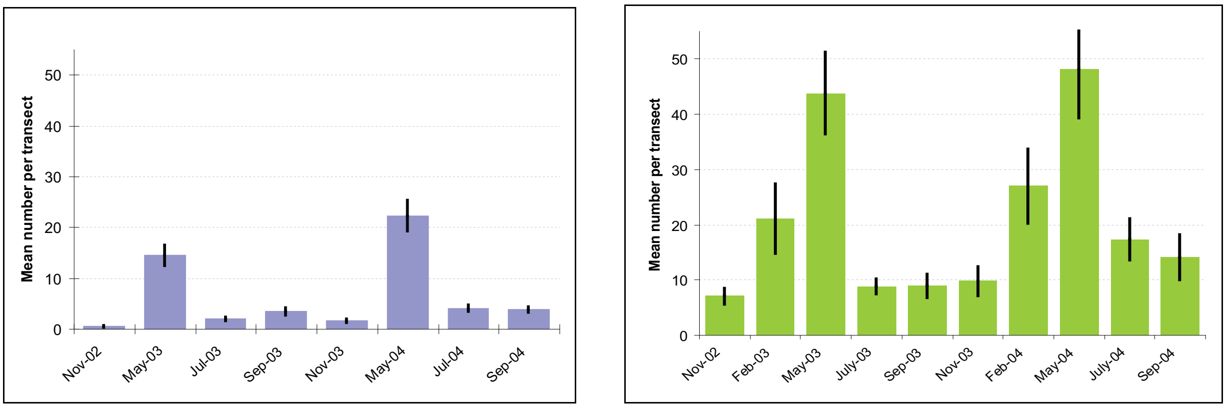


Figure 3.12: Variation in abundance of all large grass-layer arthropods measured by transects pooled for plots at Kidman Springs (left), and the DDRF (right) during each sampling period between Nov. 2002 and Sept. 2004.

Ground dwelling arthropods

Although a wide variety of ground dwelling arthropods was recorded, here I report only information for taxa that contributed more than 1% of total dry weight to the diet of bustards (see Chapter 6). This excluded, for example, two of the most abundant taxa recorded in pitfall traps: ants (Formicidae) and silverfish (Thysanura). The main taxa considered include spiders (Araneae), true bugs (Hemiptera), beetles (Coleoptera), cockroaches (Blattodea), and small (<20mm) grasshoppers or crickets (Orthoptera).

Seasonal variation in the abundance of the different taxa at the DDRF generally showed peaks in the wet and early dry season followed by marked declines (Fig. 3.13). Beetles and small orthopterans made up the largest numbers of the ground dwelling arthropods considered. Beetles were equally and highly abundant during the wet season and early dry, while orthopterans were at least 10 fold more common in the wet season (Feb) compared with other periods. An exception to the general pattern at the DDRF was the large numbers of spiders recorded during the September 2003 survey.

At Kidman Springs patterns of variation in the abundance of the different taxa were generally more variable. Of all the taxa only the small orthopterans exhibited expected trends, with a notable peak in the early dry season eclipsing numbers in all other periods. Larger numbers of some taxa in the 'Nov.03' sampling period may have been a result of patchy rainfall in the region in October and November. Spiders at Kidman Springs exhibited a similar peak to the DDRF in the latter dry season. At both sites, spider numbers were dominated by a large proportion of small (<10 mm) specimens. Overall, there were notably larger numbers for most taxa at the DDRF compared with Kidman Springs, particularly of those components especially favoured by bustards; the Orthoptera and Coleoptera. The generally low numbers of ground dwelling invertebrates for most taxa recorded at Kidman Springs may have contributed to the greater variation and apparent anomalies from expected trends for several of the taxa.

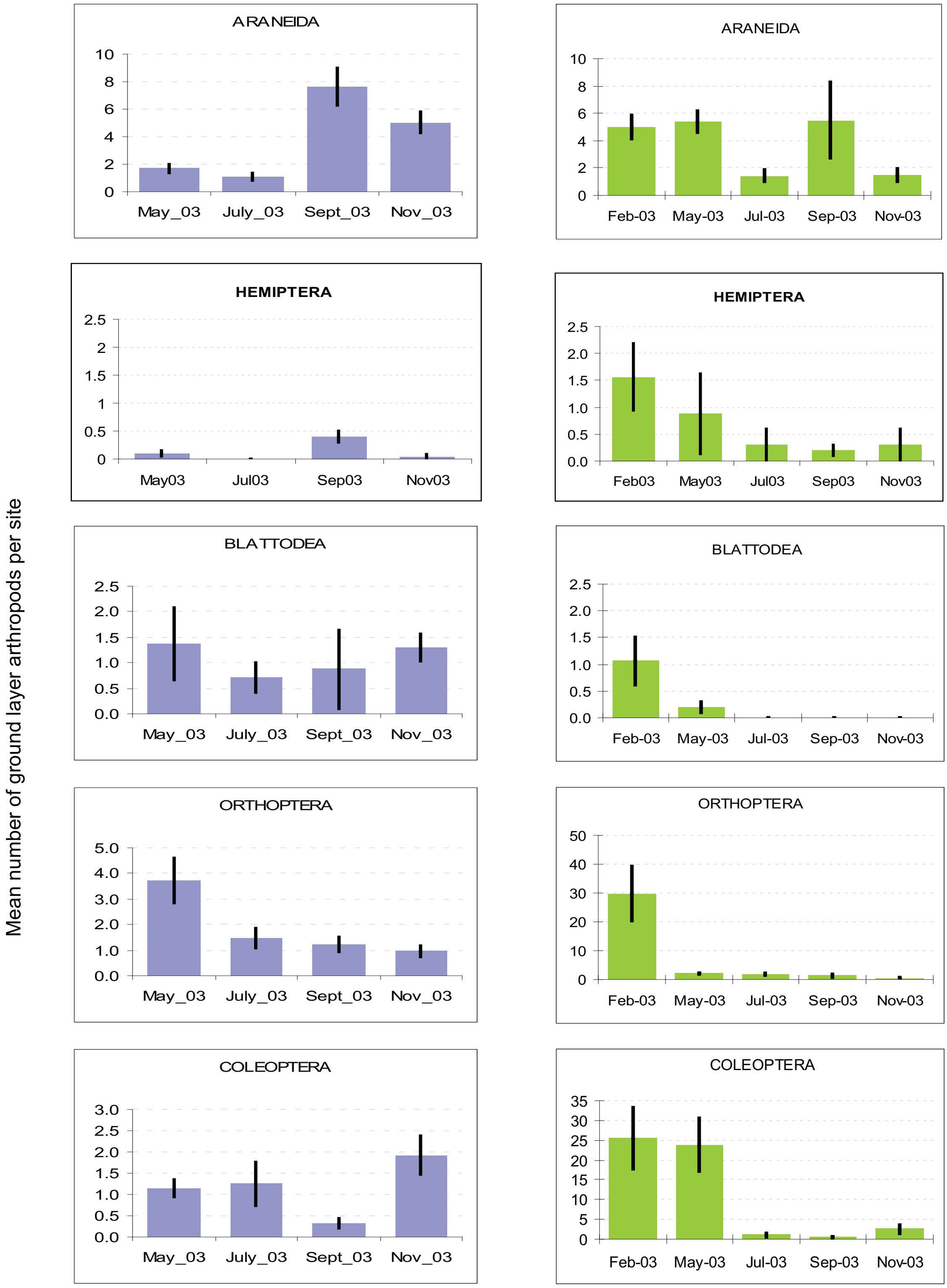


Figure 3.13: Mean abundance per plot (with standard error bars) of ground dwelling arthropods between seasons in 2003 across all sampling sites at Kidman Springs (left) and the DDRF (right). Note discrepancies in scales between taxa and between sites for Orthoptera, Coleoptera and Total arthropods and the inclusion of an additional (Feb-03) sampling period at the DDRF.

A two-way comparison of the abundance of all ground-layer arthropods considered together between sites and seasons suggested a difference between period and a site/period interaction (Table 3.10). Overall significant differences existed between May and July, and July and November (Table 3.11). There were also significantly more ground-layer arthropods at the DDRF in the early dry season (May) than at any other time at either site (Table 3.12).

Table 3.10: Two-way ANOVA results assessing total ground-layer arthropod abundance between the two main study sites and four periods of the year. (P = * <0.05, ** <0.01, *** <0.001)

Effect	d.f.	F	p
SITE	1	2.62	0.107
PERIOD	3	9.98	***
SITE*PERIOD	3	12.45	***

Table 3.11: Tukey HSD post-hoc tests results for total ground layer arthropod abundance compared between four periods of the year. (DD = DDRF, KS = Kidman Springs) (P = * <0.05, ** <0.01, *** <0.001)

	PERIOD	*May*	*July*	*Sept*
1	May			
2	July	***		
3	Sept	0.319	0.013	
4	Nov	0.261	*	0.994

Table 3.12: Tukey HSD post-hoc tests results for total ground layer arthropod abundance for the interaction between four periods of the year and two sites (DD = DDRF, KS = Kidman Springs) (P = * <0.05, ** <0.01, *** <0.001)

	SITE	PERIOD	1	2	3	4	5	6	7
1	KS	May							
2	KS	July	0.727						
3	KS	Sept	0.503	**					
4	KS	Nov	0.703	*	1.000				
5	DD	May	***	***	**	***			
6	DD	July	1.000	0.987	0.339	0.503	***		
7	DD	Sept	1.000	0.938	0.529	0.700	***	1.000	
8	DD	Nov	1.000	0.864	0.670	0.820	***	1.000	1.000

A more sophisticated analysis that aimed to assess the relative influence of habitat type, time since fire and period of the year on the abundance of ground-layer arthropods at Kidman Springs suggested that variation in abundance was best explained by time of year ('PERIOD'). However, this was a weak model that only explained 13.4% of the deviance (Tables 3.13 & Table 3.14).

Table 3.13: Model selection results for a candidate set of generalized linear models (using Poisson and log-link functions) of ground-layer arthropod abundance sampled at four different times of the year during 2003 in three habitats that varied in fire history at Kidman Springs.

(Log *L* is the maximised log-likelihood of the model, k is the number of estimated parameters,QAIC*c* is the selection criterion, ΔQ.AIC*c* is the difference between the model's QAIC*c* value and the minimum QAIC*c* value, and $QAIC_c$ weight is the Akaike weight. Shading denotes most parsimonious model with a significant level of support.)

Model	log L	k	Q.AIC_c	Δ$QAIC_c$	$QAIC_c$ weight	% deviance explained
PERIOD	-394.97	5	223.58	0.00	0.54	13.4
HABITAT + PERIOD	-393.34	7	227.34	3.76	0.08	14.1
FIRE + PERIOD	-393.44	7	227.39	3.81	0.08	14.0
FIRE + HABITAT + PERIOD	-391.63	9	231.25	7.67	0.01	14.8
Null model	-426.23	2	233.65	10.07	0.00	0.0
PERIOD*HABITAT	-380.15	13	235.40	11.82	0.00	19.7
FIRE	-424.61	4	237.15	13.57	0.00	0.7
HABITAT	-424.72	4	237.21	13.63	0.00	0.6
PERIOD*FIRE	-388.67	13	239.94	16.37	0.00	16.1
HABITAT*FIRE	-404.57	10	240.64	17.06	0.00	9.3
FIRE + HABITAT	-422.91	6	240.78	17.20	0.00	1.4
PERIOD*HABITAT*FIRE	-325.54	37	293.28	69.71	0.00	43.1

Table 3.14: Model parameters for the preferred model (from Table 3.10) of ground-layer arthropod abundance.

	Estimate	Std. Error	z	Pr(>|z|)	sig.
(Intercept)	1.997	0.071	28.17	<0.0001	***
PERIOD (July)	-0.425	0.112	-3.77	<0.001	***
PERIOD (Sept)	0.327	0.093	3.51	<0.001	***
PERIOD (Nov)	0.241	0.095	2.52	<0.05	*

*p < 0.05. **p < 0.01, ***p < 0.001

DISCUSSION

Both the DDRF and Kidman Springs exhibited patterns in food resource abundance and habitat characteristics consistent with the seasonality of the wet/dry tropics of northern Australia. Wet and early dry season peaks in grass layer biomass and key food resources were followed by general declines over a prolonged dry season. There were, however, some notable contrasts within and between sites. However, while the two study sites differ primarily in their land use, management and intrinsic naturalness, they also differ in annual rainfall and productivity, such that many of the observed differences between sites in habitat and food resource parameters cannot readily be related to any single one of these contrasts. Nevertheless, many of the outcomes presented appear in large part due to gross differences in land use and management practices between the sites.

The DDRF represents a largely artificial environment in an otherwise intact, natural savanna landscape. Established in the 1960s as an experimental research farm chartered to assess the suitability of various crops and pastoral practices in northern Australia, the site is unusual because of the variety of crop types dispersed among a larger matrix of perennial pasture grasses. Compared with broad-scale monocultures typical of agricultural practices in many other parts, the Douglas-Daly region as a whole is comparatively dynamic and varied. Nevertheless, despite the heterogeneity of crop and pasture types the overall habitat is structurally homogeneous and few of the crops are direct food resources to bustards in themselves. One notable exception is the cultivation of peanuts and pasture grasses in a small pivot-irrigated plot at the centre of the research farm. During the mid to late dry season this area provides a vigorous source of green pick for bustards and potential habitat for many arthropod taxa. Following harvesting left over peanuts represent a rich source of food at a time when many natural foods are otherwise declining in the surrounding landscape. Complementing this unusual resource peak at the DDRF is the persistence of introduced perennial pasture grasses, which under relatively low grazing intensity and through the exclusion of fire, exhibit a constancy of cover throughout the year across most of the site. Such stability may provide consistent cover and shelter, and may contribute to the observation of greater grass-layer arthropod abundance at the DDRF compared to Kidman Springs. Importantly, although there is significant seasonal variation in arthropod abundance at the DDRF, minimum arthropod numbers are notably higher compared to those at Kidman Springs. For bustards, and other components of the biota that rely on arthropods for food, such differences may be particularly important towards the mid to late dry season when food resources are generally low. Therefore, while results in this study show high seasonal variability in foods available to bustards at the DDRF, management of the site may ameliorate some of the natural seasonality.

In contrast to the DDRF, Kidman Springs represents a comparatively natural, intact savanna landscape. Within the core study region there are three main habitat types that are commonly used by bustards that form a continuum from open treeless grassland on alluvial soils to open woodland with grassy understorey. Shrub and tree density and plant species richness here reach their highest on loam earth soils. These habitats are dissected by riparian corridors and are bordered by adjacent rocky hills and escarpments that further add to the structural habitat diversity of the site. At Kidman Springs, specific habitats were also more diverse in their plant species assemblages than others. For example, woodlands over loam earth soils exhibited a greater variety of plant species than other habitats. A putative advantage of higher habitat heterogeneity and species richness for bustards may relate to the asynchronous availability of resources (i.e. high availability in one habitat may compensate for lows in resources in another habitat at specific times). One notable example is the higher availability of grass-layer arthropods in the early dry season in open treeless grasslands compared to other habitats at this time. However, this period also coincides with comparatively high availability of all resources across the entire region, therefore, the relative advantages of higher resources in one habitat over another at this time may be of negligible consequence. Overall, results here suggest that seasonality dominates resource availability with consistent trends of decline evident across the course of the dry season within all habitats.

The influence of season and rainfall on invertebrates have been reported in more comprehensive studies of specific taxa (Andersen and Müller 2000; Blanche *et al.* 2001; Orgeas and Andersen 2001; Williams *et al.* 2002). Arthropod abundance generally peaks in the wet season (Churchill 1994), with up to a 50-fold decrease in numbers of invertebrates caught between the wet season and dry season (Woinarski and Tidemann 1991). Although seasonal trends in arthropod abundance in Australia's wet-dry tropics are reasonably well documented there have been few studies that have explicitly examined the effects of patchy rainfall patterns on arthropod abundance, even though spatial patchiness in the occurrence of rainfall is a feature of the late dry and early wet season periods (Taylor and Tulloch 1985). Indeed, pre-wet season localized patchy rainfall and late dry season fires provide important contrasts in the landscape at times when resources are otherwise low. Orgeas and Anderson (2001) attributed higher abundance and richness of beetles observed in the wet-dry tropics during the middle of the wet season (Feb) compared to the end of the wet season (May) to the erratic nature of rain during the wet-dry transition. Due to logistical constraints, the study design adopted in the present study could not accommodate a thorough assessment of the effects of variable spatial patterns of rainfall, even though such patterns may have important repercussions for habitat use and the ranging behaviour of bustards, particularly late in the year.

Among the most comprehensive studies of the effects of fire on the biota of the northern savannas have been those conducted at the Kapalga Research Station in Kakadu National Park (Andersen *et al.* 2003). Although there are many possible fire scenarios, with a variety of potential direct and indirect effects on the biota (Woinarski 1999), annual late dry season fires, as examined experimentally at a landscape-scale at Kapalga, represent the most extreme, and presently dominant, fire conditions in northern Australia (Andersen *et al.* 2003; Russell-Smith *et al.* 1997). Research at Kapalga demonstrated that many components of the biota, including terrestrial invertebrates, exhibit high resilience to fire (Andersen *et al.*

2003; Andersen and Müller 2000; Orgeas and Andersen 2001; Parr and Andersen 2008; Williams *et al.* 2002). Indeed, some taxa depend on the regular occurrence of fire. Two of the most important taxa to bustards as food resources are the beetles and grasshoppers (Chapter 6). At Kapalga, grass-layer beetles and grasshoppers increased in abundance and richness following fire and were favoured by frequent fires (Andersen and Müller 2000; Orgeas and Andersen 2001). Notably there were differences in responses between ground and grass layer beetles. While grass layer beetle assemblages at Kapalga were affected by repeated fires but not by season of burn (Andersen and Müller 2000), late dry season fires significantly reduced ground layer beetle abundance and richness during the early wet season (Blanche *et al.* 2001). By comparison, primarily ground-active grasshoppers were unaffected (Orgeas and Anderson 2001).

An immediate consequence of fire is removal of the grass layer and direct mortality or emigration of arthropods from fire fronts or burnt areas. Studies of grass-layer insects in wet/dry tropics elsewhere demonstrate that a high proportion of flying insects escape from flames and rapidly recolonise following fire (Gillon 1983), although fire is also likely to cause significant mortality among many taxa (Gillon 1983). Bustards forage at fire fronts and in recently burnt areas to exploit these resources. In this study, the immediate availability of resources at a fire was not examined. However, over a longer period (in this case, after at least one growing (wet) season), there was limited evidence to suggest that the fire regimes examined at Kidman Springs affect the availability of food resources to bustards. The effects of fires on arthropod biota here may be reduced because of the relatively small-scale at which fires are implemented at Kidman Springs. Consequently, recolonisation of burnt areas from adjacent unburnt regions may be rapid. In terms of spatial scale, the fire regimes implemented at Kidman Springs may therefore not be reflective of contemporary fire regimes in northern Australia which tend to be dominated by large and intense fires. Nevertheless, high resilience to fire is a feature of the northern biota and likely a result of the extended association of the biota of northern Australia to frequent fire (Andersen and Müller 2000; Orgeas and Andersen 2001). Similar findings have been found in other Australian landscapes (Friend and Williams 1996), but contrast to areas that have been relatively recently derived from forest due to extensive clearing and burning (Gillon 1983). The consequences of fires in landscapes such as those of the cleared regions of the DDRF may therefore be notably different to natural savanna landscapes. Indeed, the apparent benefits ascribed to a continuous layer of perennial grasses (due to stability and consistent availability of cover and habitat for prey), may be nullified by fires that do occur in these areas because the continuous fuel layer it provides ensures that any fires lit leave few patches of litter or vegetation for shelter which may aid recolonisation.

In closing, this chapter examined the general patterns of bustard food and habitat resource characteristics at two contrasting sites in the northern savannas. The implications of these features are subsequently examined in the following chapters on aspects of the bustard’s ecology at these sites.

Chapter 4

Comparisons of survey methods and seasonal dynamics of bustard populations at two contrasting sites in Australia's northern savannas

Roger Potts

Chapter 4

Comparisons of survey methods and seasonal dynamics of bustard populations at two contrasting sites in Australia's northern savannas

INTRODUCTION

Estimates of population sizes, trends and distribution patterns of Australian Bustards have been largely based on coarse, large-scale surveys and disparate, often opportunistic observations. For example, reporting rates of bustards from bird atlas volunteers are predominantly based on 'incidental' sightings (Barrett *et al.* 2003; Blakers *et al.* 1984), while aerial surveys have only opportunistically recorded bustards while targeting other species (Grice *et al.* 1986). These methods, and those employing mail surveys of rangeland users presented in Chapter 2, are useful for identifying and describing spatial patterning in abundance over large scales. However, they lack the necessary detail required for assessing responses to specific environmental factors, habitat relationships and localized population trends, and provide little insight into the extent of seasonal variability in abundance, and its causes, at any site.

Bustards may employ a range of movement strategies in response to changing habitat conditions due to season, rainfall, fire and other factors, resulting in fluctuations in numbers at any given location (Downes 1982a, 1984; Marchant and Higgins 1993; Chapters 2 and 8). In some parts of the species range, perceived population declines have been attributed to various threats, such as hunting, introduced predators and habitat alteration. Elsewhere, localised increases are believed to have occurred due to increased habitat availability through land clearing (Blakers *et al.* 1984). The lack of detailed and repeated systematic surveys of bustards at specific sites makes it difficult to determine to what extent local population fluctuations are representative of dispersive movements or real changes in overall numbers. In effect, they preclude meaningful comparisons of the status of bustard populations between regions and time periods. This chapter seeks to redress this deficiency by investigating sampling methodologies and patterns in bustard abundance at two contrasting sites in northern Australia that differ fundamentally in their land use and habitat types. These sites, described in detail in Chapter 3, include the Douglas-Daly Research Farm (DDRF) and Kidman Springs in the 'Top End' of the Northern Territory.

Low population densities, marked seasonal and spatial dynamics in bustard habitat structure and productivity present challenges for surveying and monitoring the species. A primary aim of this study was to develop and assess effective survey methods to quantify bustard abundance and to facilitate comparisons between seasons and sites. Two techniques were employed and compared. A simple measure of bustard abundance based on number of individuals recorded per kilometre driven was used to provide an index of abundance. Such techniques, based on simple encounter rates per unit effort, provide quick and easily repeatable measures and have often been employed for estimating abundance of other bustard species elsewhere (Allan 1994; Alonso and Alonso 1996; Alonso *et al.* 2003; Moreira 2004; Morgado and Moreira 2000; Silva *et al.* 2007). Although widely employed by biologists these methods have recognised limitations and biases (Rosenstock *et al.* 2002). Critically, they fail to account for variability in detectability as a result of variable habitat characteristics and behavioural differences – factors that may be particularly relevant to bustards in the highly dynamic savannas of northern Australia. A more sophisticated technique incorporates an analytic component that models variation in detectability to derive density estimates. The method adopted here is based on line transect distance sampling (Buckland *et al.* 2001), and is recognised as among the best methods for estimating densities for medium to large sized animals over large areas (Harris and Burnham 2002). Such methods, based on vehicle-driven survey transects, have been used to monitor populations of bustards elsewhere (e.g. Seddon and Van Heezik 1996; Tourenq *et al.* 2005).

The development of survey methods presented in this chapter begins with the definition of a set of factors that may affect detectability of bustards in the course of vehicle-based surveys. The probability of detectability is expected to be positively related to group size (Butler *et al.* 2007), and negatively to increasing grass height, shrub and tree density and distance to observer. These factors are subsequently incorporated as covariates into models that incorporate detection functions to estimate bustard densities. Derived estimates are then related to simple counts of bustards (based on counts of individuals per kilometre driven), to examine the relative merits of each census procedure and to assess how the survey methodology employed here may inform future monitoring programs.

In Chapter 3, I outlined the seasonal variability of food resource availability and habitat conditions at Kidman Springs and the Douglas-Daly Research Farm. Here, I consider the extent to which this variability influences seasonal variation in abundance of bustards in each region. The salient findings from Chapter 3 were that both sites exhibited marked seasonality in abundance of food resources and in grass-layer dynamics, in line with the wet-dry season. Such predictable variability may lead to regular seasonal fluctuations in a population's abundance as individuals undertake regular migratory movements between regions to make use of seasonally changing resource availability. Alternatively, predictable conditions may facilitate sedentariness at a given site because individuals are 'guaranteed' that conditions will vary reliably hence may endure resource lows until conditions improve (Griffioen and Clarke 2002; Nix 1976).

It may also be reasonably expected that the coarse differences evident between these two sites will be reflected in the dynamics of their respective bustard populations. Notably, food resources were generally higher and grass cover more stable at the DDRF compared to Kidman Springs. The DDRF also provides a temporary and highly concentrated food resource in the mid-dry season (June to September), a period otherwise characterised by lower food availability in the broader landscape. At this highly managed site, fire is also excluded and hunting prohibited. Consequently, if bustard numbers at a site are closely related to resource availability, then numbers may be higher and more stable in this managed landscape than in the surrounding ‘natural’ savanna landscape. In comparison, Kidman Springs is typical of intact tropical savannas and has a variety of habitat types. Food resources here were lower than the northern site, and apart from during the early dry season when food availability peaks across the broader landscape, there were no significant differences in food resources between habitats during any specific survey period. Instead, variability between seasons and years was high. In addition, the short term effects of fires in and around Kidman Springs add further to the site’s heterogeneity. It may be expected that the favourability of this site to bustards is more variable than the DDRF due to potentially greater inter-and intra-seasonal variation in resources. Accordingly, numbers of bustards here may be comparatively lower than at the DDRF and exhibit greater seasonal and inter-annual variation.

In addition to the regular sampling of resources and bustard numbers, I also specifically examined the response of bustards at Kidman Springs to a fire event, given that fire is a factor that may substantially affect food availability and/or foraging efficiency in these largely natural landscapes (Woinarski 1990; Woinarski 1999). Bustards readily respond to fires by foraging at fire fronts and in recently burnt areas for invertebrates and small vertebrates escaping or killed by fires (Marchant and Higgins 1993). In doing so they may track fire events across the landscape and large numbers may aggregate in recently burnt areas until food resources are exploited.

METHODS

Study sites

Seasonal dynamics of bustard populations were assessed at the DDRF and Kidman Springs study sites as described in Chapter 3. To a minor degree, this chapter also presents 'simple' count information (see below) from two other 'southern' regions, the Barkly Tableland in the Mitchell Grass Downs region (specifically from Mittiebah, Brunette Downs and Alexandria stations) and the southern parts of the Tanami Desert (Fig. 4.1). The Barkly Tableland is characterised by a low diversity of vegetation communities. Survey effort in this region was confined to treeless Mitchell grassland areas (*Astrebla* spp.). Mean annual rainfall at Brunette Downs Station is 414 mm and is strongly influenced by the summer monsoon with approximately 90% of rainfall between November and March, with reasonably high variability between years. The southern Tanami Desert has a lower rainfall (mean of 367 mm at Yuendumu) that is more variable both within and between years than all other sites. Surveys here were conducted at Newhaven Station and along the Tanami Road between Yuendumu and Renahan's Bore. The survey area included spinifex grasslands (*Triodia* spp.) on sandy soils with areas of open shrub land dominated by *Acacia* species.

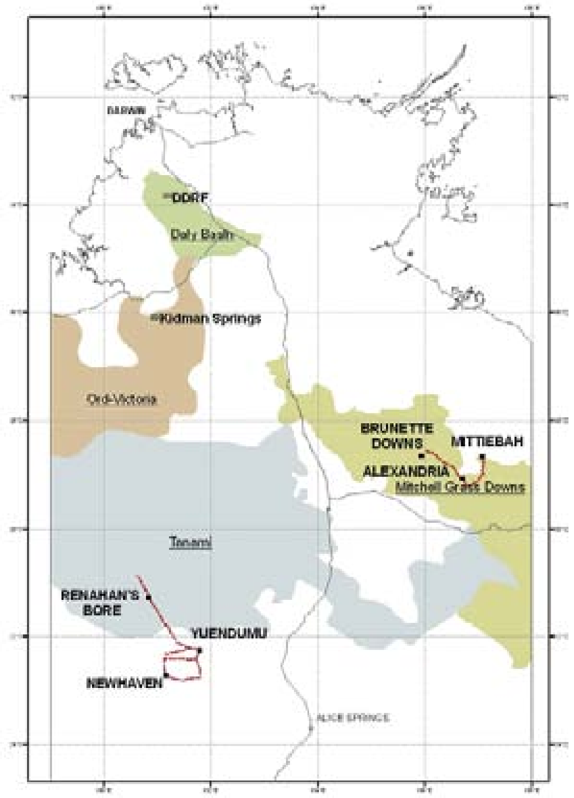


Figure 4.1: Location of place names including IBRA regions (underlined) mentioned in text including tracks (red) along which surveys were conducted at the two southern sites.

Bustard surveys

Survey technique

Vehicle-based surveys were conducted along roads and tracks within the core study regions at the DDRF and Kidman Springs (Fig. 4.2). These routes were unpaved and had very little other traffic. Individual surveys constituted a sub-section of the overall track network. Cumulatively, they were conducted to maximise coverage of each study site approximately evenly during each survey period. Although these transects were restricted to established roads and tracks it was assumed that they were randomly, or at least objectively, located with respect to bird density. Distance covered in each transect ranged between 10.7 to 22.3 km (mean = 16.0 km) at the DDRF and 10.7 to 51.4 km (mean = 32.1 km) at Kidman Springs. At Kidman Springs the relative amount of each habitat traversed during each survey was recorded according to three primary classifications as defined in Chapter 3 (i.e. open woodland on red loam earth soil ('ROW'); open woodland on alluvial black soil ('BOW') and, open treeless grassland plains on alluvial black soil ('BOP')). Six to eight surveys were conducted at each site every 2-3 months between November 2002 and November 2004, except that Kidman Springs was inaccessible during the wet season (December to April); hence the total number of survey transect periods was ten for the DDRF and eight for Kidman Springs. Transects were driven at 20-30 kph within the first and last two to three hours of the morning and afternoon respectively, corresponding to the time when bustards are most active and conspicuous. A single observer was responsible for conducting all surveys.

For each sighting (also denoted as an 'observation'), a GPS location and the perpendicular distance of an individual or centre of a group from the transect route was recorded. Only individuals located on the ground (i.e. not flying) were recorded. Perpendicular distance to individuals or centre of groups was measured exactly or estimated within fixed width distance belts of 1-10, 10-20, 25-50, 50-100, 100-150, 150-200, 200-300, 300-400 metres. The accuracy of estimated distances was regularly checked using GPS or by car odometer. Group size and sex was recorded and males were further divided into three categories based on their maturity and size: 1 = young or juvenile male; 2 = sub-adult or adult male without notable secondary sexual characteristics; 3 = large, mature males exhibiting pronounced secondary sexual characteristics (large throat sac and elongated breast plumes). However, for the purposes of analyses presented here no distinction between these male size classes was made. For each observation, mean height of grass layer (both sites) and shrub/tree density according to four categories of total cover: 0 = no cover; 1 = <33% cover; 2 = 33-66% cover; 3 = >66% cover (Kidman Springs only) were also estimated visually. Note that it was not the intention here to relate observations to habitats on the basis of grass cover and shrub and tree density, rather to use these measures for individual observations to model their effects on detection probabilities (see below).

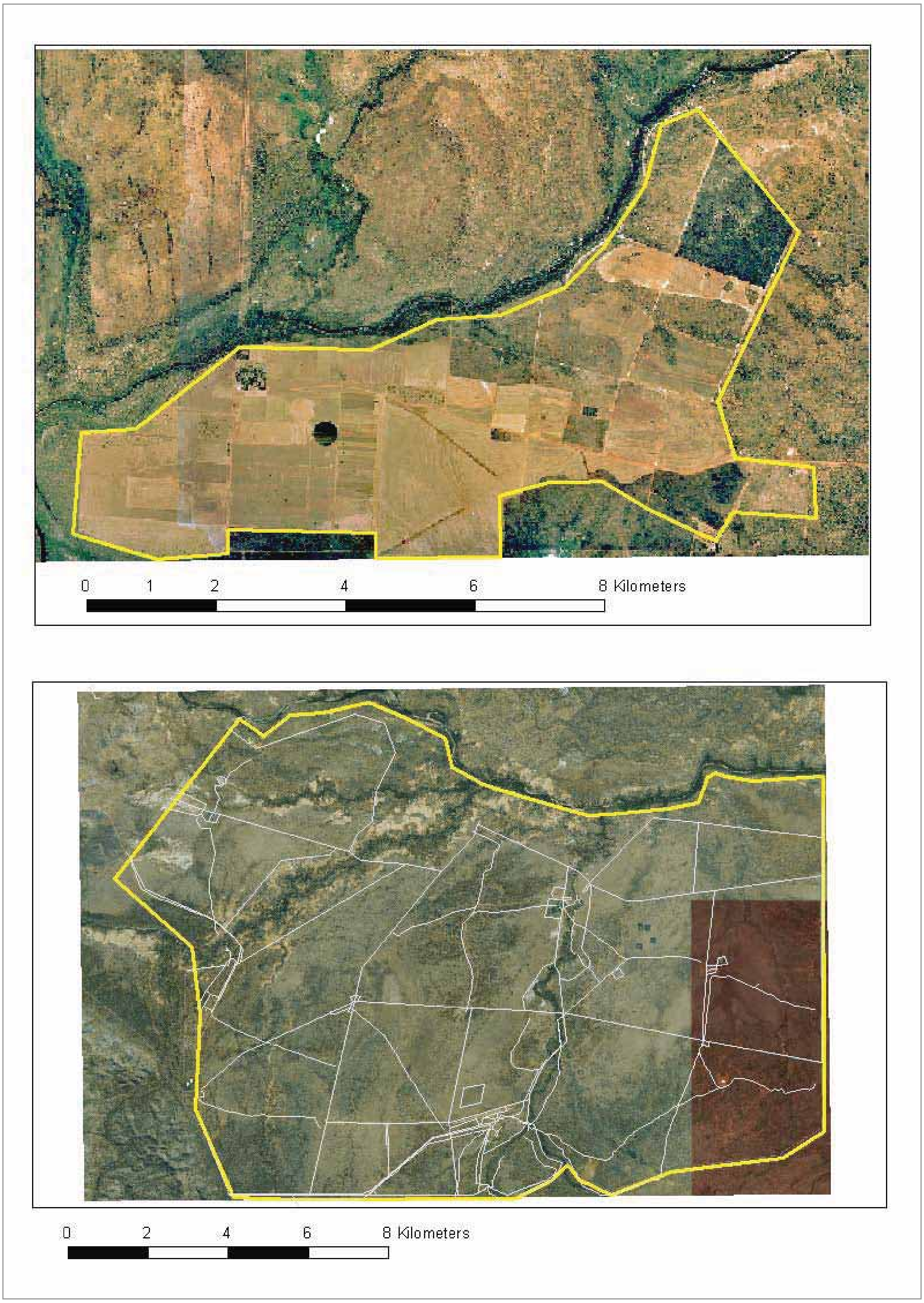


Figure 4.2: Tracks (shown in grey and yellow, and visible in the aerial photograph in the top image) along which vehicle-based surveys were conducted at the DDRF (top) and Kidman Springs (bottom). For any given survey, transect routes were chosen systematically to maximise coverage of each study site approximately evenly for each survey period. Yellow line also denotes the outer boundary of each study region.

Estimates of bustard abundance

Simple counts per unit effort

A simple index of bustard abundance was derived based on the number of bustards observed during a survey divided by the distance driven. Estimates were derived for total number of bustards, and separately for numbers of males and females. This was repeated for each survey period at each site. These estimates are hereafter referred to as 'simple counts'.

Line transect distance sampling

Modeling detectability

A more sophisticated measure of bustard abundance was used to incorporate variation in detectability of bustards under different conditions. The Distance 5.0 program (Thomas *et al.* 2005) was used to model detection functions to derive relative estimates of bustard abundance at each study site. The Multiple Covariate Distance Sampling (MCDS) engine was used to incorporate several covariates into the models. Covariates that were assumed to potentially affect the rate at which the detectability of bustards decreases with distance were chosen on an *a priori* basis and included grass height, shrub/tree density and group size. These measures were estimated at each observation as described in the previous section. Shrub/tree density was not included in models for the DDRF dataset because of the relative homogeneity of the site and the very limited occurrence of shrubs or trees at the site. Models evaluated are listed in Table 4.1. The key function + series expansion approach was used following Buckland *et al.* (2001) and included half-normal + cosine and hazard rate + cosine variations. Models were tested to determine which factors were the most important for explaining variability in detection between seasons and the most parsimonious models based on Akaike's Information Criterion (AIC) and goodness-of-fit tests (Buckland *et al.* 2001) were used for deriving density estimates.

Table 4.1: Models evaluated for deriving density estimates at Kidman Springs and the DDRF; null model with no covariates (NULL), grass height (GRASS), shrub/tree density (DEN) and group size (GROUP).

KIDMAN SPRINGS	DDRF
NULL	NULL
GRASS	GRASS
DEN	GROUP
GROUP	GRASS+GROUP
DEN+GRASS	
DEN+GROUP	
GRASS+GROUP	
DEN+GRASS+GROUP	

Distance sampling: assumptions and caveats

Distance sampling relies on satisfying several assumptions to ensure reliable and unbiased estimates (Buckland *et al.* 2001). The key assumptions are that:

i) transects are randomly, or at least objectively, located in relation to the population studied,

ii) all individuals directly on the transect route are always counted,

iii) individuals or groups are not counted more than once,

iv) individuals or groups do not move away or towards the transect line in response to the observer before distances are measured,

v) distances are measured accurately (or at least estimated with small and random error), and,

vi) the size of the object or group does not affect detectability.

The difficulty of complying with these assumptions under field conditions and logistical constraints often makes obtaining sufficiently large sample sizes difficult. Compliance may be particularly difficult for species in low densities and in relatively circumscribed areas (such as the study sites in this study). In the present study it was assumed that assumptions (iii) and (vi) could not be met consistently. Since group size is likely to affect detectability rates, with larger groups more easily detected (Butler *et al.* 2007), group size was included as a covariate in modelling of detectability. The implications of violating the assumption that individuals are not counted more than once means that unbiased density estimates cannot be guaranteed. In this case, the density of bustards may be overestimated. Because study sites differ in area, potentially leading to variable and unknown degrees of bias due to counting individuals more than once, comparisons between sites may require some caution in interpretation. However, these relative density estimates may be more reliably compared between habitats and survey periods at each site individually.

Here I present estimates of bustard densities with a measure of variation individually for each survey conducted. However, number of observations are too low for most individual surveys to make reliable conclusions. A minimum of 40 observations and a coefficient of variation of less than 20% has been recommended for any single estimate (Buckland *et al.* 2001). To satisfy these criteria in order to facilitate comparisons between seasons, data were pooled into an early-mid dry season period (February to July) and a mid-late dry/wet season period (August to November) at each of the two main sites. These periods generally correspond to periods of the year that differ markedly in their primary productivity and habitat characteristics as presented in Chapter 3.

Data analysis

Detection probabilities

Probabilities of bustard detection were derived for each survey period, for early and late dry season periods and for each of the three main habitats at Kidman Springs. These detection probabilities were compared by plotting upper and lower 95% confidence intervals, with no overlap in intervals signifying significance at least at the $\alpha = 0.05$ level.

Bustard abundance

As above, derived estimates from best models of bustard density estimates (with 95% confidence intervals) for each survey period and between seasons were compared directly for each site. No overlap in intervals signifies significance at least at the $\alpha = 0.05$ level. Differences in density estimates between habitats at Kidman Springs were similarly compared.

Resource availability and bustard abundance

Spearman rank-order correlation coefficients were calculated to examine the association between bustard density estimates for each survey period at each site and several measures of resource availability as documented in Chapter 3. These were conducted across sampling periods (i.e. seasons). At each site resource measures included grass height, grass-layer arthropod abundance, and ground-layer arthropod abundance (with separate measures for beetles, orthopterans and total arthropods). These specific ground-layer arthropod taxa were considered separately because of their relative importance to the diet of bustards (Chapter 6). At Kidman Springs an additional association with an index of fruit availability was also assessed. Bustard estimates were also related to two measures of rainfall at each site: total ‘current’ rainfall in the month leading up to the survey period and total ‘preceding’ rainfall in the month before the current month.

Group size

Group sizes, recorded during vehicle-based surveys, were compared between seasons and sites using a two-way ANOVA. Data were pooled according to periods of the year as defined earlier (i.e., May, July, September and November), but excluded February surveys at DDRF because of no analogous surveys at Kidman Springs. The frequency of group sizes for each survey period at each site according to five categories (1, 2, 3-5, 6-10, and >10 individuals) was also calculated.

Comparison of survey methods

The relationship between the simple counts of bustards, based on number of individuals recorded per kilometre driven, and abundance estimates incorporating detectability functions were examined by linear regression separately for each main study site. Statistica 6.1 (Statsoft 2003) was used for all analyses.

Short-term response to fire

In late September 2002 a small fire was initiated at Kidman Springs on a 4.1 km^2 plot in open woodland on loam earth soil (habitat code 'ROW'). Total counts of bustards on the plot were made early each morning and late afternoon for two days prior to the fire and then immediately following the fire and subsequently for 7 days. These counts, which aimed to generate absolute counts of bustards on the plot, were made while driving in and around the plot to ensure total coverage of the area, hence differed basically from the other vehicle-based surveys described above.

RESULTS

Detectability of bustards

The most salient outcomes regarding detection probabilities of bustards for individual surveys at both sites were that there were no clear seasonal patterns, there was notable variation within and between survey periods and that the probability of detection was substantially lower than 1.0 (Fig. 4.3). Comparisons between the two sites suggested that detection probabilities were generally higher at the DDRF (varying around or above 0.5), compared to Kidman Springs (with values mostly below 0.5). These differences appeared most apparent for the survey periods in the second year of the study (2004 survey periods).

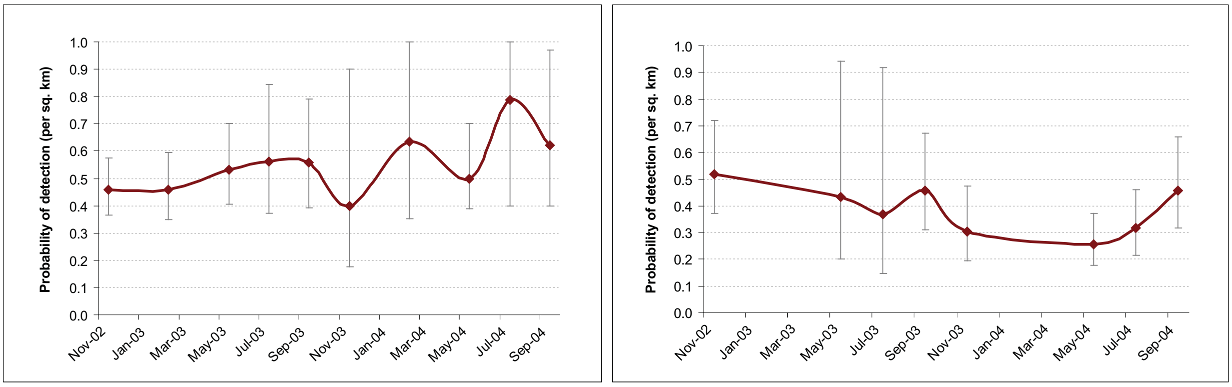


Figure 4.3: Detection probabilities (with 95% confidence intervals) of bustards during vehicle-based surveys for each survey period at the DDRF (left) and Kidman Springs (right).

In general, low numbers of observations of bustards during individual survey periods resulted in high variation in detection probabilities and bustard abundance estimates. Pooling data into early and late dry season periods decreased variability allowing for more reliable comparisons between these broad seasonal periods. However, there were no significant differences in the probabilities of detection between these two seasons at either the DDRF or Kidman Springs (Fig. 4.4). A comparison between the two sites suggests that detection probabilities were higher at the DDRF compared to Kidman Springs during the early dry season.

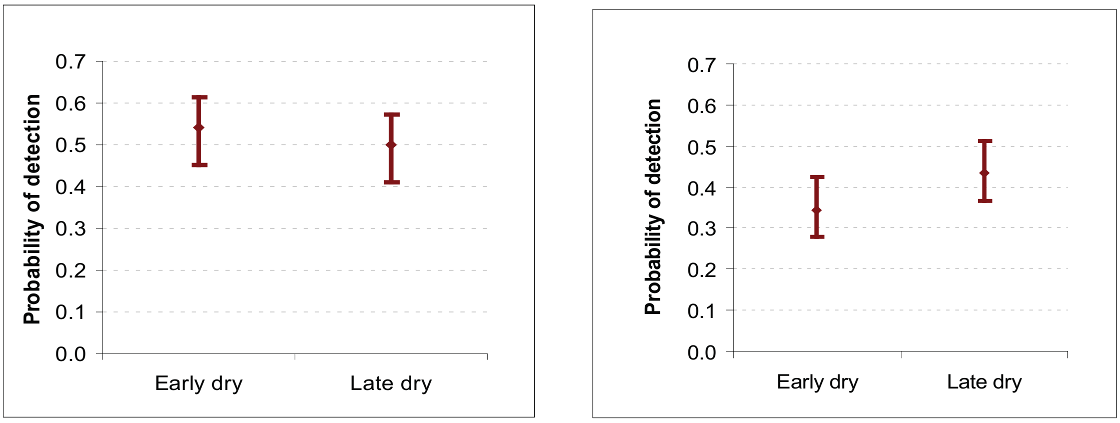


Figure 4.4: Probability of detection of bustards during vehicle-based surveys at the DDRF (left) and Kidman Springs (right) during the early dry season and late dry season (95% confidence intervals included).

A comparison of detection probabilities between habitat types at Kidman Springs suggested that detection was highest in open treeless grasslands compared with the two woodland categories, which were approximately equivalent to each other (Fig. 4.5).

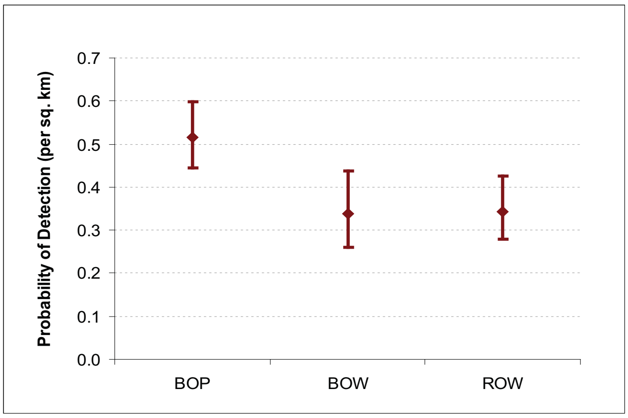


Figure 4.5: Probability of detection of bustards during vehicle-based surveys in three habitat types at Kidman Springs.

Best models

When considering survey periods individually at both sites, no models fitted the criteria of Buckland *et al.* (2001) requiring greater than 40 observations and a coefficient of variation below 20% (Tables 4.2 and 4.3). No consistent seasonal patterns emerged at either the DDRF or Kidman Springs in terms of the importance of specific covariates in models estimating bustard density. Notable instead was that null models without any covariates emerged most often as the best models. For several survey periods at the DDRF and Kidman Springs models incorporating grass height (and shrub/tree density for one period) were among the best models. However, the effects of these covariates were not significant and negligible if they did exist. Nonetheless, one notable trend was evident during the 'November 2003' survey period at Kidman Springs when the probability of bustard detection declined with increasing shrub/tree density.

Upon pooling data, thereby satisfying the methods criteria, the model that incorporated group size and grass height as covariates best estimated bustard abundance in the early dry season at the DDRF. That is, the probability of detection decreased with increasing grass height and smaller group size. In the late dry season at this site the null model was the best model suggesting that grass height and group size were less influential at that time of year.

At Kidman Springs the null model was the favoured model for the early dry season while for the late dry season period density of the shrub/tree layer exhibited a trend with detection declining with increasing density at this time.

Table 4.2: Summary statistics for best models estimating bustard density during individual survey periods at the DDRF (hn cos = half-normal + cosine; haz cos = hazard rate + cosine; # obs = number of observations; CV = coefficient of variation of the density estimate; LogL = Maximum log likelihood; k = number of parameters; AICc =Akaike's information criterion; w_{ii} = AICc weight; GRASS = β coefficient (±SE) for 'Grass height'). Note that coefficients for all covariates were not significant at α = 0.05 (except where indicated*: $P < 0.05$).

Survey period	Best Model	# obs	Effort (km)	CV	Log L	k	AIC_c	w_{ii}	GROUP	GRASS
Nov-02	NULL (hn cos)	45	129.2	0.25	-98.07	1	198.2	0.37		
Feb-03	NULL (hn cos)	34	129.2	0.25	-74.02	1	150.1	0.51		
May-03	GRASS (hn cos)	53	129.2	0.25	-121.23	2	246.7	0.47		0.04 (±0.02)
Jul-03	NULL (haz cos)	23	96.9	0.40	-51.72	2	108.0	0.78		
Sep-03	NULL (hn cos)	24	78.5	0.38	-55.65	1	113.4	0.54		
Nov-03	GRASS (hn cos)	16	78.5	0.60	-34.10	2	73.1	0.48		-0.06 (±0.04)
Feb-04	NULL (hn cos)	11	60.1	0.47	-26.25	1	54.9	0.74		
May-04	GRASS (hn cos)	30	78.5	0.35	-91.23	2	102.1	0.60		0.26 (±0.46)
Jul-04	NULL (hn cos)	29	69.4	0.44	-69.91	2	144.2	0.48		
Sep-04	NULL (hn cos)	17	75.3	0.53	-40.41	1	83.1	0.54		
Early dry	GROUP+GRASS (haz cos)	180	563.3	0.17	-324.44	2	652.9	0.56	0.20 (±0.12)*	-0.17 (±0.14)*
Late dry	NULL (haz cos)	102	361.8	0.27	-300.45	2	605.0	0.67		

Table 4.3: Summary statistics for best models estimating bustard density during individual survey periods at Kidman Springs (hn cos = half-normal + cosine; # obs. = number of observations; CV = coefficient of variation of the density estimate Log L = Maximum log likelihood; k = number of parameters; AICc =Akaike's information criterion; w_{ii} = AICc weight; GRASS = β coefficient (±SE) for 'Grass height'; DENS = β coefficients (±SE) for shrub/tree density according to classes of cover). Note that coefficients for all covariates were not significant at α = 0.05.

Survey period	Model	# obs.	Effort (km)	CV	Log L	k	AIC_c	w_{ii}	GRASS	DENS (no cover)	DENS (<33%)	DENS (33-66%)
Nov-02	NULL (hn cos)	25	223.2	0.32	-56.79	1	115.7	0.41				
May-03	NULL (hn cos)	6	184.5	0.65	-12.81	1	28.6	0.80				
Jul-03	GRASS (hn cos)	16	211	0.52	-32.52	2	69.9	0.45	-0.05 (±0.09)			
Sep-03	GRASS (hn cos)	26	194.5	0.29	-56.19	2	116.9	0.32	0.08 (±0.05)			
Nov-03	DENS (hn cos)	24	148.6	0.26	-44.82	3	96.8	0.48		32.03 (±3.38)	1.65 (±1.47)	-0.38 (±0.43)
May-04	NULL (hn cos)	17	244.5	0.37	-27.75	1	57.7	0.35				
Jul-04	NULL (hn cos)	16	234.2	0.41	-29.40	1	61.1	0.63				
Sep-04	NULL (hn cos)	19	232.3	0.41	-41.37	1	84.9	0.41				
Early dry	NULL (hn cos)	55	874.2	0.19	-148.87	1	299.7	0.40				
Late dry	DENS (haz cos)	94	798.6	0.15	-260.11	6	530.7	0.49		28.21 (±2.93)	3.32 (±1.31)	0.11 (±0.13)

Comparison of survey methods

The simple measure of bustards sighted per kilometre driven at the DDRF was strongly related to the more sophisticated measure of bustard abundance ($r^2 = 0.89$, $F = 67.9$, df = 1, $p < 0.001$) (Fig. 4.6). A less pronounced relationship also existed at Kidman Springs ($r^2 = 0.53$, $F = 8.4$, df = 1, $p < 0.05$). The stronger relationship at the DDRF confirms what is intuitively evident, that simple counts may be more reliable in open, structurally simple habitats. However, these relationships should be qualified by considering the notable variation in estimates derived from the line distance method.

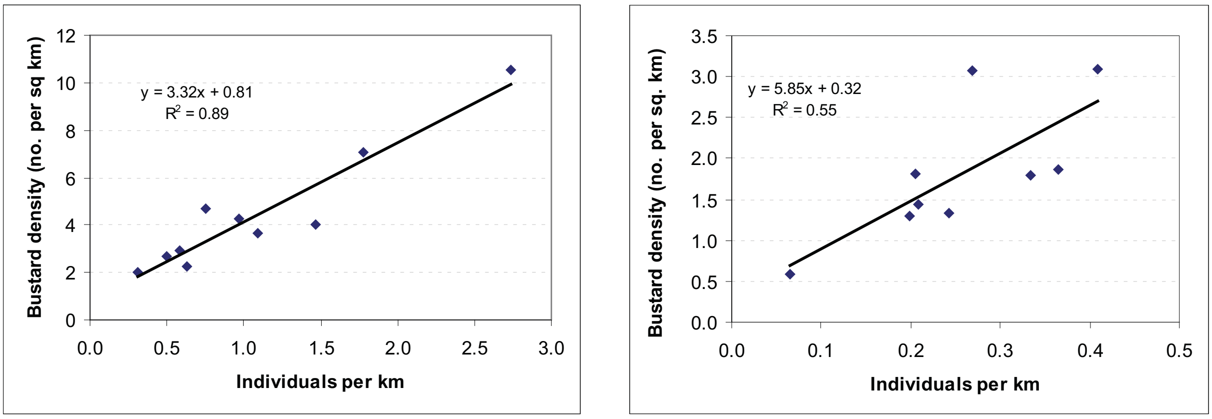
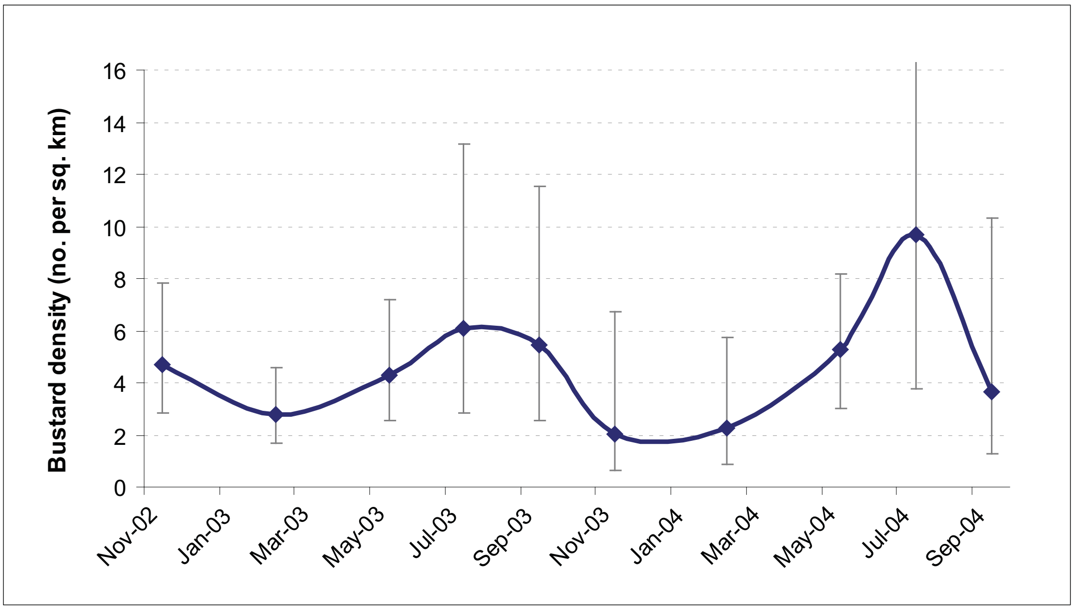


Figure 4.6: Relationships between the number of bustards recorded per kilometre driven and the bustard density estimate derived from distance sampling at the DDRF (left) and Kidman Springs (right). Note the different scales on each axis and slope values between the two sites.

Seasonal abundance estimates

For both years of the survey study at the DDRF, bustard abundance values were consistently highest in the mid-dry season (July) and lowest in the wet season (Fig. 4.7). Fluctuations in bustard abundance here were considerable but regular. The greatest difference between periods occurred when abundance indices were 5 times greater in the mid-dry season (July04) compared to the late dry (Nov03)/ wet season (Feb04). However, given the variability associated with counts during specific survey periods there was overlap in the variation between periods. A comparison of early to late dry season periods at this site suggested that these periods were similar (Fig. 4.8). This was largely a function of the groupings of individual surveys into these general seasons cancelling each other out. This demonstrates that pooling data here is a compromise between a loss of resolution in bustard estimates for periods of the year and a gain in the precision of the estimate by increasing sample size.

The abundance of bustards at Kidman Springs was notably lower for most periods compared with the DDRF (Fig. 4.7). Unlike the DDRF seasonal trends were less apparent. Abundance was lowest in the early dry season of 2003 but numbers subsequently increased during the year and remained relatively high until the mid-dry season of 2004 when they declined. Here too, comparisons between individual surveys were compromised by high variation for individual surveys as a result of too few observations per survey period. Pooling data suggested greater numbers in the late dry compared to the early dry season (Fig. 4.8).



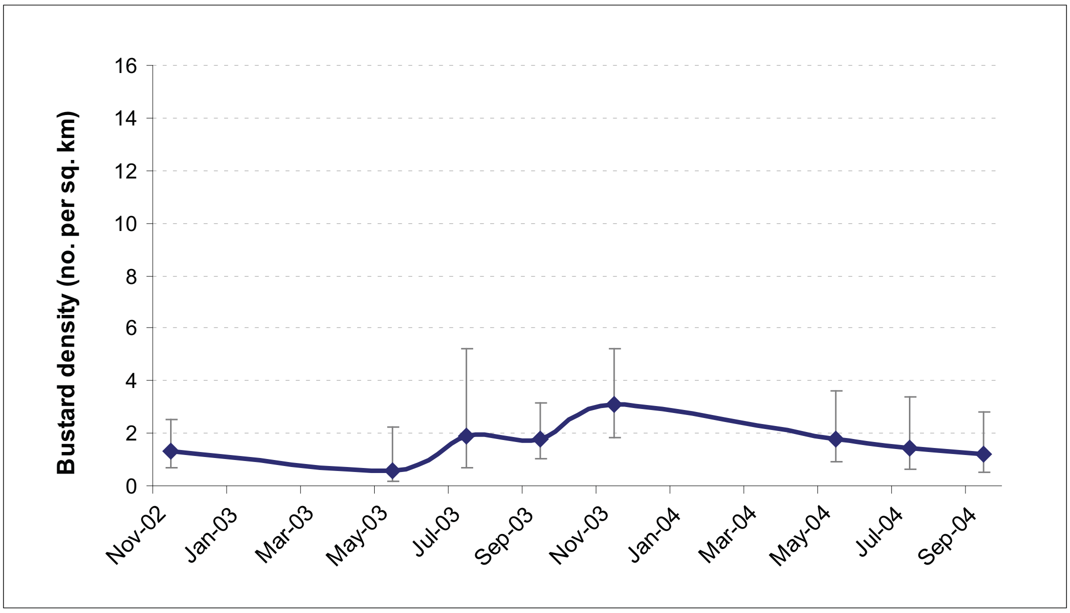


Figure 4.7: Bustard abundance at the DDRF (top) and Kidman Springs (bottom) for each survey period between November 2002 and September 2004 (included are 95% confidence intervals).

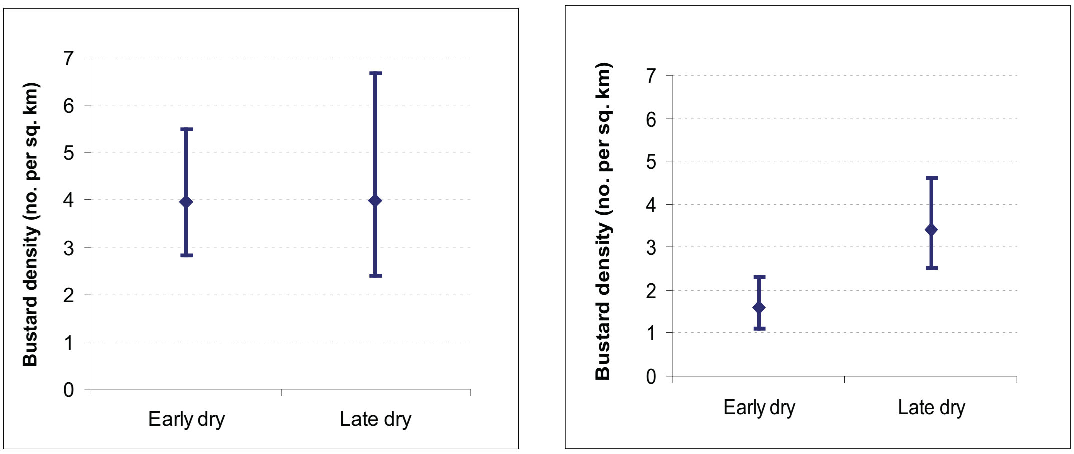


Figure 4.8: Bustard density estimates at the DDRF (left) and Kidman Springs (right) for the early dry and late dry seasons. Early dry season survey period include all surveys pooled conducted between May and July (including February at the DRRF) and late dry season include all surveys from August to November. Included are 95% confidence intervals.

Comparing bustard density estimates between the three main habitat types at Kidman Springs, when data from all survey periods were combined (there were too few observations per habitat per season to generate density estimates separately), suggested that abundance of bustards was twice as high on open treeless grasslands on alluvial soils (BOP) than in open woodland habitat on the same substrate (BOW), and higher than wooded habitats on loam soils (ROW) (Fig. 4.9). However, this result is qualified by some overlap in 95% confidence intervals because of the marked variability in estimates.

A measure of proportion of observations for each habitat according to three seasons suggested that the largest proportion of observations in the BOP was recorded in the early dry season (May) and that about half of the observations were also recorded in this habitat in the mid and late dry seasons (Fig. 4.10). Note that in Chapter 5 it is demonstrated that two females tracked intensively over four seasons at Kidman Springs exhibited a marked affinity for open treeless plains in the early dry season, but used wooded habitats more at other times of the year.

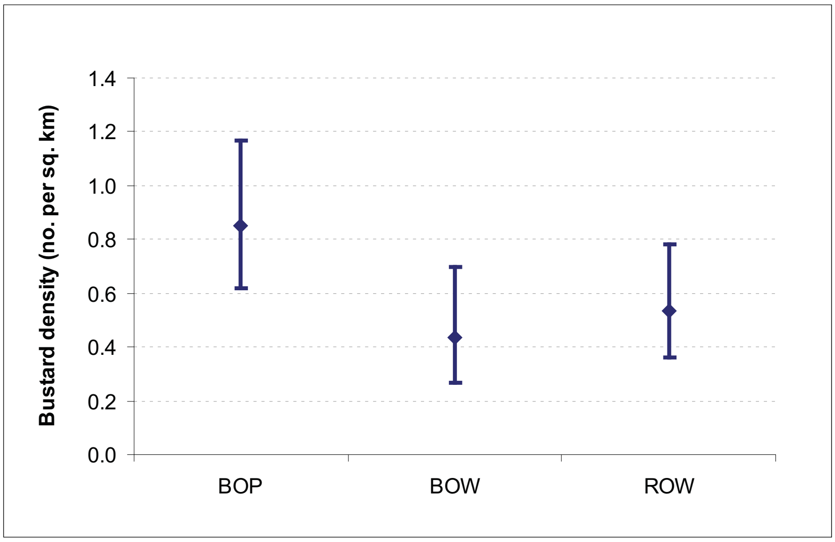


Figure 4.9: Bustard density estimates at Kidman Springs according to three habitat categories (BOP – open treeless grassland on black soil; BOW – open woodland on black soil; ROW - open woodland on loam earth soil). Included are 95% confidence intervals.

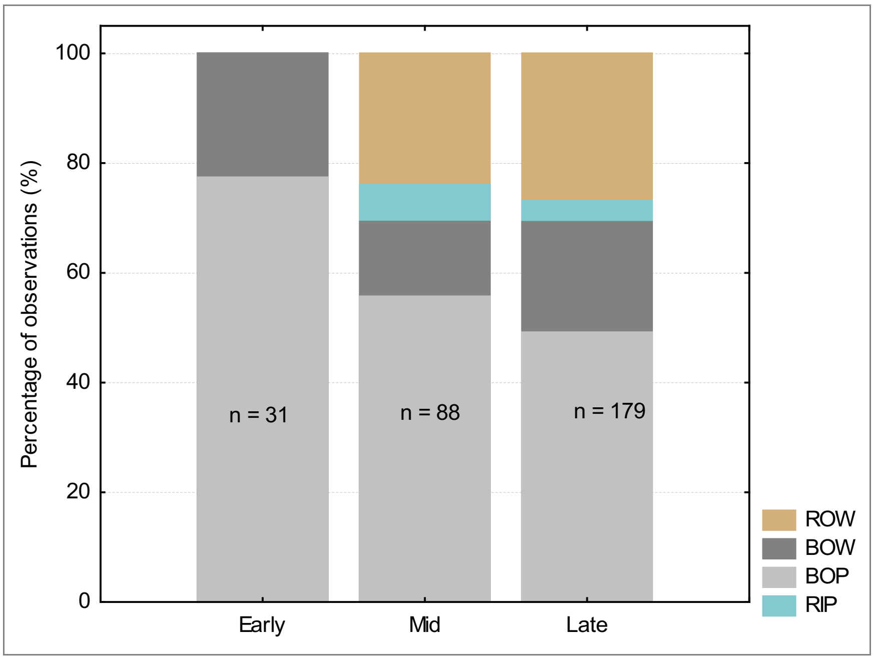
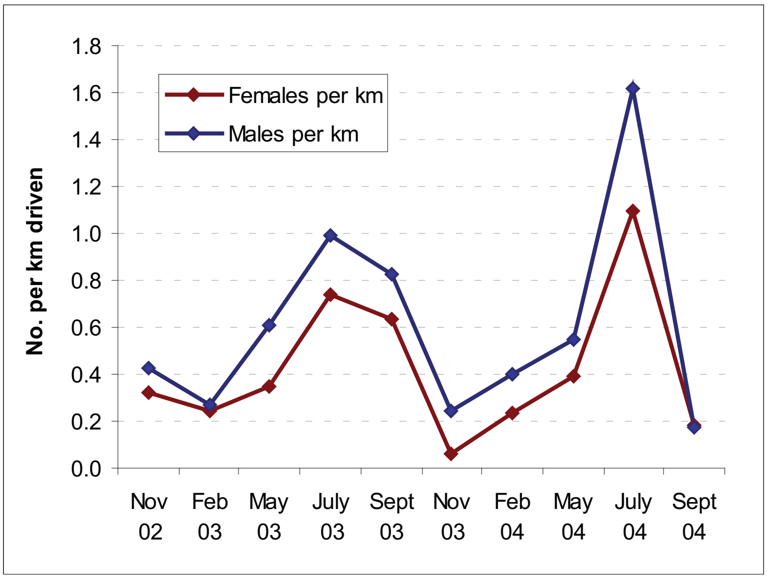


Figure 4.10: Proportion of observations of bustards at Kidman Springs in four habitat types in three different seasons. (Note that this figure is repeated (Fig. 5.15) and discussed in more detail in regard to habitat use in Chapter 5). Habitat codes are: ROW = open woodland on red loam soils; BOW = open woodland over alluvial soils; BOP = open treeless plains on alluvial soils; RIP = riparian The latter was not considered in analyses in this chapter. Seasons were defined as: Early dry season (March-May); Mid dry season (June-Aug.); Late dry season (Sept.-Nov.). No surveys were undertaken during the wet season because of restricted access to the site. (n = number of observations).

Relative abundance of males and females

An indication of the relative abundance of bustards of each sex, measured as numbers recorded per kilometre driven, suggested that males were generally more common than females (Fig. 4.11). However, this perceived difference may be due to differences in detectability arising from innate differences in size and behaviour between the sexes. Nevertheless, notable was the almost complete absence of males at Kidman Springs in the early dry season (May) in 2003. This contrasted sharply to numbers observed in the late dry season in both 2003 and 2004.



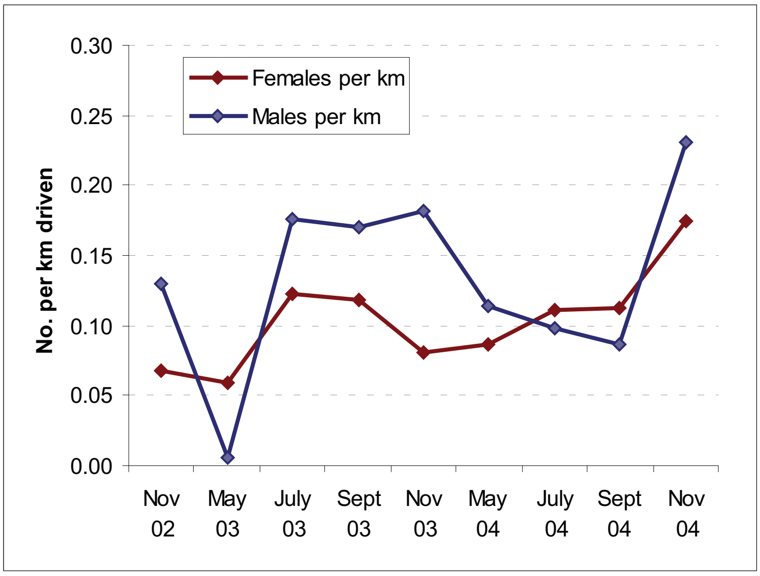


Figure 4.11: Number of bustards of each sex per kilometre driven at the DDRF (top) and Kidman Springs (bottom) during each survey period. Note the different Y-axis scales between sites. Number of kilometres driven (survey effort) per survey period is listed in Table 4.2

Relative abundance in other regions

The close correlation between simple count data and the line distance methods in simple open habitats, suggests that the less sophisticated counts are particularly useful under these circumstances. Such counts of bustard abundance conducted in the two more arid southern sites suggested that numbers here were appreciably lower than measurements from the two principal sites estimated for the same periods (Table 4.4). Within these two more arid regions, bustard abundance at the Tanami Desert site was less than that in the Barkly Tableland. Overall, the results suggest that during the periods surveyed bustard numbers were much higher in the northern than the southern sites and that numbers at the DDRF are exceptionally high by national standards, particularly in the mid-dry season period.

Table 4.4: Relative abundance of bustards measured as number sighted per kilometre driven from the southern Tanami Desert and Barkly Tableland, including comparable estimates for the relevant periods from the DDRF and Kidman Springs.

Region	Date	Effort (km)	Total bustards sighted	Bustards /km
Tanami Desert	Feb. 2004	1012	18	0.02
	July 2004	961	21	0.02
Barkly Tableland	July 2003	554	33	0.06
	July 2004	607	28	0.05
DDRF	July 2003	97	172	1.77
	Feb. 2004	60	38	0.63
	July 2004	69	190	2.74
Kidman Springs	July 2003	211	77	0.36
	July 2004	234	49	0.21

Resource availability and bustard abundance

Correlations across sampling periods of the association of bustard abundance estimates with individual measures of resource availability, grass height and grass cover revealed no significant relationships between any of these measures at either the DDRF or Kidman Springs at $\alpha = 0.05$ (Table 4.5). Similarly, no association was noted for either rainfall in the current month or in the period preceding surveys. Trends in bustard abundance and selected resource measures are presented in Figure 4.12 for the DDRF and Figure 4.13 for Kidman Springs.

Table 4.5: Comparisons of bustard density estimates across seasons at each site in relation to resource variables based on Spearman rank correlation tests. No results were significant at p = 0.05.

	DDRF		Kidman Springs	
	r_s	n	r_s	n
Grass arthropods	-0.05	10	0.03	8
Total ground arthropods	-0.20	10	-0.09	5
Ground arthropods (Coleoptera)	-0.21	5	-0.26	5
Ground arthropods (Orthoptera)	-0.20	5	-0.17	5
Index of fruit availability	n/a		-0.18	8
Grass height	-0.19	5	-0.10	8
Grass cover	-0.21	5	-0.11	8
Rainfall current period	-0.55	10	0.17	8
Rainfall previous period	0.04	10	-0.57	8

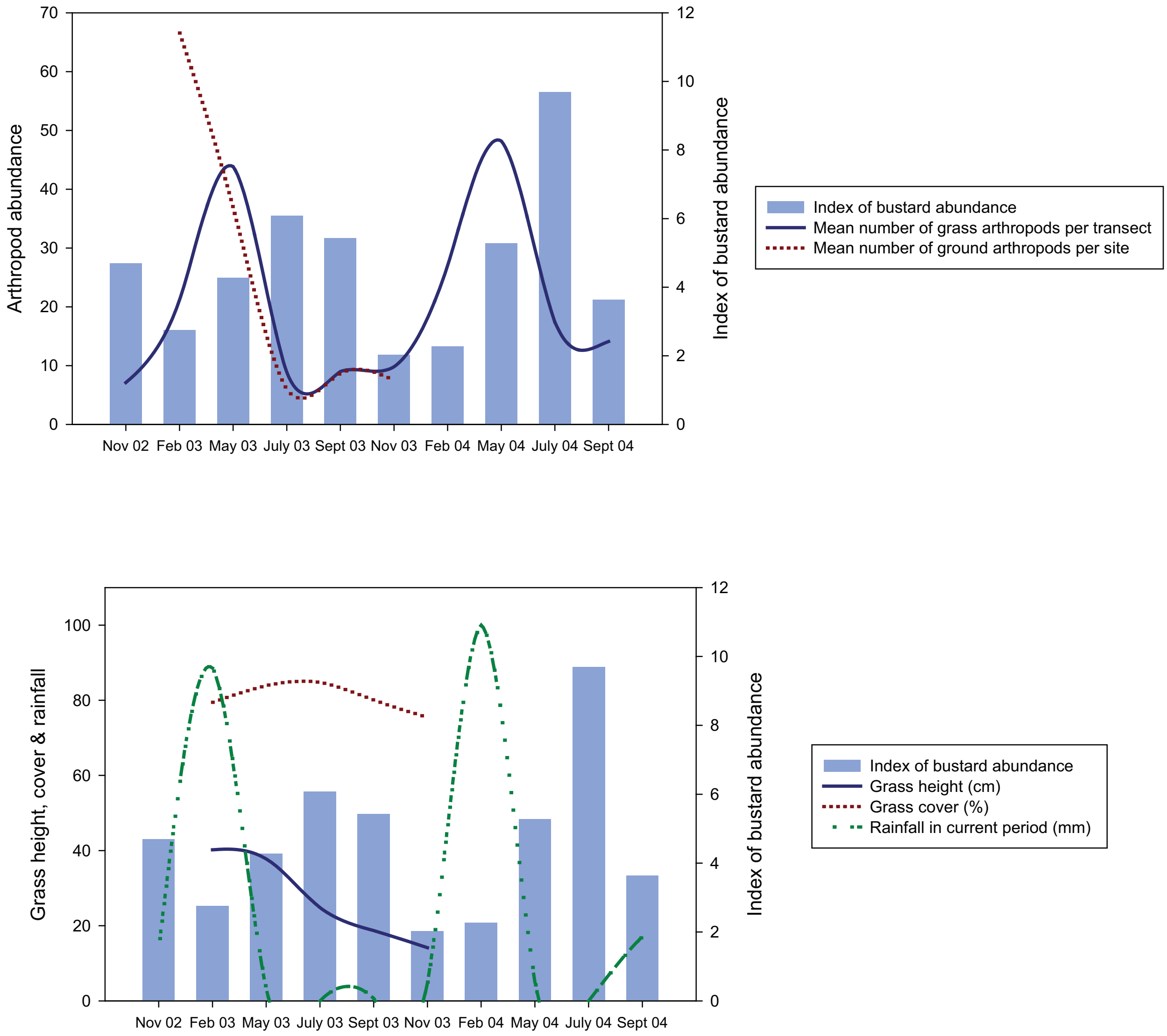


Figure 4.12: Trends in bustard abundance and selected food resources, habitat characteristics and rainfall (range standardised) at the DDRF. Note that the left side Y-axis represents different measures as denoted in the graph legend.

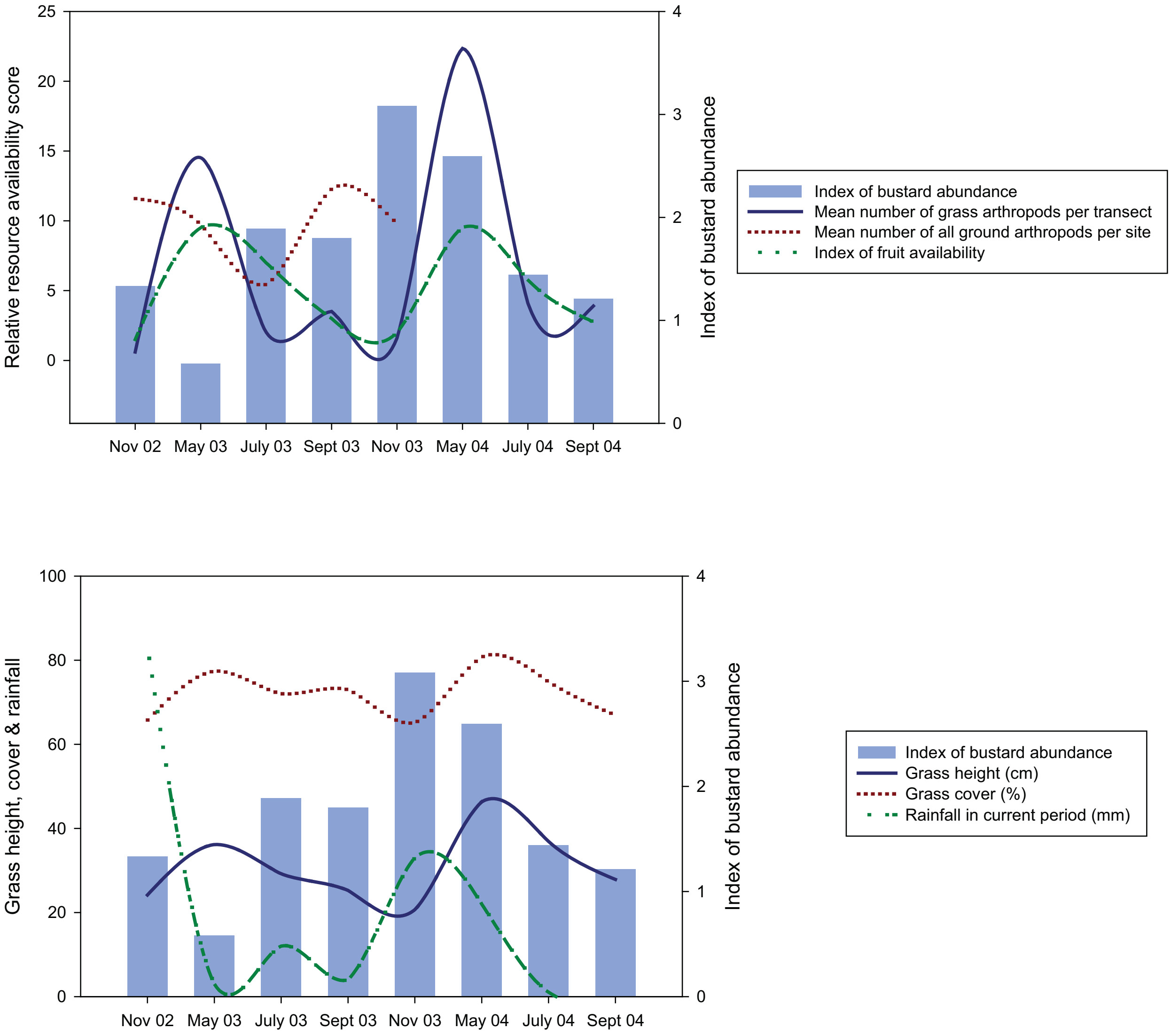


Figure 4.13: Trends in bustard abundance and selected food resource, habitat characteristics and rainfall (range standardised) at Kidman Springs. Note that the left side Y-axis represents different measures as denoted in graph legend.

Group size

Overall, group sizes were larger at the DDRF than at Kidman Springs (F = 14.9, df = 1, p <0.001) (Table 4.6). Mean group size at the DDRF was 3.7 (±0.4) individuals per group (n = 239) (range = 1 to 49) compared with 2.2 (±0.1) individuals per group (n = 223) (range = 1 to 13) at Kidman Springs. Group sizes were also significantly different between periods of the year (F= 19.2, df =3, p<0.001), with the group size highest during the middle of the year (July) compared to all other periods, and higher in the early dry season (May) compared to the late dry season (November) (Table 4.6). Figure 4.14 illustrates the relative proportions of observations according to five categories of group size between survey periods pooled across years for each site.

Table 4.6: Two-way ANOVA results comparing group size between site and time of year (period) and results of a Tukey HSD post-hoc test (below) demonstrating differences in group size between four periods of the year for data pooled between the DDRF and Kidman Springs (P = * <0.05, ** <0.01, *** <0.001).

	Df	**F**	**p**
SITE	**1**	**14.9**	***
PERIOD	**3**	**19.2**	***
SITE*PERIOD	**3**	**2.0**	**0.114**

	May	July	Sept
July	**		
Sept	0.48	***	
Nov	*	***	0.21

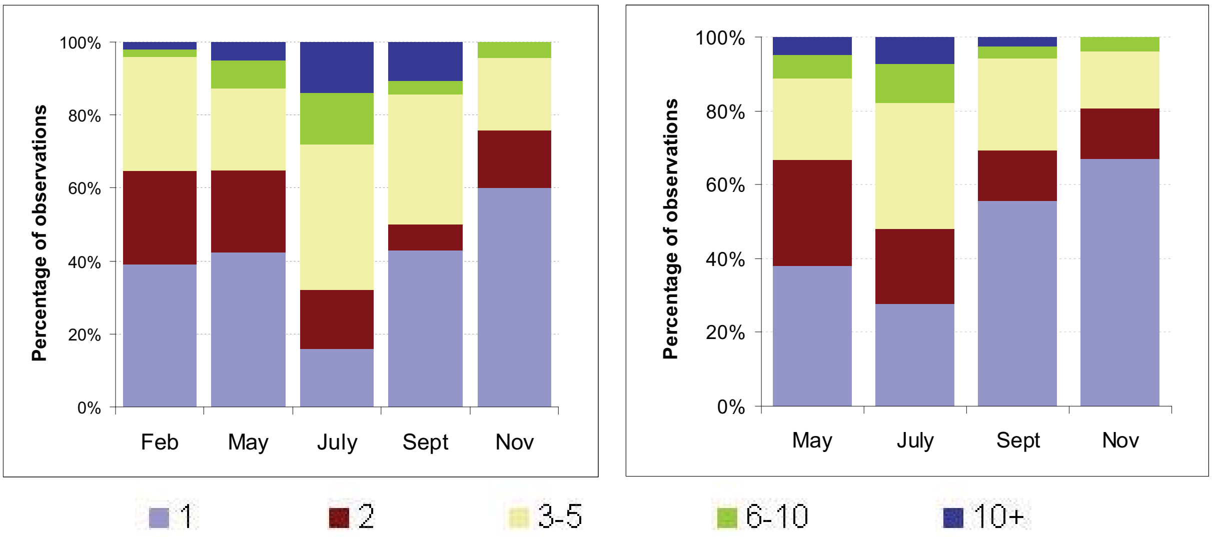


Figure 4.14: Frequency of bustard group size observations according to five size categories for surveys pooled according to time of year at the DDRF (left) and Kidman Springs (right).

Response to a fire at Kidman Springs

Bustards exhibited a slightly delayed response to a small-scale fire initiated at Kidman Springs in the late dry season (Fig. 4.15). Following the initiation of the fire in the mid-morning of September 28, numbers of individuals on the burnt plot peaked the following morning and then gradually declined over the following days until no individuals were sighted on the plot after 5-6 days. The absence and low numbers of bustards on the plot on October 1 coincided with a larger fire that began as a result of a lightning strike some three kilometres away the previous night. This may have attracted individuals away from the study plot resulting in a lower number of bustards on the plot in the following days and possibly its early abandonment.

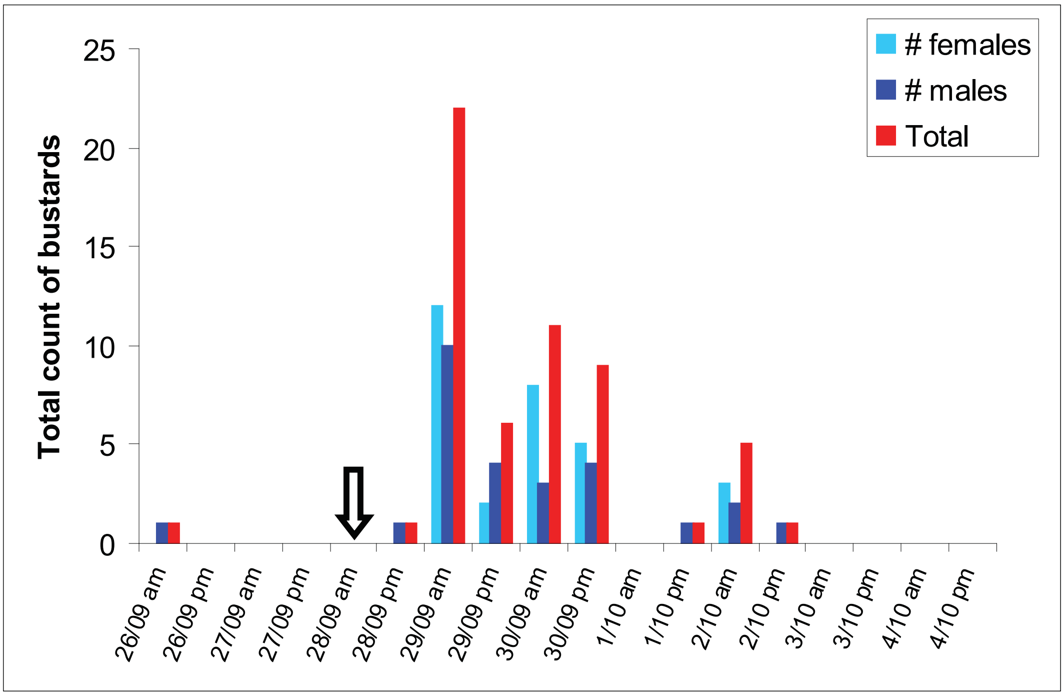


Figure 4.15: Response of bustards, measured as absolute number of males, females and total number of individuals, to a fire on a 4.1 km^2 plot in open woodland at Kidman Springs in the late dry season of 2002. Arrow indicates initiation of fire on the morning of September 28.

DISCUSSION

Survey methodologies and implications for future monitoring

This study presents the first attempt in Australia to regularly monitor bustard populations across a sequence of seasons, and to compare these patterns between a largely natural site and a highly modified horticultural landscape. The abundance patterns that formed the focus of this study were based on two techniques for estimating abundance, a simple count (with abundance reported as mean number of individuals per kilometre of transect), and a more sophisticated method based on a line transect distance procedure that incorporates an analytic component that models variation in detectability to generate density estimates. Both methods have relative strengths and weaknesses that should be considered in their application and when interpreting results. While the simple count method is easily applied, it is likely to be affected by unconsidered biases relating to variability in the probability of detecting individuals due to differences in habitat characteristics, behaviour and other factors. This limits extrapolation or comparison of results between different areas and times.

The line distance method seeks to overcome this limitation by explicitly incorporating the effects of predefined and measured factors that affect the probability of sighting an individual or group. However, this method is also subject to specific assumptions and limitations that warrant further consideration and need to be accounted for when interpreting results. In the present study, because of logistical constraints, for most survey periods there were low numbers of observations relative to survey effort leading to significant variation within and between survey periods. Furthermore, because of the relatively circumscribed areas of the study sites, it is likely that one of the assumptions of the line distance method was compromised, namely that individuals may have been counted more than once. This arose because, although transects were systematically located so as to cover each entire study site approximately evenly during each survey period, some parts of the track network were surveyed on more than one occasion, and individuals may have moved within the study site between individual surveys. In effect, the implications are that the derived density estimates may be an overestimation of the density of bustards at the site, and that comparisons between sites (and to other regions) may be compromised or require caution in interpretation.

Notable outcomes of the line distance technique in this study were that the probability of detection for most survey periods was substantially lower than 1.0, that detectability varied considerably within and between surveys and that there were no recognisable inter-seasonal patterns in detection probabilities or in the importance of specific covariates affecting probability. That the probability of detection was lower than 1.0 for most survey periods suggests that only a proportion (often less than half) of all bustards along the survey routes were counted. Bustards were more often ‘missed’ in the more complex habitats of Kidman Springs as evidenced by the relative differences in probabilities between the DDRF and Kidman

Springs, and between the higher detection probabilities in the treeless open grasslands at Kidman Springs than in other habitats at the site. However, given the notable variability within survey periods and the lack of clear seasonal trends it appears there were no obvious seasonal trends in detection rates.

The *a priori* chosen factors thought to influence the detectability of bustards in the northern savannas included group size, density of shrubs/trees and height of grass layer. Detectability should decrease with increasing grass height and shrub and tree density, and increase with increasing group size (Butler *et al.* 2007). However, the relative influence of these factors may be contingent on prevailing environmental conditions, the behaviour of bustards which may vary between seasons and years, and the synergy between these different influences. In Australia's northern savannas grass heights are highest in the late wet and early dry season periods (Chapter 3) suggesting that detectability may be lower at this time. However, as demonstrated in the present study, in the early to mid dry season bustards tend to form larger groups more often and congregate on open treeless grasslands where they are more easily observed (see also Chapter 5). In effect, these factors may counteract the influence of decreased detectability due to grass height. Conversely, in the late dry season when grass heights are substantially lower, bustards are less likely to group, and at Kidman Springs tend to use habitats of greater shrub and tree density more often (Chapter 5). In this study, it was the null model (without any of the covariates) that most often appeared the best model for estimating bustard abundance.

Comparison between methods

Comparison of the two techniques for estimating abundance suggested that there was a very high correlation between these two procedures with a particularly strong relationship in the structurally simple habitats characteristic of the DDRF and parts of Kidman Springs. Simple index counts are widely used by biologists and have been commonly employed in surveys of other bustard species (Alonso *et al.* 2003; Moreira 2004). An advantage of such surveys is that they are easily employed. This study suggests that they may be legitimately used in simple open habitats such as the Douglas-Daly rivers region, or the open grassland regions of the Barkly Tableland. Furthermore, the line distance method is likely to be less robust (or require far greater survey effort) in regions of lower bustard abundance (e.g. central Australia) because the method relies on sufficient sample size or number of objects observed to provide robust estimates of the detection function and its variance. Where sufficient sample sizes cannot be acquired it may be more appropriate or logistically practical to use simple counts. Nevertheless, comparisons between different habitats, or within habitats that vary in the dynamics of their structural composition over time, need to consider differences in detectability between different habitats. Given their simplicity such counts may be employed for surveys and monitoring programs using lay volunteers and amateur ornithologists. For example, vehicle-based counts by volunteers have been used to assess patterns of distribution and abundance of raptors over large scales (Baker-Gabb 1987), and such methods have been proposed to monitor bustards, emus, and other highly mobile, conspicuous species (Garnett and Crowley 2000).

Bustard abundance

In addition to several of the caveats listed above regarding interpretation of results based on survey methodology, the DDRF and Kidman Springs differ not only in levels of management and habitat modification, but also in annual rainfall and productivity such that observed differences in population dynamics between the sites cannot unambiguously be attributed to any specific individual differences in site characteristics. Nevertheless, the substantial differences in innate naturalness between the sites are likely to play a significant role in affecting bustards between sites. The principal contrasts between the two main study sites regarding bustard abundance patterns were that the highly modified site supported substantially higher bustard numbers, and that there were different patterns between the two sites in seasonal variation. Coarse comparisons of both northern sites to more southerly arid regions also suggested pronounced differences in bustard abundance between the tropical savannas and more arid regions. These findings correspond to findings presented in Chapter 2 and other, generally more anecdotal accounts (Barrett *et al.* 2003; Blakers *et al.* 1984; Grice *et al.* 1986). The considerable variation in abundance estimates apparent across the species' range has been mirrored for other closely related species elsewhere. For example, densities of Houbara Bustard *Chlamydotis undulata* range from values as low as 0.03 to 0.10 per km^2 in Saudi Arabia (Seddon and Van Heezik 1996) and 0.001 to 0.2 per km^2 in other parts of Asia (Tourenq *et al.* 2005) up to 2 to 4 per km^2 in the Negev Desert in Israel (Lavee 1985).

Seasonal patterns in abundance

Assessing seasonal trends in bustard abundance at each site in this study was hampered by low numbers of observations and high variability within individual survey periods. Nonetheless, some general trends consistently emerged. At the DDRF, in both years of the study, there were fewer bustards in the late wet and early dry season compared to other times and notable peaks in abundance during the mid-dry season. At Kidman Springs variation between survey periods was similarly high, however, consistent trends between years were not as clear cut. In May 2003, there were very few records of bustards and almost no males sighted. Pooled data revealed that there were notably more bustards later in the year compared to the early dry season at this site. In part, these results are consistent with seasonal patterns in bustard abundance reported by landholders in the northern savannas (Chapter 2), and by general observations of bustards in the Barkly Tableland by Downes (1982a). These post-breeding (i.e. early dry season) lows in northern Australia are consistent with patterns observed for other bustard species elsewhere in the world. For example, numbers of the Great Bustard in Europe reportedly peak during breeding displays (Morgado and Moreira 2000) and are also lowest immediately following the breeding season (Alonso *et al.* 2000; Morales *et al.* 2000; Morgado and Moreira 2000). Much of this seasonal variation is attributed to post-breeding season dispersal by males (Alonso and Alonso 1992) (and see below). However, differences in numbers between sexes observed in this study should be qualified by the potentially considerable differences in detectability due to pronounced differences in size and behaviour. For example, during the breeding season males display noisily in open or raised areas, making them particularly conspicuous at this time. Females, by comparison, are smaller, more drab in appearance and shy, and rely on their camouflage to protect their nest and young. Such inherent differences may be an explanation for the apparently greater numbers of male than female bustards recorded per kilometre travelled.

Seasonal variations in group size appear to be a feature of many bustard species. Larger group size among Houbara and Great Bustards has often been attributed to patch richness with larger flocks observed in areas of high resource concentration (Lavee 1985; Martinez 1991; 1992; Morgado and Moreira 2000; Seddon and Van Heezik 1996). Similar explanations may be offered for observations of the Australian Bustard in this study. Groups were often sighted at peanut crop patches at the DDRF during the mid-dry season and on open treeless grassland plains at Kidman Springs in the early to mid-dry season when resources in these areas were significantly higher than in surrounding habitats (see Chapter 3 and below).

Bustard numbers and resource availability

As demonstrated in Chapter 3, most measures of food resource availability were significantly higher at the DDRF for most seasons than at Kidman Springs. The combination of stable cover, a diversity of crop types within a relatively small area and availability of a highly productive and rich source of food during an otherwise lean time presents unique and highly favourable conditions for bustards. Consequently, the DDRF represents an artificially favourable environment which supports densities of bustards that are exceptionally high by national and international standards. A marked seasonal flush of a single, highly productive food resource (irrigated peanut crop and pasture) was responsible for large numbers of bustards in the mid to late dry season. These high numbers appear to be a result of local movements of bustards from surrounding areas. For example, numerous individuals were regularly observed flying to and from the irrigated area from an adjacent property to the north of the Douglas River (pers. obs). Also contributing to these large numbers is the greater detectability of bustards on these patches relative to surrounding habitats.

Besides the ostensibly atypical situation at the DDRF (because of the relationship between bustard numbers and irrigated crops), there was no evidence of a link between variations in bustard numbers and food resource availability at the site scale at either the DDRF or Kidman Springs. Indeed, peaks in resource availability during the early dry season generally coincided with lowest abundances of bustards at both sites. This reflects findings from similar studies of related species elsewhere (e.g. Seddon and van Heezik 1996). There are several possible explanations for these observations. The measures of resources I used in this study aimed to document patterns in their relative abundance. However, they may not necessarily reflect availability or accessibility of these resources to bustards. For example, high numbers of bustards in recently burnt areas do not necessarily infer greater resource abundance in these areas, rather that resources may simply be more accessible or visible to them.

In an analogous study of the Houbara Bustard, Seddon and van Heezik (1996) found no association between changes in bustard numbers and resource availability in a conservation reserve in Saudi Arabia. They attributed seasonal fluctuations in numbers primarily to the movements of migratory bustards and suggested that low numbers observed in spring, when food resources peak, were a result of the outward movement of migrants to their breeding grounds where they may be presumably exploiting similarly productive conditions.

In a similar scenario whereby seasonal movements occur there may be factors other than the availability of food that are more influential in regulating bustard abundance in northern Australia. In this case, a plausible explanation relates to the mating system of the species. Both the DDRF and Kidman Springs were selected as study sites in large part due to their robust bustard populations. At both sites, bustards consistently aggregate at lekking or display sites (Chapter 7). Lek sites may act as foci for bustards in the surrounding landscape whereby, through conspecific attraction, bustards aggregate in the build-up to and during the breeding season in relatively concentrated densities (Alonso *et al.* 2000; Jiguet *et al.* 2000; Lane and Alonso 2001; Morales *et al.* 2000; Morgado and Moreira 2000; Osborne *et al.* 2001). Consequently, these study sites may not be more broadly reflective of bustard densities in the wider landscape. In northern Australia, after the breeding season in the late wet and early dry season, conditions are broadly productive across the entire savanna landscape at the same time. Bustards, uninhibited by the constraints of social and mating behaviour associated with the breeding season, may at this time disperse over a broader area in order to take advantage of opportunities to exploit new areas with reduced competition. Subsequently, following this period of post-breeding season dispersal, bustards then move back towards traditional lekking areas in preparation for the following breeding season and the cycle starts anew. Future survey efforts may be aimed to assess this possibility by quantifying the distribution of lekking areas in a region and the relative numbers of bustards at lekking and non-lekking areas during and after the breeding season.

Short term response to fire

Fire is a pervasive feature of the northern savanna landscape and is of importance to many bird species (Woinarski 1999). Australian Bustards have been reported to exhibit a strong affinity for fires which they track across the landscape, often appearing in large aggregations where they feed on animals escaping from or killed by the fire front (Boehm 1947; Marchant and Higgins 1993). Although limited, the results presented here represent the first quantified before-and-after fire study for Australian Bustards. They clearly corroborate the anecdotal record, and demonstrate a substantial short-term response to a single fire event. The densities of bustards in the burnt area (>5 km^{-2} within 2 days after the fire) were markedly higher (by about two orders of magnitude) than those reported for the same area immediately prior to the fire. Similar but more anecdotal observations of large aggregations have been noted at other fires at both study sites. Elsewhere, others have also noted very high densities of bustards at fires. For example, Berney (1907) estimated 23 bustards/km^2 after a bushfire in north Queensland (although no indication was made as to how he came up with this number). This result demonstrates rapid local movements of bustards in response to landscape-scale variability in resource availability. The abrupt decline in bustard numbers in the burnt area (within five days of the fire) suggests that these post-fire resources may be rapidly depleted, and/or that subsequent fires elsewhere in the landscape may recast spatial variations in relative resource availability, with rapid responses by bustards. In this case, the sudden decline of bustards in the monitored burnt area coincided with a fire that began as a result of a lightning strike less than 3 kilometres away to the north a couple of days after the monitored fire occurred. Subsequent surveys revealed unusually high numbers of bustards in that area, suggesting that the birds that had been on the smaller monitored patch may have moved to the newly burnt area. In Chapter 8, I present further information collated from satellite tracking of individuals in the Kidman Springs area which documented specific movements and cues in response to fire events in more detail.

Chapter 5

Habitat use and local ranging behaviour of the bustard in northern Australia

Bruce Doran

Chapter 5

Habitat use and local ranging behaviour of the bustard in northern Australia

INTRODUCTION

Previous observations and general studies have reported that the Australian Bustard exhibits a broad preference for open habitats preferring grasslands, low shrublands, grassy open woodlands and other structurally similar but artificial habitats such as croplands, golf courses and airfields (Downes 1982a; 1984; Marchant and Higgins 1993). It also responds readily to fire and large numbers are often found on recently burnt country, even in more densely wooded areas. Broad classifications of bustard habitat associations in the Northern Territory suggest the best quality habitat, supporting the largest concentrations of bustards, is at the margins between tussock grass plains and semi-desert scrub (as found for example in the southern regions of the Victoria River District and Barkly Tableland in the Northern Territory (Downes 1982a; Downes and Speedie 1982)). The ecotones between open plains and open woodlands are also regarded as preferred nesting areas (Downes 1982a; Downes and Speedie 1982; Marchant and Higgins 1993). These general accounts provide a broad context for describing the habitat preferences of bustards. However, there have been no detailed studies of bustard habitat selection at specific sites and there is limited information on how habitat preferences vary seasonally.

Information regarding ranging behaviour is similarly scarce. Over larger scales, bustards have been reported to undertake nomadic movements in some parts of their range and adopt more sedentary strategies or migratory movements in other parts (Bravery 1970; Marchant and Higgins 1993; Ziembicki and Woinarski 2007, Chapter 2). In the northern savannas, according to Downes and Speedie (1982), variability in localized climatic conditions often determine which specific areas may be best for bustards in any particular year. This suggests that bustards move readily, and by implication (since the suitability of these areas varies randomly in space and time), nomadically between areas of high productivity. Similar reports also suggest that bustards opportunistically track fires across the landscape (Boehm 1947; Marchant and Higgins 1993). On local scales (i.e. 1 to 100 km^2), information regarding patterns of home range use by Australian Bustards is non-existent.

In this chapter I examine habitat preferences and home range dynamics of bustards at two sites in northern Australia. The general definition of 'home range' adopted in this study follows that of Kernohan *et al.* (2001) who define the concept as 'the extent of area with a defined probability of occurrence of an animal during a specified time period'. Accordingly, precise definitions of the bustard's home range in this study vary and relate to specific study objectives . First, I examined habitat use and ranging behaviour at the beginning of the breeding season (in northern Australia this period corresponds to the late dry season between approximately September and November) and aimed to compare these characteristics between sexes and at two sites that differed in their land use and intrinsic 'naturalness'. According to the 'food-exploitation hypothesis' home range size is inversely related to food availability (Village 1982). Given the marked differences in relative food resources measured between the DDRF and Kidman Springs, according to this hypothesis, it may be expected that home ranges will be smaller at the DDRF because of the high resource availability at this site relative to Kidman Springs. I acknowledge, however, that there are other differences between the sites that could not be controlled for.

The early breeding season in the late dry is a critical period for bustards. It represents a period of hardship due to low water and food resource availability (Chapter 3; Woinarski *et al.* 2006). Also at this time, males use specific display territories on dispersed leks which females in turn visit to chose potential mates (Chapter 7). Consequently, it may be expected that females range broadly at this time to assess displaying males, while low food resource availability may require individuals to range further to satisfy nutritional requirements. The extent of male home ranges in turn may be a compromise between the need to establish and display at leks and the need to forage at a time when food resources are low. The specific aims of the study then were to determine, i) the extent to which females range between male display sites; (ii) the relative size of male and female territories; (iii) whether the breeding season ranges of males overlap, and (iv) whether bustards exhibit specific habitat preferences at this time.

These analyses are then extended to examine patterns of ranging behaviour and habitat use between seasons at Kidman Springs, a site typical of intact savannas in northern Australia. The focus here was on two females that were tracked using satellite telemetry. I specifically aimed to assess whether these two individuals exhibit specific habitat preferences between seasons, whether they show year round fidelity to the breeding (lekking) area (see also Chapter 7) and whether their home range sizes vary between seasons. I acknowledge the constraint here of small sample size which limit broader generalisations, however, note that the level of detail and longevity of the tracking period for these individuals is unprecedented for a terrestrial Australian bird species.

METHODS

Study sites

Kidman Springs and the Douglas-Daly Research Farm (DDRF) were again the two main study sites (see Chapter 3). However, the majority of work (i.e. the assessment of seasonal and breeding season habitat use and home ranges) was undertaken at Kidman Springs. Only ranging behaviour during the breeding season was assessed at the DDRF.

Trapping procedures

The cryptic, mobile nature of bustards required a trapping technique that was both portable and easy to assemble and use at short notice. The most effective method for catching bustards was with a rocket net gun. The model used was a Paxarms™ Net Projector MK9 (Fig. 5.1). Bustards were located by driving slowly along tracks within the study sites until an individual or group was sighted. An individual was then slowly approached by vehicle to within effective firing range of the net-gun (10-15 metres) which was discharged by an operator from the passenger side of the vehicle. During the study 42 bustards were captured in this way. Earlier in the study two other individuals were captured using walk-in cage traps, and one incapacitated individual was caught by hand.

Figure 5.1: The Paxarms™ Net Projector MK9 used for capturing bustards.

Radio and satellite telemetry

Morphological measurements were taken of each individual following capture (see Appendix 1) and an Australian Bird and Bat Banding Scheme (ABBBS) stainless steel band (size 13 for females, 14 for males) fitted to the tarsus of each individual. A variety of radio and satellite tracking devices were trialed and used during this study (Table 5.1; and Fig. 5.2). Individuals were released at the point of capture.

Table 5.1: Summary characteristics of radio and satellite transmitters deployed on bustards during the study.

	Transmitter type	Manufacturer	Power source	Accuracy[1]	Transmitter weight (g)	Minimum weight (g) of tracked bird[2]	Transmitter dimensions (mm) (L x W x H)
A	Satellite & Radio	Sirtrack™	Battery	ARGOS & VHF	150	5000	105 x 20 x 24
B	Satellite	Microwave Telemetry™	Solar	GPS	70	2333	98 x 34 x 24
C	Radio	Sirtrack™	Battery	VHF	55	1833	44 x 22 x 22
D	Radio	Sirtrack™	Battery	VHF	20	666	38 x 20 x 10

[1] see text below for details regarding accuracy and capacity of transmitter types
[2] based on a transmitter weight of ≤ 3% of total body weight.

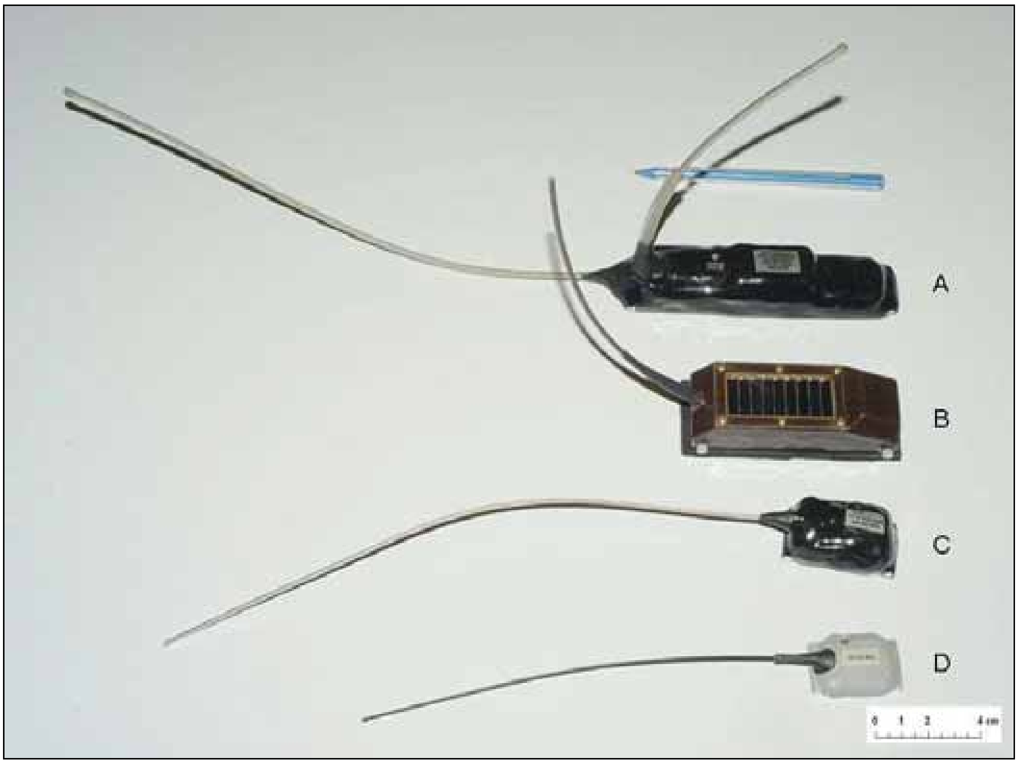


Figure 5.2: Satellite and radio-telemetry transmitters used during the study (see also Table 5.1).

Radio-telemetry

Radio transmitters were attached using super glue to feathers on the back or tail of individuals or were attached as backpacks using harnesses made of Teflon Ribbon (Bally Ribbon Company™). The harness design was based on one effectively used for Houbara Bustards *Chlamydotis undulata macqueenii* in the Middle-East (Judas *et al.* 2006; Combreau *et al.* 1999; M.Lawrence, pers comm.) and was also the method used to attach the larger satellite transmitters (Fig. 5.3).

Radio-telemetry was employed in the early breeding season to assess the ranging behaviour and habitat use of male and female bustards in detail at the two main study sites. Either an ATS 2100 (Advanced Telemetry Systems Inc., USA) or a Telonics TR-2 (Telonics Inc., USA) portable receiver was used in conjunction with a 3-element Yagi™ antenna. Tracking was conducted between September and November from 2002 to 2004, with the majority of individuals tracked in the 2003 and 2004 seasons. The radio-tracking schedule ranged from 10 to 31 days and generally consisted of acquiring three locations per individual per day with the aim of acquiring a fix in the morning, at mid-day and in the late afternoon. These periods correspond to the morning and afternoon periods of activity and a midday period when the birds are generally resting (see Chapter 6).

ARGOS satellite transmitters

The advent of satellite telemetry has greatly enhanced the capability of gathering data at spatial and temporal scales beyond that possible with conventional radio-telemetry techniques. There are two satellite telemetry systems mainly used by biologists: the CLS/Service Argos Data Collection and Location System (or simply the ‘ARGOS system’) and the NAVSTAR Global Positioning System. Both systems were employed during this study (but see note[1]). ARGOS is carried on Tiros-N weather satellites operated by the U.S. National Oceanic and Atmospheric Administration. The system relies on an orbiting satellite receiving UHF radio signals emitted at successive intervals by a ground-based transmitter and uses the Doppler shift to calculate the location of the unit on the ground. Location estimates are then relayed from the satellite to ground-based receiving stations and subsequently to processing centres for redistribution to individual researchers. Because the accuracy of the Argos-based system is variable and dependent on several factors, a scale of location quality classes was established to provide users with estimates of location accuracy (Table 5.2). However, tests of these estimates under varying conditions suggest the actual errors often exceed specifications (Britten *et al.* 1999), although the technology and accuracy of the system is improving (Rodgers 2001). Consequently, locations obtained from ARGOS transmitters are suited to documenting broad-scale movements, but are not suitable for detailed studies of habitat use or local-scale ranging behaviour.

Table 5.2: ARGOS accuracy location classes and estimated accuracy range.

Class	Accuracy
3	<150 m
2	150 m – 350 m
1	350 m – 1000 m
0	>1000 m
A	>4000 m
B	>10,000 m
Z	Invalid location

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[1] Although ARGOS transmitters are discussed in this section, data from these transmitters were not used in the analyses presented in this chapter. The discussion appears here because data from GPS satellite transmitters were used, warranting a general introduction of satellite telemetry. ARGOS (and GPS) satellite transmitters were used to assess broader scale movements discussed specifically in Chapter 8.

In this study, the ARGOS-based transmitters used were manufactured by Sirtrack™. These operated on a 12/156 hour duty cycle, meaning that they would turn on for 12 hours every 156 hours (or once a week for 12 hours). By convention, the recommended maximum weight of a transmitter should not exceed more than 3% of the total body weight of an animal to be tracked. In practice, this meant that these units were only deployed on bustards heavier than 5 kilograms, restricting their use to mature males. The units were also fitted with conventional VHF radio transmitters enabling individuals to be tracked by conventional radio-telemetry as described above.

GPS-based satellite transmitters

Telemetry systems based on the NAVSTAR Global Positioning System overcome the uncertainties associated with Argos-derived accuracy estimates. GPS-based systems also theoretically allow for 24 hour per day position estimates as they are not dependent on the timing of orbital satellite passes. The system relies on a GPS receiver on the ground that determines its position by simultaneously synchronizing with three or more satellites to obtain geographical coordinates. The level of accuracy is within 10m of the true location 95% of the time (Rodgers 2001). The units are capable of collecting multiple daily fixes over an extended time. The spatial and temporal resolution of GPS data, therefore, provide unprecedented levels of detail for examining space use and movements of wildlife.

The units employed in this study were Microwave Telemetry's™ 70 gram solar-powered GPS transmitters. These were programmed to operate on a duty cycle of 16 hours on, 8 hours off (with the off period occurring overnight between 22:00 and 6:00). While turned on, the units were programmed to attempt a GPS fix every hour leading to a theoretical maximum of 16 location fixes per day. Data were logged within the unit and transmitted for retrieval via the Argos satellite system every three days.

Inherent in many studies of habitat use based on satellite telemetry is the potential for bias in the acquisition of location fixes because of the effects of vegetation characteristics (e.g. signal transmission may be compromised in denser vegetation or in habitats with closed canopy cover). This source of potential error for habitat use studies may be particularly significant for species that use different habitats (particularly when a significant component of this habitat is dense), and when it is an explicit aim of the study to compare relative habitat preferences. The savanna habitats of northern Australia which bustards favour are open with low canopy cover and shrub and tree density. Although it was an aim of this study to assess habitat use of bustards in detail, and to examine the potential effect of tree and shrub density and canopy cover on bustard habitat use, it was assumed that such a bias was unlikely here because of the 'openness' of available habitats at Kidman Springs.

Figure 5.3: Backpack harness design with GPS transmitter (top left), a mature male bustard captured at its display site with attached unit (top right), and a female with attached unit (bottom).

Range assessment

Numerous methods have been developed by wildlife biologists for estimating home ranges (Kenward 1987; Rodgers 2001; White and Garrott 1990). However, there are few consistent and unambiguous criteria for choosing between methods and there is often considerable variation in home range estimates depending on sampling effort and which estimators are used (Borger *et al.* 2006; Girard *et al.* 2006; Girard *et al.* 2002; Horne and Garton 2006). To avoid such problems many authors have recommended that multiple methods be used (Harris *et al.* 1990). The choice of a preferred method for assessing ranging behaviour largely depends on the specific aims of a study and should be chosen with due consideration of the relative strengths and weaknesses of each technique. In this study, I employ two methods: that based on the minimum convex polygon (MCP) and the fixed-kernel model.

Home range estimators

The minimum convex polygon measure of home ranges has been widely used by biologists, particularly in pioneering studies of ranging behaviour and habitat use patterns (White and Garrott 1990). The method is limited and often criticized for its many shortcomings: it can dramatically inflate range estimates because of its sensitivity to outliers and it does not account for preferred areas within an individual's range (Burgman and Fox 2003; Girard *et al.* 2002). Despite its shortcomings it may be useful under certain circumstances. It was adopted in this study to specifically compare the extent of area over which males and females range, and to determine the degree of interaction between males and between females and displaying males (i.e. over what area do they roam and how many display sites do females visit). Calculation of MCPs also allow comparison with several studies of other bustard species which have exclusively used the method in the past. Since it was the primary intention here to define the full extent over which bustards use an area, all fixes including outliers were used in the analyses.

It is clear from even a cursory glance of the point location data derived by satellite and radio-telemetry in this study that individuals (particularly females) tend to have multiple areas of activity. MCP methods, by simply delineating the outer boundaries of space used, are inherently insensitive to location points within their boundaries. The kernel density method circumvents this limitation because it is sensitive to all location fixes. In this respect, an important part of the method is the selection of an appropriate bandwidth or smoothing factor. The bandwidth determines the resolution of range areas and its choice may vary depending on study goals, sample size and patterns of space use by a study species (Gitzen *et al.* 2006). In my analyses, I consistently adopted a constant bandwidth of 500 for all range calculations. It was derived by visually comparing range kernels calculated using different bandwidth values and was chosen to achieve a balance between incorporating broad areas around single sample points, and restricting the influence of sample points where several repeated fixes occurred within close proximity of each other. In this sense it represent a mid-range value that has also been favoured among similar studies (e.g. Pope *et al.* 2004). Furthermore, use of a constant value facilitates more effective comparisons between ranges estimated in this study because biases associated with the bandwidth are uniform, so in effect are cancelled out.

In this study, two utilization contours were employed for analyses. A 95% kernel utilization contour defined the bustard's overall range and a 50% contour its core area. These proportions are arbitrarily assigned, however, they are generally accepted and widely applied in studies of home ranges and habitat selection (Pope *et al.* 2004; White and Garrott 1990). The Home Range Extension (HRE) for ArcView GIS (Rodgers and Carr 1998) and Hawth's Analysis Tools (Version 3.27) for ArcMap (Beyer 2004) were used for calculating range estimates.

Ranging behaviour and habitat use during the breeding season

As discussed above, radio-tracking was used for periods during September to November at the DDRF and Kidman Springs to assess home range and habitat use in the early breeding season. Individuals that were tracked using GPS satellite transmitters in the Kidman Springs region were also included for up to a 31 day span in the middle of the September to November period.

Logistical constraints often mean home range sampling regimes are a compromise between sampling a representative set of individuals within a population and obtaining sufficient data for each individual. Larger sample size (i.e. number of location fixes acquired for an individual) generally equates to larger and more accurate estimates of home ranges (De Solla *et al.* 1999; Girard *et al.* 2002; Horne and Garton 2006; Worton 1987). Researchers often aim to determine the minimum number of fixes required for an individual to generate unbiased, reliable home range estimates. However, simply considering number of fixes without regard to the overall time over which sampling occurred is inadequate because the number of days over which sampling occurred is often more important (Borger *et al.* 2006). To examine the reliability of my breeding range estimates in relation to sampling regime two measures were used. First, increment area analysis (Kenward 1987) using the minimum convex polygon measure was performed on the fixes for each animal to determine the minimum number of fixes required to provide a reliable estimate of home range area. Second, a regression was performed across individuals to determine whether a significant positive relationship existed between number of fixes and days of sampling and home range size. Should no relationship exist it would indicate that ranges were stable.

Seasonal habitat selection and ranging behaviour

Data from two sources were used to assess seasonal habitat use at Kidman Springs. The primary source of seasonal habitat use data was derived from satellite tracking of individuals at Kidman Springs. This dataset was based on two individuals (both females) that were tracked continuously for 4 years. The dataset was screened to exclude duplicate location fixes and also omitted periods when these two individuals were nesting.

A second source of data was derived from the vehicle-based surveys of bustards at Kidman Springs (see also Chapter 4). Surveys were driven along roads and tracks in the core study area of Kidman Springs to record the presence of bustards at the site. Each observation of an individual or group was classified according to habitat type (as defined below, see also Fig. 5.4 and Chapter 3). The proportion of observations within each habitat type was determined according to season (that is, each survey period was assigned to one of four seasons as defined below). This provided a measure of the relative abundance of bustards in different habitat types between seasons. Note that this approach is affected by the placement of tracks relative to the environmental variation of the study site.

In this study I defined seasons as:

i) *Early dry season* (March to May) – this period is the bustard's post-breeding season and overlaps with the end of the wet season. It is a period of great productivity and is regarded by Aboriginal people in northern Australia as 'harvest time' because of the many different bush foods available.

ii) *Mid dry season* (June to August) – at this time the weather is cool and the humidity is low. Grasses senesce. Surface water becomes increasingly scarce. There is little or no rainfall.

iii) *Late dry season* (September to November) – this is the hottest time of the year and there is limited surface water. Grasses are completely dry and the biomass has been significantly reduced. Much of the savanna has been burnt by now. This period corresponds to the early breeding season.

iv) *Wet season* (December to February) – the rainy season. Heavy rains cause flooding of rivers and low-lying areas. Significant grass and forb growth. This is the main part of the bustard's breeding season in northern Australia.

Data analysis

Home range size

Wilcoxon matched-pairs test were used to compare the two different types of home range estimation techniques (kernels at 95% and MCP) for all sites and all seasonal home ranges combined respectively.

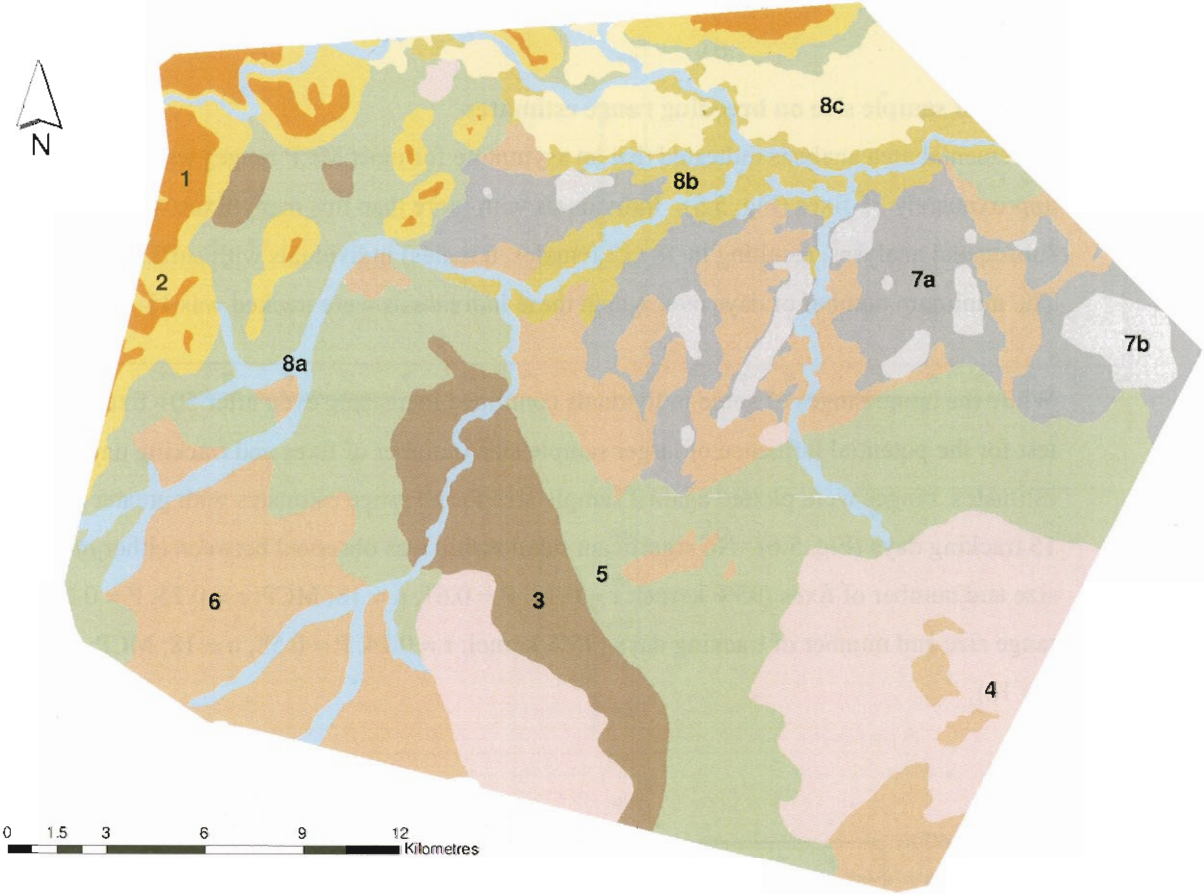
One-way ANOVAs were used to compare range sizes during the breeding season between sexes and between sites. A three-way mixed model ANOVA was used to compare differences in seasonal home range measures using year and bird (ID) as random factors and season as a fixed effect. Prior to comparisons all range data were $\log_{10}$ transformed to meet the assumptions of the subsequent ANOVA tests. Logarithmic transformation is appropriate when the variance of a sample of count data is larger than the mean. Statistical analyses were conducted using Statistica 6.0 (Statsoft 2003).

Habitat selection

Compositional analysis was used to assess habitat preferences following Aebischer (1993) and employed the Resource Selection program (Leban 1999). Compositional Analysis uses MANOVA to analyse two sets of data in which variables are represented as proportions. It is used to determine the statistical significance of differences and the rank order of differences between the variables (Aebischer *et al.* 1993). The technique provides a relative ranking of preference for each habitat type by comparing the log-ratio of proportion of habitat used relative to overall habitat availability within a defined study area. To examine seasonal habitat use I delineated total habitat availability for the Kidman Springs site by defining a minimum convex polygon based firstly on all fixes of all individuals (plus a buffer of 200 metres) tracked during the breeding season, and then solely for the two individuals tracked in detail using all fixes for the entire period they were tracked for.

Habitat types at Kidman Springs were classed on the basis of land units defined by McLeod and Van Cuylenburg (in prep.) with some modifications. First, the number of units was reduced to reflect the main habitat categories available in the study area. An additional category was identified within the alluvial plains land unit to distinguish between open treeless grassland and open woodland. Open treeless grassland was mapped using Quickbird™ (from 2007) and Landsat™ imagery (from 2005). This resulted in a total of 11 habitat types (Fig. 5.4 and see also Fig. 3.5). In the presentation of results here I emphasise the three primary habitats that were considered during resource sampling (Chapter 3) and seasonal surveys (Chapter 4), and which make up most of the core study region at Kidman Springs. Namely, open woodland on red loam soil (ROW), open woodland on alluvial black soil (BOW) and treeless grassland on alluvial black soil (BOP). In addition, I denote riparian areas as 'RIP'. These acronyms are subsequently used in the presentation of results, however, I retain numerical values for the remaining habitats as defined in Fig. 5.4.

Rankings were based on habitat use measured as the proportion of range area within a habitat category defined by the 95% kernel density estimate. Where a habitat was available but not used, the zero value was replaced with 0.001% (an order of magnitude less than the smallest recorded non-zero percentage present) since a log-ratio transformation of zero is invalid (Aebischer *et al.* 1993).



🟧	1	PLATEAU SURFACES Open woodland with grassy understory
🟨	2	ESCARPMENT &/or STEEP SIDESLOPES Open woodland with grassy understory
🟫	3	ROLLING TO SLEEP HILLS: Open woodland with grassy understory
🟥	4	UNDULATING TO ROLLING HILLS. Open woodland with grassy understory
🟩	5	GENTLY UNDULATING TO ROLLING HILLS. Open woodland with grassy understory
🟧	ROW 6	LEVEL TO UNDULATING PLAINS Open woodland with grassy understory
⬛	BOW 7a	LEVEL TO UNDULATING ALLUVIAL PLAINS: Open woodland with grassy understory
⬜	BOP 7b	LEVEL TO UNDULATING ALLUVIAL PLAINS Treeless open grassland
🟦	RIP 8a	RIVER SYSTEMS DRAINAGE AREAS & BACKPLAINS: Open woodland
🟨	8b	RIVER SYSTEMS, DRAINAGE AREAS - severely eroded areas Open woodland
⬜	8c	RIVER SYSTEMS & BACKPLAINS - levees & terraces. Open woodland.

Figure 5.4: Simplified representation of habitat types and the defined study area at Kidman Springs. Note that figure 3.5 provides a more detailed description of habitat unit characteristics.

RESULTS

Effect of sample size on breeding range estimates

Incremental area analysis indicated that an asymptote for most MCP ranges was reached by approximately 35 fixes (Fig. 5.5). Individuals with more than this many fixes were included in subsequent analyses, resulting in 18 (12 females, 6 males) individuals with sufficient data for analysis. The minimum number of days over which these individuals were tracked was 15.

While the home ranges of some individuals continued increasing even after 50+ fixes were acquired, to test for the potential influence of larger sample size (number of fixes and tracking days) on home range estimates, ranges were plotted against sample size for all range estimates with greater than 35 fixes and 15 tracking days (Fig. 5.6). No significant relationship was observed between either measure of range size and number of fixes (95% kernel: r = 0.13, P = 0.61, n = 18; MCP: r = 0.25, P = 0.32, n = 18), or range size and number of tracking days (95% kernel: r = 0.14, P = 0.58, n = 18; MCP: r = 0.07, P = 0.78, n = 18).

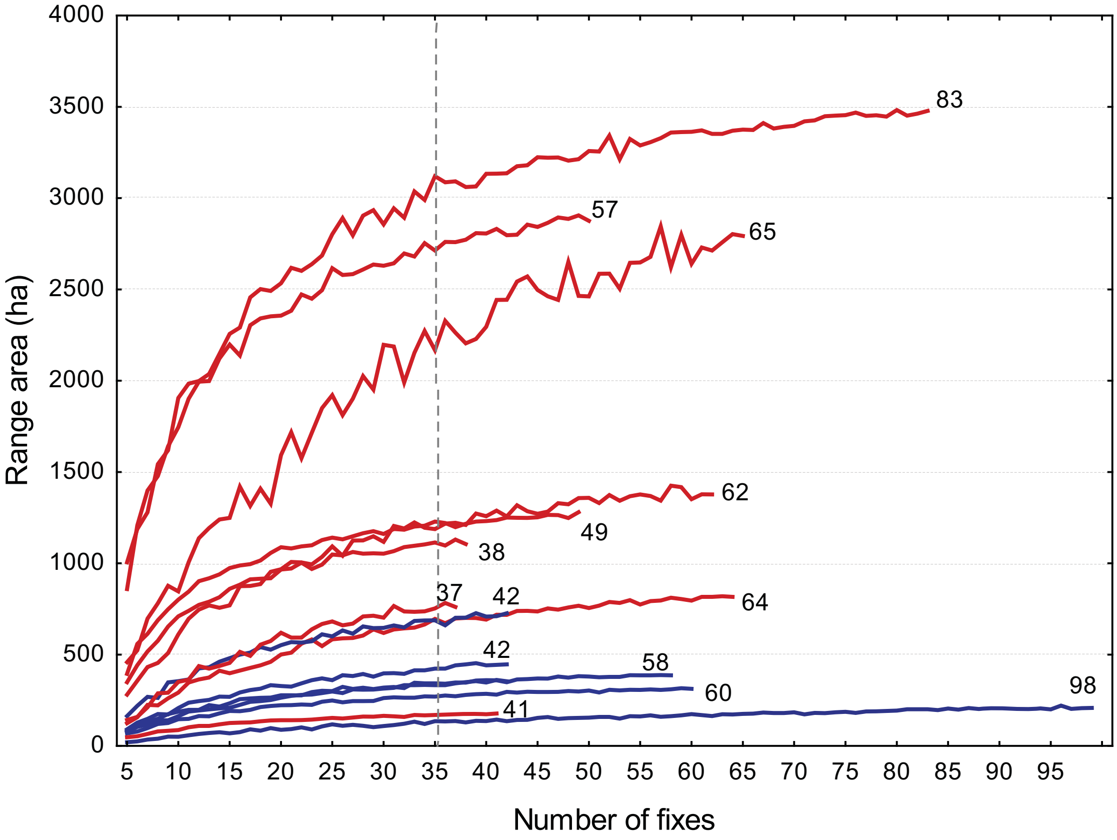


Figure 5.5: Number of location fixes in relation to breeding range area based on the MCP estimator for a sub-sample of 15 tracked bustards (females are denoted by red lines, males by blue). Vertical dashed line defines the minimum number of fixes (n = 35) used for estimates of home range areas.

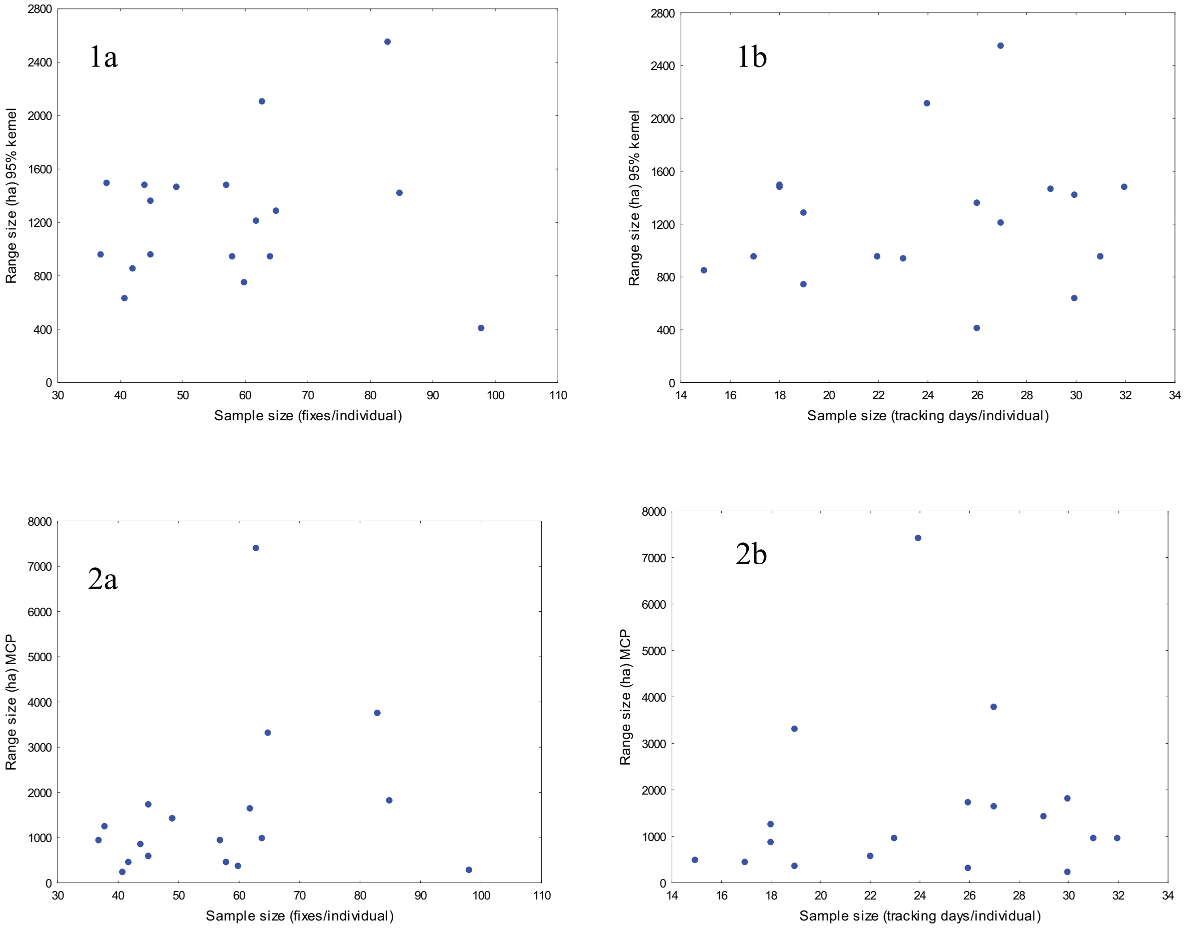


Figure 5.6: Estimated home range sizes across different individuals during the breeding season based on: 1) the 95% kernel estimator, and 2) minimum convex polygons, as a function of sample size measured as: a) number of fixes/ individual, and b) number of tracking days/ individual with at least 35 fixes and 15 days respectively.

Breeding season range size and habitat use

Range size

The mean home range (±s.e.) of females measured by 95% kernel analysis during the breeding season was 1404.5 (± 147.9) hectares, and 2104.9 (± 560.9) hectares by MCP (Table 5.3; Fig. 5.7, 5.8 & 5.9). Mean home ranges for males during this time were 894.7 (± 143.2) and 495.1 (±82.6) hectares respectively. Both estimates comparing sexes were significantly different (95% kernel: F = 4.5, d.f = 1, p = 0.03; MCP: F = 4.9, d.f. = 1, p = 0.02), indicating that females have larger home ranges at this time (Table 5.4). Mean core ranges (50% kernel) were 175.3 (± 18.5) hectares for females, and 218.8 (± 36.1) hectares for males, and not significantly different (F = 2.5, d.f = 1, p = 0.11). Most males (83%) tended to have unimodal home ranges, whereas most females (85%) had distinctly multimodal range distributions (Fig. 5.9).

There was no detectable difference in any of the range estimates between sites (Table 5.4) and there was no statistically significant difference between the 95% kernel or MCP-based range estimates (Z = 1.02, n = 18, P = 0.31).

Table 5.3: Range estimates for individual bustards (including means and variation for sexes and sites) tracked during the early breeding season at the DDRF and Kidman Springs based on kernel density estimates and MCPs.

ID	Sex	Site	Number of fixes	Tracking period (days)	Range (ha) (95% kernel)	Core range (ha) (50% kernel)	MCP (ha)
11	male	DDRF	42	18	1479.4	369.9	856.4
13	male	DDRF	42	22	954.5	223.1	574.3
27	female	DDRF	37	31	947.7	126.7	922.3
28	female	DDRF	49	29	1459.6	231.2	1425.3
30	female	DDRF	38	18	1496.2	219.3	1248.3
32	female	KS	83	27	2543.2	133.1	3744.2
33	male	KS	42	15	846.4	178.9	455.6
34	female	KS	64	23	936.6	109.9	945.7
35	female	KS	65	19	1278.4	92.4	3287.8
36	male	KS	60	19	738.4	172.9	358.6
37	female	KS	85	30	1422.1	145.3	1788.3
38	female	KS	45	26	1354.5	217.6	1727.8
39	female	KS	63	24	2102.9	200.3	7400.7
40	male	KS	98	26	404.6	113.2	283.2
41	male	KS	58	17	945.1	254.7	442.4
42	female	KS	41	30	628.3	121.0	208.9
43	female	KS	62	27	1207.8	195.5	1637.9
44	female	KS	57	32	1476.3	311.0	921.9
	female (n =12)		689	316	1404.5 (±147.9)	175.3 (± 18.5)	2104.9 (± 560.9)
	male (n = 6)		347	117	894.7 (± 143.2)	218.8 (± 36.1)	495.1 (± 82.6)
	KS (n =13)		823	315	1221.9 (± 164.1)	172.8 (± 17.6)	1784.8 (± 563.0)
	DDRF (n = 5)		213	118	1267.5 (± 129.3)	234.0 (± 38.9)	1005.3 (± 150.1)
	All sites, both sexes (n=18)		1036	433	1234.6 (± 121.8)	189.8 (± 17.3)	1568.3 (± 412.6)

Table 5.4: One-way ANOVA results comparing range sizes (n = 18) between sex and site during the early breeding season for two different range estimation techniques (K = kernel estimate; MCP = minimum convex polygon). Significant values are indicated in bold.

		50%K		95%K		MCP	
	df	F	p	F	p	F	p
Sex	1	2.500	0.110	4.500	**0.030**	4.900	**0.020**
Site	1	2.831	0.091	0.073	0.930	0.021	0.979

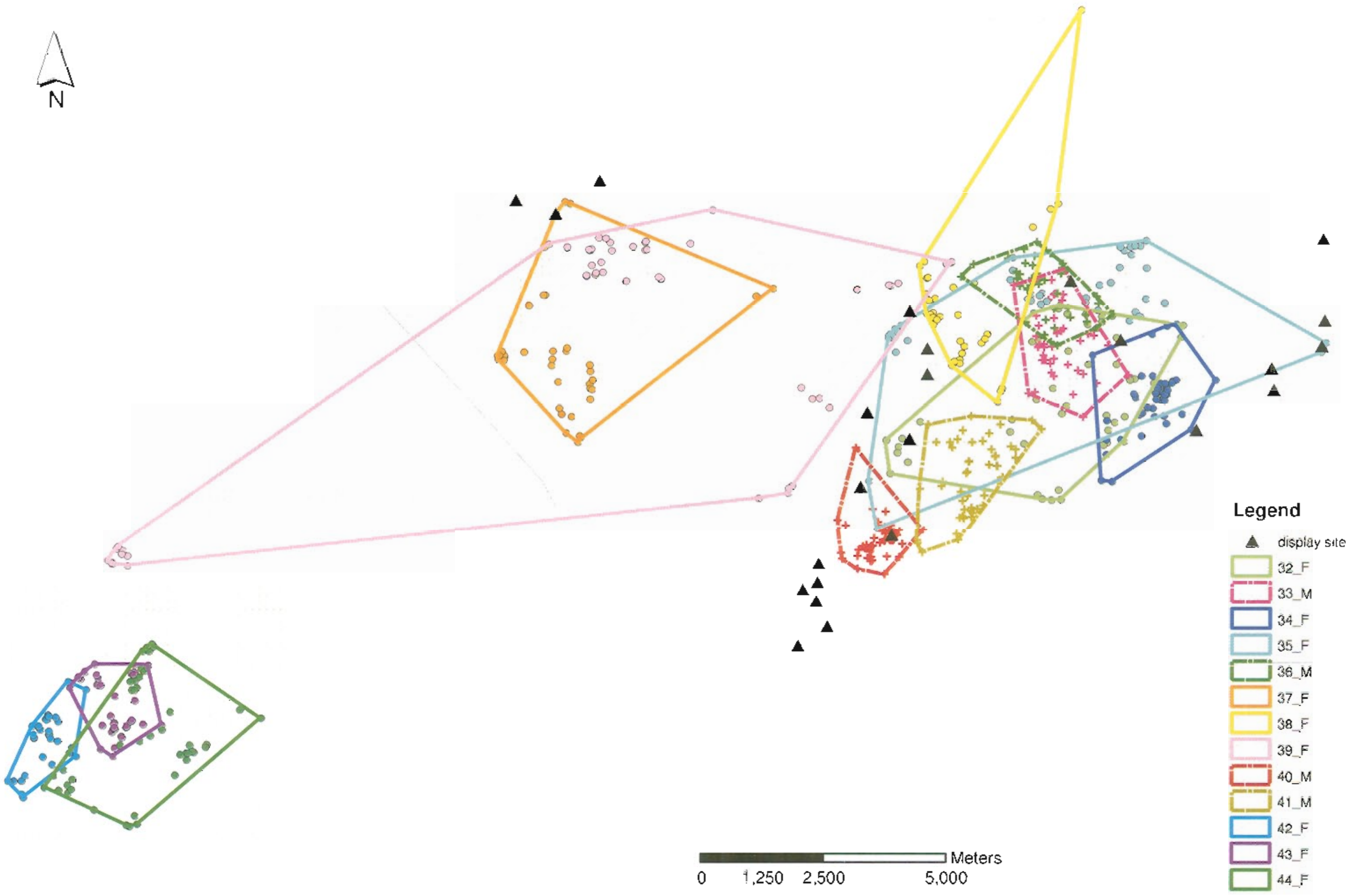


Figure 5.7: Ranges (represented by minimum convex polygons and incorporating all fixes) for bustards tracked for a portion of the early breeding season at Kidman Springs and surrounding areas. Fixes and MCP's for females are depicted as circles (•) and solid lines; males as crosses (+) and dashed lines. Note that ranges shown include bustards tracked at different times and not all the individuals in the study area were tracked. All known display sites of males (▲) between 2002 to 2004 within the core study region (gray line) are also shown.

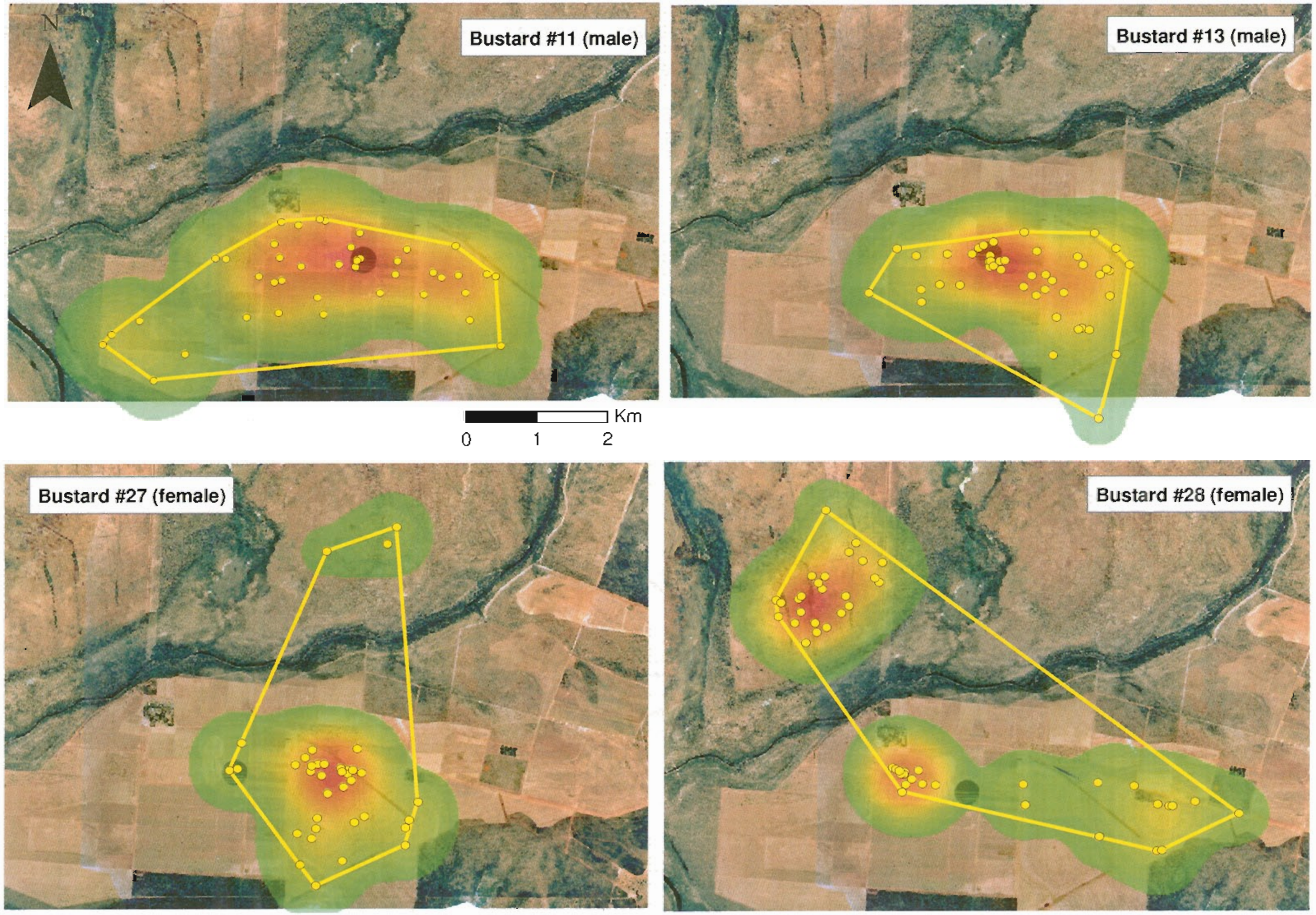


Figure 5.8: Comparison of home range estimates based on MCPs (yellow line) and kernel density estimator (green-red area) for a sub-sample of individuals at the DDRF. Gradations in the kernel graphic represent percentile areas used ranging from 5% (red) to 95% (green). Individual location fixes are denoted as yellow points.

Figure 5.9: Ranges of individual male (M) and female (F) bustards estimated using kernel density models during the early breeding season at Kidman Springs. Gradations in the kernel graphics represent the probability of use of an area ranging from 5% (dark blue) to 95% (light green). Shown also at bottom centre is the position of the core study region at Kidman Springs as depicted also in Figs. 3.1, 3.5 & 4.1 in relation to bustard home ranges.

Habitat use

Collectively, bustards did not use habitats in proportion to their availability during the early breeding season at Kidman Springs ($\chi^2 = 63.9$, d.f. = 8, $P < 0.0001$) (Table 5.5). A simple ranking of habitat preferences ranked habitats in the order: ROW > RIP > BOP > BOW > 8b > 2 > 5 > 4> 8c (Table 5.6). However, among the top four ranking habitats the only significantly detectable difference was greater selection for treeless grassland on cracking clays ('BOP') compared with open woodland on cracking clays ('BOW') (Table 5.6). Notably, these two habitat types differ fundamentally in shrub and tree density and canopy cover. There were no other detectable differences between the top four ranking habitats, but all were used more than the remaining habitats. This suggests the top ranking habitats are generally used interchangeably during the early breeding season and that bustards exhibit a general affinity for open woodlands and grasslands on plains, over similar habitats on rises, hills or rocky slopes which were only very rarely used or avoided entirely. Of significance also was the lower importance of severely eroded riparian areas ('8b') compared to most of the top ranking habitats despite their geographical location between the most valued habitats (i.e. between 'ROW' or 'BOP' and 'RIP').

It should be noted that no location fixes were obtained in habitats '2' and '4'. Their presence as a component of bustard habitat use here is an artifact of the kernel density estimate technique (i.e. a small proportion of the kernel area overlaps these habitats because of the bandwidth chosen for analyses). These habitats, along with habitat '3', were avoided by bustards in the breeding season during this study.

Table 5.5: Mean proportions of 95% kernel home ranges and fixes for bustards tracked during the early breeding season, and relative proportions of total availability of habitat types at the study site at Kidman Springs (see Fig. 3.5 or 5.4 for habitat codes and descriptions). Among the top four habitats (boxed) the only significant difference was between habitats BOW and BOP (*) (Table 5.6). Note that the discrepancy between portions of home ranges within habitat types where there are no fixes is an artifact of the kernel density estimate technique.

Habitat	% home range	% fixes	% available habitat on site
2	0.2	0	0.8
3	0	0	7.9
4	0.1	0	1.7
5	3.0	1.8	20.3
ROW	39.8	43.5	29.1
BOW*	27.9	29.0	13.9
BOP*	10.6	12.8	3.5
RIP	11.8	8.2	9.3
8b	5.6	4.0	6.9
8c	1.0	0.7	6.4

Table 5.6: Pairwise comparisons of habitat types used by bustards in the early breeding season as measured by the 95% kernel density estimate in relation to their proportional availability in the study area at Kidman Springs. A positive log-ratio indicates the proportion of habitat in the home range (row) was used more than the proportion of available habitat in the study area (column). Rank based on 1 (most) to 9 (least) preferred habitat. (P = * <0.05, ** <0.01, *** <0.001). (Figures 3.5 & 5.4 list habitat codes and descriptions).

		Habitat availability								
	Habitat	2 Mean (±s.e.)	4 Mean (±s.e.)	5 Mean (±s.e.)	ROW Mean (±s.e.)	BOW Mean (±s.e.)	BOP Mean (±s.e.)	RIP Mean (±s.e.)	8b Mean (±s.e.)	8c Mean (±s.e.)
Habitat use	2									
	4	-0.84 (±0.83)								
	5	-0.57 (±1.13)	0.26 (±1.41)							
	ROW	6.17***(±0.64)	7.02***(±0.51)	6.75***(±1.22)						
	BOW	4.48**(±1.37)	5.33**(±1.31)	5.06*(±1.95)	-1.68 (±1.42)					
	BOP	5.12**(±1.21)	5.96***(±1.16)	5.69*(±1.89)	-1.05 (±1.29)	0.63*(±0.28)				
	RIP	5.51***(±0.91)	6.35 (±0.85)	6.08***(±1.24)	-0.66 (±0.79)	1.02 (±1.58)	0.39 (±1.51)			
	8b	2.19 (±1.28)	3.03 (±1.56)	2.76 (±1.58)	-3.98*(±1.46)	-2.29 (±1.17)	-2.92*(±1.18)	-3.31*(±1.30)		
	8c	-1.59***(±0.36)	-0.75 (±0.98)	-1.01 (±1.26)	-7.77 (±0.81)	-6.08***(±1.39)	-6.71***(±1.25)	-7.10 (±1.00)	-3.78*(±1.25)	
	Rank	6	8	7	1	4	3	2	5	9

There were too few male home ranges recorded at Kidman Springs to facilitate reliable comparison of male and female habitat use patterns. Ranges for both sexes at Kidman Springs were pooled for overall assessment of bustard habitat use during this period. However, a simple graphical comparison of male to female habitat use suggested that females used more habitat types and males were more likely to use open treeless grasslands (BOP) which females used much less of at this time of year (Fig. 5.10).

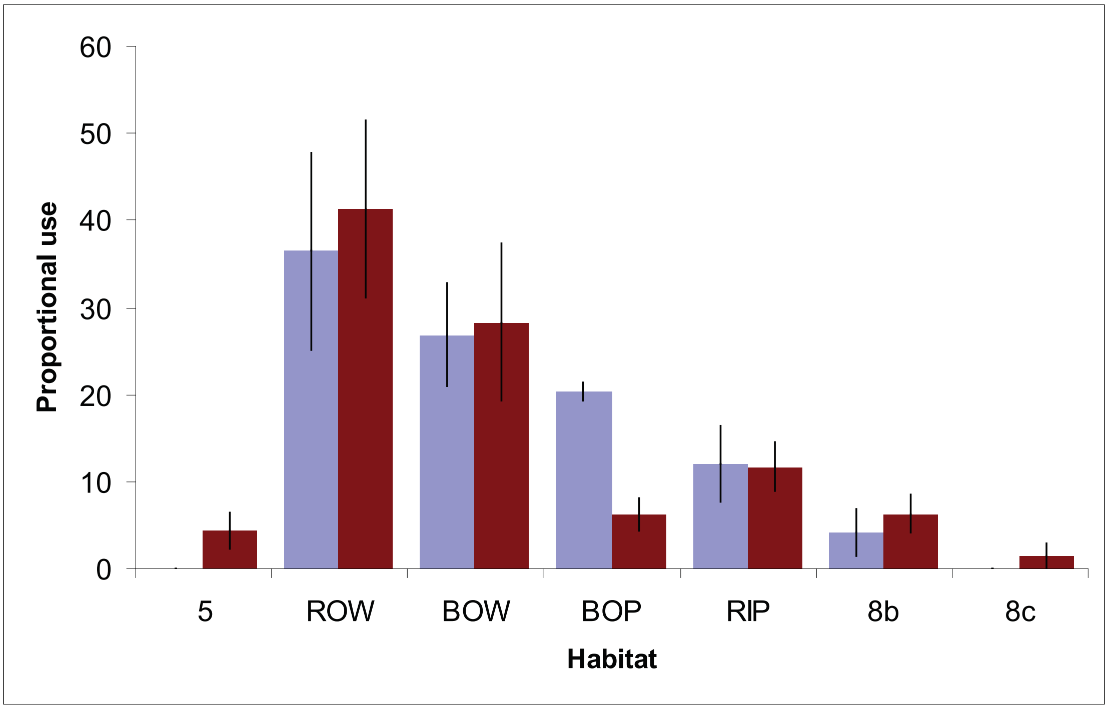


Figure 5.10: Habitat preferences of male (blue) and female (red) bustards during the early breeding season at Kidman Springs, expressed as proportion of each habitat used (± s.e.). Refer to Fig. 5.4 for habitat codes and descriptions.

Seasonal ranging and habitat use

Assessment of seasonal habitat use and ranging behaviour by bustards was examined here primarily on the basis of satellite tracking of two individual females. While this sample size is obviously very small, and appropriate limitations regarding interpretation of results are acknowledged, the dataset was exceptionally detailed. The total duration of transmission of individual transmitters for which data are presented here was 1358 days for individual 42548 and 1361 days for individual 47734. However, there was a large difference in the number of location fixes obtained for each individual: 4952 fixes were obtained for bustard 42548 and 9899 fixes for bustard 47734 (Table 5.7; Fig. 5.11). The number of fixes for individual seasons ranged from 99 to 567 fixes for bustard 42548, and 375 to 883 fixes for bustard 47734. The number of fixes per day ranged from 0 to 16 (16 was the maximum possible for a 24 hour period because of the duty cycle employed), with a mean of 8.4 fixes per day (Fig. 5.12).

Table 5.7: Seasonal home ranges and home range for whole tracking period for two satellite tracked female bustards at Kidman Springs (after duplicate location coordinates removed) based on kernel and MCP estimates including number of location fixes obtained per season.

	42548				47734			
Season	# fixes	50% K (ha)	95% K (ha)	MCP (ha)	# fixes	50% K (ha)	95% K (ha)	MCP (ha)
mid 2004	567	109	458	7627	883	205	2367	4509
late 2004	379	177	1871	11933	420	153	2334	11843
wet 2004	380	148	860	1530	757	241	1121	3152
early 2004	206	106	865	2586	824	185	1595	7765
mid 2005	550	261	1690	6778	827	166	1403	15651
late 2005	184	141	1296	2695	386	184	2165	3274
wet 2005	277	124	637	1937	619	141	2109	3674
early 2005	409	473	1949	3663	690	295	3027	18221
mid 2006	474	174	1080	1098	690	216	1509	10121
late 2006	99	132	889	579	375	214	1013	29058
wet 2006	154	153	725	2556	534	265	2106	3289
early 2006	240	167	1072	5163	584	193	1627	11226
mid 2007	430	234	2091	6400	764	116	1491	2610
late 2007	154	227	1519	1152	379	186	1725	9500
wet 2007	333	115	622	4550	709	508	2819	1980
early 2007	106	191	694	3795	458	133	1367	5164
Early	961	234 (±82)	1145 (±279)	3801 (±528)	2556	196 (±18)	1854 (±302)	6817 (±1935)
Mid	2021	169 (±22)	1393 (±206)	4089 (±2652)	3164	196 (±34)	2176 (±332)	10205 (±3922)
Late	816	194 (±34)	1329 (±357)	5475 (±1482)	1560	222 (±15)	1563 (±224)	13423 (±5499)
Wet	1144	135 (±9)	711 (±55)	2643 (±670)	2619	235 (±92)	1850 (±331)	4813 (±1707)
Both individuals combined								
Early	3517	218 (±41)	1525 (±261)	7198 (±1850)				
Mid	2376	177 (±12)	1602 (±184)	8754 (±3338)				
Late	5185	185 (±19)	1511 (±207)	6849 (±1612)				
Wet	3763	212 (±46)	1375 (±299)	2834 (±360)				
Total	14841							

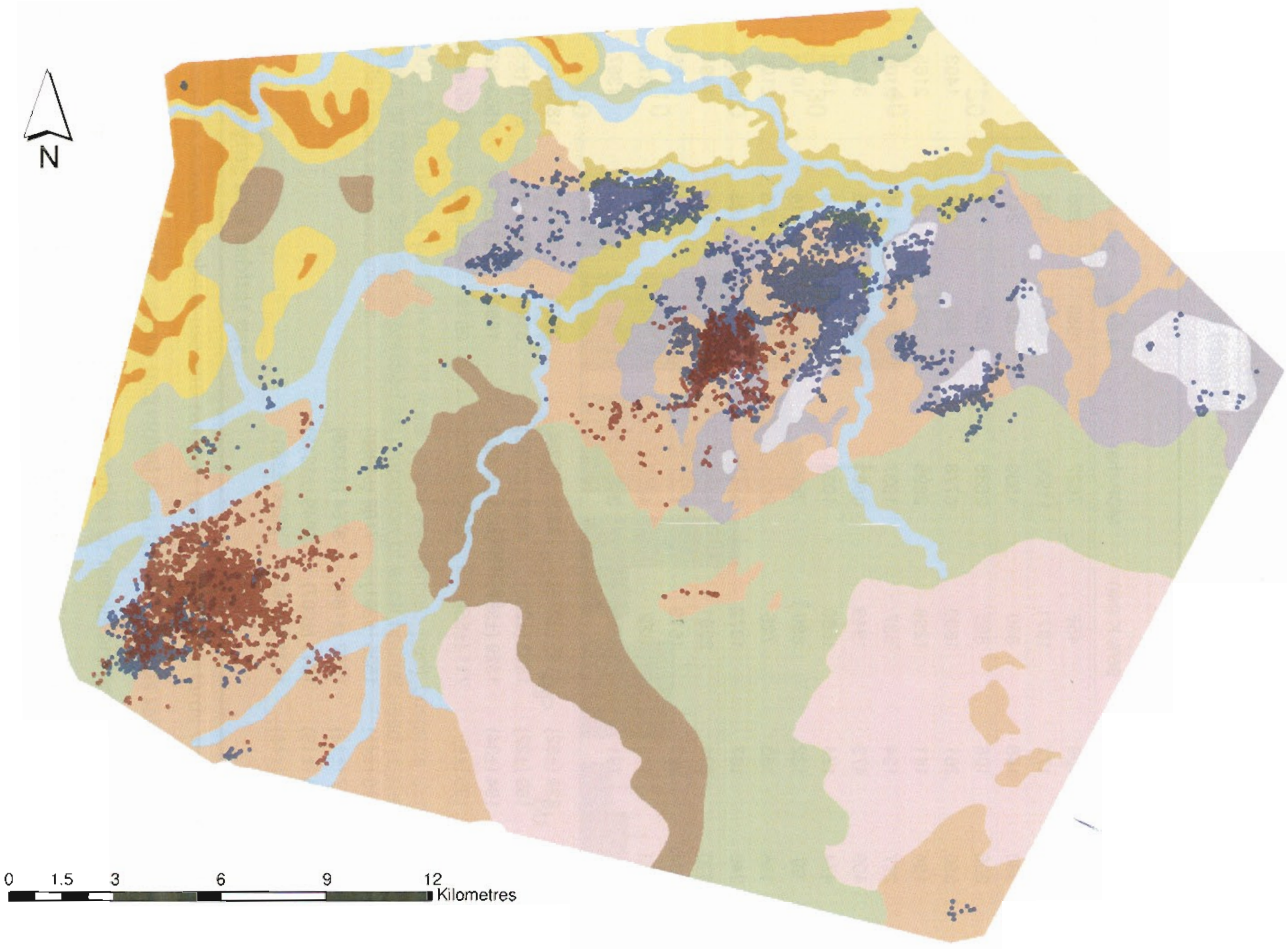


Figure 5.11: Point locations of two female bustards tracked by satellite telemetry in the Kidman Springs region between May 2004 and March 2008. Background map consists of the study area used to assess proportions of available habitat and represents main habitat types as also depicted in Fig. 5.4.

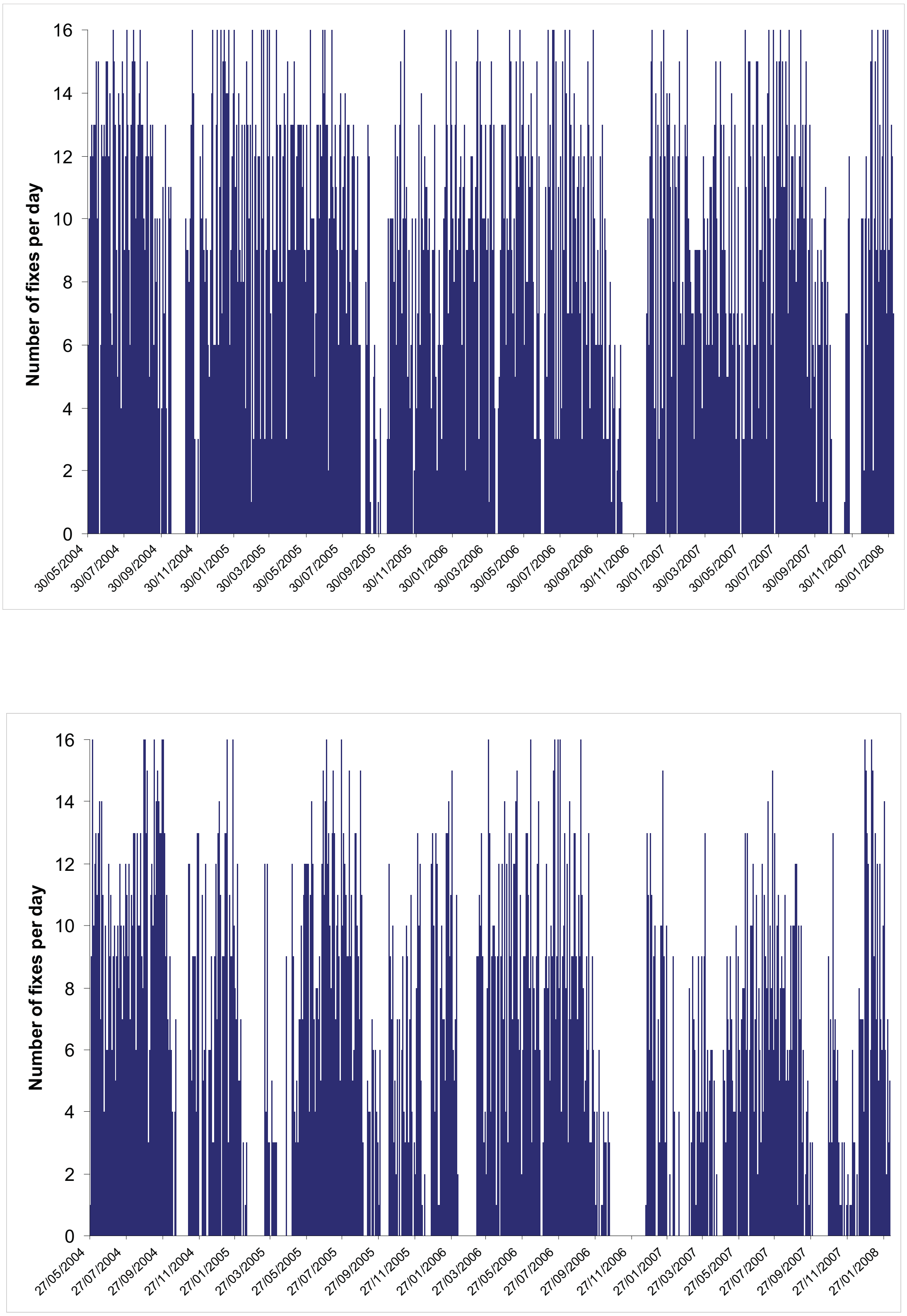


Figure 5.12: Number of GPS fixes per day for two female bustards tracked by satellite telemetry between 27/05/2004 and 10/02/2008. Maximum possible number of fixes per day is 16. (Individual 47734 at top; 42548 bottom).

Seasonal range size

Home ranges measured by kernel estimates for individual seasons ranged from 458 to 2091 hectares for bustard 42548 and 1013 to 3027 hectares for bustard 47734 (Table 5.7). These differences were more pronounced for each individual when calculated using MCPs (579 to 11933 hectares for bustard 42548; 1980 to 29058 hectares for 47734). There was a very highly significant difference between the two estimates when all ranges were combined ($Z = 4.75$, $n = 32$, $p < 0.001$).

Bustard 47734 consistently had larger range sizes than bustard 42548 (KD: $F = 14.49$, $p = 0.0009$; MCP: $F = 8.31$, $p = 0.008$), suggesting that there may be significant variability in range size between individuals (Table 5.8). However, these differences did not extend to core regions ($F = 1.61$, $p = 0.236$).

Table 5.8: Three-way ANOVA for each of the home range measures of satellite tracked bustards at Kidman Springs

		50% K		95% K		MCP	
	df	F	p	F	p	F	p
ID	1	1.61	0.236	14.49	**0.0009**	8.31	**0.008**
year	3	0.60	0.631	1.00	0.4108	0.25	0.863
season	3	0.18	0.904	0.63	0.5999	1.70	0.193
ID*year	3	0.91	0.473	0.05	0.9855	1.45	0.250
ID*season	3	1.75	0.226	0.98	0.4174	1.26	0.311
year*season	9	1.26	0.367	0.44	0.8811	0.50	0.854
ID*year*season	9	0.94	0.509	0.48	0.8576	0.84	0.588

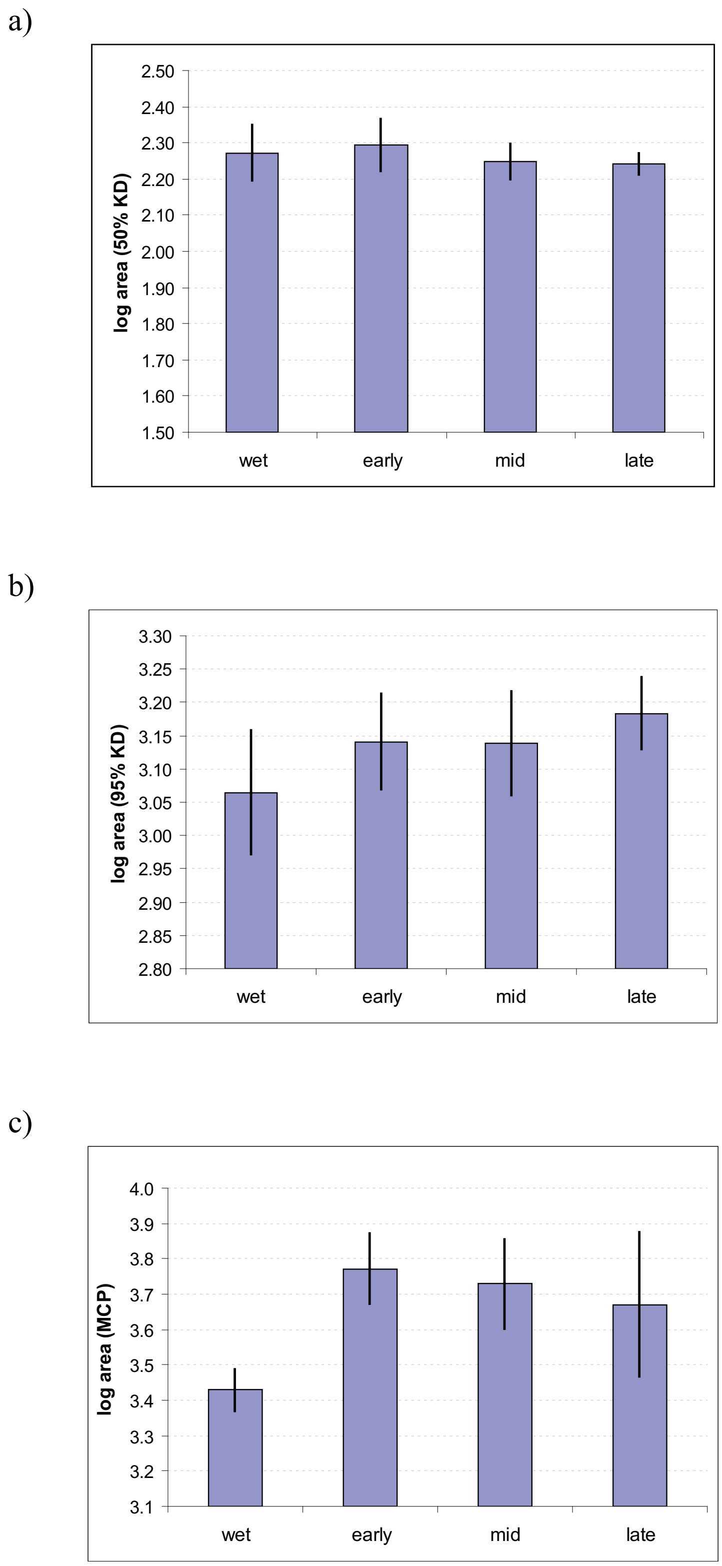


Figure 5.13: Variation in home range sizes (log10 area) within and between seasons at Kidman Springs between 2004 and 2008 measured as (a) 50% kernel (core range), (b) 95% kernel, and (c) minimum convex polygon.

Seasonal patterns of habitat use

Besides a brief visit to the plateau (habitat '1') by 47734 during the early dry season, habitats '1', '2', '3' and '4' were not used in any season despite cumulatively accounting for almost 27% of available habitat in the study area (Table 5.9; Fig. 5.14). These habitats were not considered in subsequent analyses. Up to six habitats were used every season (ROW, BOW, BOP, RIP, 8b and 5). Of these habitats ROW, BOW and BOP were favoured in most seasons but the relative preference for these varied between seasons, although not always significantly (Table 5.10). Habitat '8c' was generally avoided, but appeared as an artifact of the kernel density estimate method in some seasons.

Wet season: Bustards exhibited a pattern to their habitat use during the wet season ($\chi^2 = 31.6$; d.f. = 6; $P<0.0001$). There was a detectable difference between open woodland on red loam soil ('ROW') compared with less favoured eroded riparian areas ('8b'), and a general preference for the top five ranked habitats over the two least favoured. However, there was little to suggest significant differences in habitat use between the top four ranked habitats rendering the ranking between these categories largely insignificant. The ranking matrix was ROW > BOW > BOP > RIP > 8b > 8c > 5.

Early dry season: There was a distinct preference for open treeless grasslands ('BOP') over all other habitats during this early dry season ($\chi^2 = 22.8$; d.f. = 6; $P<0.001$). This was the only season during which the ROW habitat was not the highest ranked habitat. The ranking matrix listed BOP > ROW > BOW > RIP > 8b > 5 > 8c. There were no discernible differences between the second to fourth ranked habitat categories, but a notable difference between these and the lower ranked habitats.

Mid dry season: There was again a significant deviation from random habitat use during the mid-dry season ($\chi^2 = 19.7$; d.f. = 6; $P<0.01$). The most salient differences were again between habitats characterized by open woodland (ROW and BOW) or treeless grassland (BOP) compared with similar habitats on undulating, hilly or steep terrain and eroded riparian areas. The top two ranked habitats (ROW) and (BOP) did not differ significantly from each other. However, treeless grassland was favoured over more densely vegetated open woodland on the same black alluvial soils (BOW). The two lowest ranked habitats were used significantly less than the other habitat types. The ranking matrix was ROW >BOP > BOW > RIP > 8b > 5 > 8c.

Late dry season: Habitat preferences again deviated from proportional availability ($\chi^2 = 27.7$; df = 6, $P < 0.001$). ROW habitat was again the highest ranked habitat which was significantly preferred over riparian habitats and habitat '5' but not over the other habitats. The ranking matrix was ROW > RIP > BOP > BOW > 5 > 8b >8c. Notable here was the higher use of RIP than in other seasons.

Table 5.9: Mean proportions of 95% kernel home range areas and fixes for the two bustards tracked between seasons within each major habitat group, and relative proportions of total availability of habitat types at the study site at Kidman Springs (see Fig. 5.4 for habitat descriptions).

Habitat	early dry (% range)	early dry (% fixes)	mid dry (% range)	mid dry (% fixes)	late dry (% range)	late dry (% fixes)	wet (range)	wet (% fixes)	% habitat available
1	0	0.2	0	0	0	0	0	0	2.6
2	0	0	0	0	0	0	0	0	4.7
3	0	0	0	0	0	0	0	0	6.5
4	0	0	0	0	0	0	0	0	13.0
5	2.7	1.6	1.4	1.6	6.4	4.2	1.0	0.8	28.3
ROW	47.1	36.7	57.3	55.0	63.9	69.8	63.6	63.4	18.6
BOW	19.1	19.0	19.3	17.3	12.9	13.6	15.8	18.6	8.9
BOP	19.0	34.5	14.7	23.8	6.6	7.3	10.5	13.2	2.7
RIP	6.2	2.8	4.8	1.0	7.9	2.5	4.6	1.4	6.0
8b	5.5	5.2	2.4	1.4	2.3	2.3	4.4	2.6	3.9
8c	0.5	0	0	0	0	0.2	0.1	0	4.7

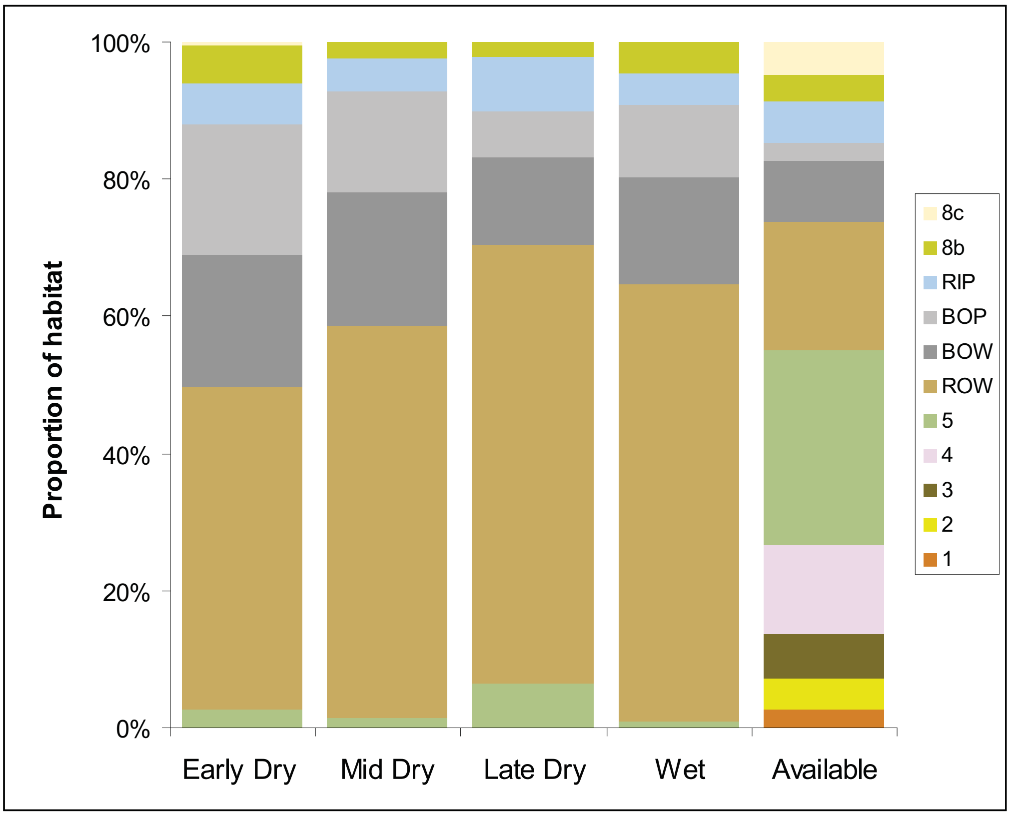


Figure 5.14: Proportional habitat use by two tracked female bustards measured by 95% kernel home range estimates in four seasons, including overall proportion of available habitat in the study region. Seasons are defined as: Early dry season (March-May); Mid dry season (June-August); Late dry season (September-November); Wet season (December-February).

Table 5.10: Pairwise comparisons of habitat types used by bustards tracked between seasons as measured by the 95% kernel density home range estimate in relation to their proportional availability in the study area at Kidman Springs. A positive log-ratio indicates the proportion of habitat in the home range (row) was used more than the proportion of available habitat in the study area (column). Rank is based on 1 (most) to 9 (least) preferred habitats. Matrix of means and standard errors obtained by averaging each element over all ranges in each season for the two satellite tracked bustards (P= * <0.05, ** <0.01, *** <0.001) (see Fig. 5.4 for habitat codes and descriptions).

Wet season: χ^2 = 31.6; df = 6, P < 0.0001

Habitat	5	ROW	BOW	BOP	RIP	8b	8c
ROW	9.24 (±1.11)						
BOW	8.24 (±1.60)**	-2.00 (±1.35)					
BOP	7.27 (±1.85)**	-2.97 (±1.93)	-0.97 (±1.27)				
RIP	6.92 (±1.61)**	-3.31 (±1.51)	-1.31 (±1.93)	-0.34 (±2.04)			
8b	5.34 (±1.70)*	-4.90 (±1.86)*	-2.90 (±1.47)	-1.93 (±1.16)	-1.58 (±1.38)		
8c	2.04 (±1.59)	-8.19(±1.07)***	-6.19 (±1.23)**	-5.22 (±1.56)*	-4.88 (±1.39)**	-3.29 (±1.33)*	
Rank	7	1	2	3	4	5	6

Early dry season: χ^2 = 22.8, df = 6, P < 0.001

Habitat	5	ROW	BOW	BOP	RIP	8b	8c
ROW	6.12 (±1.51)**						
BOW	5.88 (±1.54)**	-0.23 (±0.42)					
BOP	7.11 (±1.54)**	1.00 (±0.36)*	1.23 (±0.17)***				
RIP	4.18 (±2.09)	-1.94 (±1.19)	-1.71 (±1.10)	-2.94 (±1.09)*			
8b	1.63 (±1.91)	-4.48 (±1.90)*	-4.25 (±1.62)*	-5.48 (±1.66)*	-2.54 (±1.59)		
8c	-1.29 (±1.22)	-7.41(±1.35)***	-7.17(±1.14)***	-8.4 (±1.19)***	-5.47 (±1.52)**	-2.92 (±1.44)	
Rank	6	2	3	1	4	5	7

Mid dry season: χ^2 = 19.7, df = 6, P < 0.05

Habitat	5	ROW	BOW	BOP	RIP	8b	8c
ROW	7.66 (±1.43)**						
BOW	6.12 (±1.52)	-1.54 (±1.36)					
BOP	7.11 (±1.53)**	-0.54 (±1.32)	0.99 (±0.13)***				
RIP	5.32 (±1.49)	-2.34 (±1.05)	-0.76 (±1.85)	-1.79 (±1.83)			
8b	2.50 (±1.41)	-5.16 (±1.68)*	-3.61 (±1.52)*	-4.61 (±1.50)*	-2.81 (±1.63)		
8c	-1.24 (±1.33)	--8.90 (±0.71)***	-7.36 (±1.25)***	8.35 (±1.24)***	6.56 (±1.12)***	3.74 (±1.4)*	
Rank	6	1	3	2	4	5	7

Late dry season: χ^2 =27.7; df = 6, P < 0.001

Habitat	5	ROW	BOW	BOP	RIP	8b	8c
ROW	3.82 (±1.19)*						
BOW	-0.39 (±2.23)	-4.21 (±1.90)					
BOP	0.52 (±2.24)	-3.29 (±1.79)	0.91 (±0.29)*				
RIP	2.86 (±0.97)*	-0.96 (±0.27)**	3.25 (±1.86)	2.33 (±1.79)			
8b	-2.41 (±1.54)	-6.23 (±1.72)**	-2.02 (±1.37)	-2.93 (±1.45)	-5.27 (±1.58)*		
8c	-5.18 (±1.16)**	-9.01 (±0.71)***	-4.79 (±1.65)*	-5.71 (±1.58)**	-8.04 (±0.64)***	-2.77 (±1.35)	
Rank	4	1	5	3	2	6	7

At Kidman Springs, results from vehicle-based surveys corroborated findings from the satellite-tracked individuals (Fig. 5.15). There was a noticeable preference for open treeless plains and open woodland on cracking soils in the early dry season. No vehicle-based surveys were undertaken at Kidman Springs during the wet season because of access difficulties. Note also that the area considered here, and therefore the relative areas and types of available habitat, was different to that defined for analyses of habitat preferences using the telemetry data because the vehicle-based survey area was restricted to a smaller part of the study region due to track and access constraints. In practice, this excluded most of the habitats that were least used by the two satellite tracked female bustards (i.e. habitats 1, 2, 3, 4 and 8c).

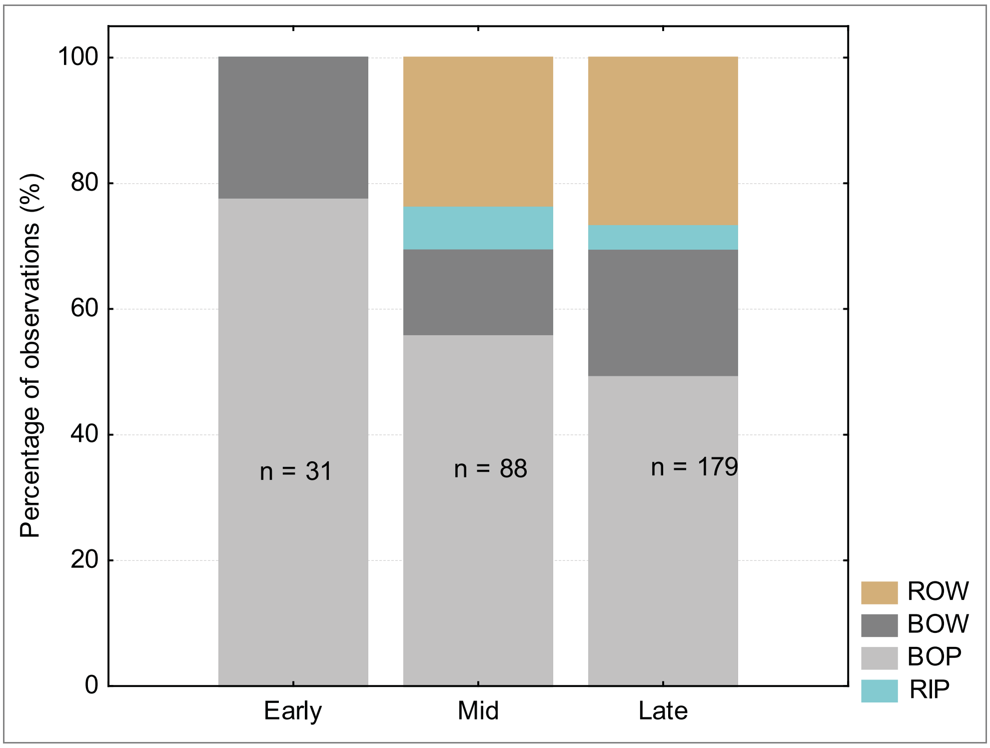


Figure 5.15: Seasonal habitat use by bustards at Kidman Springs determined by vehicle-based surveys. Habitat codes are; ROW = open woodland on red loam soils; BOW = open woodland over alluvial soils; BOP = open treeless plains on alluvial soils; RIP = riparian (refer also to Figure 5.4). Seasons were defined as: Early dry season (March-May); Mid dry season (June-Aug.); Late dry season (Sept.-Nov.). No surveys were undertaken during the wet season because of access difficulties. (n = number of observations).

DISCUSSION

Caveats and study limitations

Sample size

Before I discuss the implications of the results of this study a brief exploration of issues associated with the effects of sample size on range estimates and related caveats is warranted. Much of the discussion of seasonal habitat use is based on tracking of two individual female bustards at one site. I acknowledge that such a small sample size limits generalization to the wider population and effectively renders an assessment of seasonal habitat use largely descriptive. Nevertheless, the dataset used here represents an unprecedented and exceptionally detailed information base for two individuals tracked over several seasons. Furthermore, comparison of habitat use by these two females is highly consistent with information collated during vehicle-based surveys, reinforcing the findings. For reasons outlined below, there were few males compared to female bustards tracked during this study, in one case limiting comparisons of habitat use between the sexes. Despite small sample sizes for some analyses presented here notable patterns emerge, although their interpretation requires caution.

A note regarding capture myopathy

An initial intention of this thesis was to focus on the movements and habitat preferences of mature male bustards, particularly as they related to patterns of distribution and use and fidelity to display sites on leks (see also Chapter 7). Consequently, at the commencement of the field study, efforts were focused on capturing, tagging and tracking males on breeding grounds. In the early stages of the study it became evident that several individuals (four known cases – all male) exhibited symptoms consistent with capture myopathy. Capture myopathy is a muscle condition brought on by stress of capture, restraint and transportation. Symptoms include muscular stiffness, lack of coordination, paralysis, metabolic acidosis, or death (Montane *et al.* 2002). It has been documented among a range of birds including, among others, waders (Rogers *et al.* 2004), wild turkeys (Spraker *et al.* 1987), partridges (Hofle *et al.* 2004), and several mammals (Montane *et al.* 2002; Shepherd *et al.* 1988). Males of some species appear to be particularly susceptible to the condition (Rogers *et al.* 2004). At the time of this study there was limited published literature concerning the syndrome, although it has also been subsequently documented among Little Bustards (Ponjoan *et al.* 2008). Following these initial problems, the study’s focus shifted, and was largely restricted to tracking females. Nevertheless, the initial problems, coupled with the inherent challenges of capturing the species in the field, further limited sample sizes during this study.

Home ranges

In the early breeding season female bustards ranged over larger areas than males, exhibited multimodal rather than unimodal home range use and their ranges encompassed several male display sites. During this period males begin to establish or return to leks and display arenas, which females in turn visit to choose potential mates. On several occasions during the study, tracked females were observed within close proximity of displaying males, and on one occasion a female moved directly between one displaying male and another approximately 2.5 kilometres away. These observations suggest females actively range between displaying males and leks to assess potential mates, satisfying one of the key criteria used to define a lekking species – that females are free to choose their mates (Chapter 7, Bradbury 1981).

In contrast, the smaller, unimodal ranges of males during the early breeding season appear to be related to their concentration around their display sites (see Chapter 7). Male bustards also spend significantly less time foraging during the display season than at other times of the year, suggesting that movements in search of food at this time are comparatively restricted (Fitzherbert 1978; Chapter 6). During this time their weight and physical condition deteriorates significantly (Fitzherbert 1978; 1982).

In Chapter 3 it was documented that food resource availability at the DDRF was substantially higher than at Kidman Springs for all periods of the year, including during the late dry season when resources are comparatively low on a landscape scale. The 'food-exploitation hypothesis' predicts that home-range size is inversely related to food availability and has been documented among a range of species (e.g. Kie *et al.* 1991; Larter and Gates 1994; Village 1982). It may be expected then, given the marked differences between the two sites, that home ranges of individual at the DDRF may be smaller than those at Kidman Springs. However, no such difference between sites was observed. A likely explanation for this observation is that other behavioural factors are important. In this case, the need for females to range between males at display sites, and the need for males to remain on their territories at this time, may override the need to range further to gather food.

Despite the competition that exists between displaying males on leks (Johnsgard 1994; Chapter 7) their overall home ranges are not mutually exclusive during the early breeding season. On the lek, displaying males are often within visual (or at least audible) proximity of each other. Similar to other bustard species that exhibit exploded lekking (Hingrat *et al.* 2004; Hingrat *et al.* 2007), defending of display sites by Australian bustards appears to occur on small, localised scales. When not on display sites, males often socialize in small groups while foraging or roosting together.

There are no detailed studies of the biology of the Australian Bustard in the field with which to compare findings from this study. Studies of the Houbara Bustard in Morocco found that the annual home ranges of males were unimodal and much smaller than the multimodal ranges of females reflecting the differences observed between male and female Australian Bustards during the breeding season in this study. During the display season the ranges of Houbara Bustard males measured approximately 8 km^2 as they concentrated around display sites, comparing very closely to the observed breeding season male range of 8.95 km^2 in this study. In Saudi Arabia, a study of the Houbara Bustard found no differences in home ranges between sexes but that the ranges of individuals were significantly larger during spring (breeding season) than at other times (Combreau *et al.* 2000).

Seasonal home ranges estimated by the MCP method in this study were significantly larger and exhibited more variability than ranges determined using kernel density models. Marked variability between individual ranges were characteristic of similar studies using MCP estimates for other bustard species (e.g. ranges of Houbara Bustards in Saudi Arabia varied between 116 to 977 km^2 with core areas between 13 to 128 km^2 (Combreau *et al.* 2000)). The higher and more variable home range estimates between individuals in this study may in large part be an artifact of using the MCP as the home range estimator, given the method's inherent susceptibility to outliers which tends to over-estimate range size (Burgman and Fox 2003). This discrepancy underlines the importance of ensuring that home range estimates are compatible when comparing between different studies. It also highlights the need to choose an estimator that specifically addresses the study's aims. Here, the use of MCP was a useful method for demonstrating that the female home range may overlap many male display sites, but inappropriate for demonstrating the multimodal nature of space use.

Habitat use

At Kidman Springs, bustards almost always avoided habitats where the topography was anything but flat, even though the vegetation assemblages in these areas were structurally indistinguishable from habitats on flatter substrates. This general finding was expected and corresponds to what is known of the broad habitat preferences of most bustard species, including that of the Australian Bustard (Alonso and Alonso 1990; Downes and Speedie 1982; Lane *et al.* 2001; Launay *et al.* 1997; Marchant and Higgins 1993; Salamolard and Moreau 1999). On a small number of occasions individuals were noted in woodland on undulating or gently rolling hills, and on one occasion a satellite tracked female moved on to a plateau outside its overall home range at Kidman Springs. Such aberrant movements may have been in response to local fires in the region. On at least one occasion this was known to have been the case (see Chapter 8).

Among the most specific habitat preferences of bustards was their tendency to concentrate on open treeless grassland plains in the early dry season. One of the primary reasons for this preference may relate to the higher abundance of preferred foods in this habitat at this time compared to other habitats (Chapter 3). The significance of these areas to bustards has important implications for the management of the species' habitats. 'Woody weed' infestation is a significant issue in the northern savannas (Crowley and Garnett 1998; Dyer *et al.* 2001), and has been cited as a threatening process for several bird species (Garnett and Crowley 2000). It is a widespread and well documented phenomenon in the Victoria River District (Dyer *et al.* 2001; Dyer 2001; Fensham *et al.* 2005; Lewis 2002; Sharp and Bowman 2004; Sharp and Whittaker 2003). Its occurrence and intensity varies between habitats and appears particularly pronounced on the alluvial plains favoured by bustards (Sharp and Whittaker 2003). Infestations have been primarily attributed to overgrazing by cattle, which has led to a transformation of much of the herbaceous vegetation to a largely non-flammable state, resulting in significantly fewer effective fires and subsequent higher rates of woody weed establishment (Sharp and Whittaker 2003). In the VRD much of the peak woody weed establishment occurred in the 1970s following significant pastoral intensification in the region (Sharp and Whittaker 2003). The effects of infestation have steadily intensified since, with large areas of formerly open plains increasingly wooded as these species have matured and propagated. In the Kidman Springs study area, open treeless plains accounted for less than 4% of the total area of available habitat, yet included almost 80% of bustard observations recorded during vehicle surveys and over one-third of fixes recorded for the two satellite tracked females during the early dry season. Open areas are also critical for displaying males in the early breeding season (Chapter 7). As this apparently irreversible transformation from open to wooded habitats continues (Sharp and Whittaker 2003), and these critical habitats contract further, the region may become progressively less suitable to bustards, eventually leading to their local demise. Indeed, the overall lower abundance of bustards in the early dry season (Chapter 4) may signify that a significant component of the local population may move away from these regions at least seasonally because of limited availability of preferred habitats at this time. Whether limited habitat availability is a driver of movements in this case or a consequence of normal post-breeding season dispersal as observed for other bustard species (Alonso *et al.* 2001; Alonso and Alonso 1992; Morales *et al.* 2000), or the dispersive movements to exploit productive conditions over the broader landscape as discussed in the preceding chapter remains unknown.

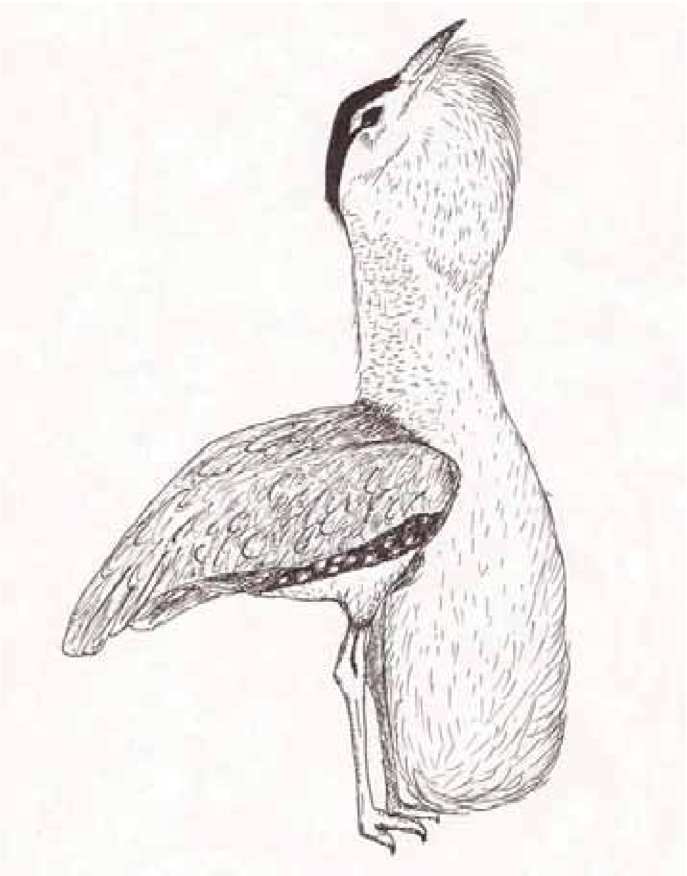
The seasonal progression from the highly productive wet season through the dry season in the tropical savannas is characterized by a general reduction in biomass of the herbaceous layer as grasses senesce, and the cumulative impact of fires and grazing takes effect. The habitat preferences of bustards alter accordingly. The importance of open treeless plains gradually decreases as more wooded areas increase in importance and individuals disperse across a variety of habitats. By the late dry season there is no significant preference for specific habitats, other than the universal avoidance of "hilly" or steep terrain, and the use of open areas by displaying males (Chapter 7).

One of the primary factors influencing habitat preferences of many bustard species relates to the availability of cover (Martinez 1994; Salamolard and Moreau 1999; Silva *et al.* 2007; Silva *et al.* 2004; Van Heezik and Seddon 1999). Bustards are dependent on their visual acuity and camouflage for predator avoidance. The degree of cover that bustards prefer may ultimately be a compromise between the need for effective vigilance and adequate concealment. Consequently, bustards favour habitats that are neither too sparse nor too dense, or may rely on different degrees of cover for different purposes. The Little Bustard *Tetrax tetrax*, for example, favours mid-height vegetation that does not exceed the bird's height but in which they can effectively hide when required (Martinez 1994; Silva *et al.* 2004). Habitats that are too sparse in cover provide little option for hiding, particularly while individuals are roosting in the hotter part of the day or are nesting. Conversely, habitats that are too dense reduce the ability of individuals to detect and escape from potential dangers by leaving them more open to ambush and by impeding their ability to take flight if required because of their somewhat cumbersome take-off. The quality of cover changes seasonally within and between habitats in naturally diverse savanna habitats as found at Kidman Springs. Following wet season rains, open grasslands provide large expanses of favourable habitat whereby bustards have far-ranging vision and adequate cover. As the dry season progresses and grasses senesce and are removed by fires and grazing, the cover qualities of these grasslands decrease. With a more depauperate grass layer, open woodland and shrub lands assume more importance to bustards. The reported preference of bustards for breeding in the ecotone between open plains and open woodlands (Downes 1982a; Downes and Speedie 1982; Marchant and Higgins 1993) is reflective of the diversity of habitats bustards require and largely relates to the different needs of the sexes. In the breeding season a balance is required between the requirement of males for open display areas and the needs of females for areas of higher cover where they can nest, raise chicks and forage. This juxtaposition of open and wooded habitats is likely to be most important in more dynamic environments such as those found at Kidman Springs because of the significant amplitude in habitat suitability. Such contrasts are more muted in the more highly managed, artificial environments of the DDRF which retain a relatively consistent grass cover year round and are more likely to satisfy the different needs of male and female bustards.

Conspecific attraction may also influence habitat selection. Its significance is likely to vary through the year and affect certain components of the population more than others (Seddon and Van Heezik 1996; Van Heezik and Seddon 1999). For example, during the early breeding season females and subordinate males are attracted to displaying mature males in open habitats. In this case, their use of these habitats is governed by the preference of mature males for open display areas that maximize their visibility (Chapter 7, Yang *et al.* 2002).

Bustards also exhibited some affinity for riparian areas at Kidman Springs. Their association with such areas is common in arid zones where drainage lines and watercourses act as refuges and represent areas of high productivity in otherwise dry and for extended periods, relatively unproductive landscapes (Badman 1979; Gibson 1986; Gibson and Cole 1988; Marchant and Higgins 1993; Wyndham 1978). In the northern savannas, riparian areas were only used occasionally but were used throughout the year. The attraction of these areas relates to their use as water source for drinking and their suitability as day-time roost sites because of the greater cover they provide. Use of these areas tended to be highest in the late dry season, the hottest and driest part of the year, when their value was greatest. Although bustards occasionally used riparian areas, they almost entirely avoided the open, highly degraded parts of riparian corridors. At Kidman Springs these areas were often located between the open grassland or open woodland favoured by bustards and the intact riparian areas they used. These areas are generally bare of vegetation, highly eroded and characterized by convoluted topography. As such they are neither suitable as display sites nor for supplying cover and food resources.

In closing, although over much of their range bustards tend to occupy seemingly featureless, open, flat environments, they do in fact exhibit notable preferences and have specific requirements for particular habitat features. In the savannas of northern Australia, bustards are dependent on a subtle diversity of habitats that satisfy the different seasonal requirements of male and females.



Chapter 6

Diet and activity patterns of the Australian Bustard in the tropical savannas of northern Australia

Nicole Bartsch

Chapter 6

Diet and activity patterns of the Australian Bustard in the tropical savannas of northern Australia

INTRODUCTION

Diet and activity patterns are fundamental aspects of a species' biology but remain poorly known for the Australian Bustard. Much of what is known about the species is based on descriptive or anecdotal accounts by amateur naturalists and casual observers, while the only detailed study of the bustard's behaviour was based on a captive population in southern Australia (Fitzherbert 1978). In spite of the lack of targeted, systematic studies of the bustard, the list of known food items consumed by the species is extensive, reflecting a broad, omnivorous diet that includes seeds, fruits, leaves, flowers, green shoots, various invertebrates and small vertebrates (Barker and Vestjens 1989; Marchant and Higgins 1993). However, the relative importance of different food types has not been assessed, nor is it known whether there are seasonal, regional, or gender-related variations in the bustard's diet.

The marked seasonality of rainfall that characterises monsoonal northern Australia drives substantial variation in food resources available to the biota. A short but intense wet season produces a glut of many resources that then gradually decline over the extended dry season leading to resource lows by the end of the year (Woinarski *et al.* 2005). However, despite this general pattern there are seasonal and inter-annual variations in the relative abundance of specific resources, such that peaks in different resources may be asynchronous, while some foods may be available continuously. The broad diet of the Australian Bustard suggests that it is particularly well-placed to exploit such variation by making use of food resources opportunistically according to their availability (Downes 1982; Marchant and Higgins 1993). At the DDRF and Kidman Springs it was demonstrated how potential foods of bustards vary seasonally in their abundance (Chapter 3). In general, ground-dwelling invertebrates (e.g. beetles, true bugs and spiders) increased sharply towards the late dry season and were high during the wet season, larger invertebrates (e.g. grasshoppers) peaked at the beginning of the dry season, while the fruits of several plants were most abundant in the early-mid dry season, but were also found throughout the year. Due to logistical constraints, the present study focused on the bustard's diet in the mid-late dry season. While this precluded broader inter-seasonal comparisons, this period is an important time for bustards as it coincides with general lows in resource availability and the commencement of breeding in the north. If bustards are wholly opportunistic in their foraging then it may be expected that their diet would reflect the availability of food resources at this time.

Another characteristic feature of the northern tropical savannas is the broad-scale homogeneity of the landscape, particularly of those components favoured by the bustard: the open woodlands and grasslands. For many species, the uniformity of the landscape translates to extensive geographic ranges and limited spatial turnover in species composition (Woinarski *et al.* 2005). Consequently, many of the foods that bustards use are likely to occur broadly across the region, suggesting there may be limited regional variation in diets or that certain foods may be commonly and widely used. In this landscape, local variation is likely to be most closely associated with fire history. Bustards exhibit an affinity for fires or recently burnt areas because of increased food availability or accessibility (Marchant and Higgins 1993). They are known to chase prey escaping from the fire front, but also forage extensively for killed or exposed foods on recently burnt substrates. Furthermore, by foraging in both recently burnt and unburnt habitats it is probable that bustards can access a greater variety of food types.

The extreme sexual size dimorphism in bustards may also contribute to differences in both diet and behaviour, particularly to time allocated to foraging. Males are approximately three times heavier than females, suggesting their diets are likely to differ in quantity, size or type of food items. This in turn may equate to differing activity and foraging patterns between the sexes. If the size and type of food consumed by males and females is similar, then it may be assumed that the larger size of males means they require more time to satisfy their energetic requirements.

Marked seasonal variation in food availability may also translate into significant seasonal differences in time allocated to foraging. When resources are low, more time may be spent foraging, while conversely, foraging efficiency is likely to be higher when food resources peak in the early wet season, so the amount of time allocated to foraging is predicted to be lowest at this time. Finally, bustards exhibit an exploded lek mating system, whereby males display on lekking grounds in order to attract mates. In captivity in southern Australia, Fitzherbert (1978) found that male bustards spent considerable lengths of time (on average 70% but up to 95% of daylight hours at peak times) displaying over several months in the breeding season. It was also demonstrated that larger males spent more time in display than younger, smaller males. It is predicted that a similar pattern exists for bustards in the field in northern Australia.

METHODS

Diet analysis

Study area

The dry season diet of bustards was investigated by examining the gizzard contents of 33 bustards harvested by Aboriginal people from several locations in Australia's northern savannas (Fig. 6.1; Table 6.1). The majority of samples were collected from the vicinity of Kalumburu in the north Kimberley in Western Australia. Samples were also collected from the Victoria River District and from three other locations in the Northern Territory.

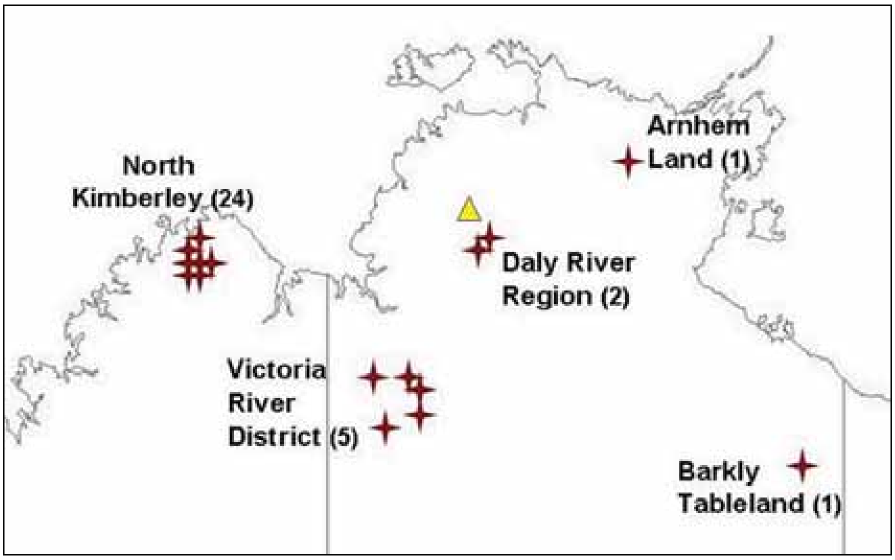


Figure 6.1: Locations where gizzards were collected in five general regions of northern Australia. The number of gizzards from each region is indicated in brackets. The yellow triangle is the location of the activity pattern study at the Douglas-Daly Research Farm.

Gizzard collection and diet composition

Bustard gizzards were mostly collected during the mid-late dry season, generally reflecting the harvesting patterns of bustards by Aboriginal people. This period also coincides with the onset of the bustard's breeding season in northern Australia. Hunting is limited during the wet season because of restricted access to the preferred habitats of the species. Many Aboriginal people also avoid eating bustards during the wet season in northern Australia because of the apparently high internal parasite loads of the birds at this time (Bill Harney, pers. comm.). During this study, collection of gizzard samples was undertaken opportunistically, often by people while on extended hunting expeditions in remote regions. Consequently, there were limited opportunities to formalise a sampling protocol to facilitate diet assessment in a systematic manner. The collection of samples during the mid-late dry season also precluded broader seasonal comparisons of diet composition. Nevertheless, the information collected provides a unique opportunity to examine bustard diet at a critical time of the year for bustards in the northern tropical savannas.

Following collection, gizzards were removed from bustards and stored in 70% ethanol. The location, geographic coordinates, sex, general habitat description and an indication of recent fire history (i.e. whether the collection site had been recently burnt i.e., within last month) were recorded for most samples (Table 6.1). In the laboratory, samples were strained through a fine sieve and flushed with water to remove fine-scale particulate matter. Gizzard contents were sorted, and food items identified to order (but more precisely whenever possible) and counted according to taxon type and size. Numbers of individuals of each taxon were calculated by considering an entire specimen or head as a single individual. When only fragments of specimens were found, counts were made following the recommendations of Calver and Wooler (1982).

The dry weights of invertebrates were calculated directly for whole intact specimens. When this was not possible an estimate of the length of the specimen was made and length:dry weight regression equations were used to estimate dry weight (Brady and Noske 2006; Gowing and Recher 1984). Whenever possible taxa-specific equations were used from sources based on invertebrates collected in the Australian monsoonal tropics (e.g. Brady and Noske 2006).

Differences in digestibility present potentially significant biases for the analysis of diet based on gizzard contents. While this bias is more acute for faecal analyses (because of more thorough digestion), the degree of digestion of gizzard contents may be more variable. The gizzard is a muscular stomach that grinds food, usually with the aid of grit in the form of small stones (termed ‘gastroliths’). The extent of digestion is a function of the type of food consumed and the time since its consumption. In general, the longer the food item has been within the gizzard and the softer and smaller it is, the more it has been broken down and the more difficult it is to detect or identify. Larger and harder food items may therefore be over-represented in analyses compared to softer, smaller items. For example, in the case of bustard foods, the mandibles of insects or *Grewia* seeds are more likely to persist and be detected in the gizzard than the bodies of annelid worms or soft fruits that have small seeds. Nevertheless, while this is a source of potential bias, during the dry season in northern Australia the availability of such softer foods to bustards is low.

Opportunistic observations of unusual food items consumed directly by bustards during the broader study were also recorded, but not included in the analysis of gizzard contents.

Data analysis of diet

Diet similarity among regions, sexes and fire history was assessed using a multidimensional scaling ordination (MDS) based on the mean abundance of each major food category (without regard to size of item) across the individual gizzards using PRIMER v.6. Abundance data were 4th root transformed to take into account the effects of rarer food items. ANOSIM analyses were conducted to test whether there were significant differences in diets between locations, sexes and recent fire history. One-way ANOVAs tested for differences between Kimberley and non-Kimberley sites and burnt and unburnt habitats with respect to three measures of diet diversity: total number of food item taxa (richness), the Shannon-Weiner diversity index and Pielou's evenness index. The latter measures how evenly the numbers of individual food items were distributed among the food taxa. A Kolmogorov-Smirnov test was used to test for differences in frequency of invertebrate size classes between the sexes. The latter two analyses were conducted using Statistica v.6.0.

Table 6.1: Location details of gizzard samples collected for diet analyses in the tropical savannas. Recently burnt refers to whether the habitat in which the individual was harvested had been burnt within a month preceding its collection. Information that was not recorded is denoted by a question mark.

ID	Region	Collection site name	Date collected	Latitude	Longitude	Habitat	Recently burnt	Sex
1	North Kimberley	Sanz Crossing	18/6/2000	14°25’	126°40’	Open woodland	no	male
2	North Kimberley	?	30/6/2000	?	?	?	?	?
3	North Kimberley	Sanz Crossing	18/6/2000	14°25’	126°40’	Open woodland	yes	female
4	North Kimberley	?	18/6/2000	?	?	?	?	?
5	North Kimberley	?	18/6/2000	?	?	?	?	?
6	North Kimberley	?	18/6/2000	?	?	?	?	?
7	North Kimberley	?	18/6/2000	?	?	?	?	?
8	North Kimberley	King George	28/7/2000	14°15’	126°58’	Open woodland	yes	male
9	North Kimberley	King George	28/7/2000	14°15’	126°58’	Open woodland	yes	male
10	North Kimberley	King George	28/7/2000	14°15’	126°58’	Open woodland	yes	male
11	North Kimberley	King George	28/7/2000	14°15’	126°58’	Open woodland	yes	male
12	North Kimberley	Grey Pool	21/7/2000	14°35’	126°45’	Sparse open woodland/plain	no	male
13	North Kimberley	Carson	21/7/2000	14°30’	126°45’	Open plain on black soil	yes	female
14	North Kimberley	Carson	21/7/2000	14°30’	126°45’	Open plain on black soil	yes	female
15	North Kimberley	Kalumburu	18/7/2000	14°12’	126°38’	Open woodland on sandy soil	yes	?
16	North Kimberley	Lariman Road	29/9/2000	14°35’	126°45’	Sparse open woodland/plain	yes	?
17	North Kimberley	Lariman Road	29/9/2000	14°35’	126°45’	Sparse open woodland/plain	yes	?
18	North Kimberley	Lariman Road	29/9/2000	14°35’	126°45’	Sparse open woodland/plain	yes	?
19	North Kimberley	Lariman Road	29/9/2000	14°35’	126°45’	Sparse open woodland/plain	yes	?
20	North Kimberley	Pompangala	27/7/2000	14°19’	126°38’	Open woodland	yes	male
21	North Kimberley	Young Creek	28/8/2000	14°30’	126°40’	Sparse open woodland	yes	?
22	North Kimberley	Young Creek	30/8/2000	14°30’	126°40’	Sparse open woodland	yes	?
23	North Kimberley	Young Creek	30/8/2000	14°30’	126°40’	Sparse open woodland	yes	?
24	North Kimberley	Carson Boundary	25/9/2000	14°30’	126°45’	Open woodland	yes	male
25	Daly River Region	Benung (Wagiman)	23/9/2003	14°47’	131°39’	Open woodland	no	female
26	Daly River Region	Munjang (Wagiman)	11/7/2003	14°22’	131°32’	Open woodland	no	male
27	Victoria River District	Kidman Springs	27/9/2003	16°13’	130°57’	Open woodland/plain	no	male
28	Victoria River District	Fitzroy Station	21/11/2002	15°47’	130°47’	Open woodland on red soil	no	male
29	Victoria River District	Fitzroy Station	23/7/2003	15°46’	130°45’	Open woodland on red soil	no	female
30	Victoria River District	Auvergne Station	20/7/2003	15°43’	129°58’	Open tea-tree woodland, clay soil	yes	male
31	Victoria River District	Yarralin	18/5/2003	16°26’	130°53’	Open plain on black soil	no	male
32	Barkly Tableland	Mittiebah Station	11/7/2004	18°34’	136°08’	Open woodland on black soil	no	male
33	Arnhem Land	Bindaluk Track	16/10/2005	13°32’	133°23’	Low sandstone, open woodland, spinifex	no	male

Activity budgets

Study site

Assessment of bustard activity patterns was undertaken at the Douglas-Daly Research Farm (Fig. 6.1). Chapter 3 describes this study site in more detail. This site was favoured for this component of the study over Kidman Springs because of the open nature of the habitat, year-round access to the site and reliable occurrence of the birds. In contrast, continuous observation of bustards at Kidman Springs is more difficult because it is inaccessible over the wet season, is characterised by densely wooded areas and has a lower population density of bustards.

Sampling protocol and data analysis

Activity patterns were sampled by the Instantaneous Sampling Method (Altmann 1974). This technique involves recording an individual subject's current activity at preselected moments in time. The scan intervals employed in this study were one minute intervals. This method allows for determining the percentage of time that individuals devote to various activities. The percentage of time is estimated from the proportion of samples in which a given activity is recorded. The behaviour of bustards was noted according to 18 separate categories which were later amalgamated into six general classes (Table 6.2).

Table 6.2: Behaviours of the Australian Bustard grouped into six general classes

Behaviour class	Description
Foraging	Walking feeding, pecking at ground or at vegetation, chasing prey, drinking
Rest	Standing, sitting or roosting, vigilance
Mating	Standing display, walking display, chasing or following female, copulation
Locomotion	Walking, flying
Maintenance	Preening, dust-bathing
Interaction	Antagonistic behaviours including chasing opponent, fleeing aggressor

All observations were made from a four-wheel drive vehicle using 10x25 Leica™ binoculars at distances of no more than 200 metres. Sampling was conducted during daylight hours extending from 30 minutes before sunrise to 30 minutes after sunset. Individuals were observed for between 15 to 60 minutes at a time. Three classes of bustards (denoted as 'sex' in the reporting of results) were targeted for observations: females, subordinate males and mature males. In order to compare activity patterns between breeding and non-breeding males, the difference between male classes was based on their maturity; mature males were distinguished by their larger size and well-developed secondary sexual characteristics (i.e. presence of a conspicuous throat-sac).

Time of day comparisons in behaviour were made according to three periods of the day: morning (from 30 minutes before to three hours post sunrise); evening (three hours before sunset to 30 minutes after) and midday (the period between the morning and evening periods). Because of the variation in day length throughout the year, this middle period of the day varied in length while the other periods were static. The number of observations within each period for each season and sex category were tailored to be approximately equivalent. Seasonal comparisons were based on three periods of the year: early-mid dry season (April to August); late dry season (September to November); wet season (December to March).

Comparisons of time spent in any one activity were made by calculating the proportion of time in every daylight hour for each bustard category and season. There was a specific emphasis on comparing time spent foraging. Accordingly, foraging time was compared between the three classes of bustards, three periods of the day and the three seasons using a three-way ANOVA. Proportional data were Arcsine transformed. Tukey HSD *post-hoc* tests revealed between which variables salient differences existed. A two-way ANOVA was also performed to assess whether there was a difference between time spent displaying by mature males in the late dry season compared to the wet season and whether there were differences in displaying according to time of day. All analyses were conducted using Statistica v6.0.

RESULTS

Diet

Analysis of the contents of 33 gizzards revealed that bustards consumed a large variety of invertebrates, seeds, fruits, leaves and small vertebrates (Table 6.3). Individuals were also opportunistically observed to have consumed sap from a *Vachellia (Acacia) farnesiana* bush and, on two separate occasions, cane toads. These two food items are notable because they are unusual and have not been recorded in the literature. In the case of the cane toad, the observation is significant because of the toxic effect of the toads on other Australian fauna. Several other food items recorded from the literature, but not in the present study are presented in Table 6.4.

In general terms, the most common foods consumed by bustards were insects and the fruits and seeds of a small number of plants (Table 6.3; Figs. 6.2 and 6.3). By dry weight the proportion of fruits/seeds (44.5%) and insects (44.7%) were practically identical, though by number, fruits/seeds outnumbered insects 62.9% to 24.6%. The most important plants in descending order of importance were the fruits or seeds of *Grewia retusifolia*, *Cassytha* sp. and *Cucumis melo*. *Blumea* flowers were also commonly consumed. Among the most prevalent invertebrate taxa were the Orthoptera, Coleoptera, Hemiptera and Mantidae (Figs. 6.2 & 6.4). The ootheca (eggs cases) and pupa cases of mantids and other unidentified insects were also notable food items. Gastroliths, in the form of grit, pebbles or small stones, were found in 75% of gizzards.

For such a large bird, bustards consumed a large proportion of small invertebrate prey items. The frequency distribution of invertebrate lengths for male and female bustards is presented in Fig. 6.5. It should be noted at this point that there were comparatively few females in the sample ($n = 5$), although they were widely distributed across the study region. Nevertheless, females consumed significantly smaller prey items than males (Kolmogorov-Smirnov result, $p < 0.01$), with up to 82% of prey items less than 20 mm in length compared to almost 28% for males. Most of these smaller prey items were from two insect families, the Curculionid beetles (weevils) and Pentatomid bugs. Females took few large prey items: less than 15% were larger than 30 mm, compared to 53% for males. Most of the larger prey items consisted of grasshoppers (Orthoptera), stick insects (Phasmida) and praying mantids (Mantidae). The crops of male bustards also contained more food by dry weight than females (males = 35.4 ± 6.1 g; females = 24.9 ±6.7 g).

As an aside, note that of the 20 harvested bustards for which gender was recorded (Table 6.1), 15 individuals were male and 5 were female (i.e. a ratio of 3:1). The implications of this ratio will be addressed in the conservation section of the concluding chapter that discusses the potential effects of hunting on the population dynamics and mating system of the bustard.

Table 6.3: Food items recorded from the gizzards of 33 Australian Bustards and direct field observations (denoted by asterisk). Included is the number and percentage (in brackets) of gizzards containing each food item.

	TAXON	**Number of gizzards (%)**
Arachnida	Araneae	9 (27)
Crustacea	Decapoda	
	Sundatelphusidae	
	Holthusiana transversa	2 (6)
Gastropoda	Pulmonata	3 (9)
	Egg mass	1 (3)
Insecta	Coleoptera	
	Carabidae	5 (15)
	Coccinellidae	4 (12)
	Curculionidae	25 (76)
	Scarabaeidae	2 (6)
	Tenebrionidae	3 (9)
	Indeterminate	15 (45)
	Dictyoptera	
	Blattodea	8 (24)
	Mantidae	20 (61)
	Mantidae (ootheca)	12 (36)
	Hemiptera	
	Cicadoidea	5 (15)
	Pentatomidae	17 (52)
	Reduviidae	1 (3)
	Indeterminate	12 (36)
	Hymenoptera	
	Formicidae	
	Iridomyrmex purpureus	7 (21)
	Oecophylla sp.	3 (9)
	unidentified	4 (12)
	Vespidae	1 (3)
	Lepidoptera	
	Adult	3 (9)
	Larvae	9 (27)
	Orthoptera	
	Acrididae	26 (79)
	Gryllidae	1 (3)
	Tettigoniidae	7 (21)
	Isoptera	3 (9)
	Phasmida	14 (42)
	Dermaptera	1 (3)
	Unidentified ootheca or pupa	2 (6)
Myriapoda	Chilopoda	3 (9)
Plants	Flowers	
	Asteraceae *Blumea* sp.	9 (27)
	Haemodoraceae	
	Haemodorum brevicaule	1 (3)
	Fruits/seeds	
	Tiliaceae	
	Grewia retusifolia	28 (85)
	Lauraceae *Cassytha* sp.	17 (52)
	Cucurbitaceae	
	Cucumis melo	12 (36)
	Apocynaceae	
	Carissa lanceolata	1 (3)
	Cyperaceae	1 (3)
	Fabaceae	4 (12)
	Poaceae	4 (12)
	Unidentified seeds	8 (24)
	Vegetative matter	
	Wood or bark fragment	6 (18)
	Green pick or leaf fragment	4 (12)
	Sap from *Vachellia (Acacia) farnesiana**	*
Reptilia	Squamata	
	Agamidae	1 (3)
Mammalia	Rodentia	
	Muridae	1 (3)
Amphibia	Anura (indeterminate species)	1 (3)
	*Chaunus (Bufo) marinus**	*
Other	Gastroliths	25 (76)
	Feather (Bustard feathers)	6 (18)

Table 6.4: Additional food items consumed by the Australian Bustard recorded in the literature but not the present study (adapted from summaries in Barker and Vestjens 1989 and Marchant and Higgins 1993).

TAXON	
Arachnida	Scorpiones
Insecta	Coleoptera
	Dytiscidae
	Elateridae
	Cerambycidae
Hymenoptera	Tiphiidae
	Thynninae
	Diamma bicolor
Myriapoda	Diplopoda
Plant	Fruits/seeds/flowers
	Asteraceae
	Taraxacum officinale
	Capparaceae
	Capparis spinosa
	Chenopodiaceae
	Atriplex sp.
	Myoporaceae
	Myoporum deserti
	Myoporum sp.
	Polygonaceae
	Emex australis
	Solanaceae
	Lycium ferocissimum
	Zygophyllaceae
	Nitraria schoberi
	Cucurbitaceae
	Citrullus colocythis
	Roots
Reptilia	Scincidae
Aves	Small ground birds & nestlings

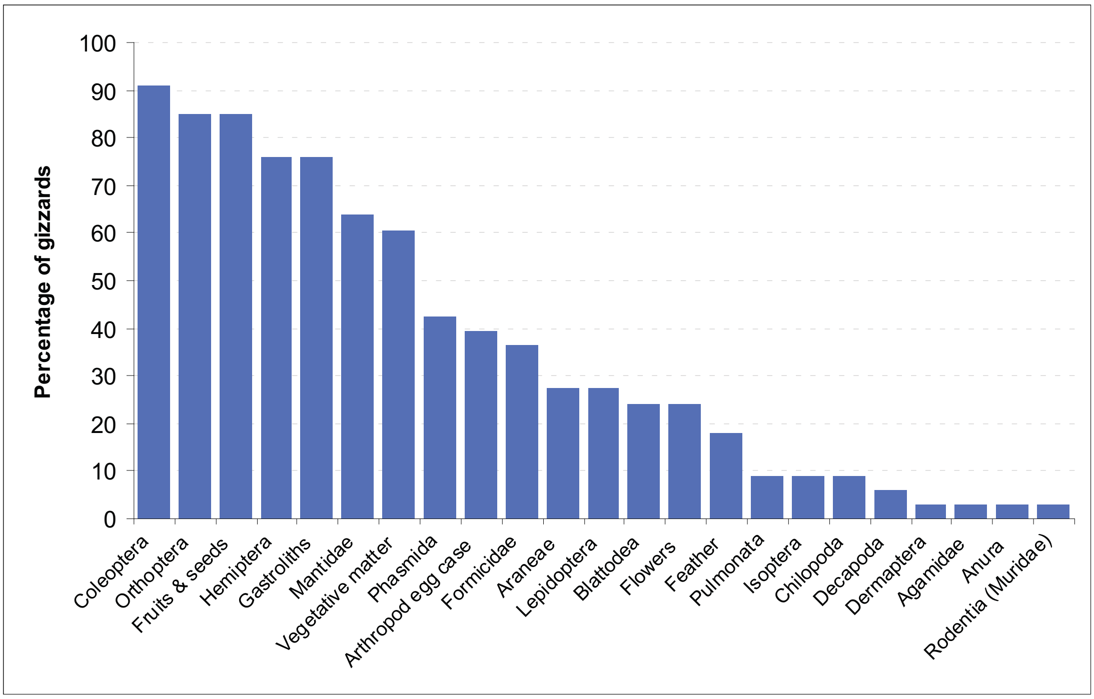


Figure 6.2: Percentage of gizzards (n=33) containing each main taxon of food items consumed by bustards.

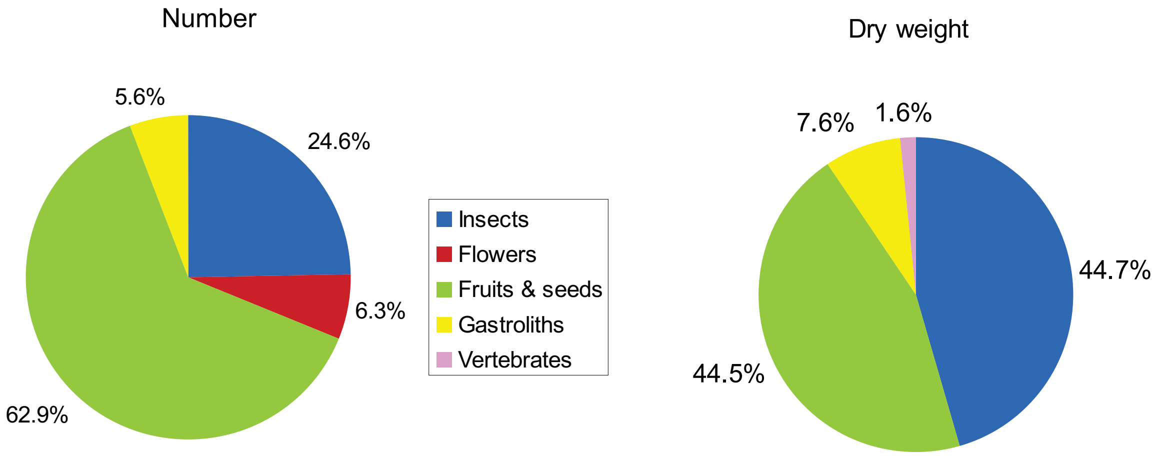


Figure 6.3: Percentage of general bustard food categories as a function of total numbers (left) and proportion by dry weight (right) present in 33 gizzards. Other taxa that nominally contributed to gizzard contents (i.e. <1%), not depicted here included Arachnida, Crustacea, Myriapoda, Gastropoda and general vegetative matter.

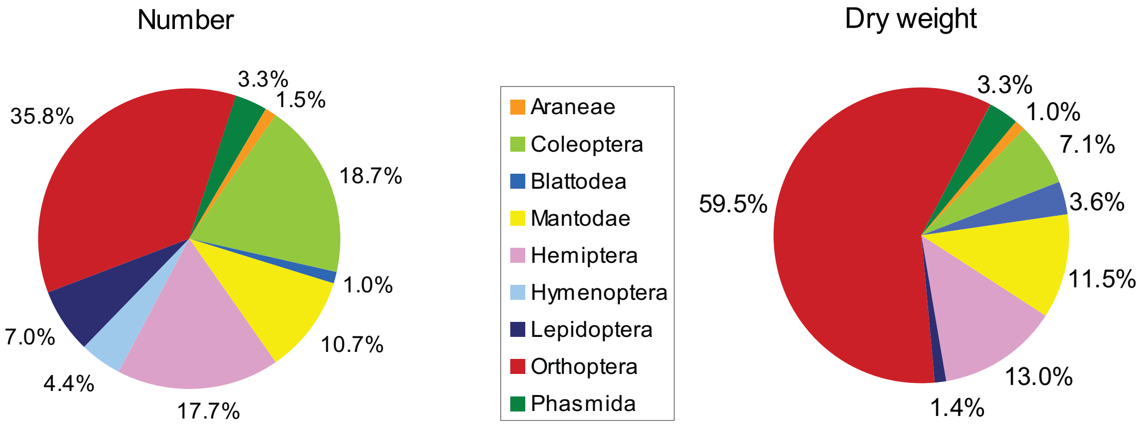


Figure 6.4: Percentage of main invertebrate taxa consumed by bustards as a function of total numbers (left) and proportion by dry weight (right) present in 33 gizzards. Other invertebrate taxa that nominally contributed to gizzard contents (i.e. <1%) not depicted here included Crustacea, Myriapoda, Isopoda, Dermaptera and Gastropoda.

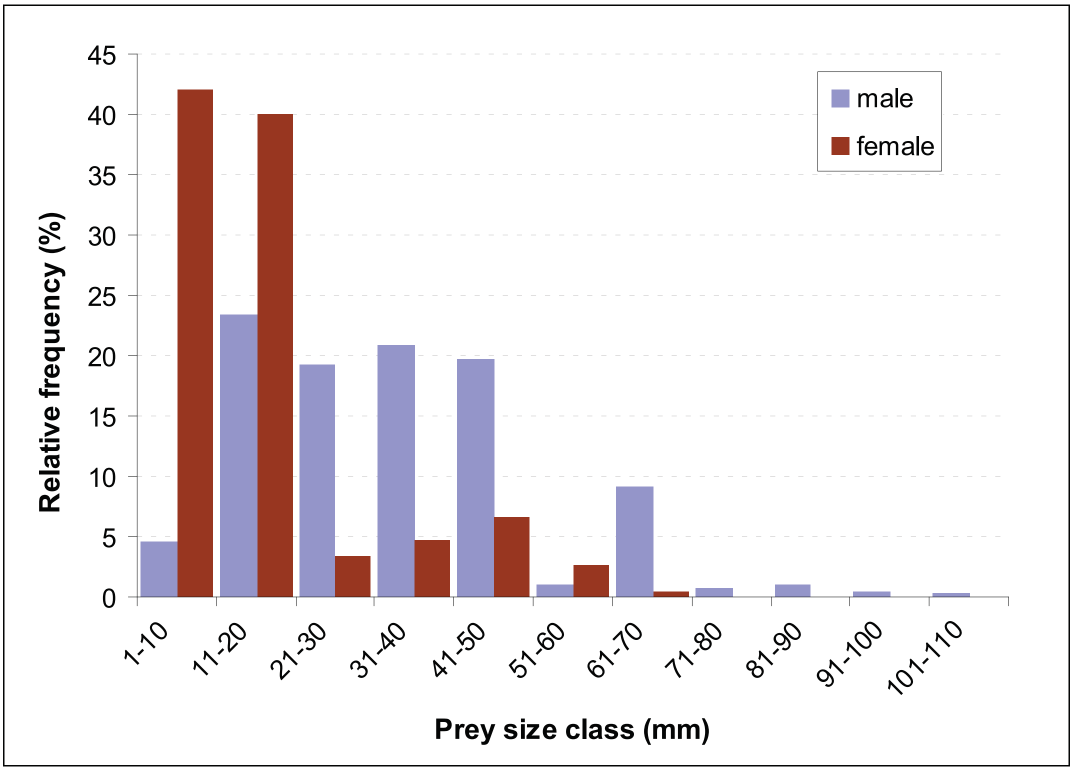


Figure 6.5: Frequency distribution of arthropod prey lengths consumed by male (n=15) and female (n=5) bustards.

Similarity in diet composition based on abundance of food items between gizzard collection locations and fire history was depicted in a three-dimensional ordination (Fig. 6.6). The north Kimberley sites were generally separated from the other sites in ordination space, although there was some overlap. There were too few samples from each region outside the Kimberley to make meaningful comparisons between individual regions. However, an ANOSIM comparing Kimberley to non-Kimberley sites supported the separation noted in the ordination (R-statistic = 0.30, $p < 0.01$). An analogous comparison of sites based on whether they were recently burnt or not yielded an R-statistic of 0.13, but fell just outside an $\alpha = 0.05$ level of significance ($p = 0.06$). It is important to note that there was a notable overlap between regions and fire history. That is, most sites in the Kimberley region were burnt while sites outside the Kimberley were largely unburnt. This was a coincidence and a result of the largely opportunistic rather than systematic collection of gizzard samples. It confounds interpretation of results because differences in diet cannot be confidently discriminated as a function of region or fire history, and there were too few samples in any one region with sufficient burnt versus unburnt sites to conduct an analysis of the effect of fire locally.

A SIMPER analysis examining the relative contribution of food items to differences between the Kimberley and all other regions revealed that the abundance of fruits and seeds of *Grewia retusifolia* and *Cassytha* sp. closely followed by the Orthoptera and Mantodea, were the most influential contributors to regional dissimilarity in diet composition (Table 6.5). That is, there were more *Cassytha* fruits and mantids, and less *Grewia* fruits and orthopterans, in the diets of individuals in the Kimberley than in other regions. However, the effect was relatively weak suggesting that most items were found at both Kimberley and non-Kimberley sites and that there were no clearly discriminating food items between the regions.

There was a significantly larger variety of food items consumed by bustards in the Kimberley region and in recently burnt habitats than in non-Kimberley sites and unburnt habitats as measured by both the number of taxa (region: $F = 9.6$, $p < 0.01$; fire: $F = 5.2$, $p < 0.05$) and the Shannon-Weiner diversity index (region: $F = 4.1$, $p < 0.05$; fire: $F = 6.2$, $p < 0.05$) (Table 6.6). Pielou's evenness index was not significantly different between sites or fire histories. Nevertheless, the index values were reasonably low ranging from 0.42 to 0.51 (Fig. 6.7), reiterating that although the diet of bustards across sampling regions and fire histories was broad, some foods tended to dominate while many foods were only taken in small proportions.

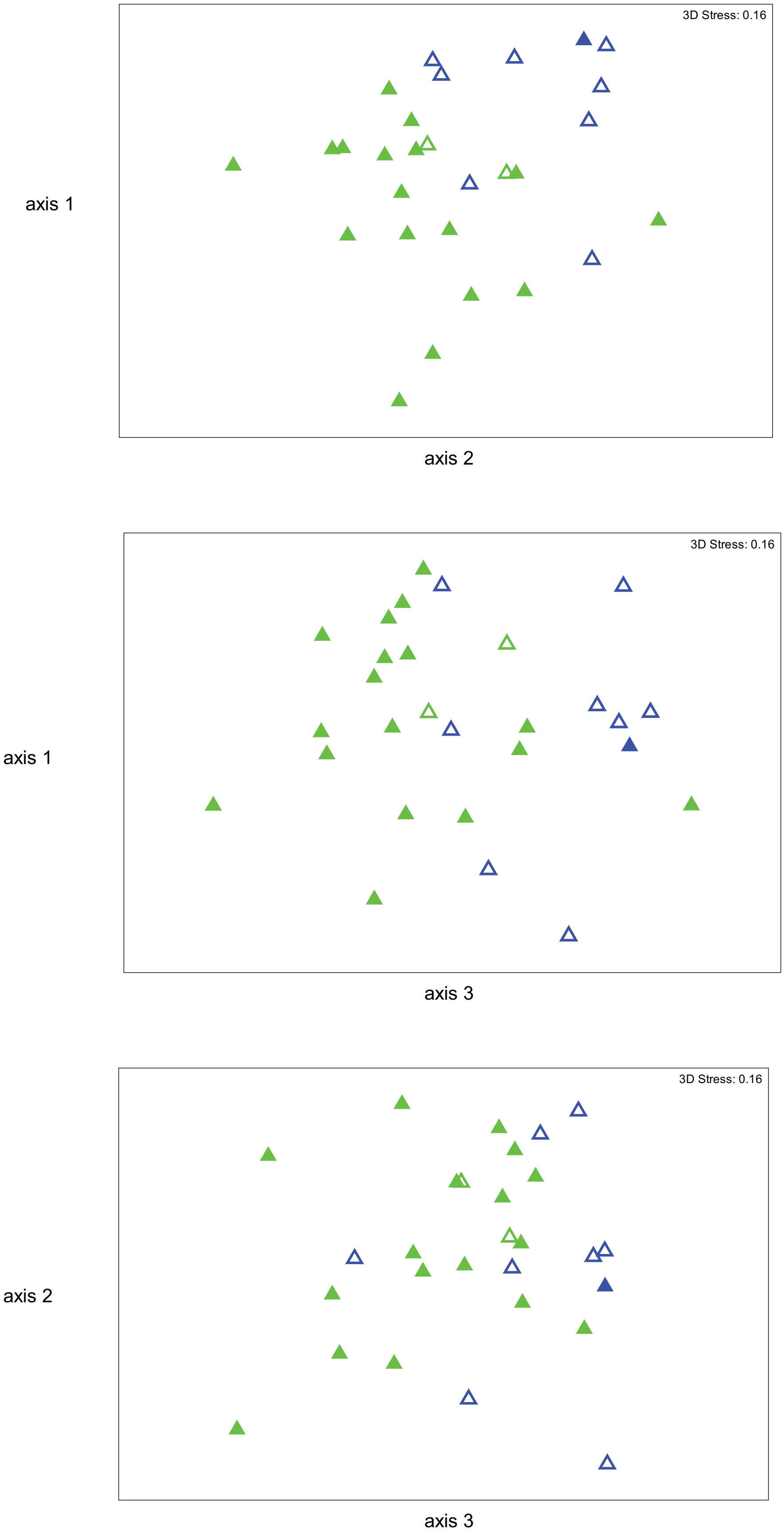


Figure 6.6: Three dimensional ordination of all gizzard samples based on abundance of major food taxa (fourth-root transformed abundance data). Regions are denoted by colour (green = North Kimberley; blue = all other regions). Samples from burnt habitats are solid shapes; unburnt are open shapes.

Table 6.5: Food items (in decreasing order of importance) contributing most to the differences between Kimberley and non-Kimberley samples. Average dissimilarity between groups = 57.5%.

Taxon	Mean Kimberley	Mean non-Kimberley	Dissimilarity (%)	Cumulative dissimilarity (%)
Grewia retusifolia (seeds)	2.57	2.94	7.18	12.48
Cassytha capillaris (seeds)	1.76	0.41	6.48	23.75
Orthoptera	1.21	1.99	5.47	33.26
Mantidae	1.21	0.31	4.68	41.4
Gastroliths	1.42	0.90	3.99	48.34
Hemiptera	1.13	0.54	3.4	54.25
Beetles	1.62	1.23	3.03	59.52
Phasmida	0.66	0.23	2.67	64.17
Blumea sp.(flowers)	0.78	0	2.54	68.58
Pupae or egg case	0.62	0.32	2.52	72.95
Lepidoptera	0.58	0.21	2.49	77.28
Cucumis melo (fruits)	0.41	0.58	2.39	81.44
Formicidae	0.57	0.19	2.34	85.51
Cicadoidea	0.32	0.36	2.32	89.53
Araneae	0.43	0.13	1.62	92.34

Table 6.6: One-way ANOVA results for comparisons of three measures of food taxa diversity (number of taxa, Pielou's evenness index (J') and Shannon-Weiner diversity index (H')) between sites in the Kimberley region versus all others and between sites that were burnt and not burnt. Significant results (α < 0.05 level) are indicated in bold.

	Number of taxa			Evenness (J')			Diversity (H')		
	F	df	P	F	df	P	F	df	P
Region	9.6	1	**0.004**	0.9	1	0.34	4.1	1	**0.034**
Fire	5.2	1	**0.03**	3.9	1	0.06	6.2	1	**0.019**

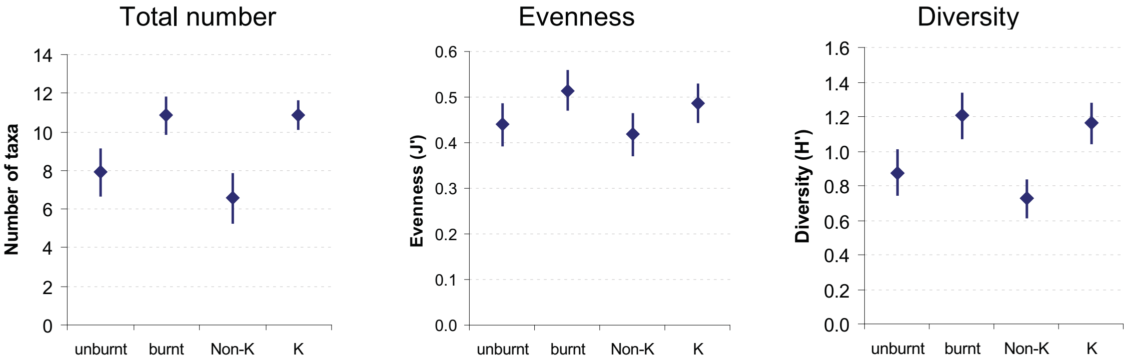


Figure 6.7: Total number, Evenness (J') and Diversity (H'), including standard errors, of food taxa recorded from 33 gizzards of the Australian Bustard according to region (K = Kimberley; non-K = all other regions) and whether the sample was collected from recently burnt or unburnt habitat.

Activity patterns

A total of 12,845 instantaneous observations of behaviour were made during 353 separate observation bouts of individual bustards. Of these, 4436 observations were made in the early-mid dry season (EMD), 4690 in the late dry season (LD) and 3749 in the wet season (W).

During the early-mid dry season foraging and resting were the two main activities of bustards, with bimodal peaks of activity in the morning and afternoon (Fig. 6.8). As the dry season progressed, these peaks became more pronounced, with more resting and less foraging during the middle parts of the day. During the late dry bustards also spent more time in locomotion. This was largely manifested by time spent walking rather than flying to and from resting and foraging sites, and was presumably a response to warmer temperatures at this time of year. Preening was more pronounced during the wet season, particularly for females. Antagonistic behaviours were uncommon, but when they occurred they were largely restricted to mature males during the breeding periods of the late dry and wet seasons. On a small number of occasions, mature males directed this behaviour towards subordinate males.

A detailed assessment of time spent foraging between seasons, sexes and at different times of the day revealed several notable differences between all factors and for all pair-wise interactions of factors (Table 6.7). Collectively, bustards spent more time foraging in the early-mid dry season than in the wet and late dry seasons ($F = 36.6$, $p < 0.001$). Mature males spent less time foraging than subordinate males and females ($F = 17.5$, $p < 0.001$), and foraging occurred less often in the middle of the day than in the morning and afternoon ($F = 25.1$, $p < 0.001$).

Table 6.8 lists the results of *post-hoc* tests identifying notable interactions between factors. In the late dry and wet seasons mature males spent considerably less time foraging compared to the early-mid dry season and compared to females and subordinate males. Subordinate males also spent more time foraging in the early dry than in other seasons. However, there were no such differences between any seasons for females. Time spent foraging in the middle part of the day was lower in the late-dry season than in the early-mid and wet seasons.

By the late dry season and during the wet season, mature males spent large proportions of the early morning and late afternoon displaying, largely at the expense of foraging. They also spent more time displaying once the rains began in the wet season compared to the late dry season ($F = 17.8$, $p < 0.001$) (Tables 6.9 & 6.10; Fig. 6.9).

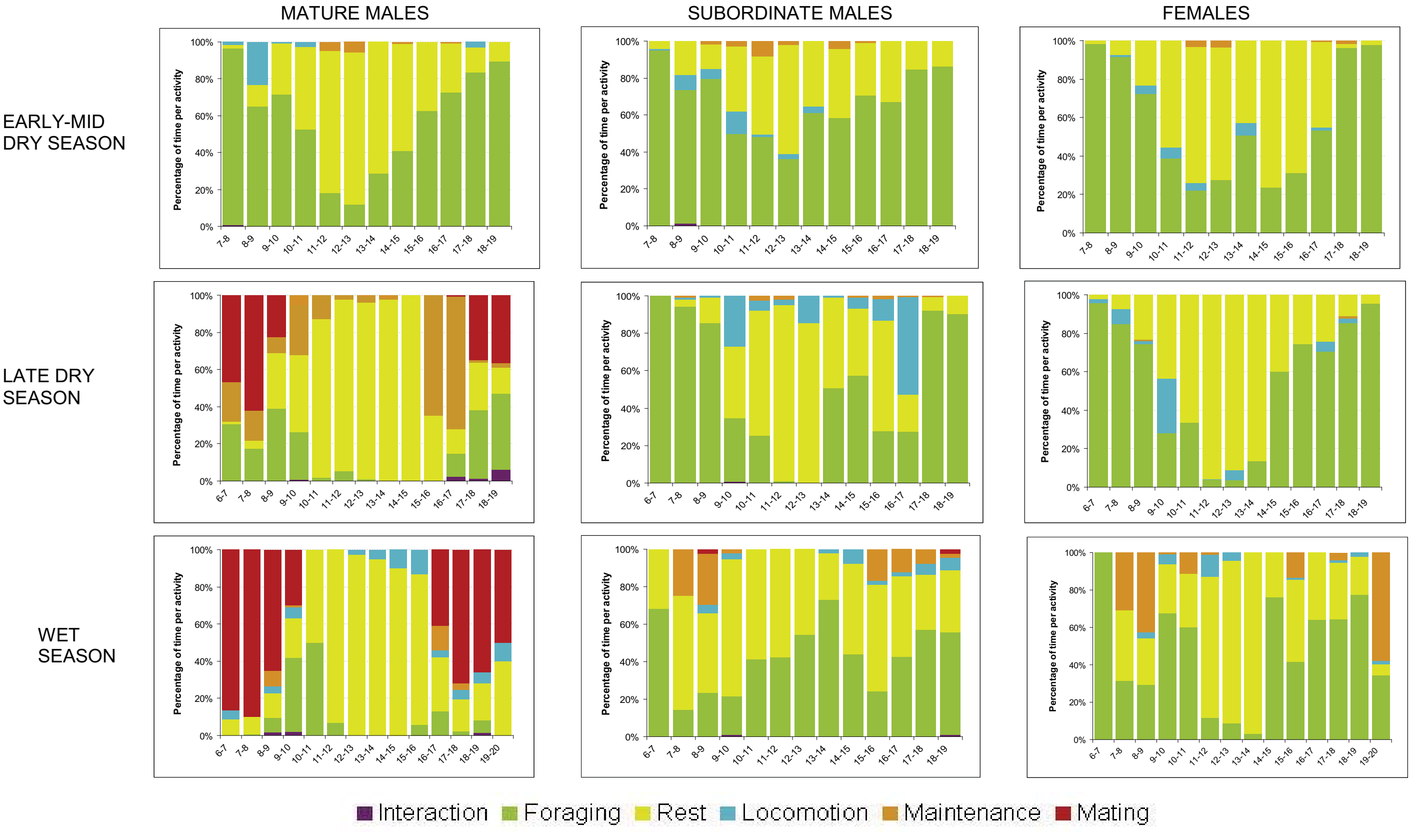
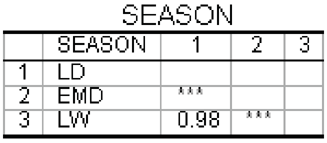


Figure 6.8: Percentage of daylight hours allocated to different behaviours by mature male, subordinate male and female bustards at the DDRF during three periods of the year (Early-mid dry = April – August; Late dry = September – November; Wet season = December – March). X-axis for all charts denotes time of day.

Table 6.7: Three-way ANOVA results comparing time spent foraging according to season, time of day and sex category and their interactions (P = * <0.05, ** <0.01, *** <0.001).

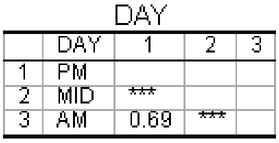
Effect	df	F	p
Intercept	1	879.89	***
SEASON	2	36.64	***
DAY	2	25.05	***
SEX	2	17.55	***
SEASON*DAY	4	8.41	***
SEASON*SEX	4	4.77	***
DAY*SEX	4	3.10	*
SEASON*DAY*SEX	8	1.17	0.313

Table 6.8: Tukey HSD post-hoc test results for analyses presented in Table 6.7 (‘Season’: EMD = early-mid dry season, LD = late dry season, W = wet season; ‘Sex’ category: M1 = mature male, M2 = subordinate male, F = female; Time of ‘Day’: AM = morning period, MID = midday period, PM = late afternoon period) (P = * <0.05, ** <0.01, *** <0.001).



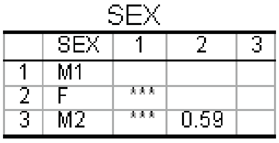
SEASON

	SEASON	1	2	3
1	LD			
2	EMD	***		
3	LW	0.98	***	



DAY

	DAY	1	2	3
1	PM			
2	MID	***		
3	AM	0.69	***	



SEX

	SEX	1	2	3
1	M1			
2	F	***		
3	M2	***	0.59	

SEX x SEASON

	SEASON	SEX	1	2	3	4	5	6	7	8
1	LD	M1								
2	LD	F	**							
3	LD	M2	*	0.963						
4	EMD	M1	***	0.420	*					
5	EMD	F	***	0.848	0.102	0.996				
6	EMD	M2	***	0.040	***	0.987	0.617			
7	W	M1	0.780	***	***	***	***	***		
8	W	F	***	1.000	0.937	0.334	0.791	**	***	
9	W	M2	0.076	0.901	1.000	**	0.054	***	**	0.847

DAY x SEASON

	SEASON	DAY	1	2	3	4	5	6	7	8
1	LD	PM								
2	LD	MID	***							
3	LD	AM	0.934	***						
4	EMD	PM	***	***	*					
5	EMD	MID	1.000	***	0.738	***				
6	EMD	AM	***	***	**	1.000	***			
7	W	PM	1.000	***	0.715	***	1.000	***		
8	W	MID	0.976	*	0.195	***	0.985	***	0.998	
9	W	AM	0.261	0.395	**	***	0.197	***	0.410	0.896

SEX x DAY

	DAY	SEX	1	2	3	4	5	6	7	8
1	PM	M1								
2	PM	F	***							
3	PM	M2	0.135	0.761						
4	MID	M1	0.303	***	***					
5	MID	F	0.963	***	**	0.882				
6	MID	M2	1.000	***	0.138	0.070	0.739			
7	AM	M1	1.000	***	**	0.544	0.999	0.991		
8	AM	F	**	0.998	0.977	***	***	***	***	
9	AM	M2	0.150	0.595	1.000	***	**	0.149	**	0.923

Table 6.9: Two-way ANOVA results assessing time spent displaying by mature males according to season and time of day and their interaction (P = * <0.05, ** <0.01, *** <0.001).

Effect	**df**	**F**	**p**
SEASON	1	17.85	***
DAY	2	15.83	***
SEASON*DAY	2	3.47	*

Table 6.10: Tukey HSD post-hoc test results for analyses presented in Table 6.9 ('Season': LD = late dry season, W = wet season; AM = morning period, MID = midday period, PM = late afternoon period) (P = * <0.05, ** <0.01, *** <0.001).

	SEASON	DAY	1	2	3	4	5
1	LD	PM					
2	LD	MID	0.488				
3	LD	AM	0.773	*			
4	LW	PM	***	***	*		
5	LW	MID	0.894	1.000	0.371	**	
6	LW	AM	***	***	**	1.000	***

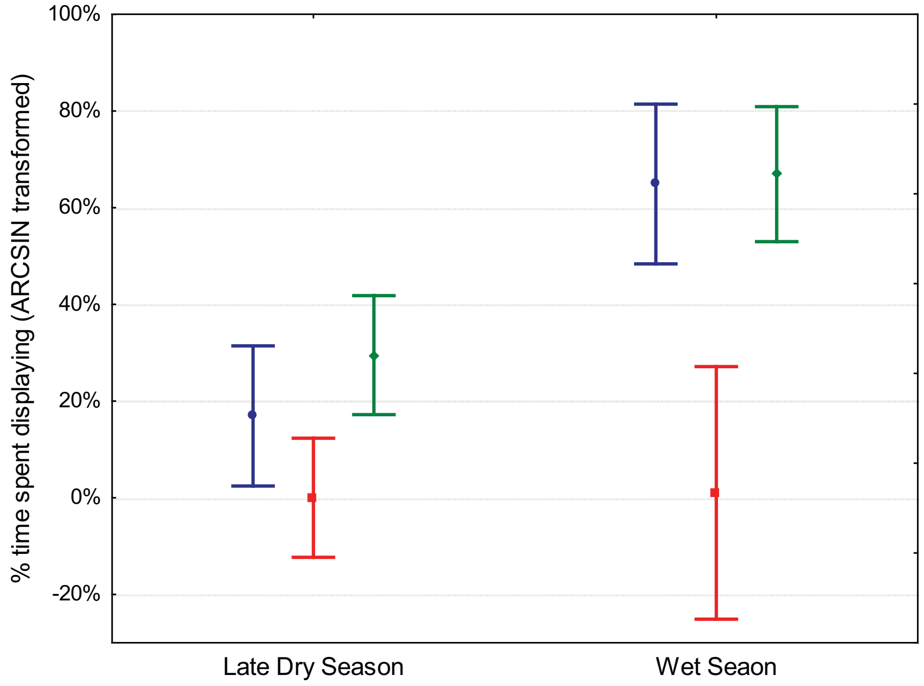


Figure 6.9: Percentage of time spent displaying by mature male bustards in the late dry and wet seasons according to three periods of the day (blue = late afternoon; red = midday; green = morning). Data were arcsine-transformed. Included are the 95% confidence intervals.

DISCUSSION

Diet of the Australian Bustard

The northern tropical savannas are characterised by a markedly seasonal rainfall, with a relatively short, but intense, summer wet season, and a long dry season. This variability results in substantial seasonal fluctuations in the relative availability of food resources. For the northern biota, this generally equates to periods of excess towards the end of the wet season, and, as the dry season progresses, a time of increasing resource depletion and hardship (Woinarski *et al.* 2005). Productivity may also vary significantly from year to year, with variation in the timing, duration and intensity of rainfall governing the subsequent food resource availability for the forthcoming dry season. To cope with this intrinsic variation, the strategies employed by the biota of northern Australia range from, moving to more productive areas or habitats, to shifting diets, tolerating lean times, or changing activity rates (Woinarski *et al.* 2005). Bustards in northern Australia may adopt several of these strategies to varying degrees depending on particular circumstances and requirements. For example, they may switch between different foods depending on availability, undertake local or broad-scale movements to more resource-rich patches, or they may opt to tolerate difficult periods.

Like most bustard species, the Australian Bustard has a broad, omnivorous diet, suggesting that diet switching may be an important means of coping with variation in food resources. Although the present study was confined to the mid-late dry season in northern Australia, the remarkable range of foods consumed matches, and in some cases extends, the cumulative breadth of foods recorded in the literature for the species (Barker and Vestjens 1989; Marchant and Higgins 1993). Despite the broad diet, however, bustards often harvested specific foods preferentially. In this study, many gizzards contained large proportions of certain foods such as grasshoppers, beetles or *Grewia* fruits, often with only nominal amounts of other foods. Other reports, though based on anecdotal observations, have noted selective feeding on ground weevils (Curculionidae) in Western Australia (McMillan 1950), and grasshoppers in the summer in Victoria (Froggatt 1921). Similarly, detailed dietary analyses of other species have revealed that the diet of the Houbara Bustard was often dominated by tenebrionid beetles (Tigar and Osborne 2000), while Great Bustards largely relied on plant foods, particularly alfalfa, at certain times (Lane *et al.* 1999).

Ultimately, the diet of bustards depends on the relative availability of different food resources and their preferences or requirements for particular foods at specific times. The intensity, timing, duration and synchrony of arthropod reproductive efforts, and the various phenological phases of food resource plants, including the persistence of these foods following production, determine food availability. However, the relationship between the relative availability of food resources and their proportional use by bustards is often complex and not always direct. In this study, interpretation of the importance of specific foods in relation to their seasonal availability is limited because of the collection of gizzard samples during one general part of the year. Nevertheless, the mid-late dry season is an important period for the biota of the wet/dry tropics. Notionally, it is the leanest period of the year in terms of food resource and water availability (Woinarski *et al.* 2005). Yet for bustards, the mid-late dry season is a critical period, marking the beginning of the breeding season in the north. According to this study, the diet of bustards at this time was dominated by insects of four main groups (Coleoptera, Orthoptera, Hemiptera and Mantidae), and the seeds and fruits of *Grewia retusifolia* and *Cassytha* sp. The fruiting phases of these food plants in the northern savannas are broad, with fruits generally occurring or persisting throughout the year (Chapter 3, Cowie, in prep. Brock 1993). These resources are likely to act as staple foods although their relative importance may vary in relation to the availability of other foods. Such a possibility has been demonstrated for other omnivorous species. During a 10 year period in a region of arid Western Australia, the main fruits consumed by emus (which have a similarly broad diet and foraging ecology to bustards) varied substantially from year to year in their abundance, but in any given year at least some fruiting plants produced good crops and were particularly important to emus (Davies 1976; 1978). Because emus are catholic in their diets, there was always food available to them because they could readily switch between different foods (Davies 1978).

Seasonal availability and use of the main arthropod taxa in the diet of bustards appears more idiosyncratic. At both Kidman Springs in the Victoria River District and the Douglas-Daly Rivers region, peak abundance of the smaller sized arthropod taxa, such as the beetles preferred by female bustards, was in the late dry season (Chapter 3). In contrast, the availability of the larger insects preferred by male bustards was generally lowest in the late dry season, peaking instead in the late wet/early dry season. If it can be assumed that a similar pattern of resource availability occurs over the broader savanna landscape (including the regions from where gizzards were collected in this study) then during the late dry season in this study males still appeared to select the rarer, but larger prey over the smaller more abundant prey. There are two related explanations for this disparity between the sexes. Fundamentally, bustards exhibit extreme sexual size dimorphism: males are significantly larger than females with larger bill gapes and sizes, so are physically able to collect and consume larger prey. Secondly, the amount of time allocated or available for foraging to breeding males is notably less than for females because of the significant proportion of time males spend displaying. Males therefore need to be more efficient in their foraging when they have the opportunity. It may be advantageous for them to target fewer but larger prey, rather than the more abundant but smaller prey that females prefer. Furthermore, the relative amount of food consumed and net energy intake of males is likely to be much lower during the breeding season than for females, as manifested by their reliance on fat stores and a significant loss of weight and body condition over the course of the breeding season (Fitzherbert 1978; 1982).

A preference for specific types of foods may also be related to particular requirements at specific times. For example, many birds have an increased need for protein-based foods prior to and during the breeding season (Reynolds *et al.* 2003). The breeding seasons of birds in the northern wet/dry tropics are highly variable, although there is a broad correspondence between the timing of breeding and the maximum abundance of their main food (Noske and Franklin 1999). Smaller insectivorous species, taking smaller prey, tend to be mainly dry season breeders, while larger species are principally late dry/early wet season breeders, when larger prey are most abundant (Noske and Franklin 1999). Noske and Franklin (1999) include omnivores among this latter category, and this is also the time when bustards breed in the north. High protein-based foods are important components of the diet of many other bustard species leading up and extending into the breeding season. For example, the proportion of animal matter in the diets of Little Bustards *Tetrax tetrax* in western France (Jiguet 2002), the Great Bustard *Otis tarda* in western Europe (Lane *et al.* 1999; Palacios *et al.* 1975), and the Houbara Bustard *Chlamydotis undulata* in Pakistan (Nadeem *et al.* 2004; Roberts 1992), all increase as the breeding season progresses. In the late dry season in the wet/dry tropics, as the breeding season commences, the small insects favoured by female bustards peak in abundance, and their availability remains high as young are reared. For males, the conclusion of the breeding season coincides with the highest abundance of their most preferred foods (grasshoppers and other large insects), just when they need large quantities of protein and fat rich foods to recover the significant weight and body condition sacrificed over the breeding season.

The dietary requirements or preferences of bustards may also have significant implications for the dynamics of their movements. Bustards are regarded as highly mobile, apparently readily moving in response to habitat conditions (Downes 1982; Marchant and Higgins 1993). However, these movements and their triggers are poorly defined and understood. They may occur as a response to resource scarcity when neither diet switching nor tolerance of food lows is viable, or as a response to greater food availability elsewhere, for example, movements in response to fires or to large grasshopper or rodent outbreaks (Marchant and Higgins 1993). While it may be readily apparent that bustards move and congregate at such extreme or noteworthy events, relating the movements or distribution patterns of bustards to more subtle or typical variations in food resource availability is generally difficult, and often contradictory. For example, as demonstrated in Chapter 4, the relationship between male bustard numbers in the Victoria River District is opposed to the availability of their preferred food resources (i.e. grasshoppers and other large insects). Numbers of male bustards were high when large insects were scarce in the late dry season, but were lowest when this food was most abundant in the early dry season. Other similar studies have had equally ambiguous results. For example, the food resource availability of Houbara Bustards in Saudi Arabia peaked when Houbara numbers were at their lowest (Seddon and Van Heezik 1996). In other cases, the vagaries of altering food preferences complicate matters; only a small proportion of the diet of Great Bustards during the early summer in Spain consisted of invertebrates even though they reached their highest abundance at this time (Lane *et al.* 1999). Such complexity and apparent contradictions exist even for species with far less complex diets. An assessment of the relationship between rainfall and food availability and the movements and breeding of an obligate granivore, the Namaqua Sandgrouse *Pterocles namaqua*, found significant regional differences in responses to food availability (Lloyd *et al.* 2001). Periods of peak food availability were not consistently associated with the breeding and movements of this species.

The ambiguity of such relationships, and the nuances of the bustard's diet, suggests factors other than proximate food availability have significant influences on bustard movements and distribution patterns. In addition, the other coping mechanisms that bustards employ in response to fluctuating food resources (i.e. diet switching or tolerance of lows), indicates a more sophisticated approach towards assessing their responses to food resource availability is required. Such an approach would need to at least incorporate the relative seasonal importance of different food resources to the bustard (including the energetic and nutritional requirements of the species); include a thorough assessment of how resources vary both spatially and temporally; and consider what other factors, such as predation pressure, moult, etc., influence movement and distribution patterns. These factors complicate the utility of the Australian Bustard as a model for assessing the movements of mobile, nomadic species, but nevertheless highlight the inherent complexity of faunal responses to climatic variability – the broader implications of which will be discussed further in the concluding chapter.

Although fire is known to be important to bustards (Marchant and Higgins 1993), interpreting its potential impact on the diet of bustards in this study was confounded by the coincidental juxtaposition of Kimberley and non-Kimberley samples with burnt and unburnt habitats, making it difficult to separate the relative influence of fire from regional differences in diet. Furthermore, although most bustards were recorded to have been harvested from recently burnt or unburnt habitats, it was not known how patchy the fires were, and to what degree bustards were foraging on burnt versus adjacent unburnt habitats prior to their collection. This possibility, however, may explain why diet was significantly more diverse for the Kimberley/burnt samples compared to the non-Kimberley/unburnt samples. At non-Kimberley sites foraging is likely to have been restricted to generally homogeneous, unburnt habitats. By comparison, if bustards were foraging in both burnt and unburnt habitats in the Kimberley, then they may have been exposed to a greater variety of food resources. However, it should be noted that the flowering and fruiting of potential plant food species for bustards have been shown to be adversely affected by early to mid-dry season fires in the region (Vigilante and Bowman 2004). This suggests that patchy, mosaic-based burning regimes are important for bustards so that a variety of resources are accessible at any given time (Vigilante and Bowman 2004).

Unusual foods

The consumption of several unusual or previously unrecorded foods, particularly the cane toad, warrants further comment. Cane toads, having been introduced to Australia, adversely affect some predator species, prey species and compete with native species for food resources. The susceptibility of a species that predates on cane toads is related to its physiological tolerance to the toad's bufotoxin and to its risk of exposure (Van Dam *et al.* 2002). While the toads are known to kill goannas and mammals (Covacevich and Archer 1975; Freeland 1984; Woinarski *et al.* 2007), the potential effects on birds have not been thoroughly investigated. However, several accounts suggest that there are bird species that eat cane toads without apparent ill effects, including the Common Koel, Black Kite, Tawny Frogmouth, Bush Thick-knee and the Australian Bustard (Covacevich and Archer 1975; Van Dam *et al.* 2002). Some may be immune to cane toad toxin, while other species eat only the non-toxic parts of the toad (Covacevich and Archer 1975; Van Dam *et al.* 2002). In this study, on two separate occasions, adult male bustards were observed to have consumed whole medium-sized (6-10 cm in length) cane toads. These observations are corroborated by Aboriginal people from the Gulf of Carpentaria region of the Northern Territory who have reported that gizzards of harvested bustards have sometimes been full of young cane toads (Joe Morrison, pers. comm.) (note that the majority of gizzards analysed in the present study were from regions where there were no, or few, cane toads at the time of collection). Finally, the consumption of sap from the trunks or branches of woody plants has not been previously recorded in the literature, although this is a food source of bustards known to Aboriginal people (Bill Harney, pers. comm.), and has been documented as a common food of the closely related Arabian Bustard *Ardeotis arabs* in parts of its range (Collar 1996).

Activity patterns

Bustards exhibited a notable bimodal pattern of activity that is common among diurnally active fauna, particularly birds (Hidalgo De Trucios and Carranza 1991; Jacquet and Launay 1997; Martinez 2000; Stirrat 2004). Both foraging and display were the two most common 'active' behaviours that occurred at higher frequencies in the morning and late afternoon. Such patterns have been observed for other bustard species (Hidalgo De Trucios and Carranza 1991; Jiguet and Bretagnolle 2001; Martinez 2000). Bimodality is often a response to daily temperatures whereby individuals avoid activity at the hottest times to avoid heat stress and excessive water loss. Bustards tended to rest in the middle of the day especially during the late dry season, the hottest time of the year. A bimodal pattern of activity was also evident during the wet season, though at this time bustards were more likely to forage in the middle of the day and display for longer, particularly on overcast days when ambient temperatures were lower.

Foraging and resting were the dominant behaviours of bustards for much of the year. The relative proportions of time spent foraging remained consistent among females, but varied for males between seasons. Display behaviour usurped foraging as the dominant active behaviour among mature males in the late dry and wet seasons, while subordinate males also spent less time foraging in these seasons than in the early-mid dry season. Significant differences in availability of food resources between seasons may influence time spent foraging, and larger males, because of their greater energy requirements, may be more susceptible to food resource fluctuations. As a general rule, if lower food availability or accessibility decreases foraging efficiency, then it may be expected that time spent foraging would increase as food resources decrease (Stephens and Krebs 1986; Uttley *et al.* 1994). This occurs among common and widespread species in the seasonal wet-dry tropics of the Northern Territory. For example, Agile Wallabies *Macropus agilis* alter their diet and foraging patterns to cope with the marked seasonal variation in food quality and availability (Stirrat 2002). Although their scope for switching between different foods is reasonably limited (since they rely on few food types), to compensate for the decline in food quality, they increase their foraging time in the dry season (Stirrat 2004). Similarly, among other bustard species, Martinez (2000) found that male Great Bustards in Spain spent more time foraging in winter when resources were lowest. Foraging subsequently decreased sharply in the spring when resources increased. In contrast, in the present study, both mature and subordinate male Australian Bustards spent more time foraging in the early-mid dry season, when resources peaked, than in the late dry season when resources are lowest.

Although the only detailed research on the Australian Bustard prior to the current study had been based on a captive population in southern Australia, Fitzherbert’s (1978) study is an instructive contribution to the species biology that helps explain the apparent paradox noted above. In captivity, as in northern Australia, male bustards spent considerable time displaying during the breeding season at the expense of foraging. Displaying occurred over several months, and at times, accounted for as much as 95% of the daily routine. Consequently, as the breeding season progressed, males exhibited significant weight loss (Fitzherbert 1978; 1982). Weights were lowest at the end of each breeding season before gradually increasing after displaying ceased. Although it was not possible to consistently weigh males in the field in this study, significant weight variations are assumed for male bustards in the north. Indeed, the physical condition of males at the end of the breeding season was often visibly poor (pers.obs.), and Aboriginal people in northern Australia avoid hunting bustards in the wet season because they report that the birds have little fat and are often infested with internal worms at this time. It appears then that male Australian Bustards spend significantly more time foraging in the non-breeding season, when foods are abundant, in order to accumulate large fat reserves in preparation for a relatively long breeding season when efforts are devoted to attracting mates. Although subordinate males do not generally display (therefore are free to forage and do not require fat reserves to the same extent as mature males do), they too spend less time foraging in the breeding season (although still comparatively more than mature males). As these males mature their foraging strategies, and associated patterns of seasonal weight variation, more closely resemble those of larger males. Indeed, as males grow they devote progressively more time to display (Fitzherbert 1978).

The apparent discrepancy between male Great Bustards in Spain and Australian Bustards in northern Australia in terms of foraging time in relation to food availability may be explained as a response to different environmental conditions, and the subsequent timing and duration of the breeding period. The breeding season of Great Bustards in western Europe is comparatively short, lasting from late March to mid-May (Hidalgo De Trucios and Carranza 1991; Morales 1999; Morales *et al.* 2003) but follows the winter, when resource availability and temperatures are low. At this time males must forage intensively not only to satisfy daily energetic costs but to build body condition in preparation for commencement of displaying at leks. They subsequently forage less in the breeding season because they are displaying, but are also likely to forage more efficiently because of high resource availability. In contrast, the breeding season of Australian Bustards is longer in northern Australia and its commencement coincides with general lows in resources. Males here therefore need to replenish fat reserves lost in the previous breeding season and prepare for the following season by making the most of high resource availability while they can. They subsequently forage less in the late dry season when they are displaying and when food resources are low by relying on fat reserves.

It is noteworthy that contrary to reports that bustards begin displaying after rains in other regions (e.g. Downes 1982a; Marchant and Higgins 1993, and references therein), male Australian Bustards at both Kidman Springs and the Douglas-Daly Research Farm began displaying up to two months prior to first rains. This suggests that bustards are well attuned to the predictability of rainfall in the north, timing their breeding season in anticipation of the highly productive period ahead. It also highlights the variable responses of bustards to resource fluctuations across their wider Australian range. The implications of different responses will be discussed in further detail in the concluding chapter.

Chapter 7

Lekking behaviour, display site selection and fidelity by the Australian Bustard in the tropical savannas

Bruce Doran

"Few bird-observers have been privileged to see the love-display of the Wild Turkey"

A.H.E. Mattingley 1929

Chapter 7

Lekking behaviour, display site selection and fidelity by the Australian Bustard in the tropical savannas

INTRODUCTION

Birds exhibit a variety of mating systems that range from faithful monogamy through promiscuity, and include various systems of polygyny (Davies 1991; Ligon 1999). Polygynous mating systems, whereby males mate with several females, account for a small proportion of mating strategies in birds. The most extreme and specialised example of polygyny in birds is lekking. Although there is no unambiguous definition of what identifies a lekking species, a general definition proposes that a lek is a male display aggregation that females visit solely to assess potential mates and for copulation (Hoglund and Alatalo 1995). Four characteristics define 'classical' lekking species:

i) males do not contribute to the care of young;

ii) there is at least some degree of aggregation of displaying males on leks;

iii) females encounter no other resource on the lek other than males, and,

iv) females are free to choose their mates (Bradbury 1981).

In addition, other auxiliary characteristics may be common to lekking species or populations. For example, lekking species often exhibit pronounced sexual dimorphism and sexual bimaturism, males undertake ritualised display and may use exclusive territories that are smaller than a normal home range, and traditional lek sites are often used between seasons and generations (Alonso *et al.* 2000; Bradbury *et al.* 1989a; Bradbury *et al.* 1989b; Hoglund and Robertson 1990; Johnsgard 1994; Lane and Alonso 2001; Morales *et al.* 2001; Widemo 1997).

Leks are described as 'exploded' when males within a display aggregation are separated by considerable distances and aggregation may not be detectable until displaying males are mapped over large areas. Such leks do not fit the classical lek mould because males may hold territories within which females may forage and nest, potentially violating the third characteristic listed above. Where these male display territories hold critical resources for females that are defended they are said to be resource-based leks

(Jiguet *et al.* 2000). Exploded lekking occupies a position between classical and resource-based leks and appears to be particularly widespread among the Otididae family (Fitzherbert 1978; Gaucher 1995; Morales *et al.* 2001; Osborne and Alonso 2000).

The Australian Bustard is regarded as primarily employing exploded lekking as its mating system (Fitzherbert 1978; Morales *et al.* 2001). However, there have been no studies of the breeding biology of the Australian Bustard in the field, and some have suggested the species may adopt variable strategies across its range, including monogamy (Marchant and Higgins 2001). Many bird species, including several bustards, are known to exhibit pronounced intra-specific variation in the adoption of particular mating strategies (Carranza *et al.* 1989). Such variation may depend on factors such as resource distribution, population density, female dispersal and habitat stability, such that a species, population or even individual, may exhibit different strategies across its range at different times (Carranza *et al.* 1989; Hoglund and Alatalo 1995; Jiguet *et al.* 2000; Ligon 1999; Morales *et al.* 2001). The widespread distribution of the Australian Bustard across continental Australia and the continent's considerable climatic variability suggests the species may adopt varying breeding strategies opportunistically depending on location and prevailing environmental conditions. In northern Australia, savanna landscapes are highly dynamic, varying seasonally and within seasons and between years as a result of fire, grazing impacts and pulses of primary productivity following rainfall events. Variable environmental conditions are likely to significantly influence habitat and resource availability, which in turn may affect the adoption of specific mating strategies through altering population dynamics and the suitability of habitats that characterise lekking and male display arenas.

In this chapter, I explore the breeding biology of the Australian Bustard at two sites in the northern savannas, with an underlying focus on aspects that may inform or influence the movement patterns of local bustard populations. General observations and anecdotal evidence suggests that bustards in northern Australia exhibit characteristics consistent with exploded lekking (Downes 1982a; Marchant and Higgins 1993). The study centres on examining male breeding behaviour by initially documenting the distribution and characteristics of male display sites. A primary aim is to assess whether bustards exhibit fidelity to specific display sites and leks between breeding seasons and in relation to changing habitat conditions between years. The use of traditional areas has potentially important implications for defining movement strategies, because, if individuals consistently return to specific breeding sites then it is unlikely they undertake irregular, dispersive movements as has been otherwise suggested (e.g. Downes 1982a). Using information presented here, and knowledge of the bustard's biology, I assess the mating system of bustard populations in northern Australia against criteria that define lekking.

METHODS

Study areas

The study was conducted at the two main study sites described in detail in Chapter 3; the Douglas-Daly Research Farm (DDRF) and Kidman Springs in the Northern Territory.

Definitions of terms

Throughout this chapter I use several terms that may be unfamiliar that I define here:

Display site – an area measuring up to approximately 200 m by 200 m at which a male has been observed displaying on at least three separate occasions during a breeding season. The dimensions defined here are subjective, however, and are based on numerous field observations which indicate that males generally use a relatively circumscribed area consistently (pers. obs).

Abandoned display site – a display site that was formerly used but subsequently abandoned. Sites may be abandoned due to change in habitat conditions but be reoccupied if the habitat becomes favourable again.

Opportunistic display – some males, particularly subordinate males with no established display site, often display opportunistically. Displays are rarely repeated in the same area. Opportunistic displaying may be common in habitats that have unusually and often temporarily, high densities of bustards, for example, where bustards aggregate on a burnt patch post-fire.

Display cluster – a close aggregation of two or more displaying males that have visual contact with each other where males are not usually separated by more than 200 metres.

Breeding season – the breeding season for bustards in northern Australia extends from approximately September to March.

Data collection

Display site locations

Display sites were located during the breeding season between 2002 and 2004, and during a single visit to each site in early December 2007. Access to Kidman Springs was restricted during the wet season so that no searches were made in any year between late-December and March. Furthermore, surveys during 2002 were conducted during single visits to each site in late October/early November, therefore these sites were not searched as intensively as in subsequent years. Display sites were located during systematic vehicle-based surveys for bustards as described in Chapter 4 that aimed to cover the entire study site on each survey occasion.

Once display sites were identified these were repeatedly monitored during each visit to each site. Display locations were recorded using a Global Positioning System (GPS) and mapped using ArcMap (Beyer 2004). Locations were considered regular display sites if males were observed displaying on the site on at least three separate occasions during a breeding season. However, limited within-season comparisons could be made at Kidman Springs due to inaccessibility following the commencement of the wet season. The location of opportunistic, one-off displaying was also noted. Since searches for display sites were conducted during vehicle-based surveys that were restricted to roads and tracks it is probable that display sites beyond the visual range of survey routes were not detected. This was considered an issue at Kidman Springs given its larger size and prevalence of wooded habitats. Accordingly, the number of display sites was likely to have been underestimated at this site. However, this was not considered the case at the DDRF where the openness of the site and extensive track network enabled all display sites within the core study area to be located.

Fidelity to display sites

Fidelity to display sites among males was assessed by monitoring identified sites between breeding seasons. An original aim of the study was to capture and wing tag displaying males in order to monitor the use of specific sites by individuals. However, due to problems associated with capture myopathy (see *Discussion* Chapter 5), this component of the study was terminated prematurely. Nevertheless, twelve male bustards were captured, wing tagged and banded during the early stages of the investigation. Three males at Kidman Springs and two at the DDRF were mature males captured at their display sites in 2003. In addition, one mature displaying male was fitted with a GPS satellite tracking unit at Kidman Springs in December 2007 (see below).

Habitat characteristics of display sites

Twenty-two habitat characteristics were measured or derived to describe the structural and biological characteristics of bustard display sites (Table 7.1). A one hectare plot centred in the middle of the display area was considered representative of the display site following preliminary observations of displaying males that suggested the position of a male varied by up to 100-200 metres around a core area. In this respect, these quadrats were the same as those described in Chapter 3. To determine whether display sites differed from surrounding non-display areas, habitat characteristics were measured at plots randomly located between 500-1000 m from each display site. These paired sites were sampled during the early breeding season (September to November) either during 2003 or 2004 (sites identified in 2007 were not included in these analyses). Sampling occurred between study sites in any given year as close as possible in time (within 2 to 3 weeks) to each other to minimise the effect of staggering sampling. Details of sampling methods of specific variables are listed in Table 7.1, and follow the conventions outlined in Chapter 3.

Table 7.1: List of original display site variables measured or derived at each one hectare sampling plot. Sixteen quadrats were located as a 4 x4 grid within the plot. Mean (±SE) were used for cover estimates.

Variable	Variable code	Description
Bare ground cover	BCOV	% of bare ground within 1m^2 quadrat estimated according to a cover scale with eight classes (0, 0-1%, 1-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-100%) and averaged across 16 quadrats
Litter cover	LCOV	% of quadrat covered by leaf litter, estimated as above
Rock cover	RCOV	% of quadrat covered by rocks, estimated as above
Perennial cover	PCOV	% of quadrat covered by perennial plants, estimated as above
Forb cover	FCOV	% of quadrat covered by forbs/ annual grasses, estimated as above
Green cover	GCOV	% of quadrat covered by green vegetation, estimated as above
Total ground cover	TCOV	% of total ground covered by all of the above (except bare ground), estimated as above
Ground cover height	GCH	Mean height of ground cover layer, estimated for each quadrat and averaged across all 16 1m^2 quadrats
Cattle dung count	DUNG	Cumulative count of cattle dung within 16 1m^2 quadrats
Species richness (grasses)	SRGRAS	Cumulative number of grass species recorded in 16 1m^2 quadrats
Species richness (forbs)	SRFORB	Cumulative number of forb species recorded in 16 1m^2 quadrats
Grass-layer arthropod abundance	ARTAB	Mean number of grass layer arthropods (>2cm) counted along five 60m walked transects
Canopy cover (0-3m)	CCOV0	Canopy cover of shrubs and trees 1-3 metres in height measured with a Bitterlich variable radius measure from four points at the corners of each quadrat
Canopy cover (3-5m)	CCOV3	Canopy cover of shrubs and trees 3-5 metres in height measured with a Bitterlich variable radius measure from four points at the corners of each quadrat
Canopy cover (>5m)	CCOV5	Canopy cover of shrubs and trees >5m in height measured with a Bitterlich variable radius measure from four points at the corners of each quadrat
Total canopy cover	TCOV	Total canopy cover of all shrubs and trees
Total Basal Area	TBA	Total basal area of all woody plants measured with a Bitterlich wedge
Canopy height	CHE	Mean height of the dominant stratum of shrubs or trees estimated visually at each quadrat
Visibility score	VIS	Estimated maximum distance a potential display male could be visible measured as the maximum distance at which a one metre high star picket was visible from four cardinal points. These values were summed to give a relative estimate of open area around a displaying male.
Podium	PODIUM	Presence/absence of an elevated substrate for display
Time since fire	TFIRE	Time in months since last fire
Fire frequency	FFIRE	Number of fires between 1990 – 2003

Data analysis

Ordination was used to examine overall differences between study areas and display/non-display sites among the suite of habitat variables. Habitat data from display and non-display sites at both Kidman Springs and the DDRF were subjected to Non-metric Multi-dimensional Scaling following range standardisation by dividing each value by the highest value of each variable to yield a value between 0 and 1. Variables were screened for inter-dependencies and redundancies using Spearman rank correlation coefficients and where pairs of variables were highly correlated ($r^2 > 0.8$), one was removed. The Bray-Curtis similarity measure was used to calculate similarity between sites. An ANOSIM (analysis of similarities) was used to test for significant differences across the set of remaining habitat variables between display and non-display sites at Kidman Springs and the Douglas-Daly Research Farm. Analyses were based on untransformed data and conducted using Primer V5.

To test for specific differences in individual habitat parameters between display and non-display sites, Mann-Whitney U tests were used for each variable independently for Kidman Springs and the DDRF.

Generalised linear modelling was used to investigate the relative influence of habitat variables on display site choice at Kidman Springs using all uncorrelated variables. This analysis was not possible for the DDRF because of too few sample sites relative to number of variables. A binomial model was used with site type (display versus non-display site) as the dependent variable and a logit link function was assumed for the models. For these analyses Akaike's information criterion was used to determine the best model, which was selected on the basis of low AIC score and parsimony (number of terms in the model). Statistica V6 (Statsoft 2003) was used for these analyses.

Adequate statistical comparisons of habitat characteristics between used and abandoned display sites were not possible because of small sample size (that is, there were too few abandoned sites during the study period). However, comparisons of selected key variables (grass cover height, visibility score, arthropod abundance, species richness of perennial grasses and bare ground cover) were made by plotting their values at used and abandoned sites to identify trends. Box-Whisker plots for these variables at all display and non-display sites were included to indicate a measure of variation.

Index of display site dispersion

A defining feature of leks is the aggregation of displaying males (Bradbury *et al.* 1989a; Bradbury 1981). Within exploded leks males may be separated by considerable distances and aggregation may not be discernible until display sites are mapped at larger scales. For example, Tarboton (1989) proposed that displaying Denham's Bustard *Neotis denhami* males may be separated by 700-2000 metres, but that these display sites seem to be organised into lek-like clustering. To assess whether the distribution of display sites were aggregated at the property scale in this study indices of dispersion were determined separately for each site following Fowler and Cohen (1990). The general premise behind the index is that a sample of count data (number of display sites per 2 km^2 grid cell – see below) with a small variance suggests regular dispersion, intermediate variance suggests random dispersion and large variance suggests clumped dispersion. Using the Poisson distribution as a basis, since it is the best model that describes a random set of objects and it can be demonstrated mathematically that in a Poisson distribution the variance of the population σ^2 equals the mean μ, it is expected that when individuals are dispersed regularly they yield samples where the ratio (i.e. the nominal index of dispersion) $s^2/x < 1$, when dispersed randomly $s^2/x \approx 1$ and when clumped $s^2/x > 1$. An objective way to then identify the critical values of the ratio that separate regular from random and random from clumped may be achieved by standardizing the variance to mean ratio by multiplying it by the degrees of freedom (Fowler and Cohen 1990). This yields a value denoted by the χ^2 symbol in Fig. 7.1.

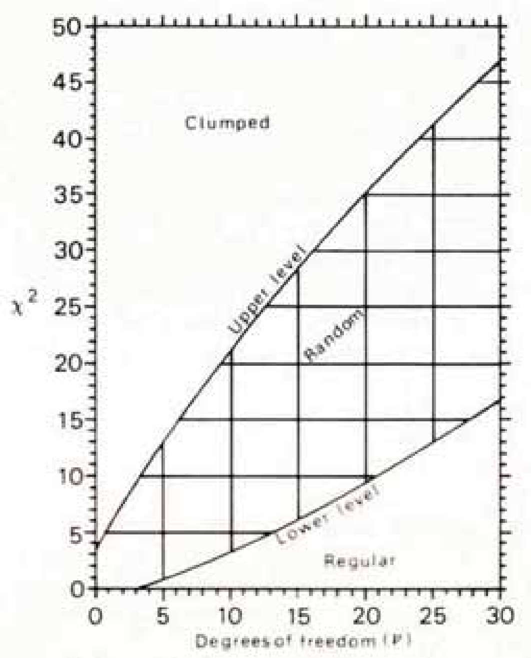


Figure 7.1: 95% confidence zone of random dispersal (from Fowler and Cohen 1990).

Sampling was conducted by dividing the study regions into 2 km^2 grid cells with each cell numbered from 1 to the total number of 2 km^2 cells at each site. Cell size was chosen on the basis of the upper linear distances reported for male bustards separated in exploded leks (Johnsgard 1994). A sample of 20 cells was chosen randomly at each study site and the number of display sites within each cell summed during the peak display period (i.e. for the survey period when the greatest number of males were observed displaying at each site). The procedure was repeated by considering a display cluster as a 'single individual' display site. The sample variance/mean ratio was then determined, standardised as noted above and the intersection between χ^2 and degrees of freedom found in Fig. 7.1.

Satellite tracking of a mature male

Supplementing observations of individual bustards at display sites were the results of satellite tracking of a mature male captured while displaying at Kidman Springs on 12 December 2007. This individual was fitted with a Microwave Telemetry^{TM} solar-powered GPS satellite transmitter (see Chapters 5 & 8 for more details), and data are presented for it up until 8 January 2009. A range of variables were determined for this individual. These included home ranges of the individual for the 2007/2008 breeding season (available data from 12/12/07 to 31/3/08); the 2008 non-breeding season (1/4/08 to 31/8/08) and the 2008/2009 breeding season (available data from 1/9/2008 to 8/1/2009). Home ranges were based on the kernel density method using a cell size of 25 and a smoothing parameter of 100. Analyses were conducted using the Hawth's Analysis Tools (Version 3.27) extension for ArcMap (Beyer 2004). The centre point of this individual's display site (based on its capture location and subsequent observations) was mapped and the minimum distance (i.e. closest distance point) the male ranged away from this site for each day that a location fix was acquired was calculated for the entire tracking period. This gave a nominal measure of its affinity for the site.

For all days on which the male was at its display site (defined as an area of 200 m radius from the central point) during the breeding season and for when 16 fixes were acquired (i.e. the maximum number of possible fixes given the duty cycle of the transmitter), the mean distance of the male from the centre of its display site was calculated for every hour. Similarly, the relative distance away from its display site was also determined over seven consecutive days in early December 2008 (a period for which there was most data) to illustrate its use of the display site over several days.

RESULTS

Distribution of display sites

Twenty display sites were identified at Kidman Springs during the main study period (2002 to 2004) and another four were identified in 2007 (Fig. 7.2; Table 7.2). Twelve display sites were documented at the DDRF (Fig. 7.3; Table 7.2). I report here the aggregation of all display sites over the course of the entire study and note that not all sites were occupied simultaneously or even in the same breeding season necessarily. Table 7.2 shows in what year specific sites were used. For the most part adjacent display sites were used by different males at the same time. For example, the cluster in the eastern part of the DDRF with sites ‘8’ to ‘12’ and the cluster in the south of Kidman Springs were all used simultaneously. However, given that sites may vary in their suitability for display within and between seasons (see below), it is probable that individual males use different sites.

Visual inspection of the configuration of male display sites suggests several separate aggregations of small numbers of males (2-6 individuals) at Kidman Springs. Distances between adjacent display sites in these aggregations ranged between approximately 244 and 1812 metres. At the DDRF, distances between display sites ranged between 117 and 1661 metres. On two occasions at the DDRF concentrated clusters of males were observed in the early dry season (November 2003 and September 2004), where up to 6 males at any one time were spaced between 50 and 300 metres of each other in an open field (Fig. 7.4). A similar cluster was observed at Kidman Springs in December 2007. At these clusters males often competed against each other in a ritualised ‘square-off’ whereby two individuals walked side by side or in tandem for periods up to 10 minutes (Fig. 7.5).

Following the procedure outlined for calculating dispersion values an index of dispersion of 44.7 for display sites at the DDRF and 62.0 at Kidman Springs was generated for each site respectively (Table 7.3). The intersection of χ^2 and ‘df’ on the graph in Fig. 7.1 suggests that indices for both sites are above the boundary of the random zone and a clumped dispersion at each site is accepted. However, removing the clusters of males at each site from the analysis resulted in random dispersion patterns at the property-scale.

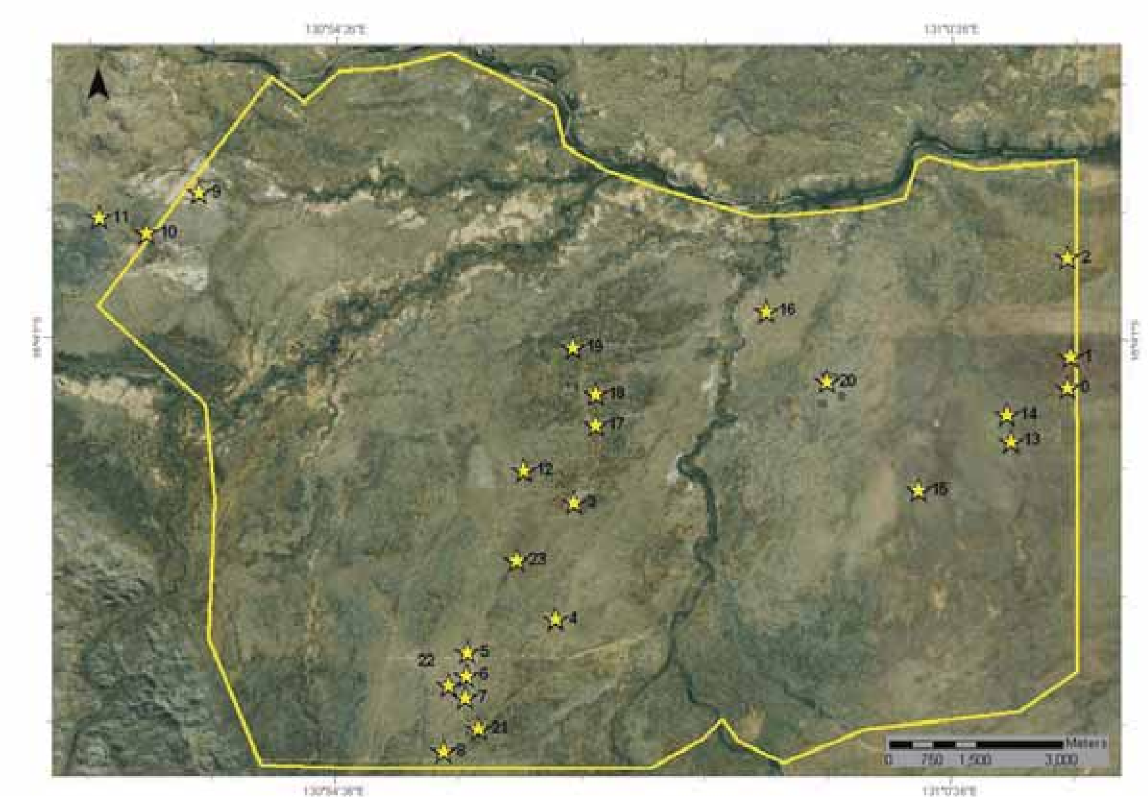


Figure 7.2: Distribution of known display sites at Kidman Springs based on all recorded locations during the breeding seasons between 2002 and 2004, and 2007. Note that not all these sites were necessarily used concurrently. Refer to Table 7.2 for more information. Yellow line denotes boundary of the study site. Background Quickbird imagery sourced from Google Earth™.

Figure 7.3: Distribution of display sites at the DDRF based on all recorded locations during the breeding seasons between 2002 and 2004. Note that not all these sites were necessarily used concurrently. Refer to Table 7.2 for more information. Yellow line denotes boundary of the study site. Refer to Table 7.2 for more information.

Table 7.2: Location, persistence and approximate distances from one display site to the next nearest display site at Kidman Springs and the DDRF. Presence of a male displaying at each display site denoted by ‘X’, absence by ‘O’, uncertain ‘-‘. Habitat categories at Kidman Springs (KS) follow those presented in Chapter 3, namely, ‘BOP’ = open treeless grassland on black soil; ‘BOW’ = open woodland on black soil; ‘ROW’ = open woodland on loam earth soil. UTM values are in WGS84 format.

Site	ID	Northing	Easting	2002	2003	2004	2007	Distance to nearest display site (m)	Habitat (KS only)
Kidman Springs	0	8221776	717023	X	X	X	X	539	ROW
	1	8222313	717077	X	X	X	X	539	ROW
	2	8224030	717050	X	X	X	X	1717	ROW
	3	8219844	708438	X	X	X	X	1049	ROW
	4	8217832	708089	O	O	X	X	1220	BOP
	5	8217269	706560	-	-	-	X	303	BOW
	6	8216866	706533	-	-	-	X	277	BOW
	7	8216491	706506	-	-	X	X	244	BOW
	8	8215552	706130	-	O	X	X	737	ROW
	9	8225264	701945	X	O	X	X	1148	ROW
	10	8224566	701033	-	-	X	X	874	ROW
	11	8224834	700201	-	-	-	X	874	ROW
	12	8220408	707552	X	O	X	O	1049	BOP
	13	8220864	716030	X	O	O	X	459	BOP
	14	8221320	715977	-	O	O	X	459	BOP
	15	8220032	714421	-	-	X	O	1812	BOW
	16	8223144	711791	-	-	X	O	1618	BOP
	17	8221186	708813	-	X	X	X	537	ROW
	18	8221722	708813	X	X	O	X	537	ROW
	19	8222527	708438	-	-	X	O	888	ROW
	20	8221910	712838	O	O	X	O	1618	BOP
	21	8215954	706748	-	X	X	O	588	ROW
	22	8216705	706238	-	-	-	X	336	BOW
	23	8218852	707418	O	O	O	X	1220	BOP
DDRF	1	8469141	740479	X	O	O	O	702	
	2	8467806	735120	X	X	X	X	614	
	3	8467285	735445	X	X	X	O	614	
	4	8468804	737247	X	X	O	O	1661	
	5	8468609	738897	X	X	X	X	1095	
	6	8468348	739960	X	X	X	X	1026	
	7	8468457	740980	X	X	X	X	1026	
	8	8468500	742517	X	X	X	O	117	
	9	8468610	742120	X	X	X	O	184	
	10	8468490	742400	O	X	X	O	117	
	11	8468640	742390	O	X	X	O	150	
	12	8468480	742250	O	X	X	O	150	

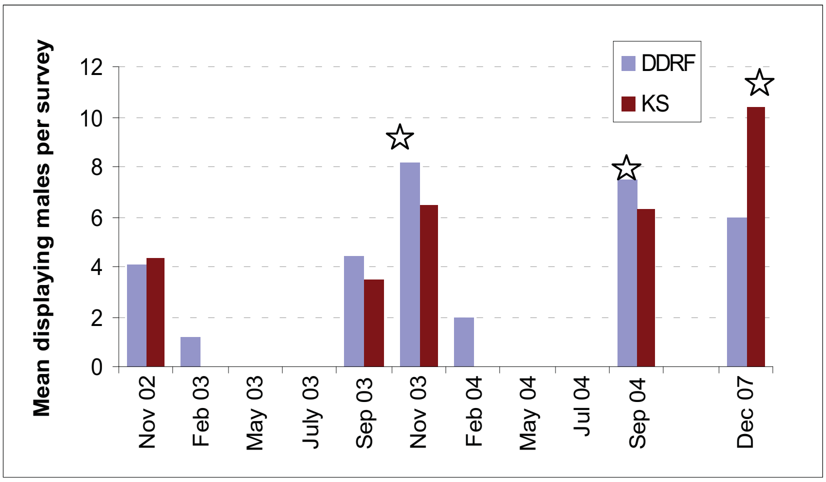


Figure 7.4: Mean number of displaying males encountered per transect during vehicle-based surveys at the DDRF and Kidman Springs (KS) between 2003 and 2004. Stars above denote periods when display clusters were observed. Note that no surveys were conducted at Kidman Springs in February.

Figure 7.5: An example of two males 'squaring-off' as commonly occurs among males at display clusters.

Table 7.3: Values used to calculate dispersion indices for display site distributions at the DDRF and Kidman Springs and respective conclusions for each site with and without clusters included.

	Number of 2 km^2 cells	Mean display sites per cell	s^2	Index of Dispersion	df	χ^2	Conclusion
DDRF	12	1.05	2.47	2.35	19	44.7	Clumped
DDRF (no cluster)	12	0.65	0.66	1.01	19	19.3	Random
Kidman Springs	46	1.00	3.26	3.26	19	62.0	Clumped
Kidman Springs (no cluster)	46	0.40	0.36	0.89	19	17.0	Random

Habitat characteristics of display sites

Ordination and subsequent analysis of similarities revealed a clear distinction in habitat between Kidman Springs and the DDRF, and between display and non-display sites at Kidman Springs (Fig. 7.6; Table 7.4). Display sites and non-display sites at Douglas-Daly Research Farm were indistinguishable reflecting the relative homogeneity and structural simplicity of the site.

Of the 17 habitat variables considered, grass cover height and the visibility score were significantly different between non-display sites and display areas at the DDRF (Table 7.5a). Seven variables (bare ground cover, rock cover, ground cover height, cattle dung count, grass species richness, arthropod abundance and visibility score) differed significantly between display sites and non-display sites at Kidman Springs (Table 7.5b). The best model to determine the importance of variables for explaining display site choice at Kidman Springs was based on one variable: "grass cover height" with low height associated with display site use. This model had an AIC_c weight of 33.0 and explained 52.6% of the deviance ($p<0.001$).

At Kidman Springs, 68% of display sites were located on red earth loam soils, the remainder on alluvial 'black' soils. At 44% of display sites at the Douglas-Daly Research Farm males used the ridges of constructed furrows as podia at least once to elevate them above the surrounding grass layer. No such podia were used by bustards at Kidman Springs although there were notably fewer such habitat features here (pers. obs.).

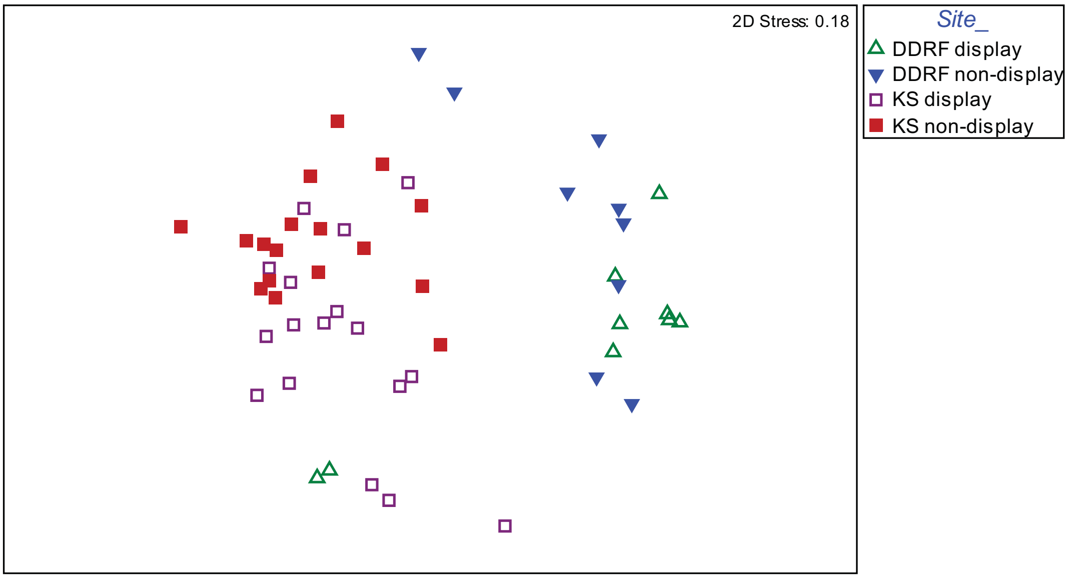


Figure 7.6: Ordination of display and non-display sites at the DDRF and Kidman Springs (KS) based on habitat characteristics (listed in Table 7.1 and following removal of redundancies) as measured on a one hectare plot at each site during 2003 and 2004.

Table 7.4: ANOSIM for sites based on habitat characteristics. Sample statistic (Global R) = 0.517

Groups	***R statistic***	***p***
DDRF display, DDRF non-display	0.073	0.15
DDRF display, KS display	0.642	**0.001**
DDRF display, KS non-display	0.809	**0.001**
DDRF non-display, KS display	0.755	**0.001**
DDRF non-display, KS non-display	0.807	**0.001**
KS display, KS non-display	0.136	**0.008**

Table 7.5: Comparisons of habitat characteristics between display (D) and non-display (ND) sites at (a) the DDRF and (b) Kidman Springs. Significant differences measured by Mann-Whitney U-tests. Significant values are highlighted in bold.

a) DDRF	Mean (± SE)			
Variable	D	ND	Z score	p-level
Bare ground cover (%)	27.1 ± 11.5	18.7 ± 8.8	1.016	0.309
Litter cover (%)	16.6 ± 3.2	13.8 ± 3	0.397	0.691
Rock cover (%)	0.1 ± 0.1	0.7 ± 0.5	-1.273	0.203
Forb cover (%)	3.7 ± 2.5	7.1 ± 2.3	-1.729	0.083
Green cover (%)	5.3 ± 2.6	6.1 ± 1.9	-0.353	0.723
Ground cover height (cm)	11.9 ± 2.8	29.3 ± 9.6	-1.548	**0.0004**
Cattle dung count	0.4 ± 0.2	0.07 ± 0.07	1.267	0.205
Grass species richness	2.4 ± 0.2	2.3 ± 0.2	0.049	0.96
Forb species richness	1.8 ± 0.3	2.1 ± 0.2	-1.008	0.313
Arthropod abundance	6.1 ± 1.3	10.6 ± 2.2	-1.635	0.102
Canopy cover (0-3m)	0.1 ± 0.04	0.1 ± 0.1	-0.121	0.903
Canopy cover (3-5m)	0.06 ± 0.1	0.03 ± 0.02	0.614	0.539
Canopy cover (>5m)	0 ± 0	0 ± 0	-	-
Canopy height (m)	0.9 ± 0.6	0.8 ± 0.5	0.121	0.903
Visibility Score	552.2 ± 52.4	344.4 ± 68.4	2.208	**0.027**
Time since fire (months)	77.8 ± 14.7	80.4 ± 12.9	-0.242	0.808
Fire frequency	0.4 ± 0.3	0.4 ± 0.3	0	1

b) KIDMAN SPRINGS	Mean (± SE)			
Variable	D	ND	Z score	p-level
Bare ground cover (%)	40.9 ± 5.6	21.1 ± 3.2	2.583	**0.009**
Litter cover (%)	9.4 ± 1.6	12.0 ± 1.6	-1.532	0.125
Rock cover (%)	4.0 ± 1.9	0.3 ± 0.2	2.161	**0.031**
Forb cover (%)	6.5 ± 1.0	6.3 ± 1.2	0.344	0.73
Green cover (%)	1.0 ±0.2	1.8 ± 0.6	-0.38	0.703
Ground cover height (cm)	12.7 ± 2.3	28.9 ± 2.1	-3.772	**0.0001**
Cattle dung count	0.13 ± 0.03	0.02 ± 0.01	3.27	**0.001**
Grass species richness	4.8 ± 0.6	6.35 ± 0.5	-1.983	**0.047**
Forb species richness	8.2 ± 0.7	9.6 ± 0.7	-1.165	0.244
Arthropod abundance	2.5 ± 0.9	4.8 ± 0.8	-2.315	**0.021**
Canopy cover (0-3m)	1.5 ± 0.4	2.2 ± 0.6	-0.837	0.402
Canopy cover (3-5m)	1.1 ± 0.2	2.2 ± 0.6	-1.084	0.278
Canopy cover (>5m)	1.1 ± 0.3	2.9 ± 0.8	-1.218	0.223
Canopy height (m)	5.1 ± 0.9	5.3 ± 0.8	-0.217	0.828
Visibility Score	410.6 ± 49.6	220.1 ± 25.7	3.24	**0.001**
Time since fire (months)	35.3 ± 4.2	34.6 ± 5.3	0.105	0.916
Fire frequency	2.1 ± 0.2	2.2 ± 0.3	-0.26	0.795

Satellite tracking of displaying male

Data are presented here for a male bustard tracked over 382 days during which 4563 fixes were obtained at an average of 11.9 fixes per day. This period spanned parts of two separate breeding seasons. Home ranges for this individual for the non-breeding season and the 2007/08 and 2008/09 breeding seasons are depicted in Figure 7.7 and 7.8 respectively. During the non-breeding season the male moved extensively over Kidman Springs and exhibited multi-modal space use. At this time it showed no specific affinity for its known display site, although this site was located near to the centre of its home range. During both breeding seasons it exhibited a strong affinity for its display site, clearly using the same site between seasons. From observations of displaying males at both Kidman Springs and the DDRF, which showed that males spent prolonged periods displaying at specific sites, it was assumed that that this individual was displaying at the site when consecutive daytime fixes from the site were acquired. However, although most of its activity was focussed on the display site it is not known whether it also displayed opportunistically (albeit for considerably shorter periods) at other sites. During the 2007/2008 breeding season peak display activity, defined by consecutive days during which the male was on or near his display site, occurred in mid-December to early January 2007 and again in early March 2008 (Fig. 7.9). In the following breeding season, peak displaying occurred in late November to late December, and followed the commencement of rainfall at the site in November. In all cases peak display activity followed notable antecedent rainfall events 1-3 weeks before.

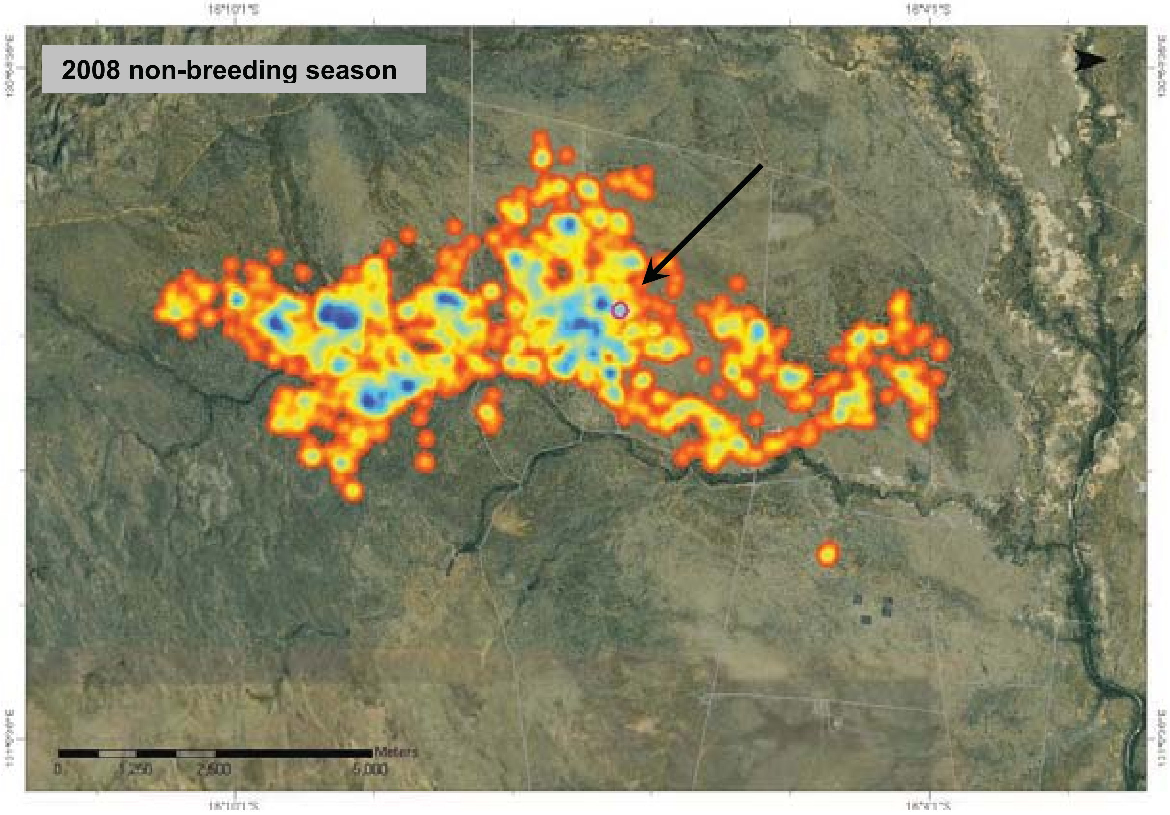


Figure 7.7: Home range of a satellite tracked male during the non-breeding season (1/4/08 to 31/8/08) based on kernel density analysis. Gradations in the kernel graphics represent the probability of use of an area ranging from very high use (dark blue) through to occasional use (red). The pink circle (indicated by arrow) denotes its display site and capture location.

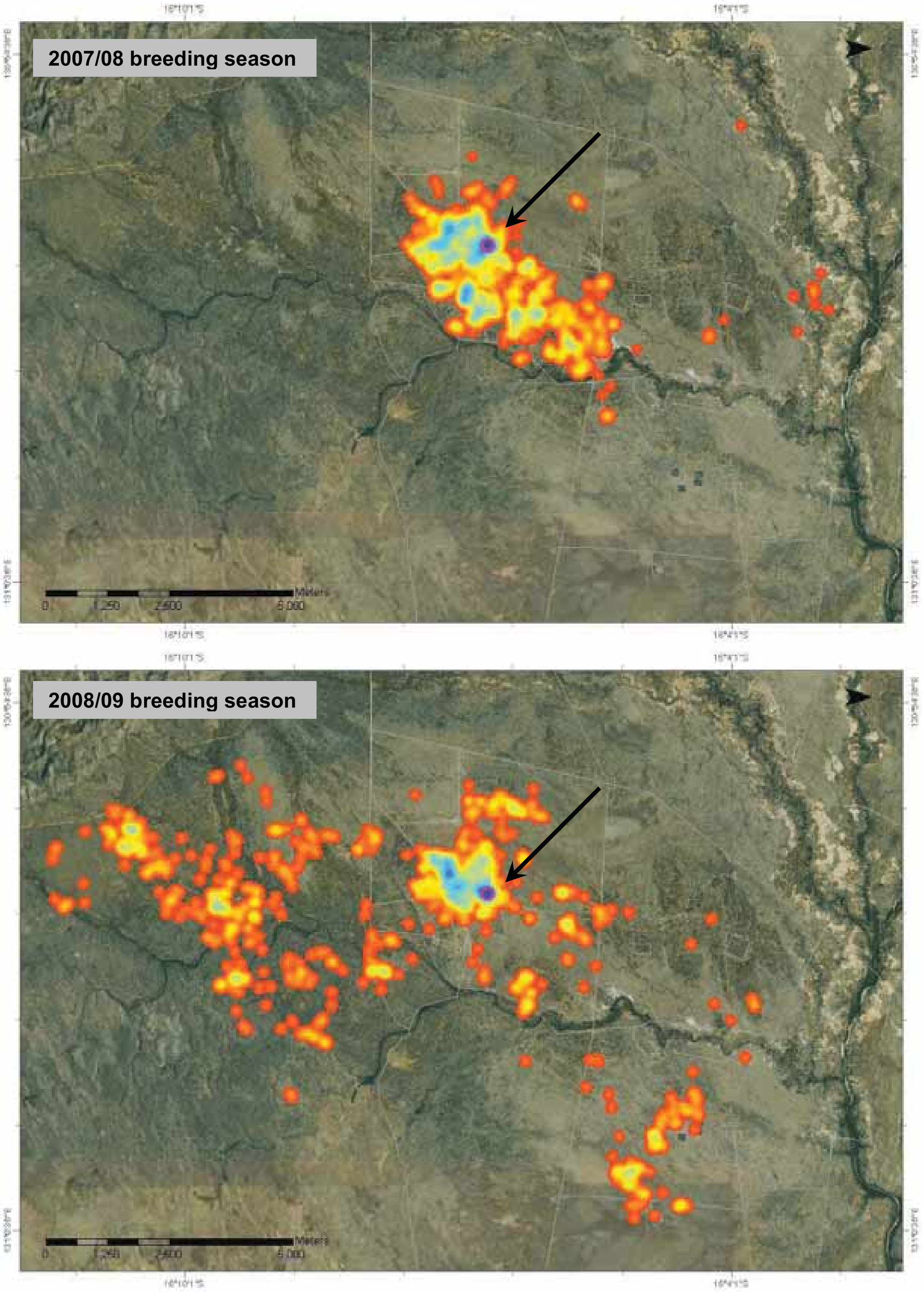


Figure 7.8: Home range of satellite tracked male during the 2007/2008 breeding season (12/12/07 to 31 March 2008) and the 2008/2009 breeding season (1/9/08 to 8/1/09) based on kernel density analysis. Gradations in the kernel graphics represent the probability of use of an area ranging from very high use (dark blue) through to occasional use (red). Pink circle (indicated by arrow) denotes the primary display site and capture location.

Figure 7.9: Minimum distance of a satellite tracked male bustard from its display site for each day a fix was made during the entire transmission period from 12/12/2007 to 8/1/2009 (blue histograms). Included are rainfall data for the period at Kidman Springs (red line). Grey areas denote periods for when no location data were acquired. Green lines separate breeding from non-breeding periods.

Daily and monthly movements in relation to display site

Analysis of the daily movements of the tracked male during peak display periods revealed that it spent most of its time within close proximity to its display site centre (Fig. 7.10). Following display at the site in the morning it often moved away from the immediate area. According to activity budgets documented for displaying males at the DDRF, individuals spent some time foraging in the mid-morning but most of the middle of the day was spent resting (Chapter 6). In the afternoons the tracked male began returning towards its display site where it remained (presumably displaying) until after sunset. It then appeared to roost overnight at the site. Depicting such patterns over several consecutive days demonstrates the variation between days in the distance and timing of movements to and from the display site but that the general pattern occurred consistently (Fig. 7.11).

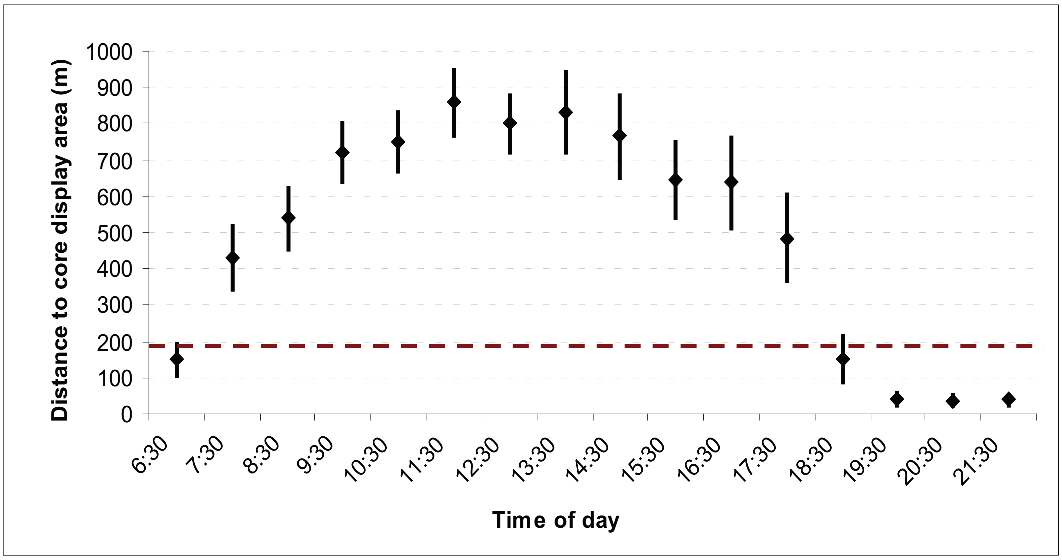


Figure 7.10: Mean distance (±SE) of a tracked male from its display site for all display days during the transmission period. Distances are based on all days that the male spent time at the display site during the breeding season (September to March) for which there were 16 location fixes for that day (n = 32 days). Red dashed line indicates the core display area representing a 200 m radius from the display site centre.

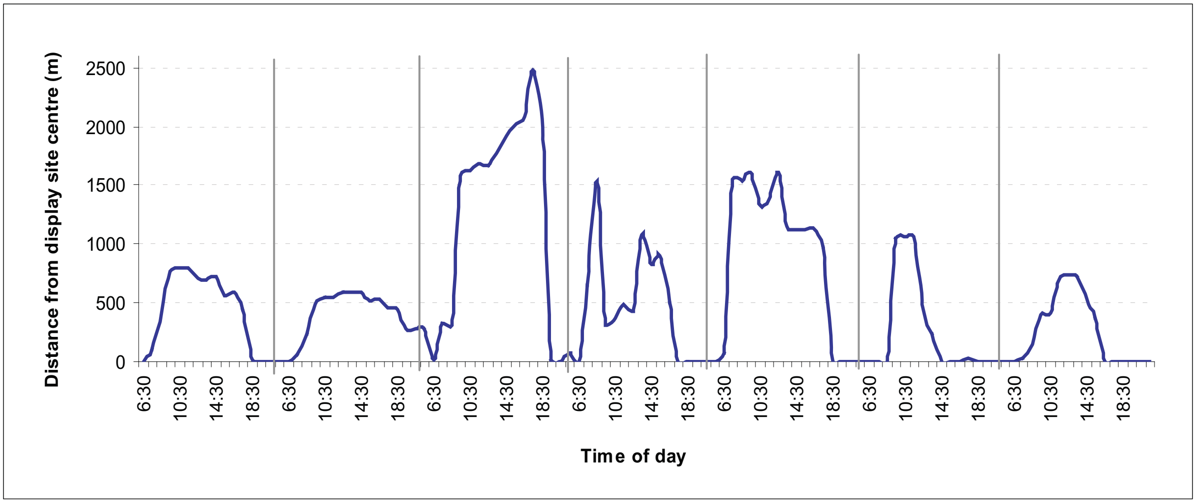
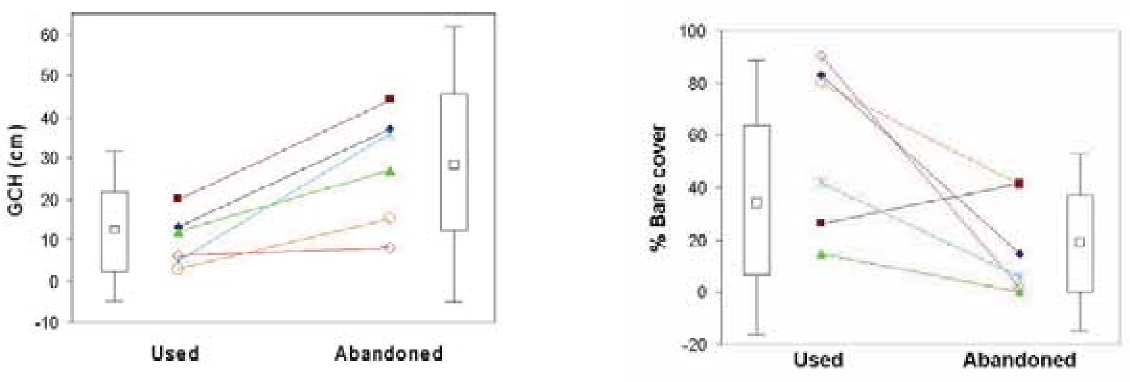


Figure 7.11: Movements of tracked male bustard relative to the centre of its display site over several consecutive days during early December 2008. Vertical lines separate days.

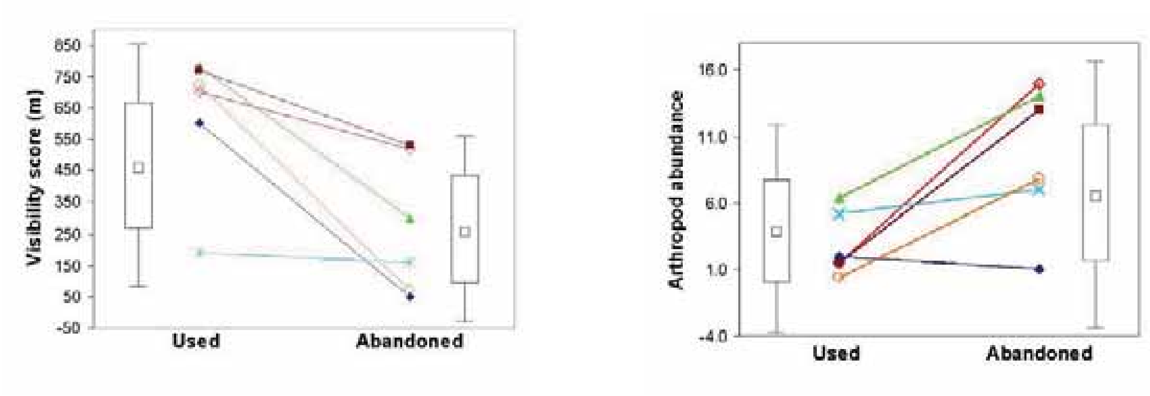
Fidelity to display sites and habitat characteristics

Due to the limited number of tagged males it was not possible to comprehensively assess fidelity to display sites by specific individuals. Nevertheless, of the five males tagged at display sites, one male at Kidman Springs and one at the Douglas-Daly Research Farm were subsequently observed displaying at the same display sites in the following breeding season. Two other males captured and radio-tagged at Kidman Springs died within a few days of capture (presumably due to capture myopathy – see *Discussion* section Chapter 5). Notably, their display sites were subsequently used by other males. As noted above, the home range of the satellite tracked individual was centred on its display site to which it exhibited strong affinity within and between consecutive breeding seasons. Display sites that were used most often between seasons occurred on laterite soils and in areas that were consistently used by cattle (e.g. waterpoints). These areas had minimal grass growth between years therefore remained open and suitable as display areas. Of six sites that were used in one breeding season and abandoned in the subsequent breeding season, three were subsequently re-used in a following year when conditions were again favourable at the site (often due to fires having occurred on the site leading up to or during the breeding season).

Sample size (i.e. number of abandoned sites compared to used display sites) was too small to test whether there were significant differences in habitat variables between sites. However, a comparison of trends among several key habitat variables between used and abandoned sites suggested that grass height and numbers of grass-layer arthropods were higher at abandoned sites, while visibility and the proportion of bare ground were higher at used display sites (Fig. 7.12). No trend appeared evident between sites in species richness of perennial grasses. The values of several of these variables among abandoned sites generally resembled those of non-display sites.


a) Mean grass cover height (cm)

b) % bare ground cover


c) Visibility score (m)

d) Grass-layer arthropod abundance

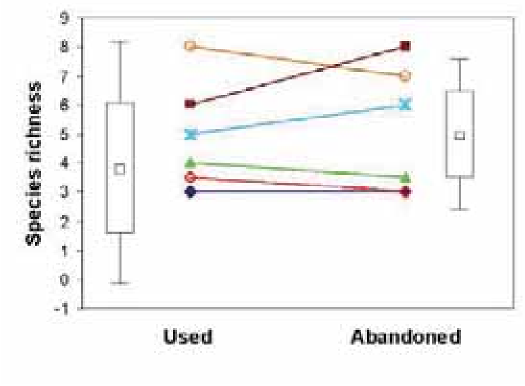

e) Species richness of perennial grasses

Figure 7.12: Trends in five key habitat characteristics between used and abandoned display sites at Kidman Springs and the DDRF. Lines connect sites that had been used in one year then subsequently abandoned. Box-Whisker plots represent variation in these variables at used and abandoned sites.

Conformity to lekking behaviour

Using the information collated in this and other chapters, and knowledge of the general biology of the Australian Bustard, it is possible to assess whether the Australian Bustard conforms to many of the standard characteristics that define lekking as defined by various authors (see Bradbury 1981; Hoglund and Alatalo 1995; Johnsgard 1994) (Table 7.7). However, it is notable that at both sites bustards appeared to exhibit characteristics consistent with both classical and exploded lekking at different times. In addition, individuals were also noted to display solitarily towards the end of each breeding season at the DDRF.

Table 7.6: Conformity of the Australian Bustard to characteristics identifying lekking species

Characteristic	Observation	Conformity
Males provide no parental care (no pair bond)	No association of adult males with young or juvenile observed or recorded from the literature[1].	yes
Males are aggregated	Display sites were aggregated at both study sites both as clumped aggregations consistent with classical lekking and as more dispersed aggregations as occurs amongst exploded leks.	yes
No resources for females on display sites or leks	No resources on display sites, but present at the larger lek scale.	yes/no
Females choose mates	Females have significantly larger home ranges than males during breeding season that overlap several male display territories. Visits by individual females to several displaying males documented.	yes/ ?
Males display	Conspicuous ritualized display characteristic of males at both sites.	yes
Pronounced sexual dimorphism	Mature males significantly larger than females.	yes
Sexual bimaturism	Documented among all *Ardeotis* species (Collar 1996; Marchant and Higgins 1993; Morales *et al.* 2001)	yes
Males have exclusive display site areas that are smaller than a normal home range	Display sites are exclusive and the area used is smaller than normal home ranges.	yes
Display site or lek fidelity	Strong inter-annual fidelity to display sites where habitat conditions remained favourable. Sites that changed within and between seasons (i.e. where significant grass growth occurred) were abandoned but were sometimes used again if conditions became favourable.	yes

DISCUSSION

Timing of display and breeding behaviour

In contrast to reports in other regions, including parts of the wet-dry tropics (Downes 1982), male Australian Bustards observed during this study began displaying prior to the commencement of rainfall, with displays occurring as early as the start of September. At Kidman Springs, this period also coincided with an increase in the daily movements of female bustards presumably to aid the assessment of displaying males on leks (Chapter 8), and suggests that breeding behaviour may be stimulated by cues other than rainfall prior to the onset of the highly productive wet season. Nevertheless, rainfall is an important cue for stimulating breeding among bustards, with peaks in numbers of displaying males occurring after the first rains in the late dry/early wet season in northern Australia. Rainfall in more arid regions is the primary stimulant for bustard breeding in central Australia (Marchant and Higgins 1993), and for Kori Bustard in Namibia (Osborne and Osborne 2001), while the Indian Bustard similarly exhibits a seasonal peak of display early in the full monsoon season (Johnsgard 1994). In the present study, males continued displaying throughout the wet season, although by February at the DDRF only a few males remained active at display sites. The breeding season in northern Australia for the Australian Bustard therefore lasts for an extended period (September to February, and sometimes in to March), contrasting to the much shorter display periods (4-5 weeks) among Great Bustard populations in western Europe (Morales 1999), and Houbara Bustards breeding in China between late April and June (Yang *et al.* 2002).

Daily patterns of display behaviour as determined for the satellite tracked male suggested it spent the early morning and late afternoon on its display site (where it also roosted overnight). In the middle of the day it retreated to nearby shelter to rest during the heat of the day. Chapter 6 documented the daily activity patterns of bustards which similarly indicated that males began displaying from sunrise until mid-morning, rested during the middle of the day when the heat presumably made displaying in the open untenable, and again returned to display in the late afternoon until sunset. By comparison, during peak display periods in captivity in southern Australia, male bustards were recorded displaying for as much as 95% of daylight hours (Fitzherbert 1978). The amount of time spent by individual males in display each day was also greater during the wet season than during the late dry season period (Chapter 6).

Distribution of display sites and lek definition

Patterns of male display site dispersion among lekking populations have been described as a continuum ranging from highly clumped to solitary displays (Hoglund and Alatalo 1995), with single populations of some species including both clumped and solitary males at display grounds at any given time (Lanctot and Weatherhead 1997; Westcott 1993). For some species, variation in aggregation patterns among a population has been shown to vary between and within years (Morales *et al.* 2001; Morales 1999). Such variability emphasises the inherent difficulties of defining the size and configuration of leks (and mating systems in general) based solely on consideration of patterns of male dispersion. In the present study, males at both study sites exhibited similarly variable degrees of aggregation within and between breeding seasons, with breeding distributions ranging from solitary displaying males to clustered groupings. Concentrated clusters of displaying males were observed at each site in the early to mid-breeding season and coincided with what appeared to be the peak display periods when there were the greatest numbers of displaying individuals at the sites following early wet season rainfall. Such highly clumped aggregations, where males are within close direct visual contact, resemble the dispersion patterns of males at classical leks. On classical leks, and as evident here, the home ranges of males are significantly smaller than females and they have no significant resources. This observation appears to be consistent with the idea that the degree of male dispersion in some species may vary with population densities (Snow 1985). In this case, clustering occurred when there was a peak in the number of actively displaying males at the study sites, rather than high bustard density in general (Chapter 4).

At both study sites, however, it was the norm for males to be more widely dispersed in a manner consistent with exploded lekking. Under this scenario males were separated by distances of up to 1 to 2 kilometres and were usually within at least audible distance of each other. The acoustic signalling of male bustards, consisting of a low, booming roar-like vocalization, appears highly effective in their open grassland and woodland habitats with the sound carrying for considerable distances. Similarly, the large size of males with their inflated and extended white feather throat sacs during display means that in open habitats, such as those at the DDRF, they may be seen for at least a kilometre or more. These characteristics make displaying males highly conspicuous to females, even in more wooded areas such as those found at Kidman Springs. On such exploded leks males may be loosely clumped or distributed uniformly (or randomly) in an area but still be aggregated on a landscape scale, with the territories having more or less resources than the surrounds. At the property-scale, and by the means used in the present study, displaying males appeared randomly dispersed. However, based on general conventions (that on exploded leks males are within audible distance of each other and may be separated by up to 1 to 2 km (Johnsgard 1994; Morales *et al.* 2001; Tarboton 1989)), it was possible to identify several small groupings of displaying males at each site. Whether such groupings may be considered separate leks or part of a larger lek is arguable. In this study, limited efforts were made to assess whether there were more display sites outside the core study regions. Therefore, it is not possible to definitively assess the relative degree of dispersion compared to the surrounding areas. Nevertheless, both sites are relatively circumscribed areas that represent favourable habitats for bustards in the more extensive, generally less suitable surrounding landscape. This is especially true for the DDRF, which along with part of an adjacent property, is largely a modified area within a larger contiguous intact woodland savanna landscape that is markedly less suitable bustard habitat. Comparably, Kidman Springs is surrounded to the north and west by escarpment and plateaus that are unsuitable habitats for bustards. Ultimately, the practical dimensions of a lek may be in part defined by the relative ranging behaviour of females during the mate choosing period in the early breeding season. Females move extensively in the early breeding season (Chapter 8) and their home ranges at this time significantly exceed those of males (Chapter 5). In this study, these ranges covered most of the display sites documented at each study site.

On other occasions, most notably towards the end of the breeding seasons at the DDRF, males were often observed displaying solitarily. Although these individuals displayed on well-known, established display sites, it is not known whether they were the same individuals that had been displaying earlier or throughout the breeding season. It is therefore not possible to say whether these individuals are unusually fit individuals maximising their capacity for accruing mates by prolonged display over the entire breeding season, or individuals of lower relative social status in the male dominance hierarchy, attempting to mate with females opportunistically at a sub-optimal periods of the year.

Characteristics of display sites

Results presented here, and studies of other lekking species, have demonstrated that males choose display sites that maximise their conspicuousness and enhance their ability to detect approaching females and predators (Deutsch 1994; Westcott 1993; Yang *et al.* 2002). At both the DDRF and Kidman Springs, displaying males exhibited a marked preference for open areas characterised by low grass cover and high visibility. These display sites, measuring up to 200 metres radius round a central point, therefore contrasted with the very small, highly circumscribed display sites of about a square metre observed for the species in captivity (Fitzherbert 1978). The most dynamic habitat variable, the inter-annual variation in grass biomass, was the most significant factor affecting the suitability of display areas and largely determined whether sites were used regularly. When grass cover increased and visibility was reduced these sites were abandoned, but were sometimes used again if conditions subsequently became favourable. That males actively choose such sites suggests habitat may be an important determinant of lek configuration and size (Westcott 1993). These choices are likely to be more constrained and dynamic at Kidman Springs because of the more heterogeneous and variable nature of the local environment. By comparison, at the DDRF the habitat is structurally more homogeneous and open, and proportionally more of the site is likely to be favourable for displaying males. It is possible that at the DDRF social forces may be more important in shaping patterns of display site dispersion than habitat availability.

Display site fidelity

Characteristic of many lekking species is the use of traditional lek sites that are consistently used between seasons and generations (Widemo 1997). A high degree of fidelity to leks has been documented for several bustard species, including the Great Bustard (Alonso *et al.* 2000; Lane and Alonso 2001) and the Little Bustard (Jiguet *et al.* 2000). In this study, both sites similarly supported leks throughout the study period. However, the internal structure of these leks in terms of the configuration and persistence of specific display sites was variable. In general, male bustards exhibited fidelity to particular display sites between and within seasons as long as habitat conditions remained favourable. Several sites that were abandoned within or between seasons (due primarily to significant grass growth) were subsequently used again when conditions again became favourable.

There was limited opportunity in this study to assess the degree to which specific males consistently used specific display sites and the degree of turnover and competition at specific sites. Nevertheless, the available evidence from two tagged individuals and the satellite tracked male suggest that individual males did use the same sites between seasons. Information from the tracked individual suggested that its ranging behaviour was centred on its single display site to which it regularly returned within and between breeding seasons. However, it was not possible to determine whether this individual also displayed (although in all likelihood substantially less often if at all) at other sites, or whether it used its known display site exclusively and to the exclusion of all other males. In addition, the inadvertent removal of two displaying males from their display sites (due to mortality as a consequence of capture myopathy) quickly resulted in their ‘colonisation’ by other males. This suggests that certain sites may be particularly favoured and consistently used by the male population in general. Notably, in all cases where sites were used repetitively, habitat conditions remained suitable for display within and between seasons.

Despite the apparent preference for specific sites, changing habitat conditions render certain sites less favourable within and between years. The highly dynamic nature of the tropical savannas suggests that bustards may need to be adaptive and opportunistic in using display sites which may entail the use of multiple sites within an area, amongst which individuals switch depending on suitability. Such a scenario may have implications for the social structure of leks according to the classical lek model. In classical leks a male’s geographical position is often governed by prevailing dominance hierarchies established between males whereby the most dominant and successful males are located in the best display positions, often in the centre of the lek (Hovi *et al.* 1994). Continued competition for favoured sites naturally results in turnover of males between specific display sites. Among populations that exhibit exploded lekking in highly dynamic environments, the ultimate patterns of display site use and lek configuration may depend on the relative influences of habitat availability as well as social factors. In dynamic landscapes such as the northern savannas, changing habitat conditions are likely to recast the suitability of display areas across the lek within and between seasons. At Kidman Springs, many of the sites that remained consistently favourable to displaying males between seasons were characterised by stony areas on laterite soils where grass growth was negligible, or where cattle grazing and trampling of the herbaceous layer kept the site exposed. A possible explanation is that these more stable sites may be at a premium and therefore be the preferred or most lucrative and successful sites. In contrast, those sites that are more dynamic, both within and between seasons, tend to be used more opportunistically by floaters – males that do not hold permanent display sites. In this sense, instability in habitat suitability may be more favourable to less dominant males than would be the case if the leks were more permanently fixed.

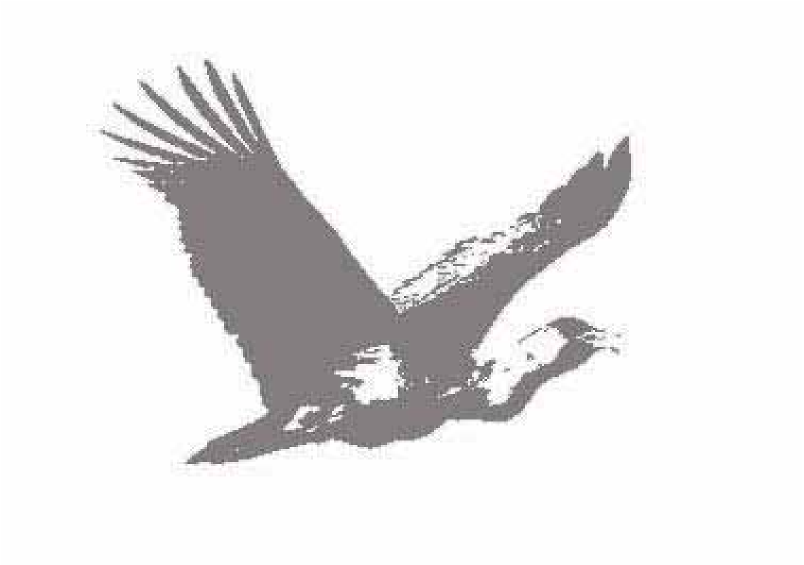
Inter-annual fidelity to particular breeding grounds also has significant implications for defining the movement strategies of the Australian Bustard. Given that the bustard has been traditionally regarded as undertaking predominantly dispersive, irregular widespread movements in response to prevailing conditions (Downes 1982a; Marchant and Higgins 1993), consistent use between years of the same lekking areas suggests that nomadic movements may not be the norm. Instead, individuals may be sedentary or movements may occur on a seasonal basis, as occurs among other bustard species, whereby individuals disperse following the breeding season only to return prior to the commencement of the following season (Alonso *et al.* 2000). However, it remains to be determined whether bustards use specific lekking areas consistently or opportunistically in more climatically erratic regions of arid Australia.

Flexibility of the mating system

Mating systems, and the lekking process itself, appear inherently flexible between and among populations of several species. Like other bustard species, the Australian Bustard conforms to general definitions of lekking, exhibiting characteristics consistent with exploded and classical lekking, as well as undertaking solitary display. However, variation in lekking behaviour, especially among species that tend towards exploded leks is high. Species often considered as exhibiting exploded lekking, upon closer examination, have proved to exhibit a variety of mating strategies (Lanctot and Weatherhead 1997). The Australian Bustard appears to exhibit similar flexibility in mating strategies across its range, and locally at the sites considered here. Such flexibility is likely to be even more pronounced in arid regions. In these areas it is unlikely that bustards regularly use the same sites for lekking or display (at least not on a regular seasonal basis) as they do in the north. Indeed, in such areas bustards may be forced to move to more favourable regions or go for extended periods without breeding. For example, the breeding of Kori Bustards in arid regions of Namibia is closely tied with rainfall and may be greatly reduced or not occur at all in drought years (Osborne and Osborne 2001). The ephemeral nature and flexibility of lekking behaviour has been emphasised as an important adaptation to variable environments (Carranza *et al.* 1989; Lanctot and Weatherhead 1997). Among Australian Bustard populations, such flexibility is yet another example of the adaptation of the species to highly variable environments.

Chapter 8

An exploratory study of the movements of the Australian Bustard as determined by satellite telemetry



'My Dreaming - Bush Turkey
- see the tracks - he goes there and there - all over my country
- he makes tracks on this big soakage on my country'

-Cowboy Louie Pwerle, Aboriginal elder, Utopia

Chapter 8

An exploratory study of the movements of the Australian Bustard as determined by satellite telemetry

INTRODUCTION

The advent of satellite telemetry and spatial information systems has provided biologists with unprecedented opportunities for studying faunal movement strategies, and relating such movements to their environmental drivers. Although these technologies have been widely employed to discern long-range migration patterns, particularly the north-south migratory movements of species from the temperate northern hemisphere (e.g. Jiguet and Villarubias 2004; Meyburg *et al.* 1995; Meyburg and Meyburg 1998), the nomadic or dispersive movement patterns of species that move with less defined seasonal regularity remain poorly studied. Such movements, that may operate over longer term cycles of climatic variability, appear common for many of Australia's birds, and their determination may provide significant novel insights into the dynamics and evolution of faunal movements generally (Dingle 2008) while also aiding in the conservation of mobile species and their habitats (Woinarski *et al.* 1992).

In an Australian context, a major focus on dispersive species has centred on the interaction between waterbirds and the availability and distribution of the wetland habitats they depend on (Frith 1967; Kingsford 1995; Kingsford and Norman 2002; Roshier *et al.* 2008; Roshier *et al.* 2001a; Roshier *et al.* 2002). Many species respond rapidly to major rainfall events and wetland inundation by moving, often over vast distances, to exploit these productive, but often only temporarily available resources (Kingsford *et al.* 1999; Roshier *et al.* 2002). The interaction of waterbirds with wetlands presents a favourable model system for assessing dispersive movements in relation to variable environmental conditions because many species are wide ranging and because wetlands are relatively circumscribed habitats that can be readily mapped in near-real time (Roshier *et al.* 2001b). However, the majority of Australian bird species use less discrete habitats, and examining their movement patterns in relation to habitat availability is arguably more challenging. The difficulties of defining and quantifying the relative availability and quality of habitat as it varies stochastically in time and space are significant, although they may be addressed by emerging technologies (e.g. Berry *et al.* 2007; Bonter *et al.* 2009; Boone *et al.* 2006; Glahder 1999; Oindo and Skidmore 2002; Osborne *et al.* 2001; Osborne *et al.* 1998; Woinarski *et al.* 2000b)).

The Australian Bustard is an example of a terrestrial Australian species that may employ a variety of movement strategies across its range. The bustard broadly relies on open habitats, and may range between or use different habitats at different times depending on, among other factors, their productivity (Downes

1982a), fire history (Marchant and Higgins 1993) and structural composition (Downes 1982a; Chapter 5). In general, in regions influenced by productive and predictable seasonal conditions, such as the wet-dry tropics of northern Australia, their movements may tend towards regular migratory patterns as individuals move to exploit seasonally fluctuating resources. Alternately, such conditions may also facilitate sedentariness, whereby populations may be supported in circumscribed areas year round (Nix 1976); Chapters 2 and 4). In increasingly unpredictable environments, such as those that cover large parts of the bustard's range, individuals or populations may be increasingly mobile and nomadic, undertaking wide ranging opportunistic movements in relation to shifting resources or habitat conditions that vary unpredictably or over longer climatic cycles (Downes 1982a; Marchant and Higgins 1993; Nix 1976).

The dynamics of these movements and the regulatory mechanisms and environmental cues that underpin them remain poorly understood. Regular annual migratory movements are believed to be largely genetically programmed and underpinned by endogenous controls (Berthold 1999). However, in the highly variable, stochastic environments that characterize much of continental Australia, it is unlikely that such movements are stimulated by tight endogenous controls (Roshier *et al.* 2008; Whitehead 1998). Instead, dispersive species must be able to detect and respond to the sudden and ephemeral presence of favourable conditions rapidly and often over vast scales. Bustards are known to respond to fires and may track such events across the landscape (Marchant and Higgins 1993). They may also move rapidly to recent rainfall events, or more belatedly, to areas where outbreaks of favoured prey such as grasshoppers or mice occur following previous rains (Marchant and Higgins 1993). In most cases, how these events are detected or known by the birds is not understood.

In this chapter I use satellite telemetry to explore the movements of bustards in regions that span a gradient of rainfall variability from the highly predictable rainfall patterns of the monsoonal wet-dry tropics to the erratic rainfall characteristic of the central deserts. It should be emphasized from the outset that this study is exploratory as it is based on a small sample size, so the chapter represents an exploration of individuals rather than a systematic assessment of populations. Nevertheless, following Nix (1976) and Griffieon and Clarke (2002) (and the findings presented in Chapter 2), some tentative general predictions may be made. First, individuals tracked in the more seasonally predictable wet-dry tropics of the north are more likely to make seasonal migratory movements in relation to the wet-dry season or are primarily sedentary. In contrast, individuals in more climatically variable regions are likely to move greater distances and more often, but with less consistent timing and direction. I also specifically assess responses to patterns of primary productivity, rainfall and fire events. Finally, I assess movements against Roshier and Reid's (2003) framework of avian movement strategies presented in the introductory chapter, and tentatively speculate on the regulatory mechanisms and cues that may govern observed movements.

METHODS

Study regions

Satellite transmitters were deployed on individuals at the two main study sites of Kidman Springs and the DDRF, at a site in Barkly Tableland region and near the township of Bedourie on the edge of the Simpson Desert in south-west Queensland. The general rationale was to track bustards from regions that spanned a gradient of annual rainfall variability (Fig. 8.1). In Australia, rainfall variability generally increases from the coast to the arid interior. In this case, Kidman Springs and the DDRF are located in the most seasonally predictable regions, with the predictability of rainfall lowest in south-west Queensland.

Barkly Tableland, Northern Territory

An individual male was fitted with a transmitter at Alexandria Station in the central Barkly Tableland in the Northern Territory. The Barkly Tableland region is bordered to the north by the Gulf of Carpentaria, to the west by the Tanami Desert and the arid interior to the south. The area is characterised by a low diversity of vegetation communities, largely dominated by extensive areas of treeless Mitchell Grass (*Astrebla* spp.) plains. The area is considered semi-arid with a mean annual rainfall at Alexandria Station of 398 mm which is strongly influenced by the summer monsoon with approximately 90% of rainfall occurring between November and March. However, total rainfall may be variable from year to year, and may be spatially patchy, particularly early in the wet season, with significant implications for productivity and the biota of the region (Fisher 1999). Rainfall during the tracking period in this study was close to average (Fig. 8.2). The dominant land tenure in the region is cattle grazing.

Channel Country, South-west Queensland

A female bustard was captured on an open plain near the Georgina River on Cluny Station approximately 12 km south-east of the township of Bedourie in south-west Queensland in October 2005. This location is in the Channel Country on the north-eastern edge of the Simpson Desert. The capture site was on an open plain dominated by hummock grassland and shrubs. The region is regarded as arid with rainfall variability in the area amongst the highest in Australia. Mean annual rainfall at the nearest weather station at Cluny is 189 mm. Notably, in June 2005, several weeks prior to transmitter deployment, there had been a significant rainfall event in the region (Fig. 8.2). Numbers of bustards at this time were unusually high, with several females observed with young (pers.obs.).

NOTE:
This figure is included on page 227
of the print copy of the thesis held in
the University of Adelaide Library.

Figure 8.1: Locations of deployed satellite transmitters in relation to annual rainfall variability. The rainfall variability index used here is defined as the 90th rainfall percentile minus the 10th rainfall percentile divided by the 50th percentile (median). The index is based on rainfall data from 1900 to 2003. Areas denoted as having a low index of rainfall variability tend to have consistent rainfall patterns from one year to the next, as occurs in the Top End of the Northern Territory. Conversely, an extreme index denotes highly irregular rainfall between years as occurs in the central desert areas and at the transmitter deployment location in south-west Queensland. (Data sourced from the Bureau of Meteorology).

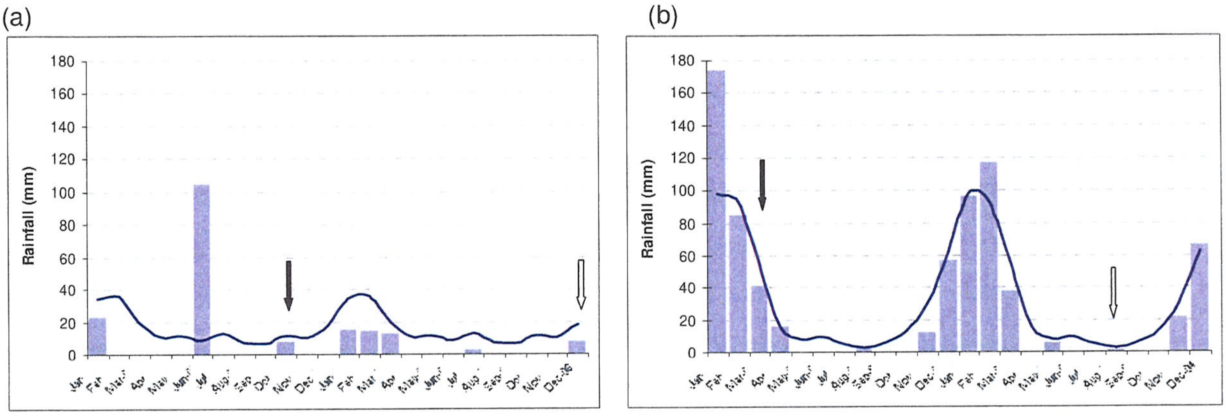


Figure 8.2: Rainfall during the study period (bars) and mean annual rainfall (line) at (a) Cluny Station (south-west Queensland), and (b) Alexandria Station (Barkly Tableland). Arrows indicate start and end of the tracking period for each individual, but note that the final location of each individual was different to its origin (Data sourced from the Bureau of Meteorology).

Definitions of terms used

Animal movements occur at a variety of spatial scales for a variety of reasons. In this study, I describe the movement patterns of bustards at multiple scales. To this end, movements were classified according to distance traveled and time spent in an area. Such a classification is inevitably subjective and classifications may overlap. Nevertheless, the following definitions were used in the analysis and presentation of results:

Small-scale movements: localized short movements ranging up to approximately 5 km that may be largely regarded as part of the daily routine and confined to a home range area. Such movements are equivalent to the 'maintenance' movements defined in Chapter 1.

Medium-scale movements: dispersive movements that are made outside the normal home range between 5 to 30 kilometres in length.

Long-range movements: larger scale dispersive movements over 30 kilometres in length between destination sites that may occur over several days and usually consist of staging areas.

Staging areas: areas used for short periods of time (< 7 days) during extended movements en route between destination sites.

Destination sites: areas used for periods longer than 7 days within a 30 km radius of an arrival location.

Satellite telemetry

Details of satellite telemetry, transmitter types and systems, and methods of deployment were outlined in Chapter 5 and will only be briefly reviewed here. Two types of satellite transmitters were used to document the movements of bustards; a system based on ARGOS and a GPS-based system. The ARGOS system relies on an orbiting satellite receiving signals from a ground-based transmitter. As it passes overhead it uses the Doppler shift to calculate the location of the unit on the ground. The accuracy of this technique is variable and dependent on several factors such that estimates of location accuracy are classified according to a scale of location quality: class 3 (<150 m), class 2 (150-350 m), class 1 (350 – 1000 m) and class 0 (>1000 m). The ARGOS-based transmitters used in this study were manufactured by Sirtrack™. Since it was an objective of this study to assess the movements of bustards over as long a period as possible a duty cycle of 12 hours on and 156 hours off was employed. That is, following continual transmission for the first 6.5 days initially, the unit would turn on for 12 hours once per week, acquire several fixes during this time, then shut off for a week. At this rate the transmitters were estimated to have a lifespan of up to 18 months (Sirtrack™, pers.comm.).

The variable quality of location accuracy classes and the duty cycle of these transmitters means these units are best suited to documenting broad-scale movements rather than for detailed studies of habitat or local-scale ranging behaviour. In this study, only fixes with accuracy classes of 2 or 3 were used, ensuring that the estimated accuracy of a fix location was within approximately 350 m. Since the recommended maximum weight of a transmitter should not exceed 3% of the total body weight of an individual (Kenward 1987), the use of these transmitters (weighing 150 g) was restricted to male bustards heavier than 5 kilograms.

Telemetry systems based on the NAVSTAR Global Positioning System (GPS) overcome the uncertainties associated with ARGOS-derived accuracy estimates. GPS-based systems also theoretically allow for 24 hour per day position estimates as they are not dependant on the timing of orbital satellite passes. The level of accuracy is within 10 m of the true location 95% of the time (Rodgers 2001). The units employed in this study were Microwave Telemetry's™ 70 gram solar-powered GPS transmitters. These were programmed to operate on a duty cycle of 16 hours on, 8 hours off (with the off period occurring overnight between 22:00 and 6:00). While turned on, the units were programmed to attempt a GPS fix every hour leading to a theoretical maximum of 16 location fixes per day. These units, being based on solar power, also have a significantly longer life span, capable of potentially transmitting for several years.

Data summaries and analysis

Inherent differences in data quality between the two satellite telemetry systems in terms of the spatial and temporal coarseness of derived location fixes necessitated different approaches to data analysis and the presentation of results. Individuals were also tracked for different periods with variable success rates in the acquisition of location fixes. Consequently, the extent of possible analyses and results presented here differ between individuals but were tailored to maximise the information obtained. In general, individuals tracked with GPS units over extended periods were examined in detail while only a cursory assessment was made for some other individuals. Additional notes are included for analyses or summaries specific to each individual in the *Results* section where relevant.

The locations and movement paths of all satellite tracked bustards were mapped and calculated using ArcMap GIS. Summary statistics are presented as described in Table 8.1. For GPS-based transmitters a measure of fix success per day is included. Where possible, movements were assessed in relation to several environmental cues for each individual as described below. Each tracked individual is referred to by the number of its satellite transmitter and detailed descriptions of movements are presented for each separately. All times presented are in Australian Central Standard Time (ACST).

Table 8.1: Description of summary statistics presented in *Results* Table 8.3

Statistic	Description
Tracking period (days)	Time between deployment of transmitter and last transmission.
Total number of fixes	Number of location fixes acquired during the tracking period.
Mean number of fixes per day	Mean number of fixes acquired per day for the tracking period.
Total distance traveled (km)	Cumulative total of all distances traveled between all fixes
Mean movement per day (km)	Mean distance traveled per day for the tracking period
Longest movement (km)	Longest single distance between consecutive fixes
Maximum distance from origin (km)	Maximum linear distance traveled from the point of transmitter deployment
Final location to origin (km)	Distance of final location from transmitter deployment site.
Maximum distance between fixes	Maximum linear distance between any two fixes acquired

Responses to environmental factors

Seasonality

The timing of medium and long range movements were assessed to determine whether they occurred over regular, seasonal cycles. For GPS-tracked individuals, daily distances moved based on the first location fix each day between consecutive days, were compared between months. Most tracked individuals were followed for less than two seasons limiting the opportunity for effectively assessing such movements over multiple seasons.

Primary productivity

While individuals may move immediately in response to rainfall it is ultimately the consequence of rainfall (i.e. increases in productivity and food availability) that are the reasons for moving, hence individuals may track areas of higher productivity opportunistically. Furthermore, as noted in Chapter 2, while rainfall may be an effective proxy for primary productivity in rangeland regions, measures of rainfall rely on sparsely distributed weather stations that may not account for the patchy nature of rainfall events. Additionally, variations in topography, substrates, vegetation and the timing, intensity and duration of rainfall events may lead to localized variations in primary productivity.

Here I relate movements and location data for the bustards tracked in the Barkly Tableland and south-west Queensland region (those individuals that made the most extensive movements) to patterns of gross primary productivity in these regions. Since movements in the Kidman Springs and the DDRF regions were highly localized similar analyses were not conducted for these areas. Gross primary productivity (GPP: $\mathrm{mol\ CO_2\ m^{-2}\ day^{-1}}$) of the raingreen component of vegetation was calculated for those months for which there were adequate bustard location records by Peter Dostine based on methods presented in

Roderick *et al*. (2001), and fPAR data and calibrations provided by Sandy Berry of ANU FSES. For the individual in the Barkly Tableland this equates to the months of August 2003, March 2004 and April 2004, while for the female in south-western Queensland data are presented for each month between October 2005 and November 2006.

Data were derived from NDVI (Normalized Difference Vegetation Index) imagery captured by sensors borne on the MODIS satellite. The NDVI is defined as:

$$\mathrm{NDVI} = (\mathrm{NIR}-\mathrm{VIS})/(\mathrm{NIR}+\mathrm{VIS})$$

where NIR and VIS are the near infra-red and visible reflectance. NDVI is a robust estimator of green vegetation cover at regional and continental scales (Roderick *et al.* 1999). NDVI data were converted to total fPAR (fraction of photosynthetically active radiation) and partitioned into evergreen and raingreen components using methods summarised in Roderick *et al.* (1999) and Berry and Roderick (2002). The distribution of raingreen fPAR corresponds to the distribution of seasonal green grasslands and herbfields, particularly on fine-textured cracking clay soils (Berry and Roderick 2002).

To examine the responses of tracked bustards to the distribution of primary productivity, all location fixes for a month were simply plotted on monthly composite images of GPP and general patterns described.

Rainfall

Coarse assessments of rainfall patterns (measured as mean monthly rainfall) were made in relation to the commencement and extent (defined as daily distances traveled) of movements for individuals tracked by GPS telemetry. Mean distances of daily movement by month were plotted against mean monthly rainfall. A measure of movement based on distance traveled between point of origin to final location in relation to annual rainfall variability at the point of origin (data derived from the Bureau of Meteorology – see Fig. 8.1) was undertaken using linear regression.

Fire

Fire data were sourced from the Bushfires Council of the Northern Territory and the Department of Land Information, Western Australia through the North Australia Fire Information (NAFI) (http://www.firenorth.org.au) and FireWatch (http://firewatch.dli.wa.gov.au) websites. These sites provide real-time fire mapping using MODIS and/or NOAA satellite imagery to map the timing and extent of fires across northern Australia.

For each region where individuals occurred during their respective tracking periods the timing, location, size and bearing of all fires that occurred within the vicinity of an individual was determined. For individuals at the Kidman Springs and DDRF sites the designated ‘vicinity’ area was within a 25 km radius of the individual (since no individuals in these areas moved further than this distance during the study). For the Barkly Tableland and south-west Queensland birds the designated ‘vicinity’ area was within 50 km of point location data for each individual. The responses of tracked individuals were assessed by determining:

a) whether a movement was made to the fire or burnt area during or for up to 4 days after the fire (time lag based on responses of bustards to a fire described in Chapter 4),
b) the minimum distances of the individual to the fire on the day(s) of the fire (N.B. when fires occurred over multiple days the closest distance was used),
c) timing of movements in relation to fire (in hours or days),
d) duration of stay on the burnt patch following arrival at the fire.

Responses of bustards to fire in the area were noted whether individuals moved or not. Wind speed and direction within the Kidman Springs region (the area for which there was available data) was plotted at the time of the fire and related to the location of the fire and individual, and the occurrence of movements.

RESULTS

Although a total of 12 individuals were fitted with satellite transmitters during the study, here I present data for seven individuals that provided suitable information for analysis. Of these, four were male and three female. Tracking periods for these individuals ranged from 152 to 1566 days. Summary statistics for each tracked individual are presented in Table 8.3. The number of daily fixes acquired for each GPS tracked individual are presented as graphs at the beginning of each individual's account.

The overall movement of individuals varied between the different regions. All five bustards tracked in the highly seasonal sites of Kidman Springs and the DDRF were relatively sedentary only making small and medium scale movements. The most mobile individual was the female tracked from the most climatically unpredictable site at Cluny Station in south-west Queensland. A male tracked in the Barkly Tableland region moved an intermediate distance between these extremes.

Occurrence of fires

A total of 47 fires occurred within 25 km of the original release sites of tracked bustards at Kidman Springs between 2004 and 2008 (Table 8.2). These fires ranged in size from less than 100 hectares to over 100,000 hectares. In addition, many other fires of varying size occurred near Kidman Springs but were not included here because no bustards in this region moved further than 25 km during the study.

Bustard #42539 at the DDRF moved 4.5 km to a fire that occurred in the region over an area of approximately 800 hectares (see below).

Four fires occurred within 50 km of the apparent movement track of male 42540 (i.e. the linear route between consecutive fixes) in the Barkly Tableland. However, due to an extended period of no transmission it was not possible to determine whether these fires had an influence on the movements of this individual (Fig. 8.18).

No fires were recorded within 100 km of bustard 42546 in Queensland.

Table 8.2: Number of fires in the Kidman Springs area according to size in three categories of distance from the original release site of individuals 42548 and 47734 between 2004 and 2008.

Area (ha)	0-5km	5-10km	10-25km	**Total**
1-100 ha	4	2	6	**12**
100-1000 ha	4	4	10	**18**
1000-10000 ha	0	1	9	**10**
>10000 ha	0	2	5	**7**
Total	**8**	**9**	**30**	**47**

Table 8.3: Details of satellite tracked bustards and summary of movements. Appendix 1 lists morphological details for each individual when available.

	42548	**47734**	**47735**	**42541**	**42539**	**42540**	**42546**
Deployment location name	Kidman Springs	Kidman Springs	Kidman Springs	Kidman Springs	DDRF	Barkly Tableland	Channel Country
Deployment location coordinates	-16.086, 130.933	-16.080, 130.932	-16.113, 130.945	-16.041, 131.033	-13.836, 131.193	-18.983, 136.613	-24.449, 139.530
Sex	Female	Female	Male	Male	Male	Male	Female
Transmitter type	GPS	GPS	GPS	ARGOS	ARGOS	ARGOS	GPS
Duty cycle	Hourly	Hourly	Hourly	Weekly	Weekly	Weekly	Hourly
Tracking period	27/5/04 - 9/9/08	30/5/04 – 23/6/08	12/12/07- 8/01/09	26/10/03 -26/3/04	10/3/04 – 10/8/04	28/8/03 – 2/6/04	3/10/05-28/12/06
Tracking period (days)	1566	1485	382+	152	152	279 (91)*	451
Total number of fixes	7099	10407	4563+	67	156	29	2676
Mean number of fixes per day	4.5	7.0	11.9	0.4	1.0	0.1 (0.3)	5.9
Total distance travelled (km)	1788	2573	1123	81	131	309	1663
Mean rate of daily movement (km)	1.1	1.7	2.9	n/a	n/a	n/a	3.7
Longest movement (km)	19.6	21.8	14.6	10.7	8.3	111.9	115.1
Maximum distance from origin (km)	20.4	20.3	8.6	17.5	11.6	112.7	418.2
Distance of final location from origin (km)	15.6	6.0	0.7	9.2	2.1	99.3	336.1
Maximum distance between fixes (km)	23.6	32.5	15.9	19.2	12.6	144.6	418.2

*prolonged period without transmission (i.e. tagged 28/8/2003, transmitted for one week then no transmission until 3/3/2004, then transmitted for 91 days).
+was still transmitting at 10/1/2009.

Movements of individuals

*BUSTARD = **42548;** SEX = **FEMALE; ** PTT = **GPS;** LOCATION = **KIDMAN SPRINGS***

Female 42548 was tracked for the longest duration of any individual in the study with a tracking period extending from 27/5/2004 to 9/9/2008, equating to 1566 days (Fig. 8.3; Table 8.3). During this time a total of 7099 location fixes were acquired at a mean of 4.5 fixes per day. Gaps in transmission, when no fixes were acquired, are also illustrated in Fig. 8.3.

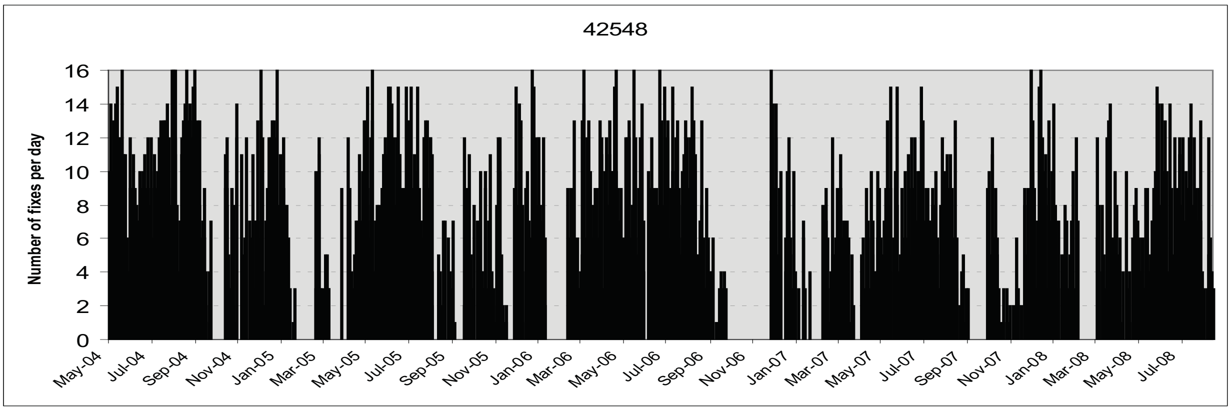


Figure 8.3: Number of fixes per day for the tracking period of female bustard 42548 at Kidman Springs.

The most notable feature of this individual's ranging behaviour was the direct, repeated movements (n = 19) it made between two intensively-used areas (designated as sites A and B in Fig. 8.4). These sites are approximately 20 kilometres apart and separated by a line of hills. Site A consists of open woodland habitat on uniform terrain over loam earth soils, while Site B has a more heterogeneous mix of open woodland and open treeless grassland habitats (see also Fig.5.11 and Chapter 5). While 78% of this female's time was spent at site A, she moved consistently to Site B in the late wet or early dry seasons (from February to May) for variable periods of time (3 to 74 days) (Fig. 8.5). Movements to site B were also made at other times (most notably in the late dry season in 2005 and 2007), and on some occasions were made repetitively back and forth between these sites within a few weeks.

The only other medium range movement this individual made was in response to a large fire that occurred in early September 2004 (Fig. 8.11). This movement of 8.5 km was made from site B towards the north-eastern front of the fire. However, the female stopped short of the fire itself, possibly because it was in steep hills - a habitat bustards tend to avoid. Therefore, while seemingly initially attracted to the fire, it spent less than 24 hours in the area before returning to where it had come from. The following section, describing the movements of bustard 47734, discusses responses to this fire in more detail.

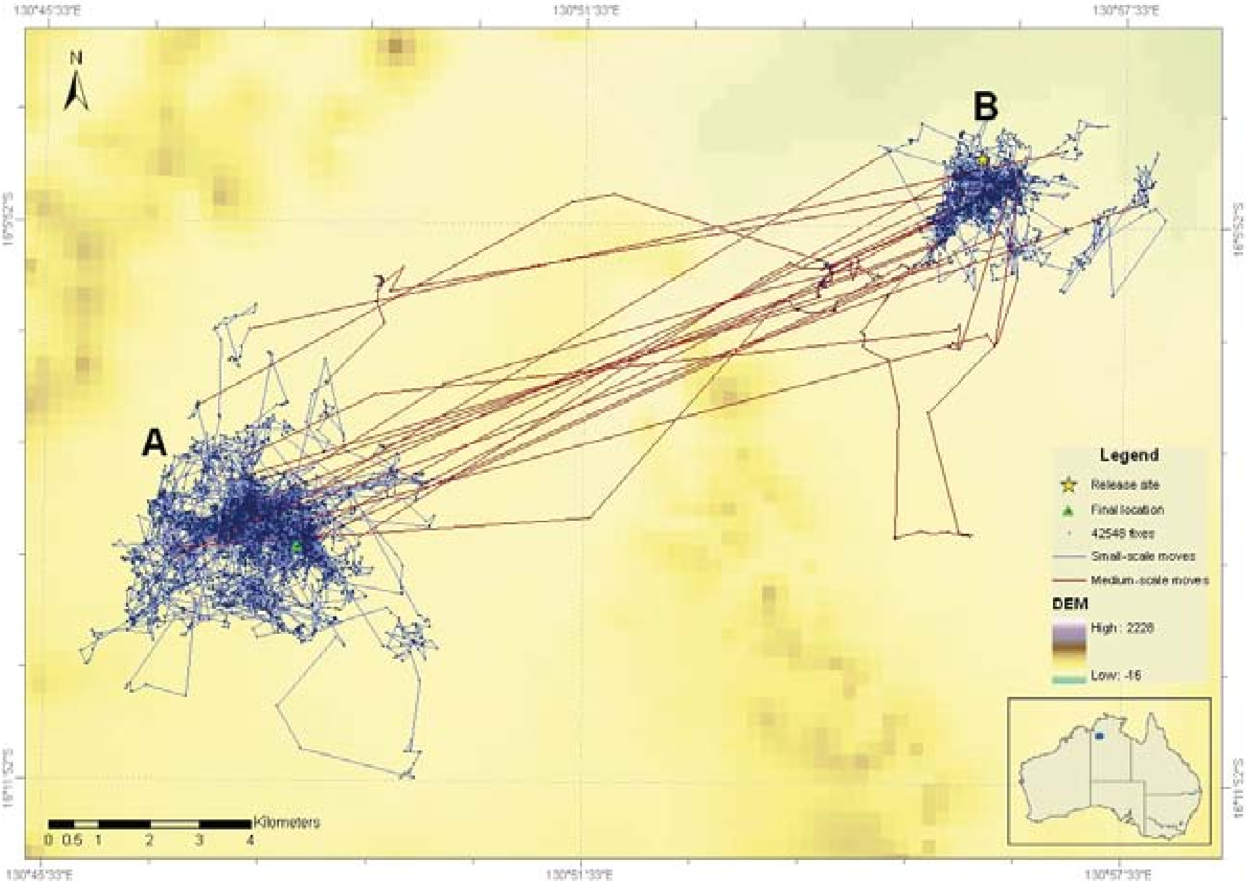


Figure 8.4: Small (blue line) and medium-scale (red line) movements of female 42548 between 27/5/2004 and 9/9/2008 in the Kidman Springs region. This individual used two general areas: area A in the south-west and region B in the north-east. Note that these areas are the same as those for female 47734 discussed subsequently. Background imagery is a Digital Elevation Model (DEM). Note also the ridge line running NNW to SSE dividing the two regions.

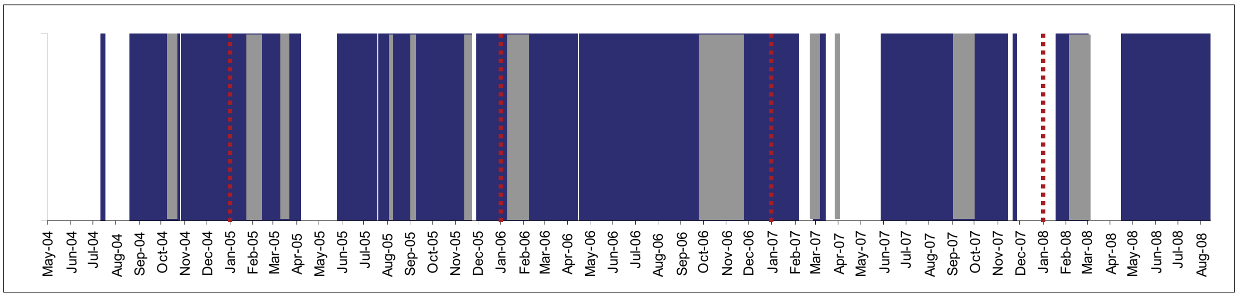


Figure 8.5: Timing of movements and duration of stay at site A (blue blocks) and site B (white blocks) at Kidman Springs during the tracking period of female bustard 42548. To clarify seasonality, red lines signify the end of January equating approximately to the middle of the wet season in northern Australia. Grey shaded regions denote periods of greater than five consecutive days when no location fixes were acquired.

This female exhibited two peaks in mean daily distance moved during the year (Fig. 8.6). Mean distances moved each month are presented for all years combined here because of the intermittent transmissions of the GPS transmitter used for this individual (i.e. the movement measurements are based on distances moved between consecutive days, however, for several months over the tracking period there were too few records to present these data for each month separately). Movements increased in the late wet season/early dry when this individual began regularly moving between sites A and B, presumably to exploit the open treeless grasslands found at site B that are a preferred habitat for bustards at this time of year (Chapter 5). A second peak later in the year coincided with the start of the breeding season in northern Australia when females range between displaying males at leks to assess potential mates (Chapter 7) and when food resources are generally low (Chapter 3).

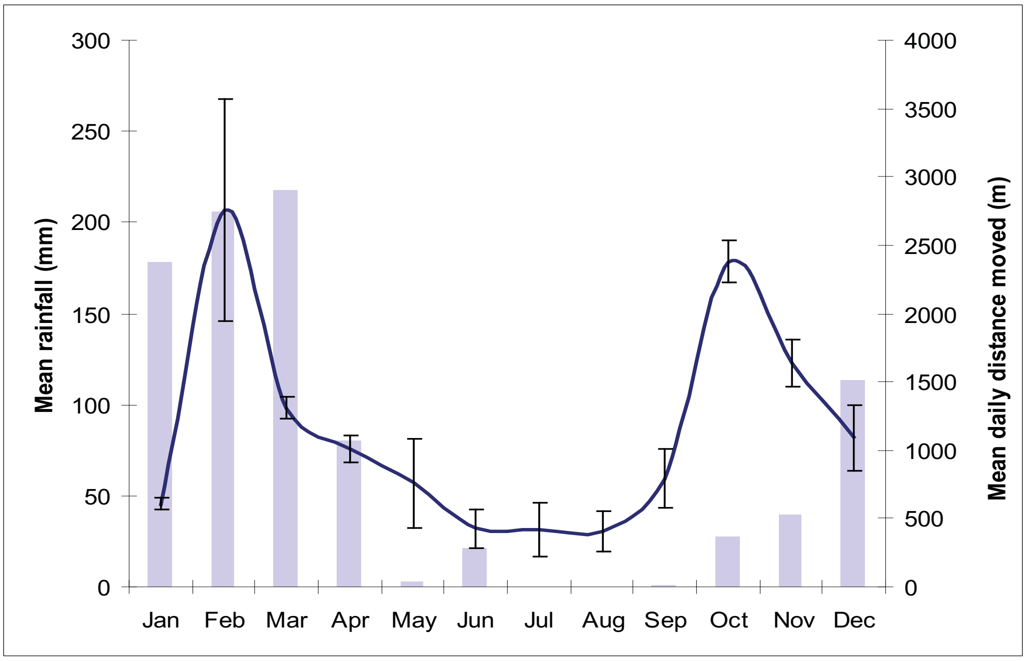


Figure 8.6: Mean daily movements (line) made according to season based on fixes between consecutive days for all years combined in relation to mean rainfall (bars) between the years 2004 to 2008.

BUSTARD = ***47734;*** *SEX =* ***FEMALE;*** *PTT =* ***GPS;*** *LOCATION =* ***KIDMAN SPRINGS***

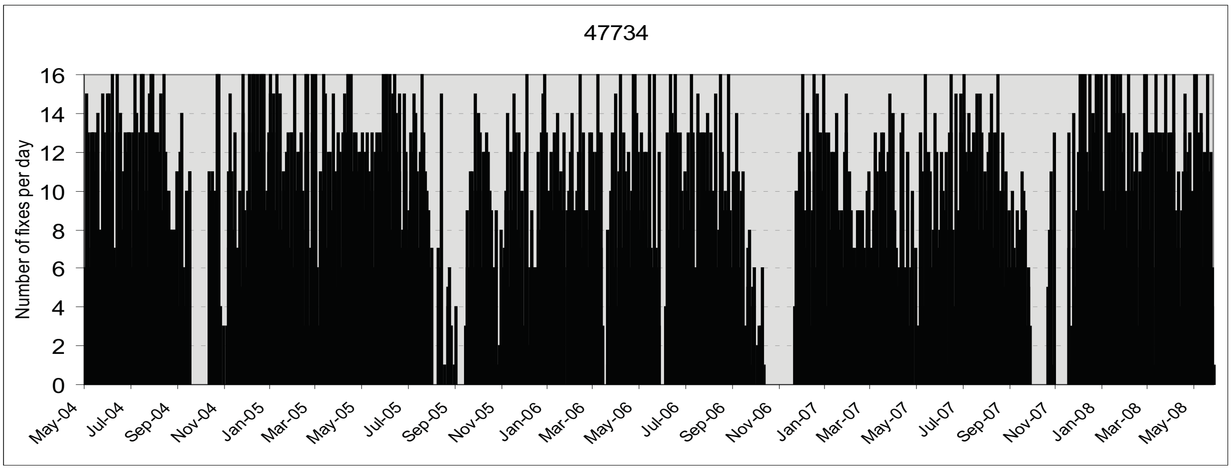


Figure 8.7: Number of fixes per day for the tracking period of bustard 47734 at Kidman Springs.

The tracking period for female 47734 at 1485 days was of similar length to bustard 42548. However, at 10,407 (mean 7.0 fixes per day), it had the largest number of location fixes of any individual (Table 8.3; Fig. 8.7). Periods when no fixes were obtained are also shown in Fig. 8.7.

As for all other bustards tracked at Kidman Springs, 47734 remained in the general vicinity, moving only locally (Fig. 8.8). This individual made repeated movements (n = 16) between Areas A and B, but spent 84% of the tracking period in Area B (Fig. 8.9). This female also ranged more widely than other individuals tracked in the Kidman Springs region, and made several ‘one-off’ movements to nearby locations for short periods of time (1 to 5 days). There were no readily discernible seasonal patterns to any of these medium scale movements. However, a regular seasonal pattern in the mean daily distances traveled was evident, with greatest mobility occurring in the late dry season (Sept. to Nov.) especially after first rains of the season (Fig. 8.10). This period coincides with the commencement of the breeding season in the north. Periods of minimal movement following these periods of high mobility in the years 2004, 2005 and 2007 indicate nesting periods when the female was generally confined to the immediate vicinity of the nest.

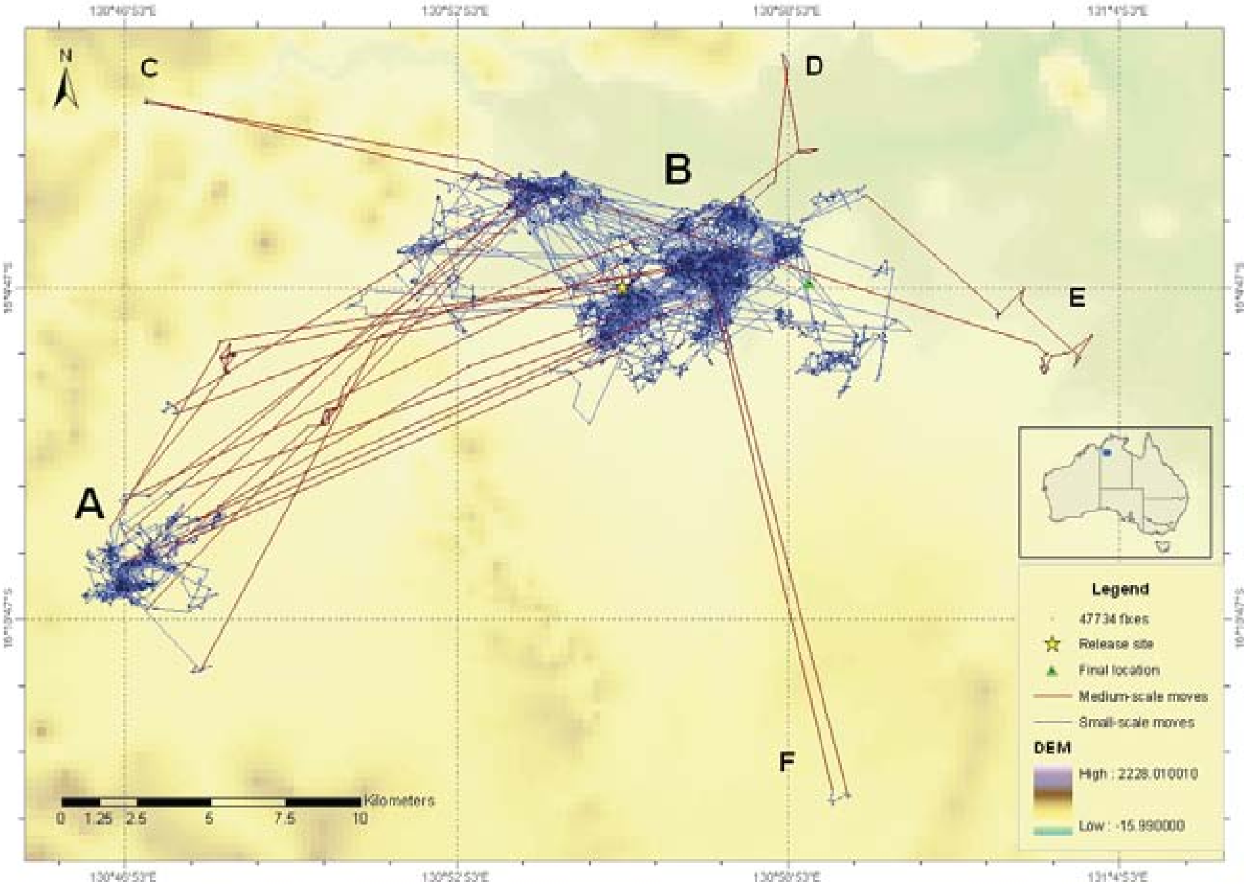


Figure 8.8: Movement paths of female 47734 at Kidman Springs between May 2004 and June 2008 showing fix locations, short (blue line) and medium (red line) scale movements. This female mostly used Area B but moved repeatedly to Area A for short periods. It also made other medium-range movements to areas depicted here as C, D, E and F. See Fig. 8.9 for timing and duration of stay at locations for these movements. Background map is a Digital Elevation Model (DEM). Note that areas A and B are the same as labelled for individual 42548 (Fig. 8.4).

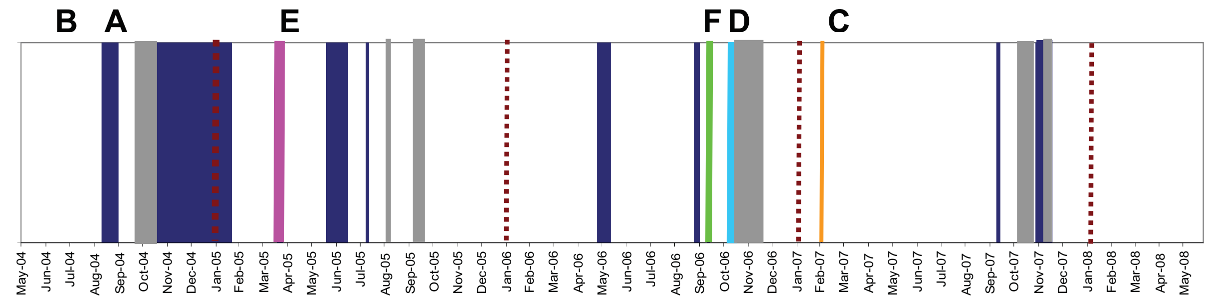


Figure 8.9: Timing of movements and duration of stay at locations in the Kidman Springs area during the tracking period of female 47734. Site codes are: A (dark blue); B (white); C (orange); D (light blue); E pink and F (green). Red dotted lines signify the end of January equating approximately to the middle of the wet season in northern Australia. Grey shaded regions denote periods of greater than five consecutive days when no location fixes were acquired.

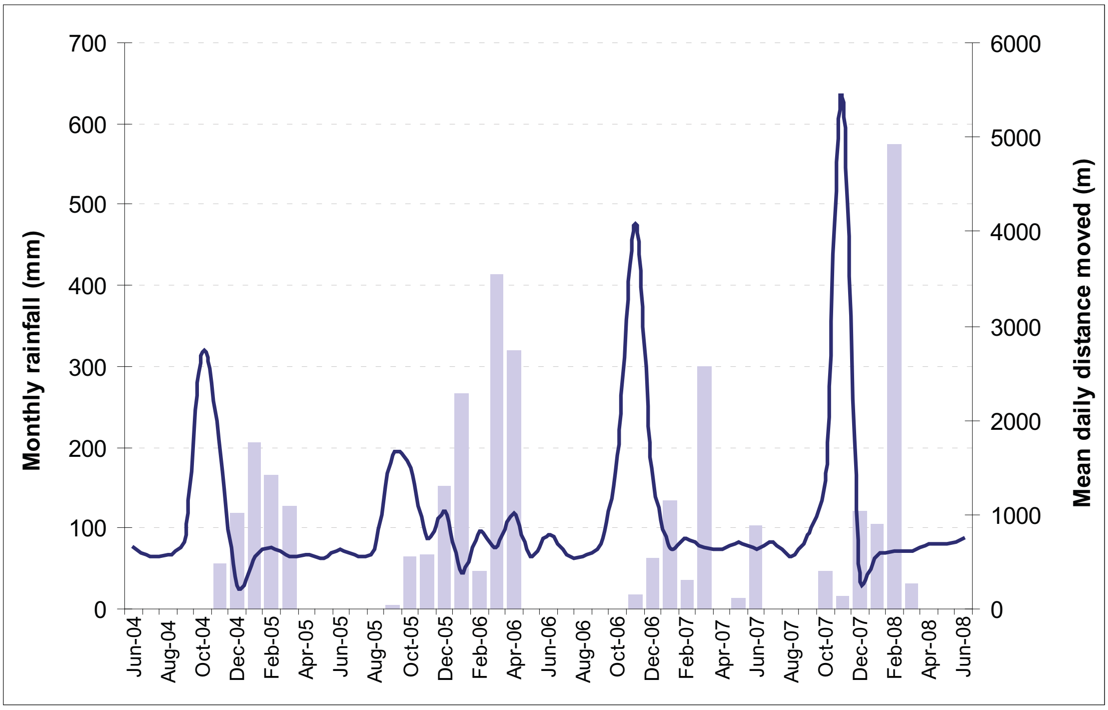


Figure 8.10: Mean distance of movements between consecutive days per month (line) by 47734 at Kidman Springs in relation to rainfall (bars). The regular seasonal peaks in the late dry season coincide with the commencement of the breeding season and resource lows. The troughs following extensive movements in most years relate to nesting events.

The first significant longer movement by 47734 of 21 km (from area B to A) was made directly to a large fire (>100,000 ha) to the south-west in September 2004 (Fig. 8.11). A simultaneous movement towards this fire (albeit to a different locality) was made by female 42548. Notably, this fire commenced in late August. However, neither individual moved towards it until over a week later. On the evening of September 7 both individuals were still in region B but had moved to the fire by the following morning. A possible explanation for these movements may relate to prevailing wind conditions. From the time the fire commenced until 6 September the prevailing wind direction was from the SE to E direction, effectively blowing away from the direction of both individuals. On September 7 and 8, the fire front had expanded to the east and the wind direction changed to a southerly, now blowing directly towards the birds. Female 47734 subsequently moved in a south-westerly direction settling at the fire in area A, where she then spent 21 days. In comparison, as discussed above, female 42548 moved in a direct southerly direction to the fire but appeared to stop at the base of the hills where the fire was before soon moving back to region B.

Female 47734 made another movement directly in response to a fire on the 5th and 6th of November 2006 (Fig. 8.12) (i.e. Area B to D in Fig. 8.8). This movement of 7.3 km to the NNE was made to a fire of approximately 1000 hectares. The fire appears to have started from a lightning strike between 4 and 5 of November. The female began moving towards the fire on the morning of the 5th and arrived either later that evening or in the morning of the following day (the uncertainty is associated with the intermittent location fixes acquired during this time). The prevailing wind direction during this period was from the NE towards the individual.

In contrast to the above observations there were two other notable examples of nearby fires that 47734 did not move to despite wind conditions appearing favourable. In late November 2005 a small prescribed fire (850 hectares) was implemented at Kidman Springs in the centre of the core range of 47734 (Fig. 8.12). Although the female was less than 2 km and downwind of the fire she did not move towards it. However, it appears she was nesting between 19/11/05 and 6/12/05 (a failed nest attempt). Another example occurred in early May 2006. A medium-sized fire (5200 ha) had been burning for 4 days approximately 5 km south of the location of 47734. Although she was again within close proximity and directly downwind of the fire she did not move towards it. In this case, movements to fires in the early dry season may be less likely because of the ubiquitous abundance of food resources at this time. That is, foraging at fires may be no more productive at this time relative to surrounding unburnt areas, whereas later in the dry season foraging at fire fronts is advantageous because food resources are generally low across the landscape.

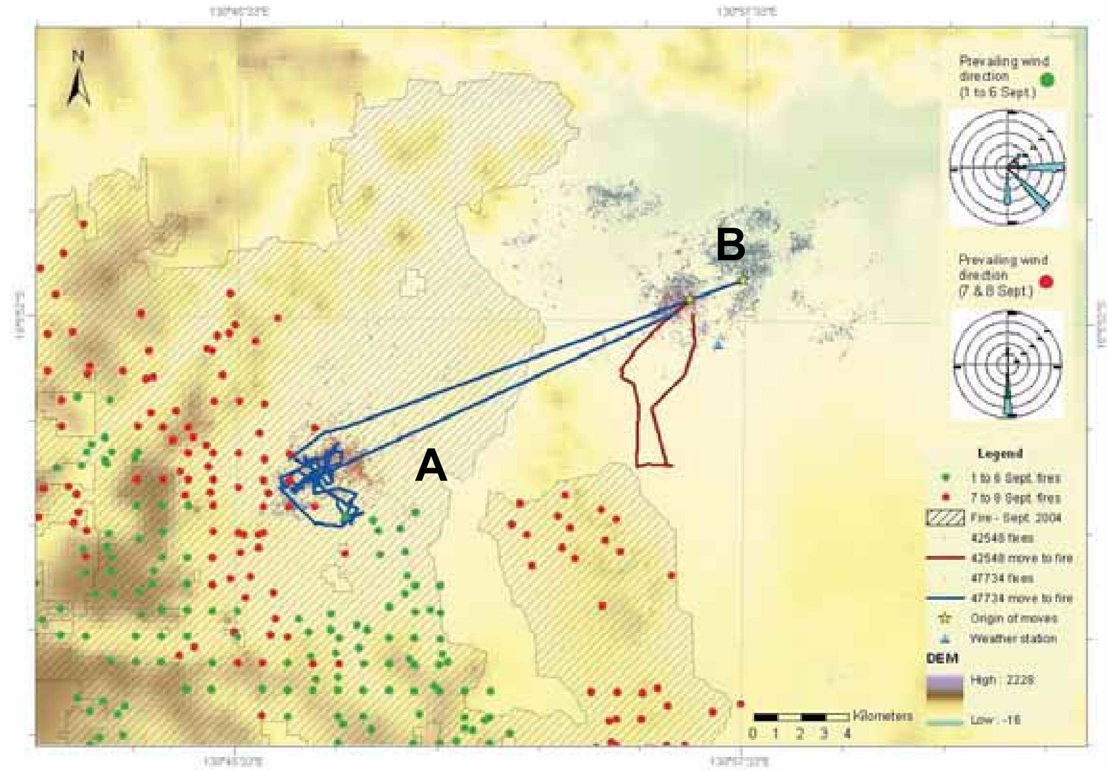


Figure 8.11: Synchronous movements of bustards 42548 (red line) and 47734 (blue line) from Area B towards a large fire in the Kidman Springs area on September 8, 2004. Red and green points indicate fire hotspots between specific dates (see legend). Hatched area shows the entire area burnt during September. Wind rose diagrams indicate prevailing wind conditions corresponding to the timing of fire hotspots. Arrow indicates direction the wind is from; frequency of recordings are indicated by length of arrow and mean speed is indicated by colour (light blue = 1-10 knots; green = 10-20 knots; blue = 20-30 knots). Notably both individuals moved simultaneously and almost immediately towards the fire only once the fire spread east and wind changed in their direction.

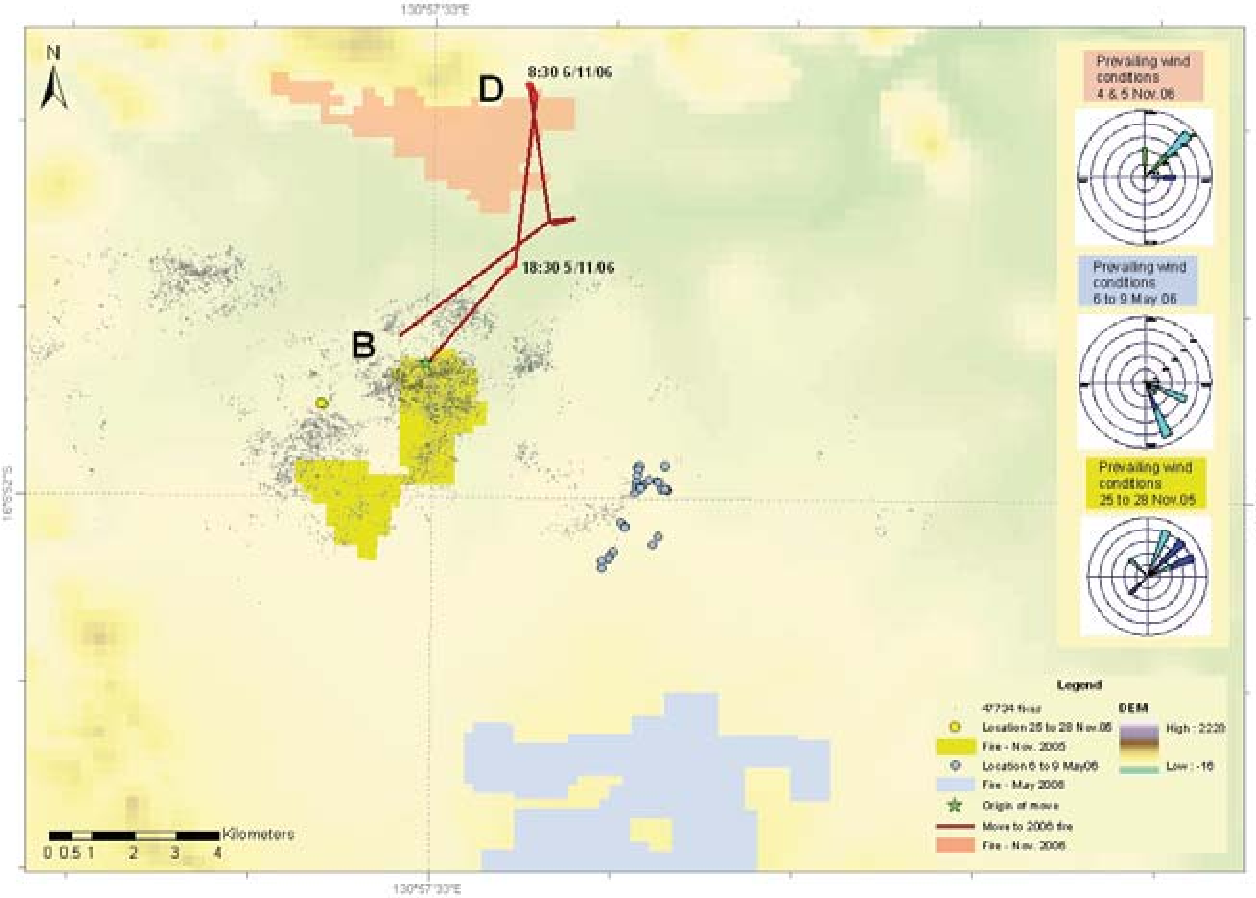


Figure 8.12: Responses of bustard 47734 to fires in the Kidman Springs area. Listed dates indicate the sequence of movements (red line) to the fire from area B to area D in early November 2006 (red area) (see also Fig. 8.8). Yellow points indicate fixes during the November 2005 fire (yellow area); blue points indicate fixes during the May 2006 fire (blue area). Wind rose diagrams indicate prevailing wind conditions corresponding to the timing of each fire. Arrow indicates direction the wind is from; frequency of recordings are indicated by length of arrow and mean speed is indicated by colour (light blue = 1-10 knots; green = 10-20 knots; blue = 20-30 knots).

BUSTARD = 47735; SEX = MALE; PTT = GPS; LOCATION = KIDMAN SPRINGS

Male 47735 was tagged at Kidman Springs in December 2007. It has averaged the greatest number of fixes per day (mean = 11.9) (Table 8.3), with a fix being obtained for over 91% of days during the tracking period. Transmission was interrupted for approximately three weeks in April 2008 and for two shorter periods in October and November 2008 (Fig. 8.13).

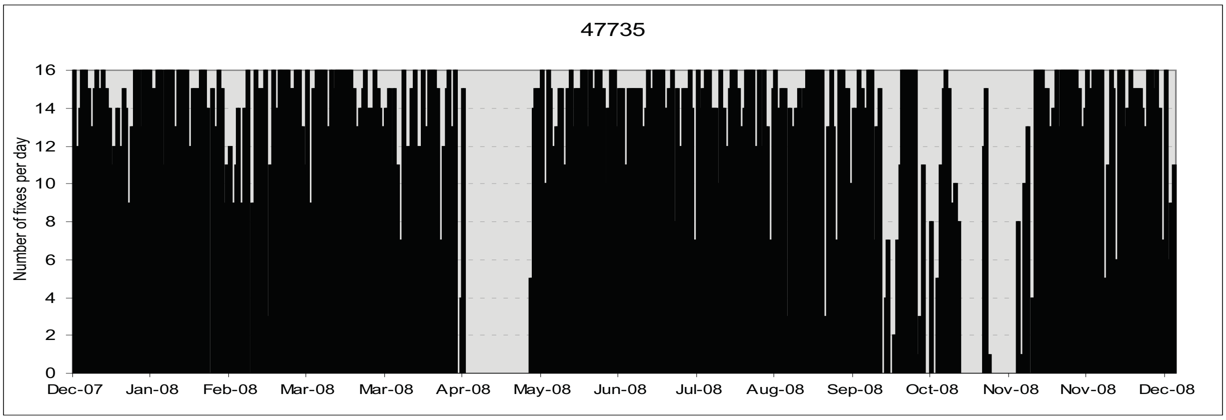


Figure 8.13: Number of fixes per day for the tracking period of bustard 47735

This male was captured at its display site which remained the central hub of its activity and ranging behaviour (Fig. 8.14). Almost all of its movements were made over a small localised area, with the furthest distance it was recorded from its capture (and primary display) site being 8.6 km. As such no medium or long range movements as defined in this study were made by this individual. This represented one of the smallest ranging areas of all individuals tracked.

During 2008 there were 5 fires within 14 to 30 km of this individual ranging in size from approximately 200 to over 50,000 ha in size. However, no movements in the direction of any of these fires were made by this individual.

Mean distance moved between consecutive days was lowest for the months of December 2007, December 2008 and March 2008 (Fig. 8.15). These periods represented peak display periods during the breeding season when much of its time was confined to its circumscribed display area (see also Chapter 7). Movement distances increased following the wet season of 2008 and peaked in the late dry season (September and November).

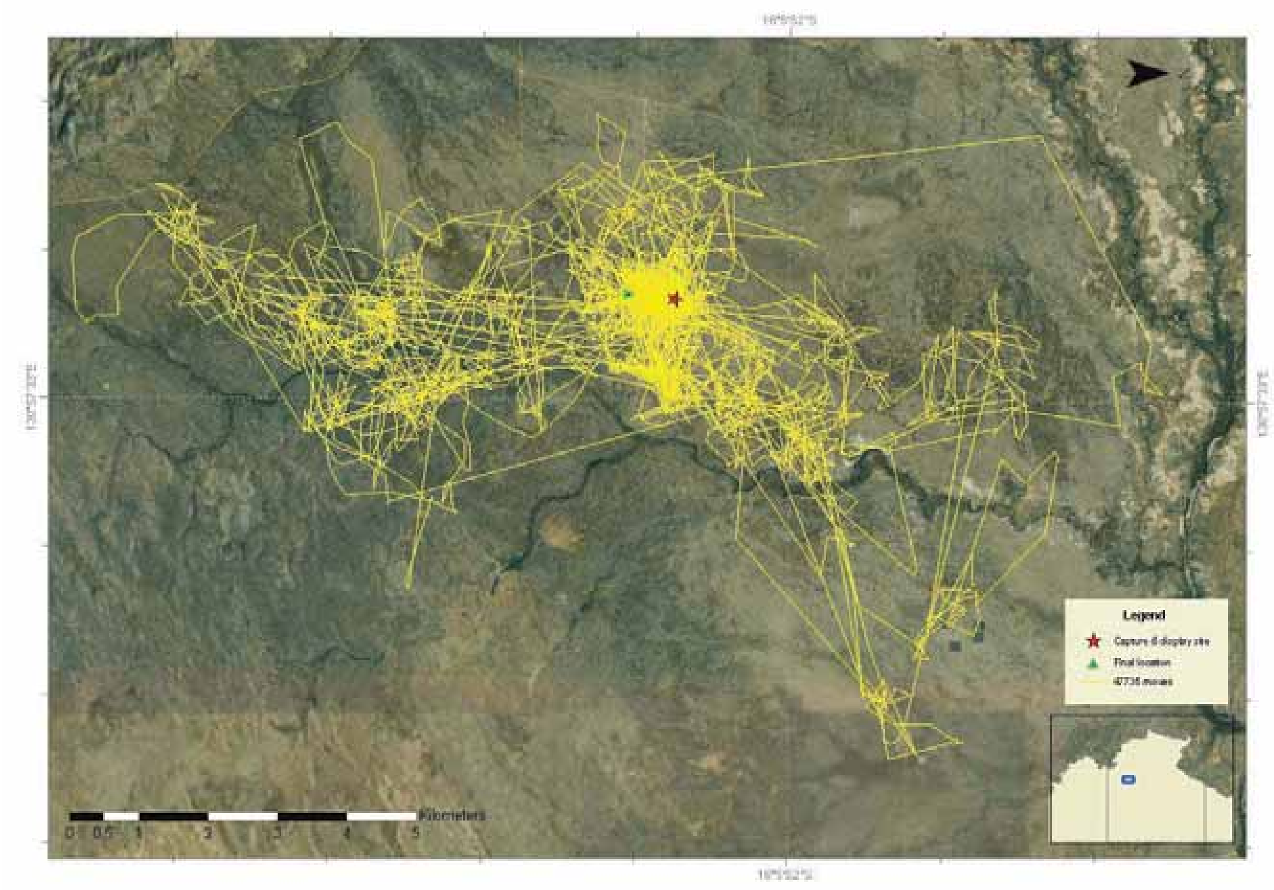


Figure 8.14: Movement paths of male 47735 at Kidman Springs between December 2007 and January 2009. Inset shows location of Kidman Springs in northern Australia. Background is Quickbird imagery sourced from Google Earth.

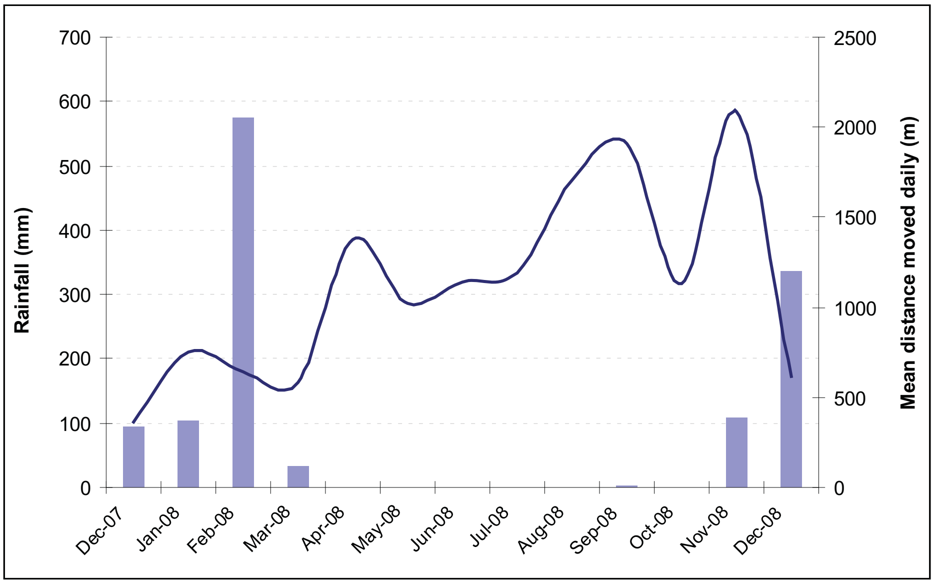


Figure 8.15: Mean distance of movements between consecutive days per month (line) by male 47735 at Kidman Springs in relation to monthly rainfall (bars).

BUSTARD = ***42541;*** *SEX =* ***MALE;*** *PTT =* ***ARGOS;*** *LOCATION =* ***KIDMAN SPRINGS***

This mature male bustard was fitted with an ARGOS transmitter at Kidman Springs in October 2003. Like the other bustards tracked at Kidman Springs it remained in the vicinity throughout the transmission period which lasted between October 2003 and March 2004 (Fig. 8.16; Table 8.3). The maximum distance at which it was recorded from the point of origin was 17.5 km. Although this was a mature male that was likely to display at leks during the breeding season, the sparse temporal and spatial resolution of location fixes makes it difficult to identify whether the male used a display site consistently.

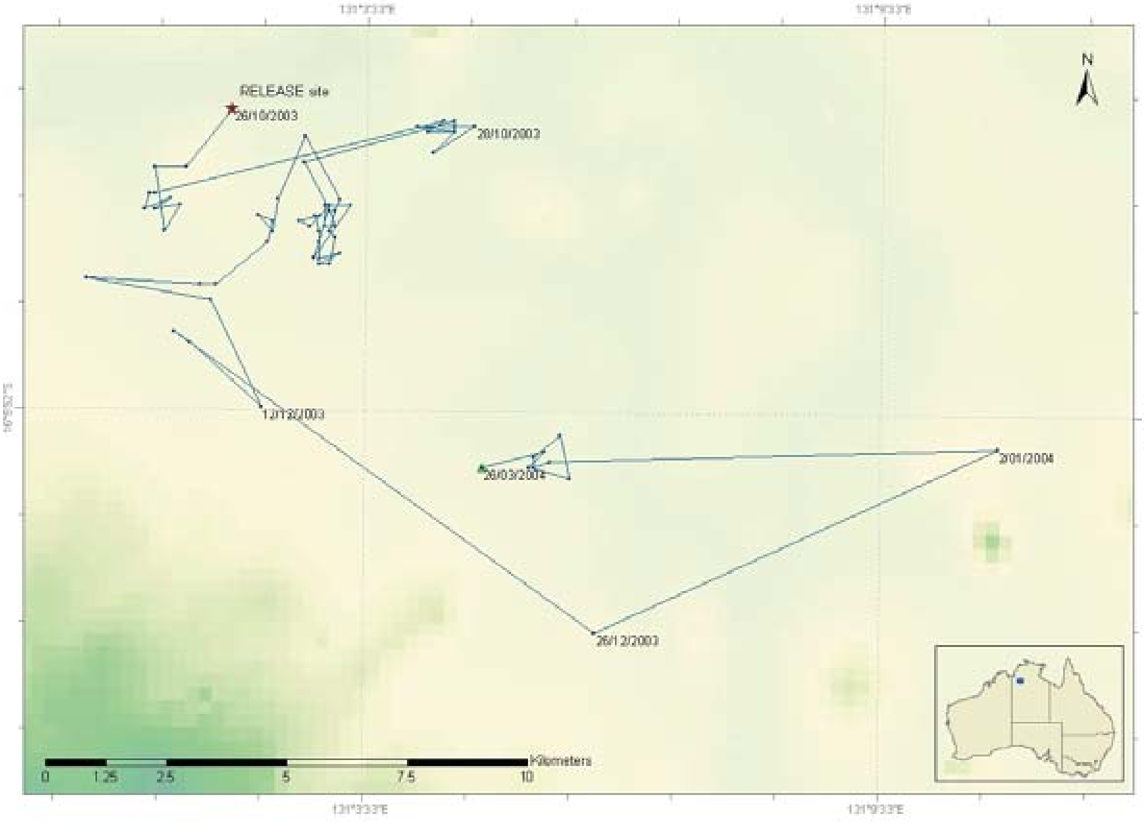


Figure 8.16: Movements of male 42541 at Kidman Springs between October 2003 and March 2004

BUSTARD = ***42539;*** *SEX =* ***MALE;*** *PTT =* ***ARGOS;*** *LOCATION =* ***DDRF***

Male 42539 was a mature male bustard fitted with an ARGOS transmitter on 10 March 2004. It remained in the general vicinity of the Douglas-Daly Research Farm throughout its tracking period until 10 August 2004 when the transmitter was located having fallen off the individual (Fig. 8.17). Between 12 March 2004 and 18 May 2004 it moved and stayed in an area across the Douglas River to the north-west of its capture site on Tipperary Station but returned to the DDRF thereafter. Much of the activity of this individual centred on the irrigated crops at the centre of the DDRF which are commonly used by large numbers of bustards, particularly during the dry season (Chapter 4). Daily movements at dawn and dusk of individuals moving between the area on Tipperary Station to the NW and the DDRF were commonly observed throughout the dry season (pers.obs).

This individual also appeared to respond to a small local fire in the region. However, the timing of the duty cycle for the ARGOS transmitter used on this individual (12 hours on/ 156 off) was such that it was not possible to pinpoint the timing of the movement accurately. A fire occurred on 25 April 2004 approximately 4.5 km to the north-west of 42539's last known position on 13 April 2004. The male was subsequently recorded at the location of the fire on 27 April, two days after the fire had commenced. He then remained in the vicinity until at least 11 May, before being located 5 km to the south on 17 May.

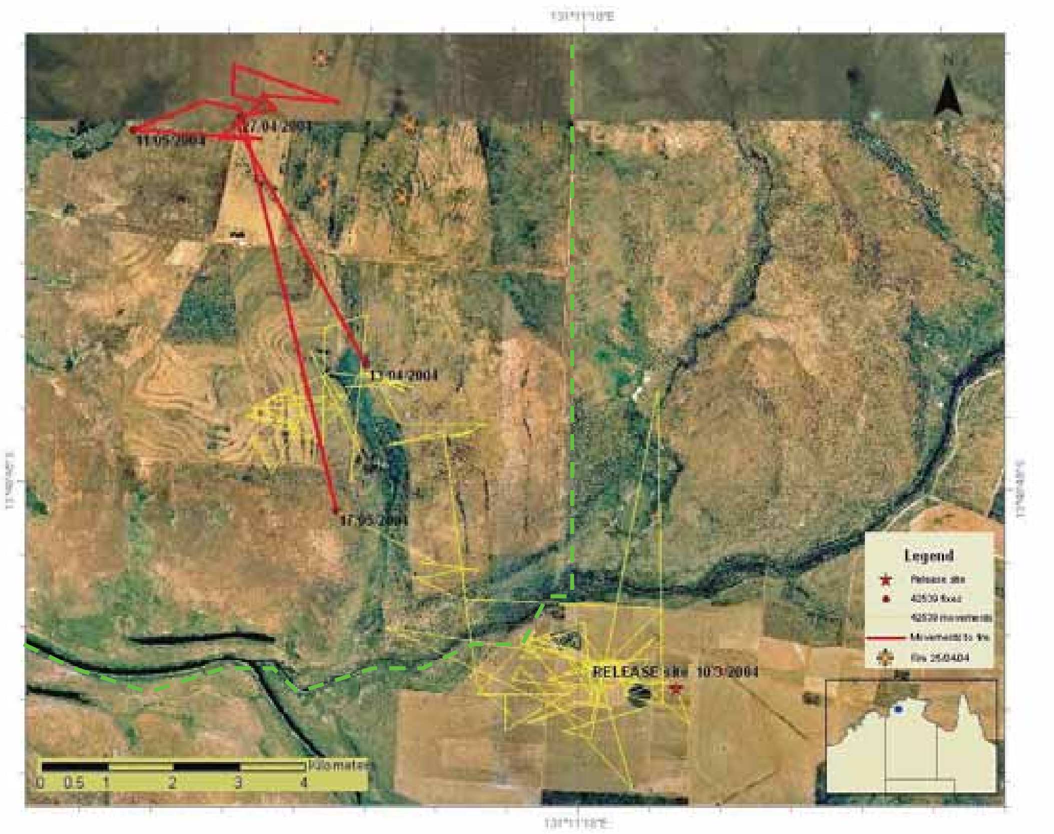


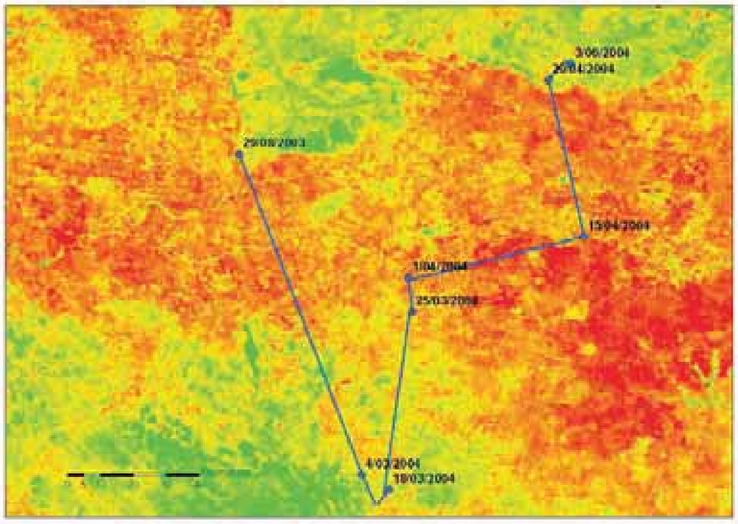
Figure 8.17: Movement path of male 42539 at the DDRF and locations on Tipperary Station (in the north-west denoted by green line) between March and August 2004. A movement to a small fire to the north-west that occurred on April 25 is indicated by the red line and includes dates of known fixes before and after the fire. Background imagery is an aerial photograph sourced from the Northern Territory Land Information System (NTLIS).

BUSTARD = ***42540;*** *SEX =* ***MALE;*** *PTT =* ***ARGOS;*** *LOCATION =* ***BARKLY TABLELAND***

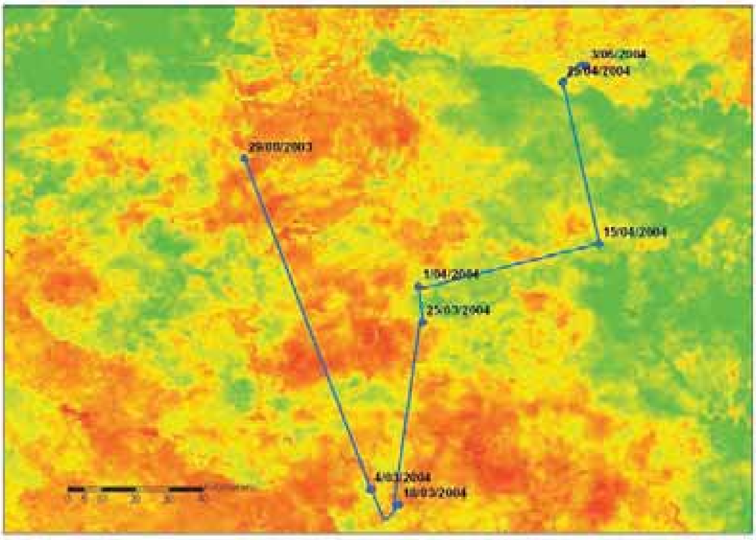
Male 42540 was captured on Alexandria Station in the Barkly Tableland in August 2003. One week after deployment contact was lost with this individual due to a transmitter malfunction, but transmission subsequently and unexpectedly recommenced in early March 2004. By then the individual had moved ~112 km to the SSE but it is not known when during this period the movements occurred (Fig. 8.18). At the time of deployment in the mid-dry season (August) the individual was in close proximity to an extensive area of relatively high vegetation greenness (Fig. 8.19). From early to mid March 2004 the individual remained in an area to the south but as the greenness of vegetation declined during the month, in subsequently moved 171 km to the north-north-east in a series of steps between March 18 and April 29. This overall movement appeared to occur towards an extensive area of high primary productivity.

Figure 8.18: Location and movements of male bustard 42540 in the Barkly Tableland in the Northern Territory between August 2003 and early June 2004, including occurrence of fires in the vicinity during this period. Note that the final location of this individual was in rocky, low undulating hill country, indicated by the darker region. Background map is Landsat Imagery overlaid with a Digital Elevation Model.

AUGUST
2003



MARCH
2004



APRIL
2004

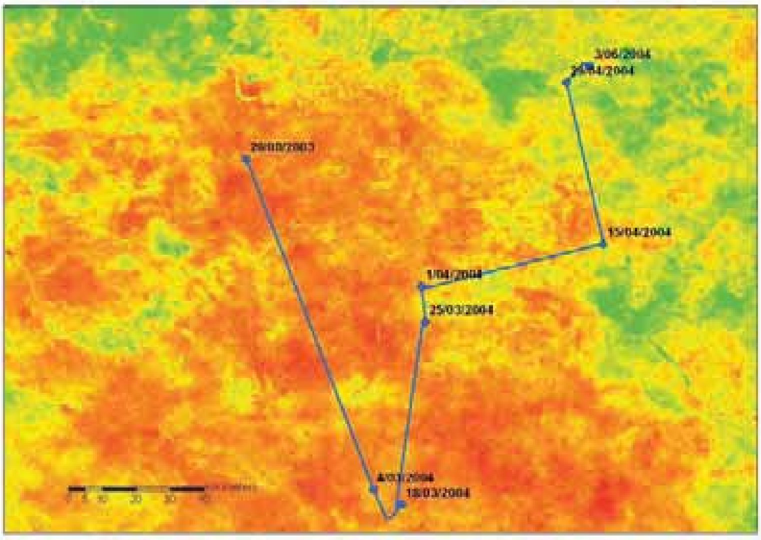


Figure 8.19: Movement track and locations by date (points) of 42540 in the Barkly Tableland region in relation to gross primary productivity (GPP) during August 2003, March 2004 and April 2004. Note that this individual was tracked using a Sirtrack ARGOS satellite transmitter therefore there were fewer location fixes than for GPS tracked individuals. Gradation in the background imagery represent areas of high (green) to low (red) gross primary productivity.

BUSTARD = ***42546;*** *SEX =* ***FEMALE;*** *PTT =* ***GPS;*** *LOCATION =* ***SW QLD***

This female bustard was tracked between 3 October 2005 and 28 December 2006 (Fig. 8.20; Table 8.3). During these 451 days there were 2676 location fixes at an average of 5.9 per day.

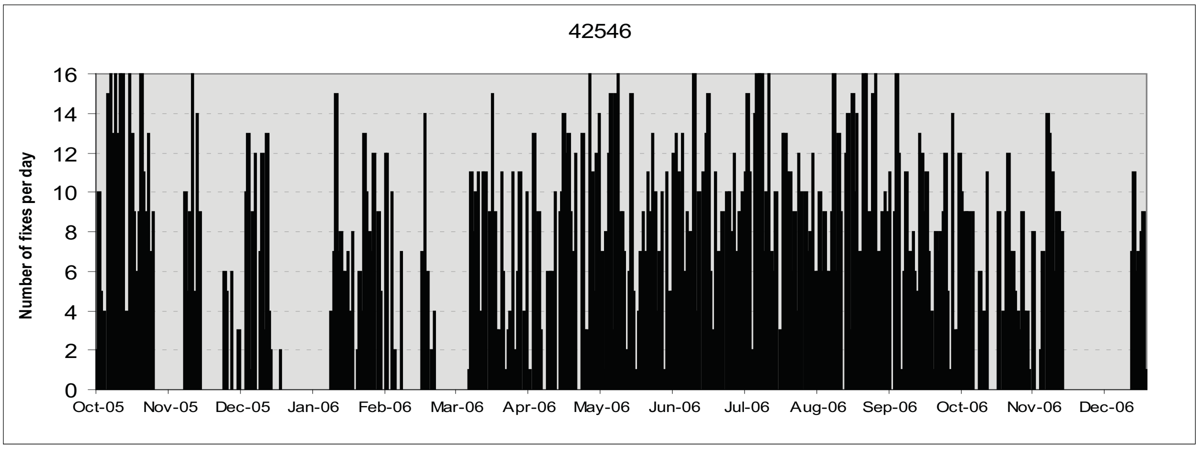


Figure 8.20: Number of fixes per day for the tracking period of bustard 42546

This individual was fitted with a transmitter 12 km south-east of Bedourie on Cluny Station in the Channel Country of south-west Queensland (Fig. 8.21). This location represents the most climatically variable site at which a transmitter was deployed during this study (Fig. 8.1). Notably, the region surrounding the capture location had received significant rainfall in June 2005 (108 mm at Cluny Station), and there was an unusually high number of bustards observed in the region at the time of capture (pers.obs). Furthermore, the captured individual, and two other females in the region, were observed with chicks. These observations highlight the favourability of this site at the time, while the apparently high bustard densities suggest there may have been an influx of individuals into the region from elsewhere following the rainfall. Consequently, this deployment offered an opportunity to assess the potential response of the female as notional habitat quality changed in favourability over time.

Bustard 42546 was the most mobile individual tracked during this study. Within two weeks following transmitter deployment in late October she commenced an extended movement northwards progressing in a series of steps following the Georgina River floodplain. The final destination on this northward movement was a location approximately 70 km west of Mount Isa, representing a total distance moved of 483 km (linear distance = 418 km) from deployment location. Maximum rate of movement between consecutive days occurred between November 10 and 13 when she averaged 46.5 km per day. These movements were made during the off period of the transmitter's duty cycle (i.e. between 21:30 and 6:30), suggesting they were made either overnight (many birds including bustards migrate at night – Collar 1996) or in the early morning (Fig. 8.22).

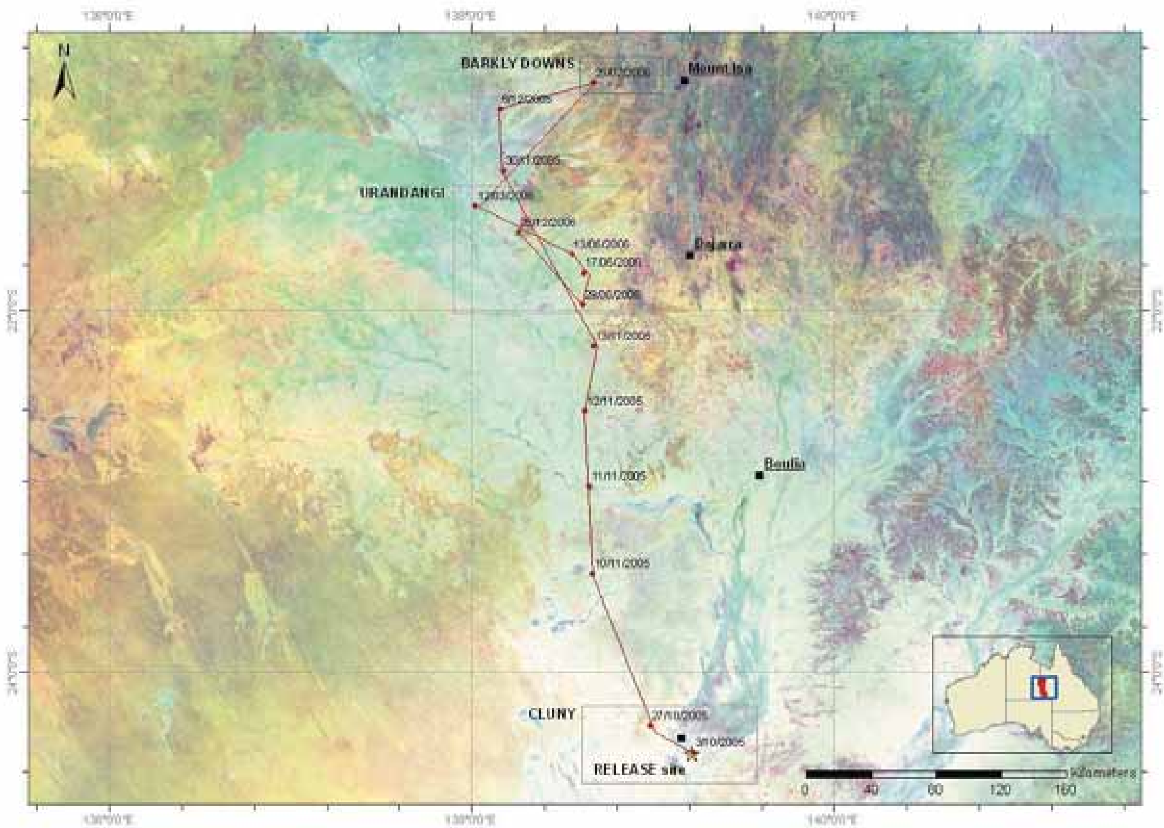


Figure 8.21: Generalized movement track of female 42546 in western Queensland between 3/10/2005 and 28/12/2006. Note that the movement path of this individual has been simplified to show the overall direction, location and approximate timing of movements. Boxed areas refer to general locations named after the closest weather station to the centre of activity. Figure 8.25 depicts the period of occupancy in each destination region. Background map is Landsat Imagery overlaid with a Digital Elevation Model.

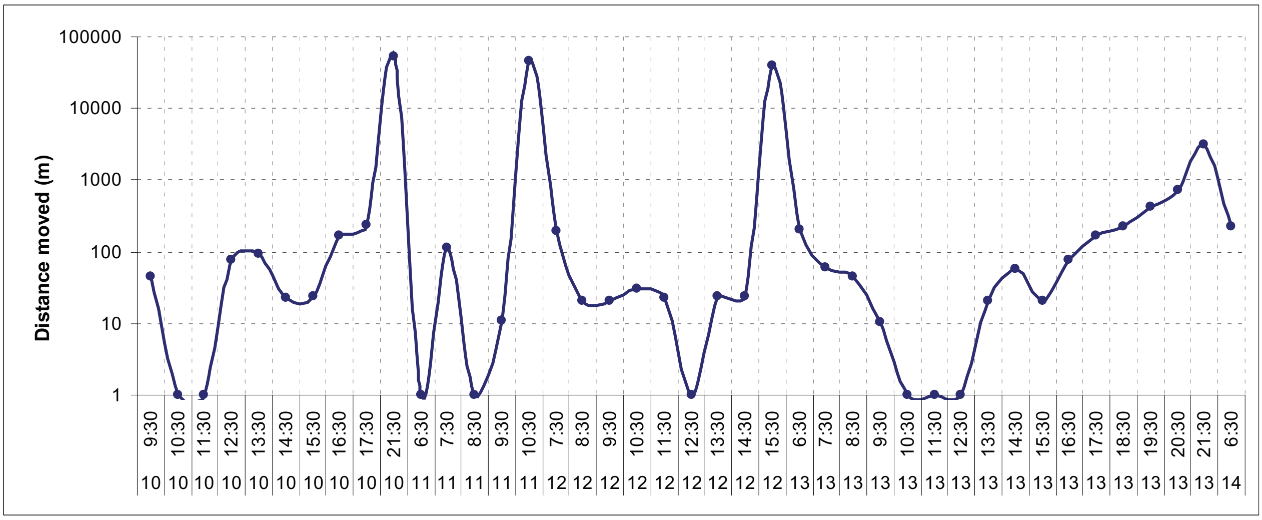


Figure 8.22: Hourly movement distances by 42546 over 4 days during a long distance northward move in November 2005. Note that the x-axis presents date (bottom figure) and 24 hour time but that only times for which fixes were acquired are included. This excluded the period between 21:30 and 6:30 because of the duty cycle employed and any ‘missed’ fixes. Note also that points refer to values for the period between the time at a point and the next consecutive time listed (e.g. a movement over 10,000 m was made sometime between 21:30 on November 10 and 6:30 the following morning).

Notably, at the time of deployment in October 2005, this female was located at the centre of a broad series of channels on the Georgina River where primary productivity was significantly higher compared to surrounding areas (Fig 8.24). She subsequently commenced her northward movement during early November following a nominal amount of rain at Cluny Station (Fig. 8.23), but as conditions were generally drying out in the south and gradually and patchily improving in the north (Fig. 8.24). Interestingly, the Simpson Desert to the west of this individual’s location in October and November was still highly productive yet, although significantly closer, the female moved northward. Having arrived in the north she subsequently moved between highly productive patches as conditions over a broader area steadily improved (Figs. 8.24 & 8.25).

In late February 2006, while conditions were still notionally favourable across the north, the female began moving southwards retracing her movements along the Georgina River floodplain. However, rather than moving back to the point of origin (i.e. where she had been captured), she moved part of the way and subsequently ranged over a broad area of productive floodplain (note particularly the period between March and June 2006) until contact was eventually lost (Fig. 8.24).

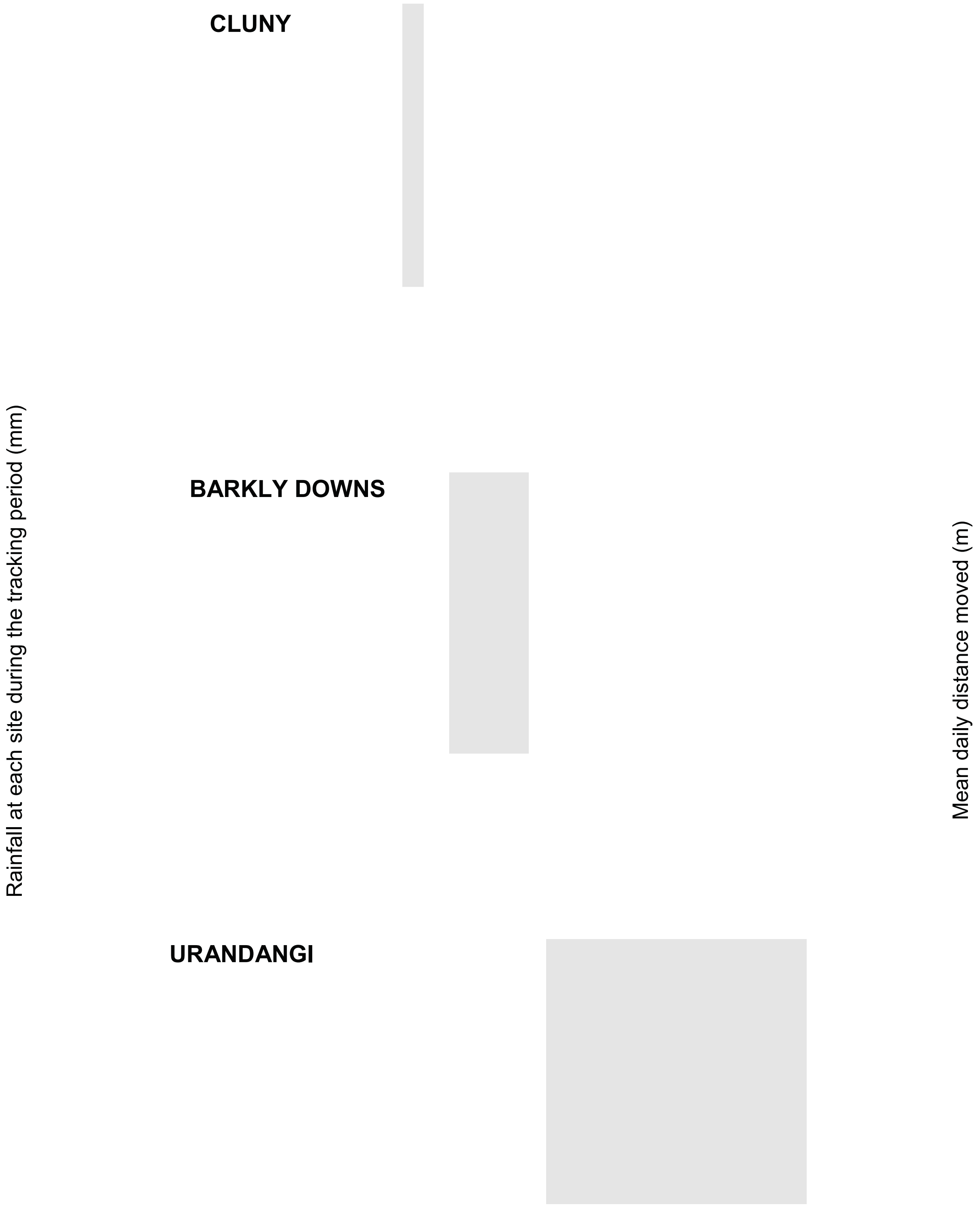
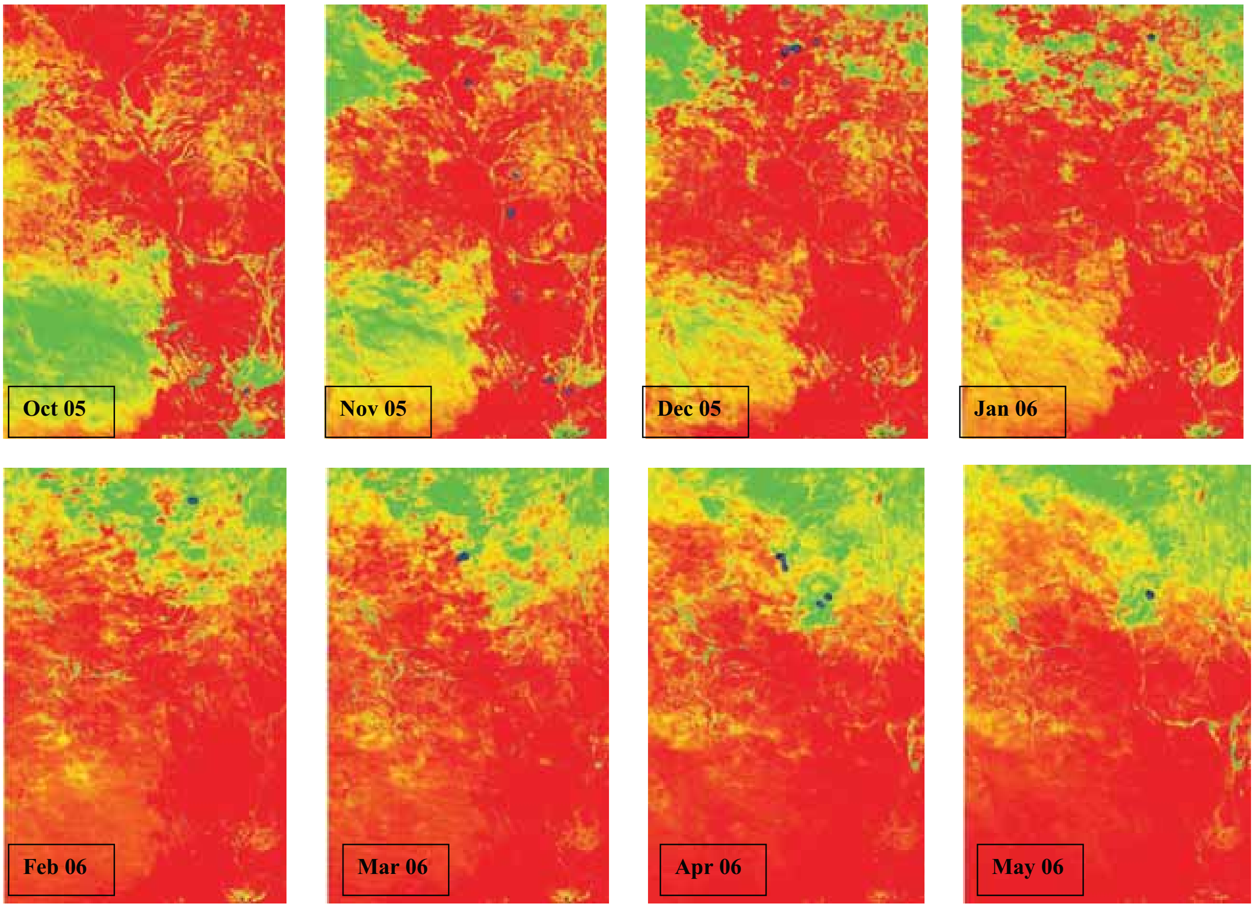


Figure 8.23: Mean daily distance moved (line) by month of female 42546 during the tracking period in relation to monthly rainfall (blue bars) at each of the three main destination sites. Rainfall for the preceding months leading up to deployment in early October 2005 are included. Also shown is mean rainfall for each site (red bars). Grey shading indicates the period of occupancy at each respective destination site (refer also to Fig. 8.23 for destination site reference).


Oct 05
Nov 05
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Jan 06
Feb 06
Mar 06
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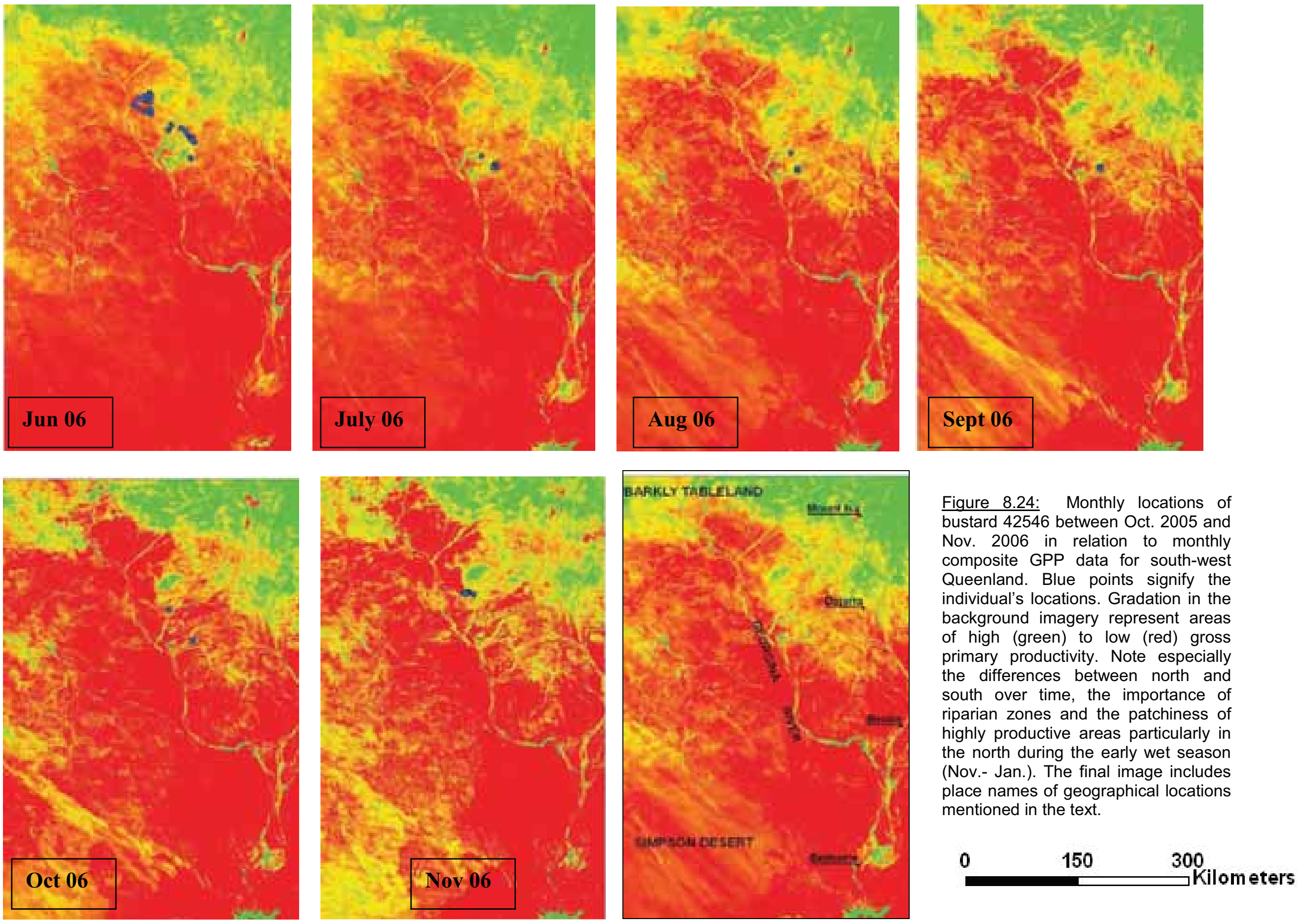


Figure 8.24: Monthly locations of bustard 42546 between Oct. 2005 and Nov. 2006 in relation to monthly composite GPP data for south-west Queensland. Blue points signify the individual's locations. Gradation in the background imagery represent areas of high (green) to low (red) gross primary productivity. Note especially the differences between north and south over time, the importance of riparian zones and the patchiness of highly productive areas particularly in the north during the early wet season (Nov.- Jan.). The final image includes place names of geographical locations mentioned in the text.

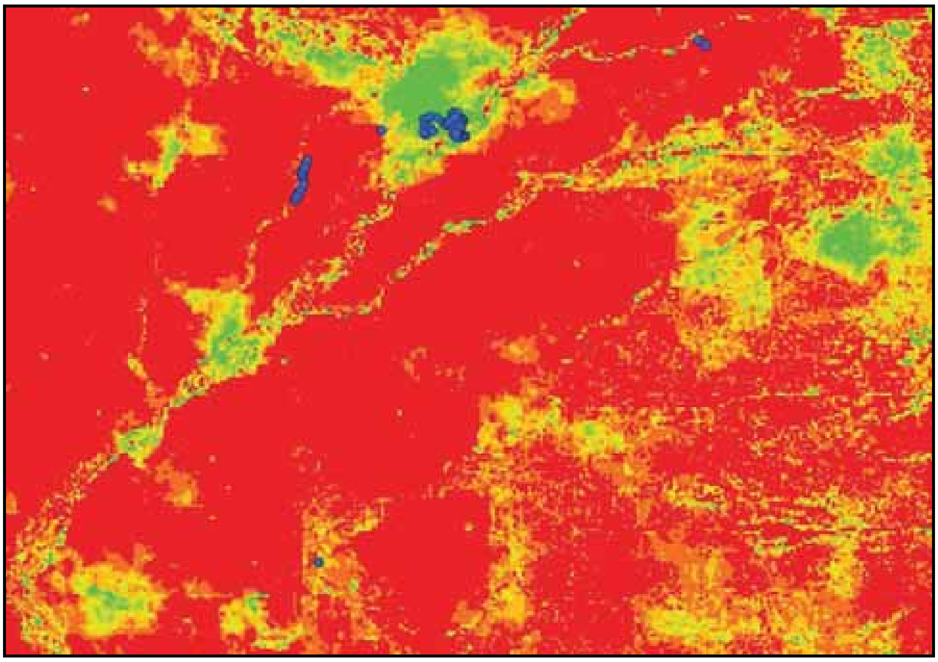


Figure 8.25: An example of use of highly productive patches and riparian areas in the early wet season (Dec. 05) by female 42546 in an area near Barkly Downs Station in Queensland. This figure represents a close up of the area also depicted in 'Dec 05' in Fig. 8.24. Blue points signify the individual's locations. Gradation in the background imagery represent areas of high (green) to low (red) gross primary productivity.

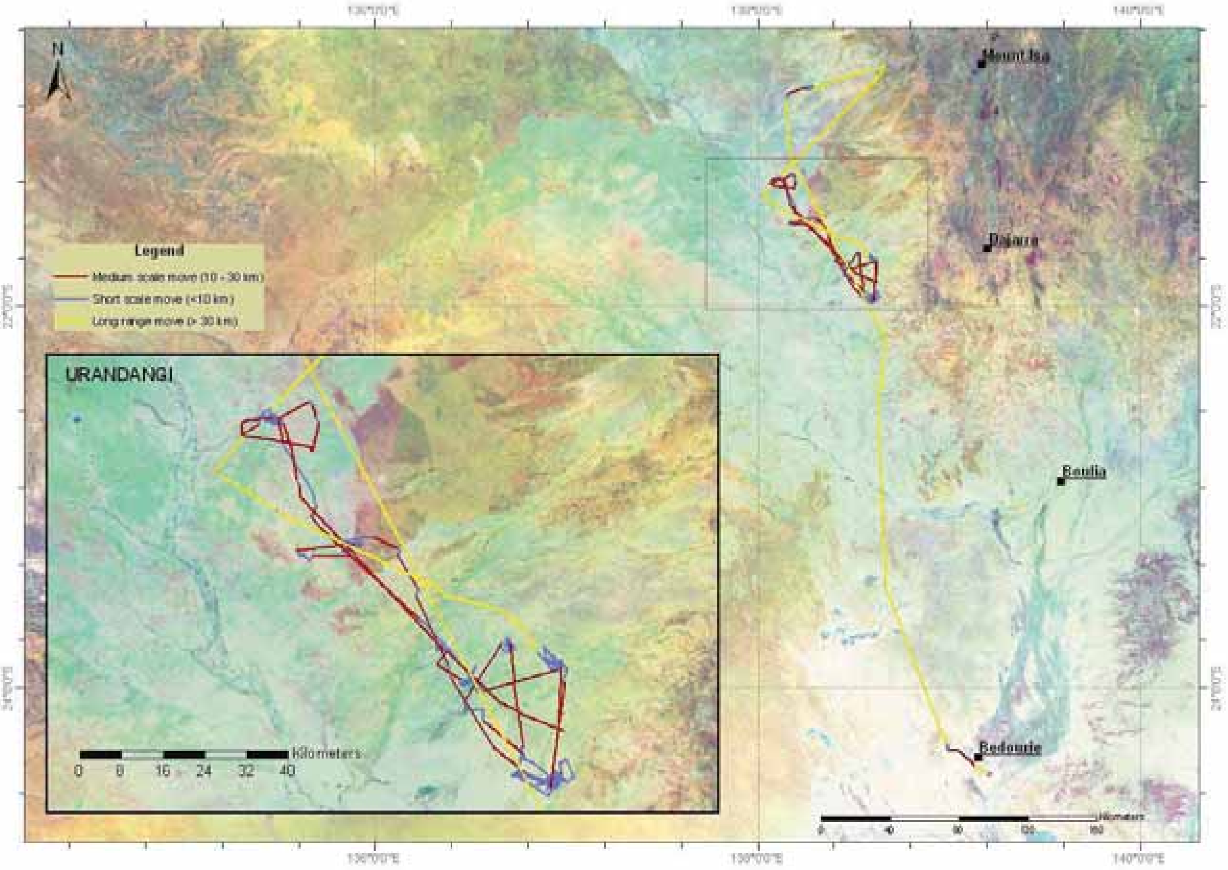


Figure 8.26: Movements of 42546 according to three distance length classes. Inset shows detailed ranging movements in the Urandangi region between 3/3/06 to 28/12/06 where this female ranged over a relatively broad part of the Georgina River floodplain (depicted as green area in the Landsat image). Background map is Landsat Imagery overlaid with a Digital Elevation Model.

Distances moved in relation to rainfall variability

A regression of maximum distance traveled for all tracked individuals against an index of rainfall variability at the point of each individual's origin yielded a highly correlated result (R2 = 0.95; $p < 0.001$), indicating that for the bustards tracked during the present study individuals in areas with greater rainfall variability moved significantly further than those in areas where rainfall was more seasonally predictable (Fig. 8.27). However, the small sample size here (and the strong cluster of values representing individuals in the Kidman Springs and DDRF areas) requires that significant caution is required in interpreting these results. More information for individuals in the highly variable rainfall areas is clearly required.

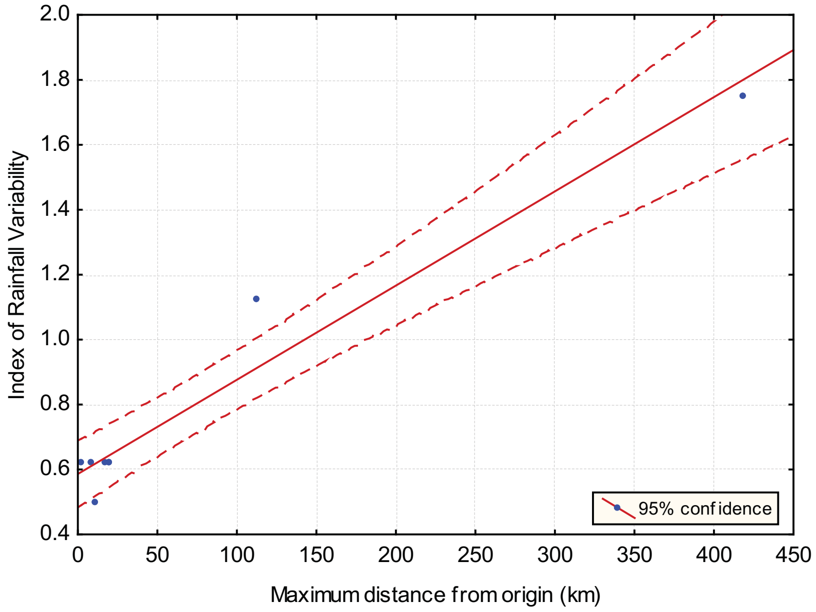


Figure 8.27: Maximum distance moved from origin of all seven tracked bustards in relation to an index of annual rainfall variability at origin (see Fig. 8.1 for an explanation for the derivation of the rainfall index).

DISCUSSION

This chapter aimed to explore the movements of bustards in regions that differed markedly in their climatic variability. Logistical constraints limited the number of transmitters deployed, particularly in more arid, remote regions. Consequently, although efforts were directed towards deploying transmitters on bustards in several different locations, by default, the majority were deployed in the main study sites in the wet-dry tropics. Before I discuss and interpret the results further I explicitly recognize the limited capacity for generalization possible in this study given the small sample sizes, and acknowledge that some of my explanations may be rendered speculative. Nevertheless, the study presents detailed information on the movement patterns for several individuals that is unprecedented for a terrestrial Australian bird. Furthermore, the results are generally consistent with predictions and findings presented in Chapter 2 and Nix (1976), and the generally more anecdotal accounts of bustard movements presented in the literature (e.g. Downes 1982a; Marchant and Higgins 1993).

Movement patterns and environmental cues

Observations in this study, and results presented in Chapter 2, demonstrate that the movement strategies of the Australian Bustard are complex and vary widely across the species' range. Variable movement strategies are common for widely distributed species, particularly for those with populations that span a spectrum of environmental conditions (e.g. Lloyd *et al.* 2001; Ward 1971), and are adaptations to cope with the particular vagaries of local environmental conditions. The complexity evident between regions is further compounded by significant differences in movement strategies adopted within populations, and even among individuals, whereby different components of the population, or individuals themselves, adopt different strategies depending on factors such as age, sex and social status.

The bustards tracked in this study exhibited movements at multiple scales. Individuals tracked in the highly climatically variable regions of the arid and semi-arid interior moved more than their counterparts in the highly seasonal, higher rainfall regions of northern Australia. All individuals in the more northern regions were largely sedentary, or made relatively short-scale movements in relation to season, local habitat conditions or stochastic events such as fires. Similar strategies have been demonstrated for related bustard species in seasonally predictable climates elsewhere. For example, in the western parts of its European range, the Great Bustard *Otis tarda* is predominantly sedentary or makes short distance seasonal movements (Alonso *et al.* 2001; Alonso *et al.* 1995; Alonso *et al.* 2000; Morales *et al.* 2000). Such movement strategies are a feature of areas with predictable conditions (Nix 1976). In contrast, the two individuals tracked in the more climatically variable regions were notably more mobile, with the female tracked in the area with the most extreme climatic variation moving most. These movements are more akin to the larger scale migratory and ranging movements of several Houbara Bustard *Chlamydotis undulata* populations (Judas *et al.* 2006; Osborne *et al.* 1997; Tourenq *et al.* 2004), and the Great Bustard in the eastern parts of its range (Streich *et al.* 2005). Large scale or more frequent ranging movements of this sort are an adaptation to low or erratically distributed resources (Dean 1997; 2004; Nix 1976; Roshier and Reid 2003).

Movements in the wet-dry tropics

While the scales of movements in the more seasonally predictable northern Australian sites were relatively limited there were notable differences in movement dynamics between individuals. The two longest, and concurrently, tracked females at Kidman Springs highlight the different strategies individuals of the same cohort may exhibit. Such variation among females has been demonstrated for Great Bustards in western Europe, with up to four different movement strategies employed within one population (Alonso *et al.* 2000). A feature of the ranging behaviour of female 42548 was its virtually exclusive use of two relatively circumscribed areas that differed in their habitat characteristics. Although most of her time was spent at a site in open eucalypt woodland, in the late wet/early dry season transition period she consistently moved to an area dominated by open treeless grassland. In this case these regular seasonal movements were made to a resource rich habitat that is preferentially favoured by bustards at this time of year (see Chapter 5). Such regularity to movements, according to simple definitions of migration as annual return movements between particular locations, are consistent with the notion of annual migration (Terrill and Able 1988), and with the scale of seasonal migratory movements made by Great Bustards (Alonso *et al.* 2001; Alonso *et al.* 1995). However, neither the exact timings of these movements, nor the period of occupancy at the destination site were consistent, highlighting a significant degree of flexibility. Furthermore, these nominally seasonal movements to a specific habitat were supplemented by moves at other, seemingly random, times of the year.

Aberrant timing to movements was more a feature of the movements of female 47734. Although this individual also moved repeatedly between the same two general areas, and also made movements to other areas that were not subsequently repeated, there was no seasonal regularity to the timing of any of these movements. In this case then, it is possible to distinguish between two types of medium-scale movements: those made to novel locations that were not subsequently repeated; and movements to already known, previously visited areas. On two occasions movements were made in response to local fires, but for others there were no discernible cues. These movements may be classified as maintenance movements, possibly as a type of commuting movement given that they occur around a central site (Dingle and Drake 2007), or are examples of local-scale exploratory or deterministic nomadism as defined in Chapter 1.

Several movements made by individuals at the northern sites were demonstrably a direct response to fire. Bustards favour foraging at fire fronts and on recently burnt patches for food made accessible by fire, and large numbers will often aggregate in these areas until food resources are depleted (Chapter 4, Marchant and Higgins 1993). Notably, all movements directed towards fires were made when tracked individuals were downwind of a fire, suggesting that olfactory cues may be an important means of fire detection. The importance of olfactory cues in navigation among birds has been argued elsewhere (Wallraff 2004), and has been suggested as a possible cue for nomadic waterbirds detecting rainfall and recently inundated floodplains in arid Australia (Roshier *et al.* 2006). Notably, distances moved by bustards towards fire here were relatively short and not all fires were responded to, even under apparently favourable conditions. There are several possible explanations for these observations. First, fires were simply not detected by tracked individuals. Detectability of a fire decreases as a function of distance and depends on factors such as fire type, timing, size and wind direction. Second, there may be a distance threshold for movements governed by optimal foraging theory. Since food resources available at fires are generally available for short periods of time (Woinarski and Recher 1997), for individuals that exhibit fidelity to core home ranges, it may not be in the individual's interest to travel too far for a limited resource knowing it will need to return to its home range area. For a similar reason, foraging at early dry season fires may be less important because of the ubiquitous abundance of food resources at this time. Third, on one occasion one of the females did not move to a nearby fire because she was nesting at the time and all her movements were restricted to a small area near the nest. Finally, for bustards in the Kidman Springs area, most fires in the region occurred in adjacent steep escarpment and hilly habitats which are generally avoided by the species. In at least one instance here, an apparent movement to a fire was abandoned presumably for this reason.

Several medium distance moves, and a general increase in daily movements, by females in the Kidman Springs area in the late dry season coincided with the commencement of the bustard breeding season in northern Australia. At this time, male bustards begin displaying (Chapter 7). Females range between these display sites and leks in order to assess and choose potential mates. This general period of increased activity often precedes significant rains. However, display activity among males may be somewhat variable, and the duration and number of displaying males increase following the first significant late dry season rains (Chapter 7). Detailed tracking of male 47735 revealed that its ranging area was strongly focused around its breeding season display site. Its daily movements steadily increased following the breeding season and similarly peaked in the late dry season. However, during the late dry season there were often extended periods when daily movements were very limited as the male spent consecutive days restricted to its display site and immediate surrounds (Chapter 7). The general increase in ranging behaviour at this time among females also coincides with general resource lows at this time of year (Chapter 3). Lower or patchy food availability may require individuals to range further or increase activity to satisfy nutritional requirements, particularly at an important time when females commence nesting. A characteristic of the northern savannas during the late dry/wet season transition is the patchy distribution of rainfall, and by implication, patchiness in areas of differing primary productivity and food resource availability (Woinarski *et al.* 2005). The daily movements of Houbara Bustards in Saudi Arabia were reported to have increased following rainfall, apparently due to the effect of rain on the distribution of food (Combreau *et al.* 2000). However, while movements may be made in relation to low and patchy food availability, no commensurate difference was detected in time spent foraging for either males or females between seasons at the DDRF (Chapter 6). In fact, for reasons outlined in Chapter 6 males spent less time foraging in the late dry season than at other times. Furthermore, in this case, increases in movement occurred suddenly rather than gradually, even though a gradual increase may be expected given the steady decline of food resources as the dry season progresses.

Males tracked in the Kidman Springs area moved less than females, and made no medium or long range movements during their respective tracking periods. Such limited ranging behaviour is consistent with the smaller breeding season home ranges of males as demonstrated in Chapter 5. However, it appears to contrast with conclusions drawn from ground surveys at Kidman Springs that indicated that the abundance of male bustards is lowest following the breeding season in the early dry season. In Chapter 4, I suggest that a primary reason for the lower numbers is male-biased dispersal from breeding areas comparable to the dispersal bias demonstrated for Great Bustards in western Europe (Alonso and Alonso 1992; Morales *et al.* 2000). However, the males tracked in this study (one over an entire season, two for at least part of the early dry season) remained sedentary. A possible explanation for this observation is that given the small sample size of tracked males there is a high probability that the observation is due to chance alone. Another possible explanation is that, since all tracked males were large mature individuals captured at display sites, these mature males are more territorial and remain near their lekking area, whereas it is the younger males without established display territories that vacate the location in the post-breeding season. This is consistent with the observation that a few large males remain in the survey area (Chapter 4), and with general hypotheses explaining movement in relation to territoriality whereby, among partially migrant populations, dominant individuals are expected to stay close to breeding territories, while subordinate individuals are more likely to move as a consequence of intra-specific competition (Gauthreaux 1978).

Movements in semi-arid and arid regions

The female tracked in the area with the most extreme climatic variation moved most. The timing of this female's movements in central Australia is consistent with the notion that for many bird species in the region there may be underlying north-south movements in relation to pulses of productivity associated with the wet-dry season in monsoonal Australia (Chapter 2; Nix 1976; Wyndham 1983; Ziembicki and Woinarski 2007). This female's initial movement northward occurred as conditions were deteriorating at the point of origin, and was in effect a directed, "persistent and undistracted" movement. The movement followed the general drainage lines of the Georgina River and appeared to bypass productive patches along the way before arriving at the southern, monsoon-influenced end of the Barkly Tableland, where conditions were improving as a result of the first rains of the monsoon season. Such a direct movement is akin to those observed for Grey Teal, whereby individuals traversed regions ignoring available wetland habitats along the way (Roshier *et al.* 2008).

Having arrived in the north, the female subsequently moved between productive patches before settling in an area for over two months as conditions gradually improved following widespread monsoonal rains. In Australia's rangelands, variability in localized climatic conditions often determine which specific areas may be best for fauna in any particular year (Stafford Smith and Morton 1990). Potentially significant inter-annual variation in greenness peaks and spatial patchiness in productivity is a feature of this grassland biome and may be particularly pronounced in the late dry season (Fisher 1999). Movements between such patches across the landscape may be regarded as an example of local-scale nomadism, and have been proposed for bustards in the Barkly Tableland region (Downes 1982; Downes and Speedie 1982), and other bustard species in similarly variable environments (Combreau *et al.* 2000).

Notable also was that this female returned southward, retracing her track along the Georgina River floodplain towards the end of the wet season but while the area she was in was still receiving significant rains. However, rather than returning to the point of origin, she settled and again ranged extensively between patches over a broad area of the Georgina River floodplain without any apparently regular pattern. Consequently, she did not return to where she had previously nested - an observation contrary to the fidelity shown to breeding sites by females in more climatically predictable regions of northern Australia (Chapter 5) and for other bustard species elsewhere (Alonso *et al.* 2000). North-south movements associated with the wet-dry season implies regularity of movements consistent with migration. However, in this case a complete (return) migration between regular sites was not undertaken. Such a scenario is consistent with the notion of facultative partial migration, whereby individuals may or may not migrate in any given year or restrict their migration to part of a nominal migratory route. However, classifying such a movement in this case is speculative. Nonetheless, whether an individual moves or restricts its migration appears to depend primarily, if not entirely, on environmental conditions (Terrill and Able 1988). For this female, her movement south may have ceased when she encountered favourable conditions along her southerly route.

An alternative to the above explanation is that the southward movement of this female was exploratory and more consistent with the notion of nomadic behaviour. In this case, the movements were undertaken over a broad area characterised by high primary productivity. Such exploratory movements may be particularly important to species that interact with temporary resources (Bennetts and Kitchens 2000; Dean and Siegfried 1997; Roshier *et al.* 2008). The rationale behind such movements is that during periods of high resource availability knowledge of the distribution of resources may be gained over broad scales at reduced energetic costs or risk compared to periods of low resource availability (Bennetts and

Kitchens 2000; Dean 1997). Subsequently, this knowledge can be used at times when resources are low, patchy or restricted to refuge areas in the landscape.

A further feature of the movement path of this female was that it was largely restricted to the Georgina River floodplain. In this case, whether these movements were exploratory or part of an underlying migratory pattern, they may have been facilitated and directed by the broad and productive floodplains of the Channel Country that run north-south. On a broader landscape-scale this area may be highly productive and serve as an important conduit facilitating dispersive movements in to regions that would otherwise not be visited, or even extend the distributions of species that otherwise favour more mesic environments (Woinarski *et al.* 2000a). Furthermore, for such reasons, the Channel Country may serve as an important refuge area, particularly in times of drought (Morton *et al.* 2001).

Although information for the male bustard tracked in the Barkly Tableland was limited in its duration and resolution, its movements were also consistent with those reported by Downes (1982a). That is, that bustards move extensively within the district during the monsoonal period (Jan. – March). In this case, there appeared to be a general movement towards a broad area of high primary productivity. Longer term tracking of individuals in this region coupled with detailed spatial information regarding habitat quality is required. Since this region is relatively homogeneous and not structurally complex it may be a favourable area for future intensive studies of the movements of bustards in relation to spatial and temporal pulses of primary productivity and key food resources.

Classification of observed movements

How do the movements of individual bustards observed during this study conform to the conceptual framework presented by Roshier and Reid (2003)? The life span of bustards in the wild is not known but, on account of their age at sexual maturity (5 years for males – Marchant and Higgins 1993) and low reproductive output the they are believed to be long lived birds, with the closely related Kori Bustard reaching 26 years in captivity (Hallager and Boylan 2004). Given that the framework relies on defining a life-time range for an individual, and this information does not yet exist, application of the framework is limited. Nevertheless, the relatively extended period of tracking for at least two individuals, and the general patterns that emerge between regions, may allow for its qualified use here. Chapter 1 describes the framework in detail. The relevant indices once more were:

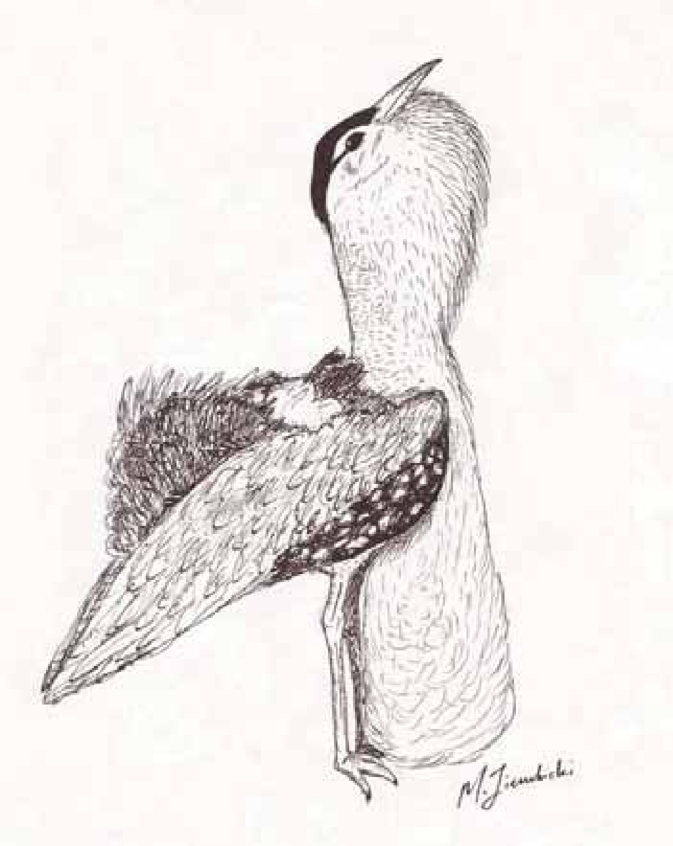
Range Stability Index (RSI) = Home range/Life-time Range

Realised Mobility Index (RMI) = Life-time Range/Geographic Range

Although the Australian Bustard's distribution is contracting, its contemporary range still occupies the larger part of continental Australia. For an Australasian endemic then it has a broad geographic range.

Individuals tracked in the seasonal wet-dry tropics were largely sedentary with relatively well-defined home ranges (see Chapter 5). For the two longest tracked individuals, home ranges (defined for any minimal period and number of fixes by incremental area analysis – see Chapter 5) was similar to life time range (defined here by the tracking period). In this case, the RSI value is high. In contrast, its small life-time range in relation to the species broad geographic range is markedly different hence its RMI is very low.

Relative to the individuals tracked in the wet-dry tropics, the two bustards tracked in the more climatically variable regions moved significantly more even though they were tracked for shorter periods. Home range estimates for the female in south-west Queensland for periods while it was sedentary were similar to individuals in the wet-dry tropics. Using these home range estimates for the entire tracking periods of these individuals, the range stability index for both is low. Although the RMI may be higher than for the sedentary individuals it may be still considered of a low-medium range given the comparatively large geographic area of the species. In chapter 2, I tentatively concluded that many of the movements of bustards even in the most variable regions were at intra-regional scales (as regions were defined) rather than at a continental scale. The most mobile individuals tracked in this study seem to support that conclusion, although longer term tracking of many more individuals is required to assess the extent of such movements adequately.



Chapter 9

Synthesis & conservation implications

NOTE:
This image is included on page 265
of the print copy of the thesis held in
the University of Adelaide Library.

Jon Altman

Chapter 9

Synthesis & conservation implications

This thesis comprises two inter-related components: a broad-scale analysis of bustard distribution and movement patterns (Chapters 2 and 8), and a site-specific investigation of key elements of the bustard's ecology at two sites in the tropical savannas of northern Australia (Chapters 3 to 7). It represents the first detailed study of the Australian Bustard in the field and includes one of the most detailed investigations of the movement patterns of an Australian terrestrial bird using satellite telemetry. It also included a near-continental scale community-based survey that aimed to assess the distribution and movement patterns of bustards across most of outback Australia. It aimed to integrate information from these multiple scales to examine the ecology and movements of bustards in relation to the inherent variability that characterises the Australian environment.

SUMMARY AND SYNTHESIS OF SALIENT FINDINGS

Variable movement strategies

A general outcome of the focus on the movement and distribution patterns of the bustard was that the species exhibits complex and variable movement strategies at multiple scales across its range. In northern Australia, bustards tend towards sedentariness and local-scale seasonal and nomadic movements. In more arid regions movements may occur over broader scales. Here too there appear to be broad seasonal patterns to these movements although they may be increasingly overlaid by more idiosyncratic, facultative responses in relation to erratic and variable environmental conditions.

Overall then, the movement strategies of bustards appear to be flexible – the birds seem to exhibit varying degrees of sedentariness, differential migration and nomadism according to climatic cycles and prevailing conditions both locally and further afield. Notably, a key consideration is that the complexity evident between regions is compounded by significant differences in movement strategies adopted within populations, and even among individuals, whereby different components of the population, or individuals themselves, adopt different strategies depending on factors such as location, age, sex and social status. Many accounts in the literature have tended to categorise species according to specific movement strategies. A net result of this thesis is to point to the need to be more circumscribed when defining movement types but more flexible in our classification or assignment of movement types bearing in mind the contexts in which the various strategies are employed.

Population dynamics

This study also included the first systematic attempt to survey the Australian Bustard and to compare seasonal trends in population dynamics in areas that differ in their naturalness and land uses. Two outcomes are worth noting. First, the more modified Douglas-Daly Research Farm (DDRF) had notably higher numbers of bustards than Kidman Springs. The DDRF represents an artificially favourable environment with consistently greater food resources supporting densities of bustards that are high by regional and national standards.

Notable also were seasonal trends in bustard abundance, particularly at the DDRF. This site had notable mid-dry season peaks in bustard numbers as a result of a concentrated area of high resource availability. In the mid dry season this resource was particularly valuable when food resources are generally low in the surrounding landscape. In this case, local movements from surrounding regions contributed to higher bustard numbers.

In spite of the notable relationship between resources and bustard abundance noted at the DDRF in the mid dry season, peaks in food resources at both sites in the late wet and early dry season coincided with low numbers of bustards. These patterns corroborate findings presented in Chapter 2 for the 'Top End' region and suggest that movements may occur away from the region at this time. The apparent discrepancy between local food abundance and bustard numbers also indicates that proximate food availability at specific sites is generally a poor predictor of bustard abundance. The most likely explanation for these observations, however, is not broad-scale movements away from the 'Top End' region as a whole but rather relatively localised post-breeding season dispersive movements. In this case, peaks in resources at the main study sites are part of broader highs across the whole savanna landscape. Leading up to and during the breeding season bustards aggregate at traditional lekking areas in comparatively concentrated densities. Towards the end of the breeding season individuals (particularly subordinate males) disperse across the landscape to make use of broadly productive conditions and to reduce competition. They later return to traditional lekking areas in time for the following breeding season.

Open plains are preferred in the early dry season

The preference of bustards for open treeless plains on alluvial soils in the early dry season is likely related to the greater concentrations of preferred foods in these areas compared to surrounding habitats. Many of the dispersive movements away from lekking sites in the post-breeding season may be made to these habitats, although more detailed information regarding movements from a larger number of individuals is required to assess this adequately.

As the dry season progresses in northern Australia there is a general reduction of grass layer biomass and food resources. With these changes bustard habitat preferences become broader, while at the same time individuals return to established lekking areas. In the Kidman Springs region, by the mid to late dry season bustards use habitats of varying shrub and tree density on flat terrain more equitably. By this time there are fewer differences in the availability of food resources between habitats while the dynamics of the grass layer also alter options for cover. Habitats that are too sparse in cover (e.g. open plains late in the dry season) provide limited opportunities for concealment and roosting, particularly in the hotter part of the day. Conversely, habitats that are too dense (e.g. wooded areas during the wet season) may make bustards more susceptible to predation. During the breeding season there may also be differences between the sexes in cover preferences, with males preferring open areas for display sites and females favouring more sheltered areas for nesting. In this respect, ecotones between open plains and more wooded habitats provide the best of both worlds by satisfying the needs of both sexes. These contrasts may be more muted in the more highly managed, artificial environments of the DDRF which retain a relatively consistent grass cover year round.

Females range further locally than do males

In the early breeding season females ranged further than males and tended to exhibit multimodal home range use. The primary reason for this difference relates to females ranging within and between leks to assess males at dispersed display sites. Satellite tracking of two females corroborated this observation with the sudden and short increase in movements in the early breeding season contrasting to what may be expected if females were ranging further simply in response to declining food resources. That is, over the dry season food resources decline gradually leading to lows in the early breeding season. If individuals were simply responding to these changes then it may be expected that distances moved would increase gradually rather than abruptly during the year. Also noteworthy was that immediately following the spike in movements there was a period of very little mobility as females were presumably restricted to the surroundings of their nest sites.

In comparison, the home ranges of males were small and centred around a single central site. During the breeding season mature males appear largely restricted to their display areas with much of their time spent in display or roosting within the vicinity. Males also spend little time foraging at this time of year hence are less likely to move to preferred foraging areas.

Notably, there were no differences detected in home range sizes between Kidman Springs and the DDRF despite obvious differences in food resource levels. It may be expected that if ranging behaviour is related to food resource availability then the home ranges of individuals at the DDRF (with significantly greater food resources) would be smaller than those at Kidman Springs. That there were no differences suggests that there are other factors that may be more important than food availability in determining the extent of local movements. In this case, as noted above, the need for females to range between males at display sites, and the need for males to remain on their territories at this time, may override the need to range further to gather food.

Bustards eat almost anything but do exhibit certain preferences

Investigation of the diet of bustards in this study from the mid to late dry season corroborates published information that bustards have very broad, omnivorous diets. Such a catholic diet presents bustards with broad options for switching between different foods depending on availability and nutritional requirements. Bustards will nevertheless harvest specific foods preferentially, gorging on preferred foods when available with a relatively small number of particularly favoured foods.

There were also notable differences in diet between the sexes, primarily in the size and type of foods preferred. Both sexes consumed seeds and fruits but females tended to consume smaller sized arthropod taxa such as beetles and true bugs. Male bustards exhibited a preference for larger insects including grasshoppers, mantids and stick insects even though these items were in lower abundance during this study than the smaller prey items favoured by females. Differences between the sexes in diet may be related to physical size differences in body size between males and females. In addition, because males spend less time foraging in the breeding season than do females, they may also opt to target fewer but larger prey rather than the more abundant but smaller prey that females prefer.

Male bustards prefer sex to eating

Due to their significantly larger size compared to females, males may be expected to forage for longer periods or consume different types of foods. As summarised in the preceding section, in the late dry season at least, males do appear to consume larger prey items. However, they spend considerably less time foraging than females at this time, and spend similar periods of time foraging to females at other times of the year. It may also be expected that they forage for longer periods when food availability is low (e.g. in the late dry season) compared to when resources are abundant (late wet/early dry season). In this study the opposite was the case. An explanation for this observation may relate to the bustard's mating system. During the breeding season males spend most of their time displaying in order to establish and defend display sites and to attract females. Consequently, displaying occurs at the expense of foraging which leads to significant weight loss by the end of the breeding season. Towards the end of the breeding season and in the early dry season when their favoured food items peak in abundance, males subsequently forage more in order to regain lost weight and body condition and to accumulate fat reserves in preparation for the following breeding season. By comparison females show no significant changes in the amount of time they spend foraging between seasons, while the differences are intermediate for subordinate males.

Males display in open areas and exhibit fidelity to leks

Males prefer open sites with low grass cover and high visibility that maximise the conspicuousness of their display routines and enhance their ability to detect approaching females and predators. Grass layer height was the most significant factor affecting the suitability of display areas and largely determined whether sites were used regularly. For the most part specific display sites were used consistently within and between breeding seasons. However, when the habitat suitability of display sites decreased (due to increased grass layer biomass) sites were usually abandoned. The configurations of leks were therefore variable within and between seasons. Sites that were abandoned were often used again in subsequent seasons if they were again suitable for displaying males. The characteristics of display sites suggest that at Kidman Springs suitable habitat may be an important determinant of lek size and configuration. In areas where there are broad expanses of open habitat favourable for displaying males as found at the DDRF social forces may be more important than habitat availability in shaping patterns of display site dispersion.

Although somewhat limited, available evidence suggests that specific males consistently used the same display sites throughout and between breeding seasons. It was beyond the scope of this study to assess the dynamics of social hierarchies within lek configurations and breeding success among males. However, it is noteworthy that the highly dynamic variation in display site suitability suggests that males must often be adaptive or opportunistic in their use of display sites and suggests that social dominance hierarchies may be complex and dynamic. Among many lekking species a male’s geographical position in a lek is often governed by prevailing dominance hierarchies established between males whereby the most dominant and successful males are located in the best display positions, often in the centre of the lek. For exploded lekking species in highly dynamic environments, the ultimate patterns of display site use and lek configuration may depend on the relative influences of habitat availability as well as social factors. In such areas changing habitat conditions are likely to quickly alter the suitability of display areas across the lek within and between seasons. Those sites that remain consistently favourable within and between seasons may be at a premium and therefore be the preferred or most lucrative sites for dominant males. In contrast, those sites that are more dynamic, or sub-optimal in their suitability may tend to be used by subordinate males. In general, highly dynamic environments where the suitability of display areas within leks change substantially and regularly may be more favourable to less dominant males than may be the case if leks were more permanently ‘fixed’. Such possibilities, while offering plausible explanations for the use of display sites within leks clearly require further investigation.

It has been proposed that in semi-arid parts of the tropical savannas and in the arid interior of the continent breeding among bustards is dependent on rainfall. However, at both main sites in this study males commenced displaying prior to the onset of significant rains suggesting there may be cues other than antecedent rainfall governing the onset of breeding. Nevertheless, the dispersion patterns of males appeared to be largely a function of densities of displaying individuals, which in turn *are* dependent on preceding rainfall. That is, in the early breeding season prior to the onset of rains, solitary males were often observed displaying at traditional sites. Following patchy rainfall in the region and for much of the breeding season the spatial arrangement of displaying males at each site resembled that of exploded leks. At the peak periods of display, following substantial rains at each site, these arrangements comprised a mix of exploded and classical leks.

Compared to many other bustard species the breeding season of Australian Bustards in the north is protracted, commencing as early as the start of September and lasting as long as in to March. However, the details of how long individual males display for, when they start and finish and how these factors relate to social dominance hierarchies in leks are unknown. For example, do the fittest, most dominant males display for the longest periods by beginning displaying early in the breeding season and lasting late into the breeding season, or do sub-dominant males display at these sub-optimal periods? Do dominant males in turn wait for optimal breeding periods following significant rains, relying more on their spatial position at leks at the height of breeding in order to mate with as many females as possible? There were limited opportunities for addressing these questions in this study. However, information for the male tracked by satellite in detail suggests that he began displaying briefly and intermittently from the beginning of the breeding season, but that he displayed most intensively and for periods of up to several consecutive weeks following a short lag after significant rainfall events.

Flexibility and opportunism are key

A recurring theme characterising the ecology and movements of the bustard is flexibility. Whether in reference to population dynamics, diet, behaviour, mating strategies or local and broad-scale movement patterns, a defining feature is plasticity and opportunism in response to prevailing conditions. This flexibility renders the bustard well adapted to the highly variable environmental conditions that characterise the Australian continent and has resulted in a geographical distribution that spans a range of biomes from the tropics of southern New Guinea to the arid interior of central Australia and the temperate grasslands of southern Australia. In this study, even in the seasonally predictable wet-dry tropics of northern Australia bustards exhibited a variety of responses to changing conditions. Such flexibility and opportunism are arguably more important in more environmentally variable environments. The ultimate responses by individuals and populations to changes are an interplay between a range of adaptations. The bustard has many options. In deteriorating ambient conditions, it may opt to tolerate difficult times, switch between a broad variety of foods depending on availability, range locally or move further afield. It may also breed under various conditions given its flexible mating system.

The original premise of my investigation was to use the Australian Bustard as a model for assessing movement patterns of a reportedly highly mobile, nomadic bird in relation to changing environmental conditions. It may be argued that given the plasticity of the bustard's responses, and that there are species with ostensibly 'simpler' ecologies, that the bustard is not an ideal 'exemplar' species for this purpose. By comparison, the Flock Bronzewing Pigeon *Phaps histrionica* is an obligate granivore with a relatively restricted diet (Dostine 2009). In a contemporaneous investigation of the ecology of the species, Dostine (2009) described the species as 'serially' nomadic over a large area outside its core range. Broad-scale patterns of Flock Bronzewing occurrence were associated with rainfall-driven patterns of plant productivity, with the species often associated with high abundance of a small set of annual or ephemeral herbs and grasses. Notably, however, many of the species' broad-scale movements are not necessarily a simple result of high rainfall and food resource availability in a given area, but rather a complex response to historical conditions at local point of origin and as well as conditions further afield. For example, a sudden mass influx of the pigeons into the Pilbara region of Western Australia (an area outside the species core range) was apparently triggered by successive productive years in the region while there was a prolonged drought in eastern Australia (Dostine 2009). A similar assessment of the relationship between rainfall and food availability and the movements and breeding of the Namaqua Sandgrouse *Pterocles namaqua*, a dispersive, obligate granivore of southern Africa, found significant regional differences in responses to food availability (Lloyd *et al.* 2001). Periods of peak food availability were not consistently associated with the breeding and movements of sandgrouse populations. Instead, the species adopted varying degrees of partial migration and nomadism and their breeding periods were unexpectedly variable and often coincided with food resource lows.

Such findings emphasise the inherent complexity of faunal responses to environmental conditions. Above all they highlight that flexibility in adaptations and responses within species, populations and even individuals should be regarded as the norm for many austral birds. Indeed, it has been argued that regular migration, which has been the primary focus of biologists investigating avian movements, is the exception rather than the rule. Flexibility in responses to environmental variation as exhibited by many of Australia's birds largely distinguishes them from the more 'hardwired', innate responses of strict migrants to seasonal environmental variability. Detailed autecological studies employing emerging technologies focusing on a greater variety of dispersive species will help untangle the complex and interacting factors that shape the responses of dispersive fauna to environmental changes. In this respect, detailed studies of Australia's birds have the potential to contribute significantly to the understanding of the evolution and dynamics of faunal movements generally, particularly in a constantly, and increasingly, changing world.

CONSERVATION IMPLICATIONS

> *It may be possible – and, indeed it is most likely – that … no longer does the noble Bustard stalk over the flats of the … Hunter … and if this be so, surely the Australians should at once bestir themselves to render protection of these and many other native birds: otherwise very many of them … will soon become extinct.*
>
> John Gould 1865

As John Gould's remarks following his famous pioneering trip to Australia in the 19th century suggest, it did not take long for the effects of European settlement to adversely affect the Australian Bustard and many other Australian birds. Although still relatively common in parts of Australia's northern savannas, the bustard has undergone large historical population declines in the more settled parts of its range. It has largely disappeared from south-eastern Australia and undergone patchy declines elsewhere. On a national scale it is regarded as near threatened, but its precipitous declines in the southern states has it listed as critically endangered in Victoria, endangered in New South Wales and vulnerable in South Australia. Recent declines in central Australia have it now similarly listed as vulnerable in the Northern Territory.

Primary threats

The decline and extirpation of the bustard in parts of its range have been variously attributed to a range of factors including hunting, altered fire regimes, pastoralism, disturbance, habitat alteration, pesticides and predation (particularly by the introduced fox) (Garnett and Crowley 2000; Ziembicki 2007). These factors assume varying importance in different parts of the bustard's range and combine in different ways to affect local populations. The bustard's widespread distribution and variable biology and threats mean that there are no simple, homogeneous prescriptions for its protection, while its variable movement strategies and specialised lek mating system pose specific conservation challenges. Here I discuss the primary threats to the bustard in light of the findings presented in this study and general knowledge of the species.

Hunting

As a valued game bird and a subsistence food source to early settlers and indigenous people, hunting has had a profound impact on bustard numbers, particularly in the more settled regions of Australia. Other bustard species have also been heavily hunted in many parts of the world and in many areas uncontrolled take of birds has been implicated as a major factor in local and regional extinctions (Goriup and Vardhan 1980). Although hunting by the general populace is now prohibited illegal hunting still occurs to some degree. Aboriginal people are also still permitted to hunt, and the bustard remains an important food resource to communities throughout central and northern Australia. However, breakdown over controls of traditional hunting, coupled with potentially greater efficiency facilitated by modern technology including motor vehicles and guns, means that hunting may have increasingly significant, localised impacts on bustard populations.

Apart from the ease with which bustards can be harvested with contemporary technology, there are inherent biological reasons for the susceptibility of bustard populations to over-exploitation. First among these is their low reproductive output. As a long lived and late maturing species with few young at a time, individuals are not quickly replaced. Furthermore, in the more arid parts of their range, breeding is largely opportunistic and dependent on favourable environmental conditions. Since these conditions are largely dependent on rainfall which may be highly variable, breeding may not occur every year in many parts of the country (Marchant and Higgins 1993; Osborne and Osborne 2001).

Male bustards may be particularly susceptible to biased harvesting or over-exploitation on account of the lek-mating system. Their spectacular plumage and preference for displaying noisily in open or raised areas, makes displaying males particularly conspicuous. Females, by comparison, are smaller, more drab in appearance and shy, relying on their camouflage to protect their nest and young. The largest males, which are responsible for most of the breeding success in lekking populations, are therefore the most likely to be harvested because they are more visible and their great size makes them prized game. Additionally, the tendency for bustards to exhibit strong fidelity to lekking grounds, means that if these sites are known to people, they are at risk of over-harvesting. In effect, leks may then act as ‘sinks’ because as individuals are removed new individuals move in to occupy vacated display sites. However, studies of other bustard species suggest that once leks become extinct through habitat alteration or over-exploitation they are not re-established (Lane and Alonso 2001). Thus, uncontrolled or illegal hunting may not only lead to direct reduction in overall bustard numbers but to a significant loss of prime males which disrupts the social structure that forms the basis of the lek mating system. In the longer term, the genetic viability of populations is potentially compromised by the selective removal of the largest and fittest of males. Indeed, the effects of excessive or biased harvesting among such lekking species may have disproportionally adverse consequences compared to species that have less specialised mating systems.

Habitat alteration

Declining numbers of bustards in some regions have been partly offset by localised increases in other areas as a result of increased habitat availability through clearing for grazing and crop agriculture. However, clearing in southern Australia has been extensive and bustards there declined as agriculture intensified and human populations increased. Temporary increases in Great Bustard *Otis tarda* numbers also occurred in Europe during the 18th century following forest clearing, however, marked declines soon followed as the intensity of land use increased and more of the cleared areas were continuously cultivated (Isakov 1974). Similarly, the main cause of the decline of the Little Bustard *Tetrax tetrax* is cited as habitat modification mainly due to agricultural intensification (Goriup 1994; Schulz 1985; Silva *et al.* 2007).

Development of northern Australia has been proposed by successive governments over recent decades with aspirations of developing the north into the 'food bowl for Asia'. The Douglas-Daly Rivers region, for example, is earmarked for further development by the Northern Territory government (Price 2003). With increased clearing and a larger human population increased intensification of land use is inevitable. Associated with such changes are increases in application of fertilizers and pesticides, mono-cropping and overgrazing by livestock. Therefore, if not managed properly the initial beneficial effects of clearing and horticultural development for bustards in these strongholds for the species are likely to dissipate as agriculture intensifies, and human populations increase.

A more insidious example of the effects of habitat alteration is the thickening of vegetation across vast areas of the northern savannas. 'Woody weed' infestation, resulting in increased density of shrubs and trees, particularly on open alluvial plains, is recognised as a significant change to savanna regions over recent decades (Lewis 2002), and is considered a threat to some bird populations (Garnett and Crowley 2000). The principal factors driving shrub and tree thickening are likely to include increasing atmospheric CO_2 concentrations and the alteration of fire regimes, particularly a reduction in the incidence, intensity and extent of burning as a consequence of the impacts of pastoralism and the cessation of traditional burning by Aboriginal people. There are two primary implications for bustards: a decrease in availability of open areas that are favoured in the early dry season and by displaying males, and secondly, the potential increase in susceptibility to predation. In an analogous example, the Golden-shouldered Parrot *Psephotus chrysopterygius* is reportedly more susceptible to predation due to increased vegetation density increasing the success of predators through ambush, especially when the parrots are feeding on the ground (Garnett and Crowley 2000). Similarly, as a ground dwelling and nesting species bustards may be particularly vulnerable to predation at nests by dingos, cats and other predators.

Altered fire regimes

Fire is an intrinsic and dominant feature of the Australian environment. Bustards are one of many species that benefit from fires by foraging at fire fronts and in recently burnt areas, and by using habitats that have been opened up by fire for other aspects of their life cycles. For bustards, mosaic burning patterns, such as those that predominated under Aboriginal fire management practices (Bowman 1998), are likely to be preferred as they result in a juxtaposition of areas of different fire history providing structural heterogeneity in the landscape and more options for food, shelter and breeding habitat requirements.

Altered fire regimes, particularly the contemporary predominance of late dry season fires, is a two edged sword for the species. Late dry season fires may be particularly useful to bustards because they provide novel foraging opportunities at a time when resources are low across the landscape. However, fires at this time of year coincide with the onset of the nesting season hence may destroy ground based nests. Extensive late dry season fires may also alter the dynamics of lek and display site configurations, and while initially providing greater availability or accessibility to food resources, lead to food lows over broad areas once the initial and short-lasting bounty has been exploited.

Predation

The bustard is one of a large suite of ground dwelling and nesting Australian birds that have been much reduced by the impact of introduced predators, particularly the European Red Fox *Vulpes vulpes* (McLeod 2004). The areas where bustards have declined most correspond closely to the distribution of foxes in Australia with very few recent breeding records from areas where foxes occur. However, since the northward expansion of foxes is limited by climatic conditions, populations in the northern parts of the continent are not as affected by foxes. As ground-dwelling birds, it is the eggs, young and females at nests that are most susceptible to predation. Furthermore, as discussed above, the impacts of predation may be exacerbated by the thickening of habitats through ‘woody weed’ infestation.

Pesticides

> *In 1882 when phosphorized oats were scattered in the Riverina, bustards died in hundreds. They were found dead on runs where no poison had been laid, and they had flown many miles after eating the grain.*
>
> E.Rolls 1969

The influence of pesticides on bustards has been cited as a significant cause for the species decline, particularly in the southern agricultural regions (Rolls 1969). Bustards are susceptible to poisons through direct ingestion of poisoned baits or by the consumption of poisoned prey such as grasshoppers and mice (Downes 1982a). Hundreds, perhaps thousands of bustards were killed by grain treated with arsenic, phosphorous and strychnine laid out over many thousands of kilometres to eradicate rabbits at the turn of the last century (Rolls 1969). Pesticide use is an ongoing concern for those species that rely on locusts and other prey items that are controlled by poisoning (Szabo *et al.* 2003).

Pastoralism

Grazing is the major form of land use in many parts of the bustard’s range and is believed to have had a severe impact on the conservation status of birds in grasslands and other ecosystems in Australia (Franklin 1999; Garnett and Crowley 2000; Recher and Lim 1990). Pastoral practices may affect birds and their habitats by direct competition for food, trampling and disturbance of nests, provision of artificial watering points which may affect the structural composition of bird communities, and through habitat alteration and destruction (e.g. removal of cover, etc). Longer term consequences of grazing include degradation of vegetation, changes to understorey and spread of weeds (Gardener *et al.* 1990; Hobbs and

Hopkins 1990; Wilson 1990). As a ground dwelling and nesting species the bustard is potentially susceptible to many of these impacts. However, to an extent, it may also be benefited by grazing. For example, in this study, several long term display sites were based at or close to the centre of piospheres. At least three such display sites were in such areas adjacent to watering points. Two of these sites were consistently used between seasons. In addition, the satellite tracked individual displayed at his site in such an area late in the wet season when surrounding areas were covered by vigorous new grass growth. Nevertheless, the sites in this study had low to moderate levels of grazing. Broad areas highly impacted by overgrazing are likely to be detrimental to bustards.

Specific conservation challenges

The specialised lek mating system

The bustard's specialised lek mating system presents specific challenges for the species conservation. However, it also presents opportunities. Leks are clearly important for bustard populations as they represent foci in the landscape at a crucial time in the species' life history. In northern Australia, the protracted breeding season means that for much of the year bustards are associated with these sites. The aggregation of bustards at lekking sites through conspecific attraction and reproductive success makes these areas potentially more susceptible to the threats outlined above. As discussed, male bustards may be more susceptible to hunting, while display site habitats may be affected by 'woody weed' infestation, intensive grazing and land use intensification. In a study of the Great Bustard in Spain, Alonso *et al.*(2004) found that during a period of overall bustard decline in Spain, numbers of birds actually increased on some leks but remained stable or declined on others. In general, larger leks increased in size while smaller leks decreased with many becoming extinct, suggesting that dispersing individuals may use number of other bustards as a cue for selecting breeding sites. Perhaps most notable was that the distribution of leks was stable and that no new leks were established, even in apparently favourable habitats (Lane and Alonso 2001). An important outcome was that once leks became extinct no new lek sites were established. Instead bustards tended to concentrate at fewer of the larger sites which may be more vulnerable to local stochastic events, and the risks of reduced genetic diversity.

The challenge of dispersive species

The bustard's variable and complex movement strategies present a particular challenge for its protection because conventional conservation practices and representative reservation cannot adequately cater for such species. The conservation of such dispersive species depends on ensuring the maintenance of suitable habitat in geographically distant and disjunct locations and over broad periods of time (Webster *et al.* 2002; Woinarski *et al.* 1992). These challenges are particularly acute for species with less regular movements than migration. While regular breeding and non-breeding sites and migratory staging posts of 'typical' migrants that move with relatively predictable regularity may be defined for some migrants, the areas used by nomads or irruptive populations are much more difficult to identify or predict. The challenge is particularly acute for those components of the fauna that use broad homogeneous habitats in comparison to more circumscribed habitats such as wetlands or rainforest patches.

A way forward?

In regions where bustards are largely sedentary or where they at least aggregate at lekking sites predictably, a primary conservation focus may be to identify lekking areas for targeted protection. A greater challenge is to protect populations in regions where movements and distribution patterns are more variable and unpredictable. However, if through methods such as those presented here, the locations of breeding areas or refugia used by bustards can be identified or predicted at particular times, then such sites can in turn be prioritised for protection at critical times. Such knowledge would effectively facilitate predictive or pre-emptive conservation planning (e.g. by developing mobile or shifting conservation zones in time and space), thereby overcoming the limitations of current static reserve design and conservation strategies. Whether they be traditionally used sites, or sites identified as described, these areas could be protected at key times by, for example, implementing hunting controls, managing for appropriate fire regimes, controlling introduced predators, and minimising stocking rates for livestock. Current strategies for the conservation of dispersive fauna are largely inadequate, highlighting the need for lateral and creative approaches for protecting bustards and other similarly mobile fauna. The bustard, a stately icon of the Australian outback, deserves nothing less. It sustained many early Australians, both indigenous and colonising, and now it is our turn to ensure its survival.