Conserving widely distributed wildlife species in an African savanna: parks, cattle-grazing and community-managed areas

Kabelo Jacob Senyatso

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Abstract

Growing evidence suggests many widely distributed low-density tropical species are declining, but whether protected areas and the increasingly promoted multi-use community-managed wildlife areas mitigate causal threats is poorly studied. Lack of monitoring data and poorly understood species ecology limit knowledge of patterns, causal mechanisms and degree of abundance or range declines. Working in an African savanna, where bushmeat hunting and cattle-grazing are considered the greatest threats to wildlife, this thesis combined three approaches to study the conservation ecology of widely distributed wildlife at three spatial scales (continent-wide; landscape; home range). The continent-wide conservation status of Kori Bustard *Ardeotis kori* was assessed by reviewing occurrence records (1863–2009) across its range (14 countries). Range contraction was quantified by examining the proportion of historical records (pre-1970) falling within the area delineated by recent records (1970–2009), finding 8% (southern) and 21% (East Africa) declines in 146 years. In contrast, qualitative evidence from historical published accounts and contemporary expert assessments suggested widespread declines in abundance; thus numbers have declined considerably but without commensurate range contraction. Examination of seasonal home range use using satellite telemetry showed that female Kori are sedentary in central Botswana, with strong site-fidelity to dry-season home ranges associated with resource-rich pan habitats; the species appears sensitive to localised habitat conditions and resource availability. However, an assessment of the differential response of Kori and 20 other large-bodied vertebrates to protected areas, wildlife management areas and unprotected areas showed most species' abundance was driven by proximity to human settlement, interpreted as sensitivity to unregulated hunting, with no effect of differential cattle stocking densities. Furthermore, the study demonstrates that cattle can affect habitat structure, but their effects on Kalahari wildlife were not perceptible, suggesting that conservationists' preoccupation in African savannas with cattle and their perceived impacts rather than unregulated hunting may be misplaced.

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Preface

The research presented in this thesis is my original work. I conceived the research ideas, led the field-work and other data collection, and am responsible for the data analysis and write-up. However, my supervisory team (Paul Dolman, Nigel Collar and Iain Lake) provided advice on research methods, statistical analysis and the write-up process.

All data chapters were written in the form of manuscripts, with Chapter 2 currently in review with *Diversity and Distributions*. In common with co-authored manuscripts I make use of the phrase ‘we’ in Chapter 2, to recognise the contributions made by my supervisory team; however, I am responsible for the contents of the entire thesis and ecological interpretation.

Acknowledgements

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Last but definitely not least is my immediate family, who have had to bear with my extended periods away in UK. I am very grateful for the support through the years. This thesis is dedicated to you all: Karabo, Didimalang, Peace, Refilwe, Kaone, Omphemetse, Tsitsi, Connie and Lefika.

Chapter One

Savanna dynamics, cattle-rearing, wildlife conservation and bustards

Introduction

Savannas: areal extent, description and determinants

Much of the world, particularly in the tropics, is currently experiencing rapid biodiversity loss largely due to anthropogenic threats (Millennium Ecosystem Assessment, 2005) and mainly as a result of land-use change (Sala *et al.*, 2000). Savanna ecosystems constitute 20% of the world's (Shorrocks, 2007) and 50% of Africa's land surface area (Du Toit & Cumming, 1999, Fig. 1.1), and of the 14 terrestrial biomes recognised in the Millennium Ecosystem Assessment, these ecosystems had the second highest wildlife species richness (amphibians, birds, mammals and reptiles, pooled) after tropical forests (Millennium Ecosystem Assessment, 2005). At the same time, savannas support more than a fifth of the world's human population, and given the significant role of humans in driving biodiversity loss, savannas therefore represent a global conservation priority; however, presently only 15% of this biome is under some form of protected area designation (Chape *et al.*, 2003).

Savannas are defined by their grass:tree ratio (Scholes & Archer, 1997) and have been characterised as 'a discontinuous tree canopy in a continuous grass layer' (Ratnam *et al.*, 2011). Mechanisms maintaining tree and grass co-existence, and preventing the development of woodland cover, remain debated (Sankaran *et al.*, 2004). It is widely acknowledged that the grass–tree balance is largely driven by a combination of precipitation, herbivory, soil nutrient and fire (Scholes & Archer, 1997; Roques *et al.*, 2001; van de Langevelde *et al.*, 2003; Sankaran *et al.*, 2005, 2008; Staver *et al.*, 2009). At continent-wide scales mean precipitation is the most important driver of both total woody vegetation cover (Sankaran *et al.*, 2005) and site-specific woody cover (Sankaran *et al.*, 2008) in African savannas. However, recent studies increasingly support the conclusion that disturbance-mediated (fire and herbivory) factors are more important than competition for resources (water and nutrients) as the main determinants of site-specific grass–tree balance (Roques *et al.*, 2001; van de Langevelde *et al.*, 2003; Staver *et al.*, 2009). Humans and their concomitant socio-economic activities affect fire regimes (for example by deliberately starting fires) and herbivore stocking rates (such as through the number and type of livestock kept), and consequently, because these are the main savanna determinants, humans can be expected to exert a strong influence on savanna vegetation structure and functioning (Scholes & Archer, 1997), with cascading effects on wildlife. Additionally, populations of some wildlife species are directly affected by humans through unregulated bushmeat offtake (Milner-Gulland & Bennett, 2003) or deliberate killing due to human–wildlife conflict (Ogutu *et al.*, 2005). The conservation of African savannas is therefore inextricably linked to humans, and safeguarding these landscapes requires strategies that address both direct and indirect anthropogenic pressures.

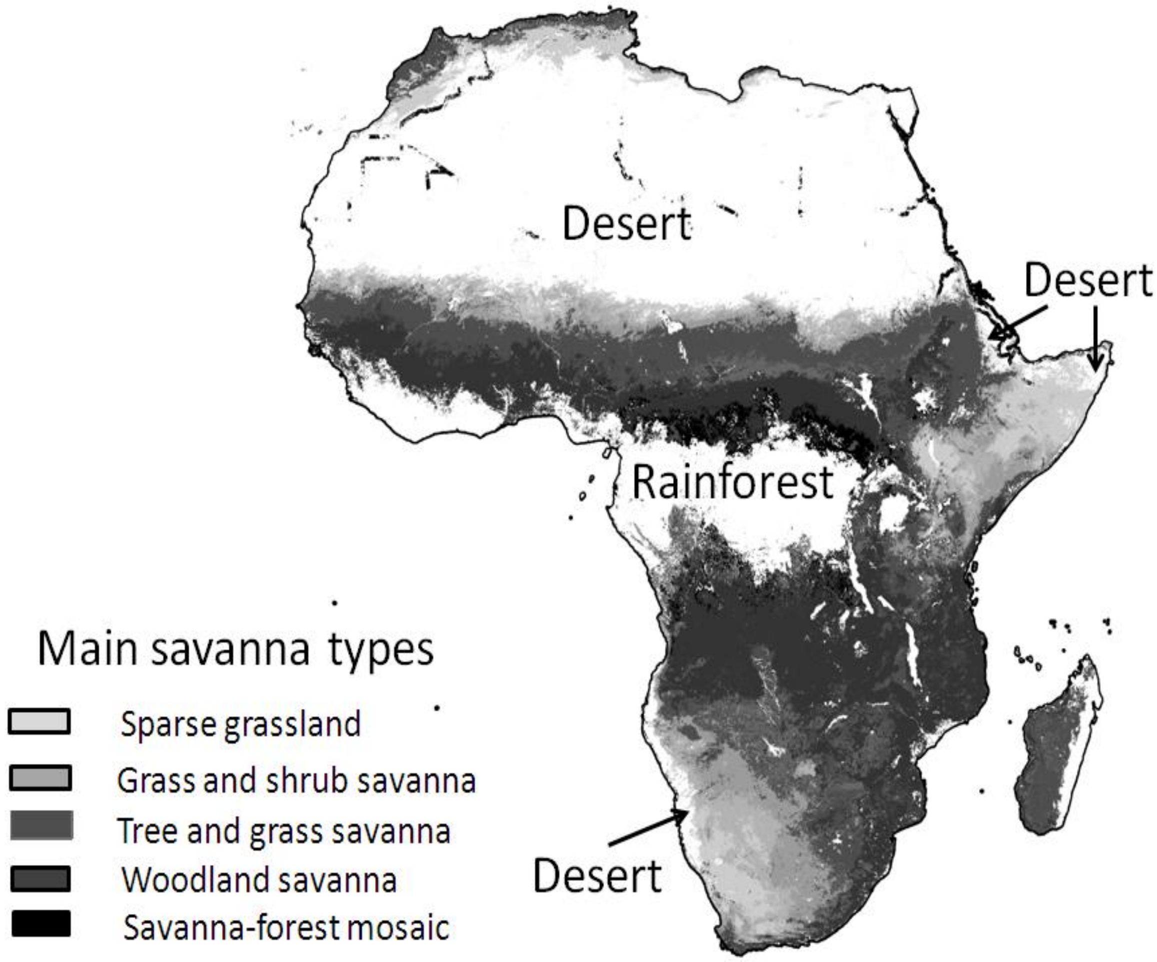

Figure 1.1. Areal extent of savannas in Africa (following Shorrocks, 2007).

Challenges to conserving African savanna ecosystems and wildlife

Studies investigating the role of humans in driving biodiversity loss in African savannas have focused principally on livestock-rearing (e.g. Du Toit & Cumming, 1999; Homewood *et al*., 2001, Ogutu *et al*., 2005). Livestock-rearing, primarily of cattle, is the principal economic activity in African savannas (Prins, 1992), and is suggested to affect savanna habitats and wildlife through two main mechanisms: bush encroachment, and livestock outcompeting wildlife for water or forage (Du Toit & Cumming, 1999).

Livestock-rearing, bush encroachment and biodiversity conservation

Robust evidence exists at localised scales that high stocking densities can result in bush encroachment (e.g. Oba *et al*., 2000; Roques *et al*., 2001), the increased density and canopy cover of indigenous woody vegetation and concomitant reduction in grass cover over time (Asner *et al*., 2004). Much of the evidence is based on exclosure experiments (e.g. Skarpe, 1990), fence-line contrasts of sites with different stocking rates (e.g. Roques *et al*., 2001) or measures of vegetation condition at varying distances from livestock-watering points (e.g. Perkins, 1996). But, owing to the small spatial scales at which existing work has been undertaken, some conceptual and practical issues remain debatable.

First, it has often been assumed that bush encroachment negatively affects wildlife conservation (Herremans, 1998; Du Toit & Cumming, 1999), possibly because range degradation has negative effects on livestock productivity (Abel & Blaikie, 1989). However, empirical evidence of pervasive negative impacts on wildlife owing to bush encroachment is lacking; moreover, recent reviews (Asner *et al*., 2004; Eldridge *et al*., 2011) show that bush encroachment does not universally result in decreased landscape productivity, contrary to the frequent supposition that bush encroachment equates to range degradation (e.g. Illius & O'Connor, 1999). Even then, at localised scales and based mostly on single-species assessment, some evidence exists for the consequences of bush encroachment for wildlife; while some authors (e.g. Spottiswoode *et al*., 2009) report negative effects as widely expected, others report positive responses (e.g. Muntifering *et al*., 2006). In the latter study, the paradoxically positive response by cheetah *Acinonyx jubatus* (which chases prey in open terrain rather than pouncing on them from a hidden position) possibly reflected positive association with increased prey density in bush-encroached areas, highlighting the need to infer directionality of impacts on empirical data rather than anecdotes.

Second, despite robust evidence that high cattle grazing pressure can result in increased site-specific woody vegetation cover (Roques *et al*., 2001), it remains debatable whether cattle account for pervasive bush encroachment observed in some landscapes (Ward, 2005; Wigley *et al*., 2010). A recent continent-wide examination of determinants of site-specific woody cover (Sankaran *et al*., 2008) considered only parks, most of which exclude cattle; thus the role of cattle in driving large-scale bush encroachment remains unstudied. This thesis aims to improve understanding on the aforementioned two issues.

Wildlife hunting and challenges in controlling bushmeat offtake

Unregulated hunting is considered a threat to most medium- and large-bodied mammals, both inside and outside parks (Milner-Gulland & Bennett, 2003). While much of the hunting is for subsistence use (e.g. Child, 1996), in many savanna landscapes there is evidence of commercially driven unregulated hunting, primarily of mega-herbivores such as elephant *Loxodonta africana* (Taylor, 2009) and black rhinoceros *Diceros bicornis* (Lewis *et al*., 1990). The extent of unregulated hunting, the species taken and the population impacts of such offtake are unknown in many countries, particularly in unprotected areas. Notwithstanding, in some unprotected areas, attempts to curb commercially-driven hunting impacts have involved the employment of community-based wildlife wardens, paid from the proceeds of elephant trophy hunting managed by the state (e.g. Lewis *et al*., 1990). This reduced elephant poaching by both residents and outsiders (Lewis *et al*., 1990). However, such an approach may be more effective at conserving high-value species threatened by economic poaching, but less so for species threatened by subsistence hunting. Notwithstanding, trophy hunting has been promoted as a tool to entice local communities to stop unregulated hunting (Du Toit, 2002), with recommendations that hunting should be in designated rather than undesignated landscapes. It has not been assessed whether unregulated hunting varies for different-sized vertebrates and whether this is mediated by possible source-sink (Pulliam, 1988) dynamics between protected and unprotected areas.

Attempted solutions to threats posed by livestock-rearing and hunting

Protected areas in Africa

When most African states were colonised in the late 19th Century, management of natural resources was still largely under the authority of traditional and customary leadership. Following colonisation, international trade with European countries in wildlife products increased drastically, aided in part by the acquisition of guns by natives, which enabled the efficient killing of many animals relative to traditional hunting techniques. Because large numbers of animals were also killed during sport-hunting by European settlers, as well as by American, Asian and European explorers (e.g. Campbell, 1997), it was important to have state-managed hunting regulation rather than subnational control that was in most cases inapplicable to non-natives. Thus for example, in response to the need for regulated wildlife trade in southern Africa, the British colonial government instigated the Cape of Good Hope's Game Law Act in 1886. Although adopted by some colonies such as Zimbabwe and Botswana (Mutwira, 1989; Campbell, 1997), this law applied only to foreigners while locals could continue exploiting the wildlife, guided by their customs and traditional law. However, the prospects of greater economic income meant many locals did not abide by traditional customs or proclamations by village chiefs, but instead resorted to commercial exploitation to meet the demands for wild game and trophies by European traders (Campbell, 1997). To ensure long-term wildlife conservation, and especially to protect wildlife from pervasive trade and unregulated use by natives, recommendations from the London Convention of 1933 were adopted across much of southern Africa in the 1930s and 1940s (Child & Barnes, 2010). Key measures in this convention were: the centralisation of wildlife management in the state, the creation of protected areas (PAs), and the curbing of commercial wildlife exploitation.

Consequently, throughout southern Africa and the rest of the continent, state-managed PAs constitute the principal means of conserving large wild vertebrates. However, the relative importance of PAs and of unregulated hunting and habitat modification remain poorly known for most of Africa's large vertebrates. Most of the PAs were designated from the 1940s to the 1970s (Myers, 1972). Although initial designations tended to involve strict PAs that prohibited all offtake of biological resources (Myers, 1972), presently the largest proportion (by area) of southern and East African PAs are managed to meet the dual goals of biodiversity conservation whilst permitting nearby communities to extract natural products from the reserves (IUCN PA management category VI, Chape *et al.*, 2003; Table 1.1).

Table 1.1. Area (km^2), number and percentage distribution of parks per IUCN Protected Area management categories in southern and East Africa, adapted from Chape *et al.*, 2003[a].

	Category	Definition	Index considered			
			No. of PAs	% of total number	Area	% of total area
Strictly protected PAs	Ia	Strict Nature Reserve: managed mainly for science	13	0.3	2,550	0.13
	Ib	Wilderness Area: managed mainly for wilderness protection	7	0.1	1,251	0.06
	II	National Park: managed mainly for ecosystem protection and recreation	217	4.5	504,692	25.65
	III	Natural Monument: managed mainly for conservation of specific natural features	24	0.5	150	0.01
	I–III	Sub-total	261	5.4	508,643	25.86
	IV	Habitat/Species Management Area: managed mainly for conservation through management intervention	463	9.5	261,122	13.27
Multi-use wildlife areas	V	Protected Landscape/Seascape: managed mainly for landscape/ seascape conservation and recreation	30	0.6	12,548	0.64
	VI	Managed Resource Protected Area: managed mainly for the sustainable use of natural ecosystems	223	4.6	556,418	28.28
	V+VI	Sub-total	253	5.2	568,966	28.92
	Unclassified	Some level of protection by states, but IUCN PA management category not assigned	3,875	79.9	628,512	31.95
		Total area protected	4,852	-	1,967,242	100

[a] Countries included are Botswana, Eritrea, Ethiopia, Kenya, Lesotho, Madagascar, Malawi, Mayotte, Mozambique, Namibia, Réunion, Seychelles, Somalia, South Africa, Sudan, Swaziland, Uganda, Tanzania, Zambia, Zimbabwe.

Based on global trends (Naughton-Treves *et al.*, 2005; Gaston *et al.*, 2008), future PA network expansion in southern and East Africa is likely to be in the management categories that allow consumptive use. The conservation effectiveness of the different

PA management categories has not been examined systematically; but, notably in East Africa, several studies have compared wildlife abundance in strict PAs to those from neighbouring consumptive reserves (Ogutu *et al*., 2005, Magige *et al*., 2009) or unprotected areas (Caro, 2001; Homewood *et al*., 2001; Rannestad *et al*., 2006). These studies focused primarily on large vertebrates, and for most species reported greater abundance in PAs relative to consumptive reserves and unprotected areas. However, none explicitly quantified the relative importance of mechanisms that may explain the wildlife species response, and importantly they also assumed PAs were largely undisturbed. This supposition may mask the understanding of processes that underlie observed patterns, particularly if the extent of human disturbance across the strict PAs, consumptive reserves and unprotected areas is taxon-specific. Taxon-specific disturbance may occur for example if people prefer to hunt some species but not others, as happened in the Serengeti where, of the two largest-bodied birds, Maasai hunted Ostrich *Struthio camelus* but not Kori Bustard *Ardeotis kori* (Magige *et al*., 2009). Recent studies (e.g. Craigie *et al*., 2010; Fynn & Bonyongo, 2010) suggest some African PAs may be ineffective at conserving wildlife, but it is unclear what the main cause is. For example, while Craigie *et al*. (2010) postulate the possibility of unregulated hunting as the main threat, Fynn & Bonyongo (2010) down-played the role of bushmeat offtake and instead argued that wildlife numbers (especially of migratory species) have declined because PAs are not large enough to provide all forage resources that the species require throughout the year, with human settlement and fencing preventing long-distance movements to exploit dry-season grazing areas. Key threats to African PAs and constituent wildlife may be site-specific or vary geographically across the continent, and consequently, conservation solutions need to be tailored to the demands of the site-specific contexts. Case studies such as this thesis are therefore important to assess the efficacy of conservation areas, including PAs, under particular circumstances.

Community-based conservation

The designation of African PAs in most cases resulted in the eviction and displacement of local communities (Myers, 1972), and subsequently restricted exploitation of previously accessible wildlife and other natural resources. However, neighbouring communities continue to incur costs from wildlife through, for example, crop damage and livestock depredation (e.g. Taylor, 2009). In realising that antagonistic relationships existed between many PAs and neighbouring communities, Integrated Conservation and Development Projects (ICDPs) were promoted in areas abutting PAs in Africa, and other developing countries globally, in the 1980s (Barrett & Arcese,1995). For example in the buffer areas of UNESCO’s Biosphere Reserves a variety of community development projects were instigated (Bridgewater, 2002). However, such substitute and compensatory economic activities associated with these buffer-zone projects provided only an indirect link between development or livelihood benefits and conservation goals (Salafsky & Wollenberg, 2000). Such an indirect linkage may not be perceived by communities, provides little incentive to cease damaging forms of wildlife exploitation (Salafsky & Wollenberg, 2000) and generally delivers few conservation benefits (e.g. Licona *et al*., 2010).

Largely due to the social movement against injustice resulting from PA designation and debates on whether communities could continue extracting resources from PAs in Latin America (e.g. Peres & Zimmerman, 2001), Asia (e.g. Guha, 1997) and Africa (e.g. Adams & Hulme, 2001; for global review see Brockington & Igoe, 2006), ‘people-based-conservation’ has been widely promoted by development agencies and states particularly following the 4th World Parks Congress held in Caracas, (Venezuela) in 1993. This approach emphasises integrated planning, co-operative management, and direct involvement of local residents and resource users. The Caracas Action Plan had four broad objectives: (a) integrating PAs into wider planning frameworks; (b) expanding the support for PAs by involving local communities and other non-traditional interest groups; (c) strengthening the capacity to manage PAs; and (d) expanding international cooperation for the financing, development and management of PAs (IUCN, 1992). To realise these four objectives, extractive reserves have been set up in forested ecosystems such as in Latin America, Asia and central Africa, while community-managed Wildlife Management Areas (WMAs) have been adopted in the savannas of southern and East Africa. The overall aims of WMAs are to engage local communities more fully in biodiversity conservation outside PAs through directly linking livelihoods to biological resources (Salafsky & Wollenberg, 2000), largely through trophy hunting and wildlife-based tourism (Du Toit, 2002; Child & Barnes, 2010; Naidoo *et al*., 2011).

Wildlife Management Areas: experiences from southern Africa

Wildlife conservation through WMAs has been attempted in Botswana, Namibia, Zambia and Zimbabwe (Table 1.2). Although there are some community-based conservation projects in South Africa, Malawi and Mozambique, these are not considered in this review because they involve game ranching within fenced reserves (for South Africa see, e.g., Du Toit, 2002), or are primarily based on non-timber forest products, with no wildlife component (for Malawi and Mozambique see, e.g., Blaikie, 2006). The ecological outcomes of WMAs in Namibia, Zambia and Zimbabwe have never been assessed, but experiences from these countries suggest at least four key conditions that WMAs must meet to have any chance of delivering on their conservation aims.

First, WMA management, user rights and benefits need to be genuinely devolved to communities, which would increase transparency in benefit-sharing and ownership; for instance 100% of the revenue in Namibian WMAs is retained by the community groups (Arntzen *et al*., 2007) in contrast to Zimbabwe where WMA management has been devolved by government to district councils who only pay 50% of the trophy hunting proceeds to communities (Child & Barnes, 2010). Because the district councils financially benefit from the scheme but do not incur any direct livelihood costs, they would probably be biased towards economically rather than ecologically based quotas, and maximising short-term profit to the detriment of wildlife conservation.

Second, strong institutional and legal frameworks are crucial. At site-level these would for example enable ordinary community members to resist the scheme being monopolised by village elites (as successfully resisted in Zimbabwe: Child, 1996). At national level, such civic empowerment was achieved, for example, through the Namibian Association of Community Based Natural Resource Management (CBNRM) Support Organizations, which enabled considerable participation by NGOs and also afforded greater coordinated organisation of WMA community groups. In contrast, the collapse of the scheme in Zambia was partly attributable to the lack of strong community-driven institutions (Lewis *et al*., 1990; Child & Barnes, 2010).

Third, WMAs need to serve the interest of the community, thus for example direct payments to traditional leaders, and not to community-managed institutions

(Lewis *et al*., 1990), probably led to the lack of continuity in the Zambian scheme following the departure of direct project financiers.

Lastly, wildlife offtake needs to be based on sound biological assessment, with the income paid to participating partners commensurate with the sustainability of the biological resources and with the livelihood costs that project partners incur, to improve links between the resources and livelihoods. In Zambia project success was short-lived because, following the departure of initial key project personnel, the percentage of revenue paid to district councils and the government's wildlife department increased from 20% to more than 70% (Child & Barnes, 2010), providing little incentive for continued community participation. Importantly, throughout southern Africa, mechanisms for assessing the ecological and financial viability of trophy hunting, and for ensuring such legal hunting is within agreed quotas, are either nonexistent or undocumented. It is assumed, but untested, that species on community-managed hunting quotas will be preferentially conserved (e.g. Du Toit, 2002; Taylor, 2009), since communities derive a direct economic income from them. It is also assumed that as long as communities earn sufficient income from trophy hunting, they will cease unregulated hunting of non-quota species, even if they do not directly benefit from the non-quota species (e.g. Lewis *et al*., 1990). These supposed natural resource–livelihoods linkages are critical to test and understand if savanna wildlife is to be conserved in the long term.

Wildlife Management Areas in Botswana

An accurate assessment of the conservation efficacy of WMAs needs to consider the socio-economic context within which they were conceived. Botswana became a British Protectorate in 1885. Subsequently, in 1933, a watershed pre-independence philosophy that significantly affected wildlife conservation was an assessment by a commission appointed 'to enquire into the position of the country from the financial and economic points of view' (Campbell, 1997). This report suggested cattle should be the highest priority economic activity, with wildlife not considered an asset worth investing in. Until independence in 1966, state investment in wildlife conservation was minimal, with initial wildlife wardens recruited in 1956, but an official wildlife department not established until 1966. Following the creation of the Department of Wildlife and National Parks (DWNP), at least five PAs were created during 1966–1972, and all four pre-1966 PAs expanded (Campbell, 1973). Outside PAs, a significant post-independence land-use designation and policy was the 1975 Tribal Grazing Lands Policy (TGLP); this set aside land for commercial cattle ranching, primarily in efforts to curb perceived range degradation in communal grazing areas (Cooke, 1985). The TGLP introduced, for the first time, a stipulation on fencing cattle grazing areas, in what were previously communal areas in which cattle-owners and non-cattle-owners cohabitated. In some areas, in a few instances, people were relocated from the ranched areas after having previously been relocated from PAs (e.g. Twyman, 2001), a double injustice.

There were discussions on creating WMAs, to serve the dual purpose of wildlife conservation outside PAs and rural economic diversification, from as early as 1983 (Cooke, 1985). However, WMAs were officially mentioned for the first time as an alternative land-use type in the 1986 Fauna Conservation Act (Twyman, 2001). The WMAs were mentioned again in the 1992 Wildlife Conservation and National Parks Act (an update of the Fauna Conservation Act). Although it is unclear when they were actually designated, or what guided their location, at least when WMAs were first conceived in the early 1980s the primary government departments involved in the process were DWNP and the Department of Animal Health and Production, who coordinate livestock production (Cooke, 1985). It appears that areas prioritised as WMAs were the low human density regions in the Kalahari Desert, and the Okavango and Chobe districts (Rozemeijer, 2009). National implementation of WMAs started in 1999, with USAID financial support to DWNP, and the initial funding was towards policy and legislation development (e.g. drafting WMA implementation guidelines: Rozemeijer, 2009); this followed and was largely based on results from a pilot USAID-funded project near the Chobe National Park, where in 1993 a WMA was devolved to a community group.

Table 1.2 Examples and characteristics of Wildlife Management Areas (WMAs) in Namibia, Zambia and Zimbabwe.

Country	Programme	Established	Conservation approach	Key biodiversity conservation achievement	References
Namibia	Conservancy program	1996	WMA boundaries proposed by communities applying to join the scheme, and each community keeps 100% of the revenue generated.	WMAs with high-value species (e.g. black rhinoceros) are profitable; at least for this species, the scheme has resulted in positive conservation outcomes notably through increased anti-poaching patrols. The extent to which co-occurring species and habitats are conserved is unclear.	Child & Barnes, 2010; Naidoo *et al*., 2011
Zambia	Administrative Management Design (ADMADE) and Luangwa Integrated Rural Development Project (LIRDP)	1980s	Promoted community-government partnerships for wildlife conservation and management, focused on four results: (a) rate of unregulated wildlife offtake (primarily of elephants), (b) sustainability of economic incentives for communities to support sustained-yield management; (c) attitudes and perceptions to wildlife, (d) level of manpower and leadership derived from the community for conservation. WMA localities pre-determined by government, but no systematic programming or formalisation of national or district-level governance structures. Lack of civic organisation (of the communities involved in the scheme) exacerbated by minimal NGO participation, because the schemes were largely driven by direct partnerships between government and local communities, principally on a project-by-project basis. Communities (household-level), paid dividends from elephants sale (80%); 20% to district councils and traditional leaders.	A few locals employed as wildlife wardens, and the increased law enforcement decreased elephant poaching. Because funds were paid to households rather than village-level governance structures, no investment was made on community-managed enterprise development, thus the schemes have left little economic legacies, and although undocumented, the initial ecological gains have probably also been lost. From the early 1990s, the schemes were effectively non-operational, and were formally closed down by the wildlife department in 2002.	Lewis *et al*., 1990; Arntzen *et al*., 2007; Child & Barnes, 2010
Zimbabwe	Communal Areas Management Programme For Indigenous Resources (CAMPFIRE)	1989 (conceived in late 1970s)	Management of WMAs devolved to district councils (Rural Development Councils, RDCs), who pay at least 50% of revenues to participating communities. RDCs comprise elected ordinary-villager representatives, councillors, and wildlife department staff. Participating districts also formed a political producer organization (CAMPFIRE Association), which represented their collective bargaining positions at each RDC, and in national forums. However, the scheme performed poorly in some districts, mostly due to historical mistrust between communities and government.	During the 1990s, rural communities’ financial stake from WMA wildlife-based income, and political, democratic and social organisation, were greatly improved, notably through lobbying by the CAMPFIRE Association. CAMPFIRE also influenced global debates, successfully lobbying CITES for continued elephant hunting, because these were their primary revenue-earner. Some positive conservation outcomes were realised, as judged by increased elephant numbers in CAMPFIRE districts; however, the impacts of the schemes on other wildlife, and habitats, is unknown.	Child, 1996; Alexander & McGregor, 2000;Child & Barnes, 2010

When they were set up, most WMAs were inhabited by human communities; however, most of them were relocated from areas designated as wildlife zones to WMA villages (Twyman, 2000), and no WMA has had new settlements established within its boundaries. The WMAs primarily make their income from trophy hunting, and Chapter 3 provides a list of the huntable species, details of zoning within WMAs (to create separate wildlife and livestock-rearing zones) and an account of how quotas are set.

A significant difference from the Namibia, Zimbabwe and Zambia WMA schemes is that in Botswana the majority of the revenue is invested in community projects rather than paid to households (Arntzen *et al*., 2007). In principle, this should enhance the ability of the scheme to deliver community-level enterprise development. However, most WMAs, especially in the drier Kalahari, have not been profitable owing to their remoteness from markets, poorly developed infrastructure, and lack of high-value species (such as elephants) that are included in quotas for WMAs in the more mesic parts of the country (Rozemeijer, 2009). Thus, for example, in 2001 a Kalahari-based WMA made approximately £18,000 from its wildlife quota, while a more species-rich but three times smaller WMA near the Okavango Delta that supported about the same number of inhabitants, had 12 elephants on its quota and made at least £1.4 million (Rozemeijer, 2009).

There is some evidence that WMA designation was top-down and some communities were coerced into joining the scheme (Twyman, 2000). However, where WMAs have been profitable, there has been less confrontation between communities and government over WMA boundaries and land-use restrictions, and in some instances communities have used WMAs to lobby for social rights (e.g. Taylor, 2006). More generally, because the civic association of WMA producer communities is weak (Child & Barnes, 2010), and there is weak institutional support from NGOs and government (Rozemeijer, 2009), most communities in WMAs often fail to meet expected obligations for continued issuance of hunting quotas (such as annually audited financial accounts), and, as a result of perceived or real financial mismanagement, quotas are sometimes withheld by DWNP, which is responsible for the annual issuance of WMA-specific quotas (Child & Barnes, 2010). Because revenue sources are undiversified, and primarily reliant on hunting quotas, this has restricted the ability of most WMAs to meet their objective of providing sustainable income opportunities (Arntzen *et al*., 2007).

As with the rest of southern Africa, the ecological effectiveness of WMAs in Botswana has never been assessed. The objectives of this scheme were primarily wildlife conservation and, secondarily, creating economic opportunities for the rural populace (Rozemeijer, 2009). However, during WMA implementation (e.g. Rozemeijer, 2009), when researching WMA outcomes and challenges (e.g. Twyman 2000, 2001; Blaikie, 2006), and when lobbying government (e.g. Taylor, 2006; Child & Barnes, 2010), the motives of WMAs seem to be reversed, because much of the effort is targeted at socio-economic processes and outcomes (such as land rights or extent of community participation), and not implications of designation for wildlife conservation.

Priorities of conservation programmes for Africa's wildlife

Focus on large charismatic vertebrates and globally threatened taxa

While the designation of PAs and WMAs gives the impression of considerable use of landscape-scale conservation approaches, in practice wildlife research and conservation programmes in Africa have primarily targeted large-bodied vertebrates, mostly on a single-species basis. Actions have focused on conservation status assessment within single parks (e.g. Harrington *et al*., 1999) and only rarely in multiple PAs (e.g. Gros, 2002), often with emphasis on translocations (particularly in small PAs, e.g. Hayward *et al*., 2007) to supplement populations. To a large extent, this has led to increased financial and research investment in single PAs or species, and less so to an understanding and mitigation of landscape-scale threats. This single-species and single PA approach persists despite the increasing recognition that the conservation of most of the large vertebrates requires consideration of landscape-scale threats, particularly the subtle impacts of human encroachment (Homewood *et al*., 2001; Fynn & Bonyongo, 2010), which have been less studied than direct anthropogenic impacts such as hunting (e.g. Magige *et al*., 2009) or habitat conversion (e.g. Thiollay, 2006).

While there has been some positive and desirable trend away from single-species focus towards conserving threatened species more broadly, this has still been largely restricted to PAs and other conservation sites such as Important Bird Areas (IBAs: Fishpool & Evans, 2001) or Key Biodiversity Areas (KBAs: Eken *et al*., 2004). This approach is valuable and practical, but it is nevertheless inadequate, because it fails to provide for a certain class of species. Thus IBAs are defined as such because they hold: (a) significant numbers of globally threatened species (as per the IUCN Red List);

(b) at least two restricted-range species (world distribution <50,000 km^2); (c) a significant component of the group of species whose distributions are largely or wholly confined to one biome; or (d) more than 1% or 20,000 pairs of waterbirds (Fishpool & Evans, 2001). This, however, means that widespread low-density species, and particularly those that do not congregate for breeding, will have low numbers in any IBA/KBA. Furthermore, the threshold for which a species can qualify as threatened under the geographic range criteria of IUCN Red List is ≤20,000 km^2 (criterion B), or if it is to meet the other criteria, evidence that its geographic range has declined by at least 30% in 10 years or three generations (IUCN, 2001). Owing to their large geographic range, widespread low-density species have therefore not been a conservation priority (e.g. Gaston & Fuller, 2008), possibly because of the assumption that their extensive geographic ranges guarantee that they occur in large enough numbers somewhere else. Consequently, there has notably been much less research, monitoring and understanding of their population trends. However, there is increasing evidence that some low-density widespread species have undergone significant and rapid population declines (e.g. Thiollay, 2006; Ogada & Buij, 2011; Senyatso *et al*., in review, Chapter 2).

Challenges to conserving low-density, widespread species

Decision-making in wildlife management and conservation increasingly demands quantitative rather than qualitative data and evidence. Therefore, while there have often been suggestions that some widespread low-density species have declined (e.g. Africa's *Ardeotis* bustards: Collar, 1996; Thiollay, 2006), if declines cannot be quantified, such species are unlikely to attract the conservation attention they deserve, unless declines are unusually rapid as occurred with Indian vultures (Pain *et al*., 2008). While much has been achieved in developing field methodologies (e.g. Bibby *et al*., 1993) and software for sophisticated analysis of population trend data, some with capacity to work with uncertainties in parameter estimates (e.g. RAMAS® Red List: Akçakaya & Ferson, 2001), gaps still exist in methodologies to evaluate range-wide trends in population numbers or geographic range extent. In much of Africa, the most comprehensive data available for most bird species are presence-only distributional records, some of which have been summarised in atlases (e.g. Harrison *et al*., 1997) and others scattered in published and unpublished literature. These distributional data, most of which are one-off sighting records, offer the best opportunity to assess range-wide conservation status of widespread bird species. There is therefore a need to develop and test robust yet cost-effective methods that can quantify long-term range-wide population trends of widespread species based on these data; this study presents one possibility.

Kori Bustard as a case study of a low-density widespread species

This thesis uses Kori Bustard as a case study to highlight the challenges over, and test a possible methodological solution to, the assessment of conservation status for low-density widespread species in Africa. This species has a large geographic range spanning 14 countries in southern and East Africa, mostly in savanna landscapes. In common with most other African birds, Kori habitat use and preference, diet, breeding and socialisation, movement patterns, and key threats are poorly understood, or only documented from small parts of the geographic range; but geographic variations in abundance and habitat occupancy make range-wide extrapolation from localised observational data close to guesswork.

Koris are thought to prefer grasslands, shrubland or fairly open and unmodified savanna habitats, based on opportunistic sight records; although they are occasionally reported in more wooded areas including Mopane *Colophospermum mopane*, Miombo *Brachystegia* and Teak *Baikiaea* woodlands (Collar, 1996; Harrison *et al.*, 1997; Allan & Osborne, 2005). While initial data from coordinated bi-annual road counts in South Africa (Young *et al.*, 2003) suggest avoidance of crop fields, Kori do use crops and other anthropogenic areas such as fallow lands, airstrips and fire-breaks (Harrison *et al.*, 1997). Kori display behaviour has been widely documented (e.g. Allen & Clifton, 1972; Hellmich, 1988), but breeding and non-breeding habitat requirements have not been studied. Observational data (e.g. Osborne & Osborne, 1999) suggest that there are routinely used areas (‘leks’) in the breeding season, mostly in open areas where displaying males can see or hear each other; for example, in Kruger National Park, display areas were ‘notoriously open, the grass short, and the small stunted trees widely scattered’ (Astley-Maberly, 1937, p. 11).

Kori diet includes invertebrates (such as beetles, grasshoppers and termites), plant matter (berries, grass, flowers and tree gum) and small vertebrates (lizards, small-bodied rodents, other birds’ eggs and nestlings, and snakes) (Allan & Osborne, 2005). The relative importance of plant versus animal matter is unknown, but the presence of a muscular ventriculus and prominent cecum, required for processing complex foods (Maloiy *et al.*, 1987), suggest plant matter and insects are probably more important than vertebrate meat. Animal matter is often obtained opportunistically by eating road kills, following wild-fires and feeding off burnt wildlife, or tracking erupting locusts and other invertebrates (Allan & Osborne, 2005); the latter two factors suggest a mobile lifestyle to exploit opportunistic food resources. Thus Kori has been thought to undertake systematic long-distance movements, based on apparent seasonal variation in the bird's abundance (e.g. Snow, 1978; Britton, 1980; Nikolaus, 1987), yet no empirical evidence exists (Chapter 5). In Namibia, however, Osborne & Osborne (1999) found that birds undertake post-breeding movements. These authors employed radio-telemetry and provided the first objective evidence of movement patterns, but findings were possibly biased owing to the difficulty (in spite of their occasional use of aeroplanes) of relocating birds. Thus, unbiased evidence for movements, as may be obtained from satellite telemetry, could be expected to reveal even wider ranging movement patterns than were found in Namibia.

The often cited threats to Kori include collision with powerlines, predation and human exploitation (Allan & Osborne, 2005), but their relative importance in unknown. Significant international trade in Kori, mainly between three African states (Somalia, Kenya and Tanzania) and Arab Gulf countries, increased drastically post-1980 (Goriup, 1987). Live trade in wild-caught Kori continues, with a total of 25 live birds y^{-1} ± 24 SD legally traded and registered on the CITES trade database (UNEP WCMC CITES, 2009) between 1990 and 2008, with most birds from Tanzania. The challenges relating to poor ecological knowledge and understanding of whether offtake quotas are sustainable have made it difficult to coordinate global, regional and country-level agreements and legal frameworks used to protect Kori (Table 1.3). Similar difficulties are expected for other low-density widespread species in African savannas.

Table 1.3. National, subregional (East and southern Africa), African-wide and global legal frameworks protecting *Ardeotis kori*.

Jurisdiction	Legislation	Main highlights	Legislative gaps
Angola	Decree no. 43/77	Legislation for creation of national parks.	Legal framework for Kori conservation outside parks.
Botswana	Wildlife Conservation and National Parks Act (1992)	Kori Bustard explicitly a protected species. Hunting or capture prohibited.	None.
Ethiopia	Forest & Wildlife Conservation & Development Proclamation (1980)	Creation of parks and regulation of hunting	Kori not included in list of legally huntable game birds thus has *de facto* protection.
Kenya	Wildlife (Conservation and Amendment) Act (1989)	Wildlife conservation and management, and park establishment	Kori not included in list of legally huntable game birds thus has *de facto* protection.
Mozambique	Law on Forestry & Wildlife 10/99 (1999); Annex 2 of Regulations of Law No. 10/99.	Outlines principles for conservation and sustainable use of forest and wildlife resources. Kori explicitly included in list (Annex 2) of species whose hunting is prohibited	None
Namibia	National Conservation Ordinance (1975)	All species of birds except huntable game birds are implicitly protected game. *A. kori* protected game.	*Status quo* suffices; could be strengthened by adding bustards to the list of protected game.
Somalia	Law on Fauna (Hunting) and Forest Conservation (1969)	Legislation for creation of national parks.	No explicit protection for *A. kori*, but wildlife hunting banned in 1977 (Law No. 65).
South Africa	National Environmental Management: Biodiversity and Protected Area Acts (2009)	Separate Acts for biodiversity conservation (species and ecosystems requiring conservation action, including trade regulation) and protected area	Kori not in list of huntable game birds but live trade permitted. Trade should be banned until evidence of non-detrimental trade produced
Sudan	Wildlife Conservation and National Parks Act (2003)	Legislation for creation of national parks. All bustards ‘completely protected’, with hunting or capture prohibited.	None

Jurisdiction	Legislation	Main highlights	Legislative gaps
Swaziland	National Trust Commission Act (1972)	Legislation for creation of national parks.	Not relevant for Kori Bustard because it is locally extinct.
Tanzania	Wildlife Conservation Act (1974)	Kori hunting prohibited. Act excludes kori in list of huntable species, but live trade allowed.	Commercial trade should be prohibited.
Uganda	Uganda Wildlife Act (2000)	Trade regulation and protected area management	Species probably extinct, thus not a priority
Zambia	Fauna Conservation Ordinance (1956)	Hunting of all bustards prohibited.	None.
Zimbabwe	Parks and Wild life Act (1975)	Bustards are ‘specially protected’ game, off-take prohibited.	None.
Subregional			
East Africa Community	None specific to biodiversity conservation	Most relevant are policies on agriculture and rural development, though biodiversity seems peripheral.	Cooperation promoted for wetlands; equivalent protocol for terrestrial habitats missing.
Southern African Development Community	Protocol on Wildlife Conservation and Law Enforcement, 1999	Promotes common approaches to wildlife conservation and sustainable use, nothing specific to birds.	Implementation weak; mechanisms through which common positions reached (e.g. on wildlife trade) required
Range-wide			
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora (1973)	In 1987 Kori listed in Appendix II. Source countries required to issue export permit and in-transit countries to issue re-export certificates, but import permits are not a requirement.	An important proviso is that permit-issuing authorities need to be satisfied that trade is not detrimental to wild birds. Such evidence not provided because it is unavailable.
African Convention	African Convention on the Conservation of Nature and Natural Resources (1968)	General policy document advocating for better environmental conservation, plus harmonization and coordination of conservation policies across Africa.	All range states signatories. Convention has no provision for species-focused programmes.

Study area

Botswana is a semi-arid country at the hub of southern Africa, with a surface area of 581,730 km^2. The country supports significant biodiversity and, based on its mammals, birds, amphibians, reptiles, butterflies and angiosperms, is among the 50 most species-rich countries in the world (World Conservation Monitoring Centre, 1994), despite 80% of the land area being characterised by sandy soils and sporadic summer (October–March) rainfall (ranging from 250 mm y^{-1} in the south-west to 650 mm y^{-1} in the north-east: Nicholson & Farrar, 1994). Although rainfall stations across the country and within the study site are limited, data from the 11 stations with long-term datasets (two of which are within the study area) suggest coefficient of variation in mean annual rainfall that ranges 0.28–0.43, based on rainfall measures over the period 1961–2003 (Parida & Moalafhi, 2008). Slight vegetation changes follow the south-west to north-east rainfall gradient with much of the south-west consisting of the more drought-resistant *Acacia* scrub while the mesic north-east has increased total plant diversity and greater woody plant density, with predominantly tree savanna and isolated stands of Mopane woodlands (Weare & Yalala, 1971; Fig. 1.2).

The country is an *in situ* conservation pioneer, having established an impressive PA estate, which is the primary locus for biodiversity conservation. The PA system incorporates some 17% of Botswana’s total land area, comprising about 7% in national parks and 10% in game reserves, while a further 22% of the country is designated as WMAs (Government of Botswana, 2001). Priority study areas examined in this thesis are the eight PAs, their neighbouring WMAs, and intervening unprotected areas in central Botswana (see Fig. 1.2).

Human population density is low across the sampling area. Based on the latest census data (from 2001), only about 10 large villages and towns in the area enclosed by the dotted square in Figure 1.2 have a human population greater than 10,000 (Government of Botswana, 2001); for the remainder of the villages (i.e. only settlements with less than 10,000 inhabitants), and based on the dataset used in this study (which utilises census data only for settlements with more than 200 people as these could be reliably mapped, see Chapter 3 for justification and data sources), the mean human population number per settlement was 1184 people ± 1498 SD (*n* = 138 settlements). Pooled across WMA livestock-rearing buffers (human settled areas of the WMA, see

Chapter 3) and unprotected areas, this translates into a mean human density of 0.092 people km^{-2} ± 0.258 SD and 0.998 people km^{-2} ± 2.407 SD for these land-uses respectively; WMA wildlife zones and parks exclude human settlements, although the Central Kalahari Game Reserve has a few small settlements whose pooled populations probably number less than 200 (see Chapter 3). The vast majority of the villagers in the study area historically depended on a combination of wildlife and non-timber forest products, but more recently (particularly after independence in 1966, and with the introduction of permit systems to regulate wildlife hunting), the relative importance of wildly collected natural resources has declined (e.g. Twyman, 2001; Sallu *et al*., 2009). However, the most frequently hunted wildlife species, the most preferred species, total numbers of wildlife killed per village or district, hunting techniques, and the extent to which hunting may be affected by socio-economic status, are poorly understood and largely undocumented; but, it is probable that throughout the study area, medium- and large-bodied herbivores, small mammals and galliformes respectively constitute the most preferred hunting quarry (pers. obs.).

Although the relative importance of income generating strategies is undocumented across much of the study site, where such data is available (e.g. Chanda *et al*., 2003; Sallu *et al*., 2009), livestock, particularly cattle, are the single most important economic activity in the smaller and more remote settlements. Due to the harsh environmental conditions and nutrient-poor soils, the major economic activities within the study area therefore revolve around small-scale livestock-rearing (based on number of cattle kept and spatial extent over which they forage, ≤10 km) on communally-managed lands. The number of cattle owned by households varies greatly, depending on household economic status (e.g. Chanda *et al*., 2003). For example, Schiess-Meier *et al*. (2007) reported that ‘owners of small cattle herds’ owned a mean 42 cattle ± 27 SD ($n = 32$) while ‘owners of large cattle herds’ owned a mean 353 cattle ± 396 SD ($n = 28$), in communally managed areas. Nevertheless, cattle stocking rates are variable depending on the land tenure, but are commonly 6 ha per livestock unit in communal lands and 12.5 ha per livestock unit in fenced commercial ranches (Abel & Blaikie, 1989). The extent to which these stocking rates vary spatially across the study area is unknown, but this is unlikely to be significant due to similar cultural motivation for livestock keeping, especially in communal areas where cattle are managed for subsistence non-commercial use. Commercial cattle ranches, typically 16 km^2 each, occur sporadically in parts of the study area (Perkins, 1996), largely under freehold tenure.

In unprotected areas, most households have three homesteads: (a) a ‘village home’; (b) a ‘cattle-post’, where livestock are kept, and with a few resident cattle herders who spend their entire time at those cattle-posts tending to the livestock; and (c) ‘arable lands’, where crop farming is practised, although this is less common in the drier south-west regions of the sampling extent (arable farming is generally negligible, and for example, crop fields of 0.2–6.0 ha are not uncommon in Botswana e.g. Jackson *et al*., 2008). The abovementioned three homesteads can be separated by up to 20–40 km (e.g. Chanda *et al*., 2003), although the physical separation is less defined within WMAs because of the more restricted areal extent of buffers for settlements and associated agricultural activities (see Chapter 3). Livestock, particularly cattle, are generally excluded from both villages and lands. In unprotected areas, at village-level, fencing is often used to separate cattle-posts from lands; this does not occur within WMAs. The exclusion of cattle from villages is less direct and is often through the prohibition of watering livestock from the same boreholes that water the human population. The vast majority of the livestock-watering boreholes, located at variable distances from villages, utilise diesel-powered engines to draw underground water.

The harvesting of non-timber forest products (e.g. Kalahari Devil’s Claw *Harpagophytum procumbens*, truffles *Kalaharituber pfielii* and wild berries such as *Grewia flava*), contributes significantly to the income of most households in the remote villages within the study area (Chanda *et al*., 2003).

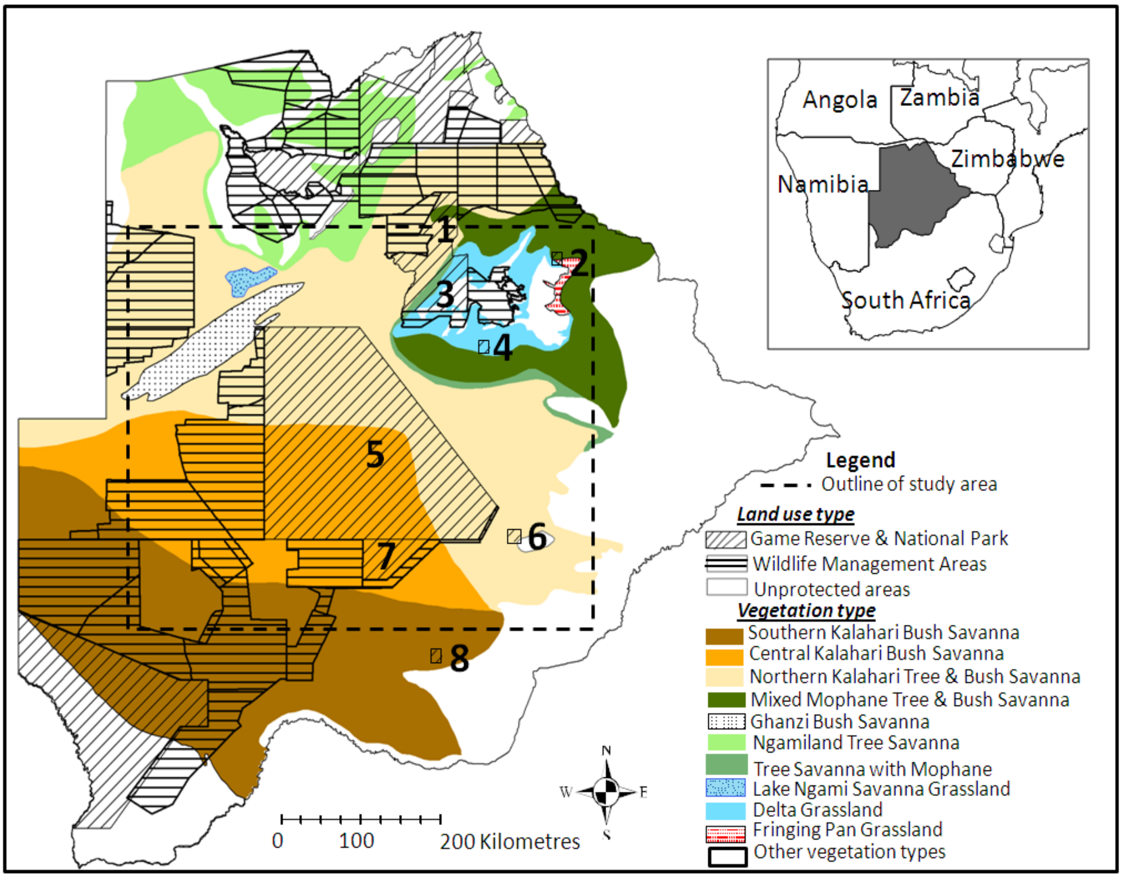

Figure 1.2. Location of the study area in the Kalahari, showing the approximate outline of the sampled area, land-use designation (Government of Botswana, 2011) and vegetation zones (following Weare & Yalala, 1971). Protected areas included in the sampling extent are (1) Nxai National Park, (2) Nata Sanctuary, (3) Makgadikgadi National Park, (4) Orapa Game Park, (5) Central Kalahari Game Reserve, (6) Dithopo Game Ranch, (7) Khutse Game Reserve and (8) Jwana Game Park.

Thesis aims and structure

This study has five main aims, each addressed in separate chapters except the second and third aims, which are pooled into one chapter. Firstly, to test if high cattle grazing pressure is associated with greater landscape-scale bush cover; although cattle can cause site-specific greater bush cover, their role in driving large-scale greater bush cover remains poorly studied. Secondly, to examine the relative importance of cattle grazing and unregulated hunting as threats to a suite of medium- and large-bodied wildlife species; unregulated hunting and cattle-induced impacts have previously been suggested as the main threats to wildlife in Botswana’s Kalahari, but hitherto, their relative importance is unknown. Thirdly, to investigate the conservation effectiveness of PAs and WMAs in the Kalahari, based on the abundance of medium- and large-bodied wildlife species in these management areas, relative to unprotected landscapes. Fourthly, using Kori as a case study, to test a new methodology to assess the range-wide conservation status of a widely distributed low-density species despite a lack of quantitative and long-term population monitoring data. The fifth aim, again using Kori as a case study, is to test the extent to which home range size and placement in an arid ecosystem are affected by season and habitat type. All five aims are geared towards improving understanding of the conservation ecology of widely distributed wildlife species in African savannas, particularly the need to ascertain: (a) the relative importance of threats; (b) the effectiveness of conservation areas; (c) the possible implications of seasonally-variable food resources on wildlife conservation; and (d) whether the widely available incidental sight records can be systematically used to produce evidence-based and objective conservation status assessments.

The thesis examines the conservation ecology of widespread low-density species across three different spatial scales: across 14 countries in southern and East Africa; in multiple PAs, WMAs and intervening areas in central Botswana; and within a single PA (Central Kalahari Game Reserve). The presentation of the research undertaken to meet the five aforementioned study aims follows the decreasing spatial scale at which analysis were done, rather than emphasise any relative importance or chronology of data analysis. Chapter 2, assesses the conservation status of Kori across its entire African geographic range, and uses this case study to develop a methodological framework for studying population and geographic range changes for widely distributed tropical birds. Chapter 3, assesses the relative effectiveness of PAs and WMAs at conserving medium- and large-bodied vertebrates in Botswana’s Kalahari ecoregion, and tests the relative importance of differential cattle stocking rates and unregulated hunting in explaining observed patterns. Comments are made on the practical implementation of WMAs, as well as the conceptual underpinnings of this model that assumes that linking biodiversity conservation to livelihoods improves conservation outcomes. Chapter 4, uses the opportunity provided by the juxtaposition of Kalahari PAs, WMAs and unprotected areas to test the degree to which increased cattle density is associated with increased woody vegetation cover, with results discussed in relation to rangeland management and mitigation of the impacts of cattle grazing. The last results chapter, Chapter 5, examines the degree to which Kori movement patterns and seasonal home range use respond to stochastic resource availability and resource-rich habitat patches.

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Chapter Two

Assessing conservation status change in an unmonitored widespread African bird species

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By Senyatso, K.J., Collar, N.J. & Dolman, P.M.

Abstract

There are no systematic, long-term, large-scale bird monitoring programmes in Africa, and the most comprehensive available data for most species are incidental occurrence records. Can such data be used to assess range-wide conservation status of widespread low-density species? We examine this using Kori Bustard *Ardeotis kori*, a large, easily identifiable species with an extensive African range. A comprehensive and systematic review of published and unpublished sources from all of the bird's geographic range spanning 14 countries in southern and East Africa provided 1948 unique locality records spanning the years 1863–2009; these included 410 non-atlas records and 97 historical (pre-1970) records. Potential range-size changes were examined by comparing minimum convex polygons to quantify Extent of Occurrence pre- and post-1970, and by testing whether more historical records fell outside the recent (post-1970) 95% probability kernel than expected by chance. Additionally, qualitative evidence of changes in abundance was obtained from historical published accounts and contemporary assessments by in-country experts. Since the late nineteenth century, range-size (measured as Extent of Occurrence) has contracted, by 21% in East Africa and 8% in southern Africa. There is strong qualitative evidence of considerable pre- and post-1970 population declines in all range states, except Zambia (slight increase) and Angola (trend unclear). In some countries declines occurred from the early 1900s. Thus, while relatively modest change in range-size has occurred in over 100 years, numbers have greatly reduced throughout the species's range. Our methodology allowed objective appraisal of continent-wide status of this species. Despite lacking quantitative population estimates and trends, and poor understanding of the species's autecology, common issues for many African species, incidental occurrence records can be used to assess range-wide changes in status. We recommend that this or similar approaches be applied to other widespread low-density species that probably also have rapidly declining populations despite apparently stable range-extents.

Introduction

Evaluating the global conservation status of low-density widely distributed species poses many challenges. Assessments are particularly difficult in developing countries, where monitoring data are sparse (Balmford *et al*., 2003). Uncertainty over older, unquantified statements on status, differences in type and extent of survey coverage between range states, geographic variations in abundance and habitat occupancy, and logistic difficulties in achieving range coverage (e.g. Houlahan *et al*., 2000) often render status assessment of such species close to guesswork. While rapid declines raise international alarms by triggering IUCN Red List criteria (IUCN, 2001), as occurred for Indian vultures (Pain *et al*., 2008), steady declines over long periods can go unrecognised and hence unremedied (e.g. Turvey *et al*., 2010).

Population and range-size changes in widely distributed African bird species have never been assessed systematically, although birds remain the best-studied class of animals on the continent. Objective baseline data are sparse. Although bird atlases have summarised sight and other records in some countries (e.g. Harrison *et al*., 1997; Ash & Atkins, 2009), none has been repeated to provide information on changing abundance or range. Repeating road transects after 20–30 years has demonstrated localised declines for some species (e.g. Thiollay, 2006), but such fine-scale systematic monitoring has not been conducted across larger spatial scales. All that otherwise exist are distributional records and anecdotal remarks on abundance scattered amongst the published literature, trip reports and museum specimen data. Could this material be combined with atlas data from discrete periods to evaluate conservation status change?

We examine this using Kori Bustard *Ardeotis kori*, a large-bodied, low-density species with an extensive African range. Kori occur as two taxonomically distinct populations: *A. k. kori* in southern Africa (Angola, Namibia, Botswana, Zambia, Zimbabwe, Mozambique and South Africa; extinct in Swaziland) and *A. k. struthiunculus* in East Africa (Somalia, Ethiopia, Sudan, Uganda, Kenya and Tanzania: Collar, 1996). It is thought to be experiencing range-wide decline (Collar *et al*., 1986; Collar, 1996), and in South Africa has twice been listed as regionally ‘Vulnerable’ (Brooke, 1984; Anderson, 2000). Nevertheless, it is globally classified as Least Concern, because perceived population declines are thought not to approach the threshold of a 30% decline in 10 years or three generations, at which it would qualify as threatened under IUCN Red List criteria (BirdLife International, 2008).

Methods

Locality data

We analysed locality and demographic data from 1863 (earliest record) to December 2009. Locality records and reports on Kori distribution and population trends were obtained from documentary evidence, coupled with input from in-country experts. We undertook systematic literature searches, without restriction on publication year, using the terms ‘*Ardeotis kori*’, ‘Kori Bustard’, ‘kori’ and alternative names ‘Giant Bustard’, ‘Large Bustard’, ‘*Choriotis kori*’, ‘*Otis kori*’, ‘Outarde kori’, ‘Riesentrappe’, ‘Greater Bustard’ and ‘Avutarda Kori’, in academic search engines (Scopus, Google Scholar, Web of Science), and also reviewed reference lists of papers mentioning the species. In addition, we searched indices of *Zoological Record*, *Recent Ornithological Literature* (www.nmnh.si.edu/birdnet/rol), the three peer-reviewed African ornithological journals (*Bulletin of the African Bird Club*, *Ostrich* and *Scopus*), plus *African Journal of Ecology*, *Koedoe* and *South African Journal of Wildlife Research*, the tables of contents of Pan African Ornithological Congress proceedings, and newsletters from ornithological societies in range states. We reviewed BirdLife International’s online monitoring database (www.worldbirds.org), country and subregional bird atlases and, where accessible, expedition reports, checklists and project reports (see Appendix 2.1).

Spatial analyses

We adopted a coarse spatial resolution due to imprecise locality data. Where authors did not provide coordinates of localities (e.g. ‘near Somerset East, South Africa’: Skead, 1968), we obtained coordinates of the nearest (≤25 km) settlement or feature from the National Geospatial Intelligence Agency (www.geonames.nga.mil/ggmagaz/geonames4.asp); localities with location errors much greater than 25 km (e.g. ‘seen along Umzimkhulwana River’: Jonsson, 1973) were excluded from spatial analyses. National bird atlas data were resolved to the centroid coordinates of occupied sampling units, which varied in resolution from 10 km point radii (Uganda) to 120 × 120 km grid-squares (Sudan). The Sudanese atlas provided only six occupancy points, while the majority of atlases used 50 × 50 km grid-squares (Appendix 2.1), for which the maximal error from centroids is 35 km, comparable to the spatial error of assigning imprecise locality records to mapped settlements and features.

Range-size of each subspecies was estimated as the mapped Extent of Occurrence (EOO; area of Minimum Convex Polygon [MCP] formed by outermost records) and, within this, the Area of Occupancy (AOO; *sensu* Gaston & Fuller, 2009) was calculated as the 95% density kernel of records (Worton, 1989). The MCPs delineate the smallest area containing all sight records, whilst meeting the constraint that none of the polygon's internal angles exceed 180° (IUCN, 2001). Kernel estimators are three-dimensional probability density functions, whose shape is determined by the number of individual records at a given locality (Worton, 1989); the shape and probability density function can then be utilised to infer which region within the areal extent from where records were derived supports a given probability (such as 95%) of the range extent. Kernel analysis was conducted assuming bivariate normal fixed-kernels, using Home Range Tools for ArcGIS (version 1.1; Rodgers & Kie, 2010). Adaptive-kernels overestimated range-size. Selecting a smoothing factor (Worton, 1989; Kenward, 2001) by Least Squares Cross-Validation failed, reverting instead to the reference smoothing factors h_{ref} (1.381 and 0.985 for southern and East Africa respectively). Therefore, to minimise over-smoothing we followed the *ad hoc* approach of Rodgers & Kie (2010), testing values from 0.2 to 1.6 times h_{ref}, in increments of 0.05, and accepted the minimal value for which the outer 95% kernel contour remained continuous and uninterrupted. This provided smoothing factors of 1.036 (i.e. $0.75*h_{ref}$) and 0.985 (i.e. h_{ref}) for the southern and East African subspecies respectively. The resolution of the largest atlas grid-squares was 2500 km^2 for southern Africa (Botswana), but 14,400 km^2 for East Africa (Sudan; Appendix 2.1); range extents were therefore rounded to a resolution of 10,000 km^2, to make measures of range change for the two regions comparable.

We chose 1970 as the date before and after which to compare range-size and abundance trends, because bird atlases for some countries are based on records collected from 1970 onwards, although other atlases date from the 1980s and 1990s (Appendix 2.1). We computed the maximum recorded (1863–2009) and recent (post-1970) EOO separately for each subspecies. The difference in overall EOO between these periods was taken as a crude measure of range change, following Burgman & Fox (2003); the Red Listing criteria also use changes in EOO to infer trends in range size (IUCN, 2001).

To investigate potential range contractions while controlling for both temporal and spatial survey effort, we tested whether the proportion of historical records outside the recent AOO was greater than expected by chance. The null hypothesis that no more than 5% of historical (pre-1970) records lie outside the recent 95% density kernel (buffered by 85 km, the maximal location error from the coarsest atlas grid-squares: 120 × 120 km) was examined using a one-tailed χ^2 Goodness-of-Fit test. We first assessed the validity of each historical record located outside the recent 95% range kernel estimate, by consulting in-country experts and reviewing the strength of evidence for purported records. We recognise that, given sparse historical records (<100) and thus limited statistical power, this is a conservative test of range contraction.

We used ArcGIS version 9.3 for geospatial analysis and SPSS version 16.0 for statistical analysis. Data are presented as mean ± SD.

Data quality

Despite civil conflicts in some range states, these did not cause any obvious gaps in survey effort (Appendix 2.1) with the exception of Angola. We therefore report tests of range changes with and without the Angola data. In contrast to southern Africa atlases, those from East Africa were not based on systematic surveys of grid-squares (Appendix 2.1). To assess whether Kori range boundaries derived from these atlases were artefacts of incomplete coverage, we inferred observer presence in apparently unoccupied grid-squares at the Kori range margin by examining records for 10 other conspicuous, widely distributed bird species (Appendix 2.2) whose ranges (in Stevenson & Fanshawe, 2004) encompass the relevant grid-squares.

Population trends

Qualitative evidence of population trends was obtained by reviewing published material and using questionnaires (Appendix 2.3) to collate contemporary in-country expert opinion. To infer pre-1970 trends we collated all published statements located during the systematic review of Kori records, in which authors made explicit reference to Kori numbers, and consistently scored the strength of evidence as: weak; or strong; and the degree of change as: substantial decline; slight decline; no change; slight increase; substantial increase; or trend unknown.

To assess post-1970 trends, we reviewed published materials reporting countrywide Kori numbers. Some materials provided national population estimates, and we report these and the applicable time-periods. In-country experts, comprising coordinators or editors of national bird atlases, bustard researchers, and active ornithologists, were asked to assess (1) national or subnational trends in numbers and range, (2) factors that may have caused these trends, (3) quality of data underlying their assessments and (4) time-periods over which their estimates apply. This analysis excluded Swaziland, where Kori went extinct pre-1970 (Parker, 1994), and Zambia, which had only six records (Dowsett, 2009). We aimed to solicit input from at least three experts for each range state.

Results

Historical and current distribution

We collated 2248 locality records, 1853 (82%) from published sources and 395 (18%) from BirdLife International's online monitoring database, the latter only populated for Botswana (*n* = 308) and Kenya (*n* = 87). The 2248 records were combined to provide 1948 unique records for one locality (or grid-square, for countries with atlases) within one calendar year. Of all unique records, 1538 (79%) were from atlases, and more records (1354; 70%) were for *A. k. kori*, largely owing to finer spatial resolution and greater geographic coverage in southern Africa atlases. Most records (1851; 95%) were post-1970 (Appendix 2.1, Fig. 2.1); however, the systematic review successfully collated 97 unique pre-1970 locality records.

We estimated recent (post-1970) EOO to be 4,060,000 km^2 (southern Africa 2,680,000 km^2; East Africa 1,380,000 km^2). The AOO enclosed by the 95% kernel was estimated at 3,420,000 km^2 (southern Africa 2,230,000 km^2; East Africa 1,190,000 km^2). The historical EOO, omitting localities 1–3 in Fig. 2.2a which had insufficient supporting evidence (Table 2.1) and were therefore excluded from subsequent analysis, was estimated at 4,652,000 km^2 (southern Africa 2,900,000 km^2; East Africa 1,752,000 km^2).

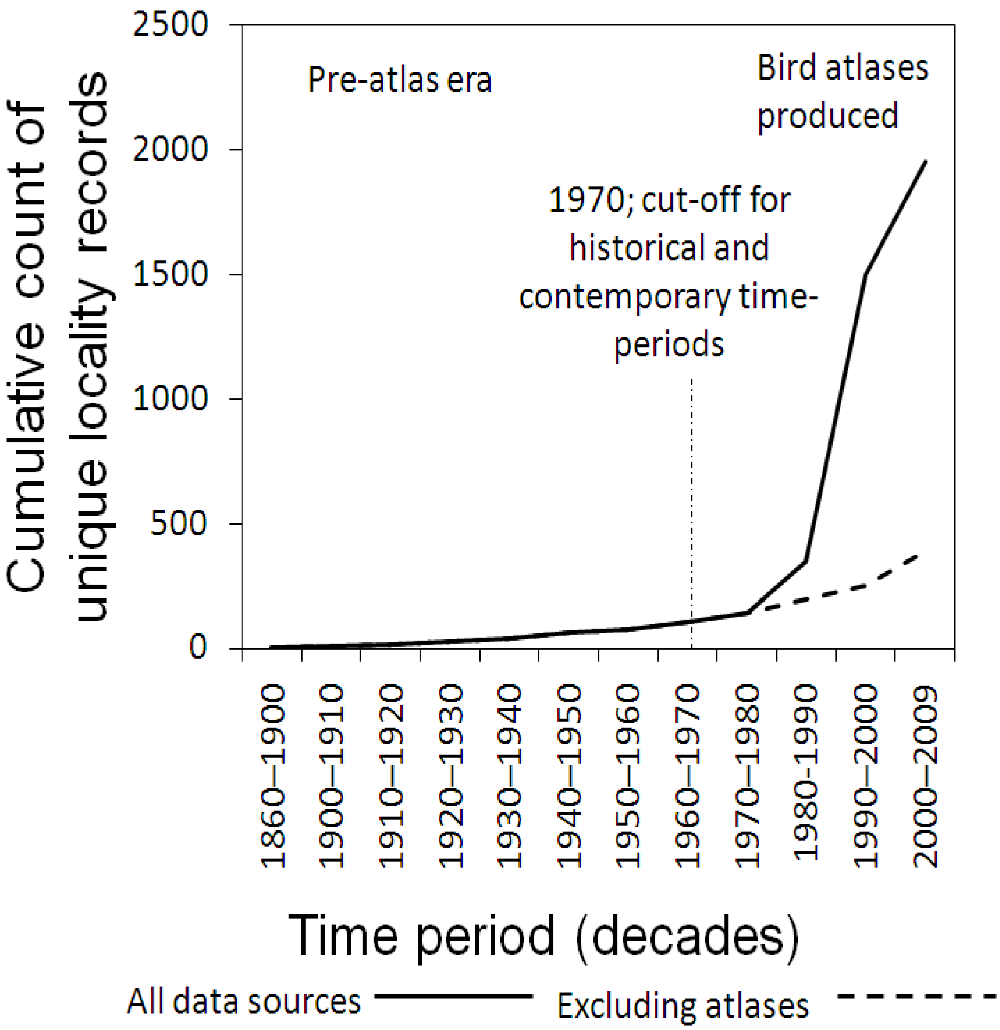

Figure 2.1. Cumulative total of Kori Bustard *Ardeotis kori* unique locality records (sightings, museum collections, hunting records and atlases) collated from published literature, in relation to year (1863 to 2009). Data post-1970 include as unique locality points the centres of all occupied grid-squares from country bird atlas projects and reflect atlas publication dates rather than sighting dates. Country-specific data sources, sample sizes, spatial resolution and time-periods for atlas data are provided in Appendix 2.1.

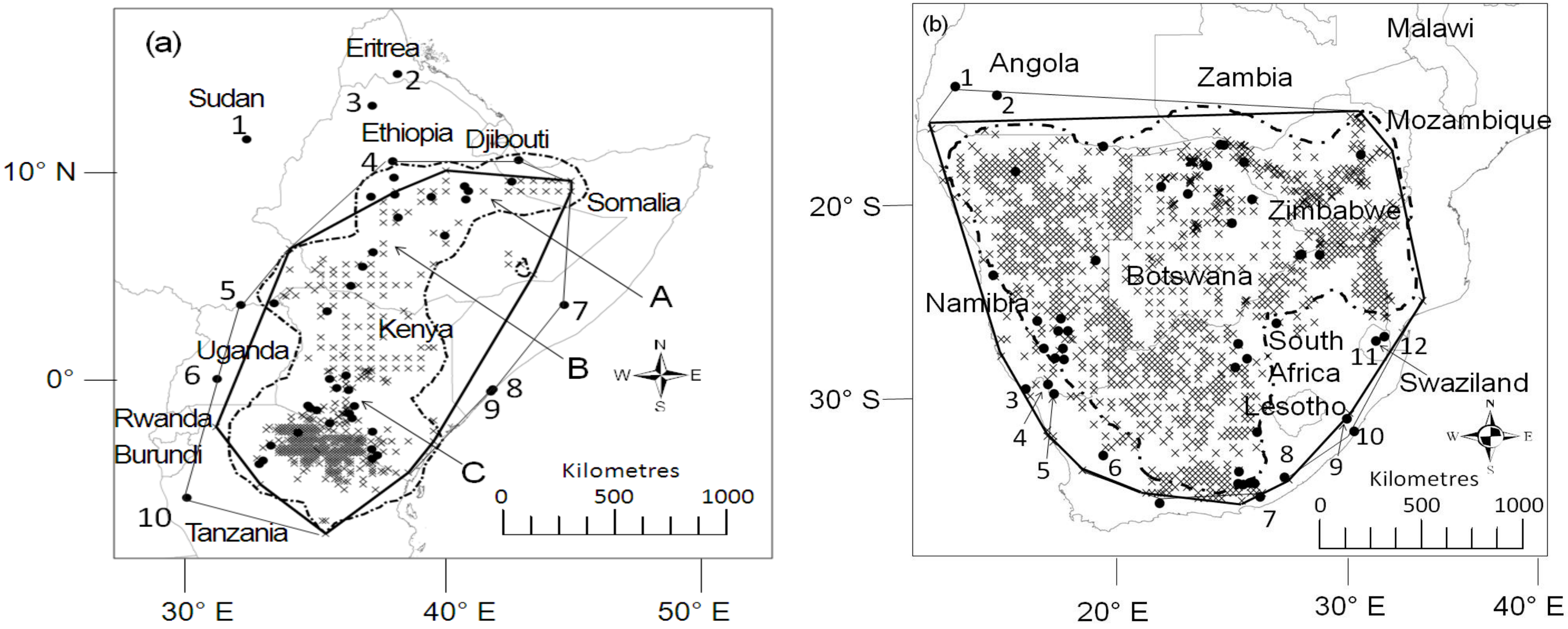

Figure 2.2. Kori Bustard *Ardeotis kori* distribution in (a) East Africa and (b) southern Africa from collated sightings, hunting and museum records and atlas data. ● pre-1970; × post-1970 (atlas and other records). Atlas records are the coordinates of centres of all occupied grid-squares in atlases listed in Appendix 2.1. Geographic range boundaries are represented as the minimum convex polygon enclosing all confirmed sightings spanning the years 1863–2009 (——) or only post-1970 data (━━) and 95% kernel density estimate (bivariate normal fixed kernels, smoothing factor h = 1.036 and 0.985 for southern and East Africa respectively) for post-1970 data (-.-.-.). Numbered localities are all pre-1970 point localities falling outside the subspecies-specific 95% kernels and are detailed in Table 2.1; East African localities 1–3 are excluded from range loss calculations as they are misidentified Kori. Arrows indicate the three localities where range-extent is limited to one confirmed occupied 50 km-wide grid-square: A, east of Harar (Ethiopia); B, Misraq Shewa Zone of the Oromia Region, south of Addis Ababa (Ethiopia); C, Nairobi–Nakuru (Kenya).

Since the 1860s, *A. k. struthiunculus* has been recorded in Sudan, Uganda, Tanzania, Kenya, Ethiopia and Somalia. Apparent records from central Sudan, Eritrea and northern Ethiopia (localities 1–3, Fig. 2.2a, Table 2.1) were probably misidentified Arabian Bustard *Ardeotis arabs*. Based on their 1949 collections in southern Sudan and a synthesis of available information, Cave & MacDonald (1950, 1955) described Kori as a common resident only in south-east Sudan. Thus Kori were either extirpated in central Sudan during 1900–1940s or, more likely, never there, with purported earlier records (e.g. Ogilvie-Grant, 1902; Butler, 1905; Lloyd, 1910) confusing the species with *A. arabs*. Meinertzhagen (1954) regarded the two as conspecific, a probably widely held view at the time. We found no evidence for ‘accidental’ Kori in Eritrea (Moltoni & Ruscone, 1944): thus, at least since the nineteenth century, the species probably never occurred there. Similarly, the record in northern Ethiopia lacked supporting evidence and was excluded on the basis of likely misidentification (Table 2.1).

We consider that post-1970 range limits in East Africa were not affected by the use of locality records rather than systematic grid-based surveys in atlas compilation, because many co-occurring widely distributed and conspicuous species were recorded from grid-squares bordering Kori range margins (Appendix 2.2). The recent Kori range-core largely overlapped the Great Rift Valley, with a narrow elongate and generally continuous range; an exception was the subpopulation in south-east Ethiopia (Fig. 2.2a). This subpopulation was probably genuinely disjunct from the core population, because co-occurring widely distributed species were reported from 9 of the 12 grid-squares surrounding it (mean 3 ± 2 SD species; range 0–6 species per 50-km grid-square), and its minimum distance to the range-core kernel was approximately 200 km. There were at least three localities where the range of *A. k. struthiunculus* was constrained to a single 50 km-wide occupied grid-square (Fig. 2.2a), although there was no evidence (except in Kenya: Lewis & Pomeroy, 1989) that these potential bottlenecks were ever wider.

Nominate *A. k. kori* has been recorded in Angola, Namibia, Botswana, Zambia, Zimbabwe, South Africa, Mozambique and, in the 1950s, Swaziland. The low number of Angolan records (n = 5) precluded inference of probable historical and current range limits in that country, although Dean (2000) suggested that the northernmost recent distribution broadly coincided with the boundaries of the arid belt in southern Angola, south of 16°S, based on assumed Kori preference for arid and semi-arid grasslands and shrublands (e.g. Collar, 1996; Allan & Osborne, 2005).

Table 2.1. Historical (pre-1970) Kori Bustard *Ardeotis kori* locality records outside the 95% kernel of recent (post-1970) geographic range. Mapped location of these numbered extralimital records are shown in relation to the kernels in Fig. 2.2a, b. * reliable records falling outside the 85 km-buffered kernels; † rejected records; EOO Extent of Occurrence.

Subspecies	Record	Year	Locality name	Source	Record reliability and relevance
A. k. struthiunculus	1†	1901	Renk, Sudan	Ogilvie-Grant, 1902	Specimen at the British Natural History Museum is in fact a misidentified *Ardeotis arabs* (G. Nikolaus pers. comm.).
	2†	Undated, pre-1944	Mendefera, Eritrea	Moltoni & Ruscone (1944)	Probably misidentified *A. arabs* given no other *A. kori* record from Eritrea; excluded from analysis.
	3†	Undated, pre-1944	Amba Ghermie, Ethiopia	Moltoni & Ruscone (1944)	Lacks supporting details (Ash & Atkins, 2009); excluded from analysis, more than 300 km from northernmost confirmed records; probably a misidentified *A. arabs*.
	4	Undated, pre-1944	Wobok, Ethiopia	Moltoni & Ruscone (1944)	Occupied atlas grid-square (Ash & Atkins, 2009). Lacks supporting details, but less than 25 km from northernmost confirmed records; included in analysis.
	5	January 1949	Acholi-Lango border, Uganda	Carswell *et al*., (2005)	Record accepted by Carswell *et al*. (2005). Very probably genuine, especially in light of *A. kori* 'common in north-eastern Uganda, on areas less than 2000 m above sea level' (van Someren, 1933).
	6*	Undated, pre-1938	Ankole, Uganda	Jackson (1938); Carswell *et al*., (2005)	No primary source; hunting report to Jackson (1938). Area 'well grassed' (Friedmann & Loveridge, 1937), typical of presumed *A. kori* habitat (Collar, 1996). Record less than 100 km from confirmed records in north-west Tanzania (Fig. 2.2a). Record accepted here, given there are no other

					large bustards in the area; may represent extinct Ugandan subpopulation or visitors from Tanzania.
	7*	Undated, pre-1944	Harar, Somalia	Moltoni & Ruscone (1944)	No primary source, but given proximity to extant Ethiopian subpopulation, record probably genuine but subpopulation now possibly extinct.
	8*	Undated, pre-1944	Giumbo, Somalia	Moltoni & Ruscone (1944)	Accepted records in Ash & Miskell (1998); no reports from area since 1950s.
	9*	Undated, pre-1944	Chisimaio plains, Somalia	Moltoni & Ruscone (1944)	Accepted records in Ash & Miskell (1998); no reports from area since 1950s.
	10*	1921	Mlenga, Tanzania	Friedmann & Loveridge (1937)	Reported by A. Loveridge who in 1920s collected many Kori specimens for Museum of Comparative Zoology, Boston, USA, thus improbably misidentified. No recent records from area (Baker *et al*., in prep.); probably a genuine range contraction.

Subspecies	Record	Year	Locality name	Source	Record legitimacy and relevance.
A. k. kori	1*	1860s	Humbe, Angola	Traylor (1963)	Specimen collected by Bocage in 1860s; present status unclear (Dean, 2000)
	2*	Pre-1960s	Mulondo, Angola	Dean (2000)	Genuine record (Dean, 2000). Pinto’s 1960 report misspelt as Mulundo, outside predicted Angolan range (R. Dean pers. comm.); present status unclear (Dean, 2000).
	3	1943	Orangemund, Namibia	Plowes (1943)	Enclosed within EOO based on post-1970 data; no influence on overall range boundary.

4	1956–1959	Aussenkjer, Namibia	Maclean (1960)	No range decline; less than 20 km from recent records (Harrison *et al*., 1997).
5	1956–1959	Viool's Drift, Namibia	Maclean (1960)	Enclosed within EOO based on post-1970 data; no influence on overall range boundary.
6	1954	Calvinia, South Africa	Skead (1955)	No range decline; less than 40 km from recent records (Harrison *et al*., 1997).
7	1960s	Grahamstown, South Africa	Skead (1967)	No range decline; less than 20 km from recent records (Harrison *et al*., 1997).
8	1863	Umgwali Reserve, South Africa	Jonsson (1973)	Enclosed within EOO based on post-1970 data, no range decline; less than 20 km from 1992 records (Colahan, 1993).
9*	1863	Richmond, South Africa	Jonsson (1973)	Locality less than 20 km from a recent (Harrison *et al*., 1997) record. While Harrison *et al*. (1997) argue all *A. kori* records in this region may refer to misidentified Denham's Bustard *Neotis denhami*, Cyrus & Robson (1980), with data collection 1970–1979, included Kori in list of 'rarer species and vagrants', with a confirmed Pietermaritzburg record (1976). This 1976 record results in recent EOO encompassing Richmond, but abundance appears drastically reduced relative to 1862–1863, when 'lots of Pou [*colloquial for bustard*] were shot near Richmond' (Jonsson, 1973). Despite possible confusion with *N. denhami*, Kori population seem to have declined.
10*	1863	Ifafa, South Africa	Jonsson (1973)	Approximately 60 km from locality 9; status and relevance the same as that record.

11	Pre-1960	Mafutseni, Swaziland	Parker (1994)	R. Girwood and R. Hardin (pers. comm. to Parker, 1994). Occurred more widely around this locality, but unrecorded post-1960, including during monthly atlas field surveys 1985–1991.
12	Pre-1960	Hlane Royal National Park, Swaziland	Parker (1994)	R. Girwood and R. Hardin (pers. comm. to Parker, 1994). Unrecorded post-1960, including during monthly atlas field surveys 1985–1991.

Kori only marginally extended into Zambia: all six published records, the earliest in 1997 (Dowsett, 2009), were within 20 km of the northernmost records in Botswana and Zimbabwe. The recent Kori range enclosed all of Namibia and Botswana, much of western South Africa, but with a noticeable absence in south-east South Africa. Elsewhere in South Africa the Kori mainly occupied areas bordering Botswana and Zimbabwe and southwards to Kruger National Park. There was a small range projection into Mozambique, restricted to areas adjoining Kruger National Park. In Zimbabwe, although the range extended as far north as 16°S, there was a gap (ranging 50–150 km; Fig. 2.2b) from south-west to north-east along the ‘central plateau’, probably owing to birds avoiding this extensively cultivated region (Rockingham-Gill, 1983).

Range-size change

Since the nineteenth century there has been a modest Kori range contraction, notably in East Africa within Somalia, Tanzania and Uganda (Fig. 2.2a). Differences between the historical and recent EOO suggested 21% and 8% declines in East and southern Africa respectively.

For the East African subspecies, marginally more reliable historical records occurred outside the buffered recent 95% kernel (5/48: localities 6–10, Fig. 2.2a) than expected by chance, given the density distribution of recent records ($\chi^2 = 2.965$, d.f. = 1, $P = 0.085$). These five extralimital historical records were a mean 150 km ± 30 SD outside the buffered kernel, and an average 290 km ± 50 SD from the nearest recent record.

This apparent decline is supported by strong qualitative evidence for historical range contractions for *A. k. struthiunculus*. In the early 1920s the species was still ‘occasionally seen’ in Jubaland (south-westernmost Somali province: Clifford, 1928), but was locally extirpated before 1950 (Ash & Miskell, 1998). In Kenya, local extinctions occurred east and west of Nairobi, and in the south-east (east of Mt Kenya, and along the coast in the Mombasa area), leaving a seemingly disjunct population on the lower Tana River (Lewis & Pomeroy, 1989). Elsewhere in East Africa, the isolated subpopulations in south-west (Ankole region) and northern Uganda (Acholi region) and south-west Tanzania appear to have died out: for example, van Someren (1933) stated ‘Kori common’ in north-east Uganda, but there are no recent records (Carswell *et al.*, 2005). In contrast putative historical records from central Sudan, northern Ethiopia and Eritrea lacked support and were discarded prior to considering range contraction.

For the southern subspecies, the proportion of historical records outside the buffered recent 95% kernel (4/49) was similar to that expected by chance ($\chi^2 = 1.032$, d.f. = 1, $P = 0.310$). Distances between all historical extralimital records and the recent buffered kernel boundary were similar to those for extralimital East African records (mean 180 km ± 90 SD, $t = 0.815$, d.f. = 7, $P = 0.442$), but extralimital historical records were located closer to recent records than was the case for East Africa (130 km ± 90 SD, $t = 3.395$, d.f. = 7, $P = 0.012$). This difference was not due to the coarser East African atlas grid-squares. Coordinates of the closest recent records were derived from atlases where the maximal error from using grid-square centroids was 35 km ($n = 4$, localities 6–9, Fig. 2.2a) or 8 km ($n = 1$, locality 10) for East Africa, and 18 km for all four southern Africa records (localities 1, 2, 9 and 10, Fig. 2.2b, Appendix 2.1). Extralimital historical records in East Africa were still located further from recent records, even after adjusting proximity measures in southern Africa by the maximum difference in grid resolution, by adding 17 km ($t = 2.967$, d.f. = 7, $P = 0.021$).

In southern Africa real range contraction probably occurred only in Swaziland and south-east South Africa, based on a lack of post-1970 records from these regions (Fig. 2.2b); this is corroborated by the only available qualitative evidence of historical large-scale range loss in the subregion (Astley-Maberly, 1937; Parker, 1994; Table 2.2). The trend in Mozambique and Angola was unclear. Parker (1999) suggested the Mozambique range was always restricted to areas bordering Kruger National Park, although the time-period over which this assessment applied was not stated, but probably largely post-1970. Of the five Angolan records (three pre-1970, two post-1970) one pre-1970 record was within the kernel boundary; although four of the five records were outside the kernel, this was probably an artefact of the kernel estimator properties. Owing to the small sample size, large inter-locality distances and remoteness, these records were excluded from the parsimonious kernel that captures 95% of record density in the smallest possible areal extent. When historical Angolan records were excluded from χ^2-tests, the proportion of extralimital localities (2/47) was similar to that expected by chance ($\chi^2 = 0.055$, d.f. = 1, $P = 0.815$), providing further evidence for minimal large-scale contraction in southern Africa.

Table 2.2. Assessment of pre-1970 Kori Bustard *Ardeotis kori* population trends from published literature. Only publications where authors explicitly comment on trends are reported, along with corresponding spatial extent and time-period. Quality of evidence is assessed as weak/strong based on the authors' confidence in ascertaining trends. Degree of purported population change is classed as: ≈ uncertain trend; = no evidence for population change; − slight decline; −− substantial decline; + slight increase; ++ substantial increase. None reported an increase.

Spatial extent	Time-period	Statement on population trend	Quality of evidence	Inferred trend	Source
Natal Province, South Africa	1860s	'Must have been abundant in Natal during early 1860s…based on Dobie's Diary (Hattersley, 1945)'.	Weak	−−	Jonsson (1973)
Kroonstad District, Free State Province, South Africa	1870s–1907	'Rarely seen here now, though it was never common'.	Strong	−−	Symonds (1907)
South Africa	1900–1970	'Numbers less than they were a century and more ago but the extent of reduction unknown'.	Weak	−	Brooke (1984)
Present-day Mashonaland East Province, Zimbabwe	Pre-1930s	'Although fairly plentiful in the Beatrice District in the past, by 1930 it was seldom seen and likely to go locally extinct in a few years'.	Strong	−−	Krienke (1931)
Eastwards of Johannesburg up to border with Swaziland and Mozambique, South Africa	1920s	'Even by 1925, when Kruger National Park was established, the bird had already lost much of its range in South Africa's Highveld region, mainly due to considerable persecution'.	Strong	−−	Astley-Maberly (1937)
South Africa and Zimbabwe	1940s–1950	'In Southern Africa reported as decreasing at a dangerous rate'.	Weak	−−	Lynn-Allen (1951)
Swaziland	Pre-1960	'Hunted to local extinction prior to 1960, with subsequent bush encroachment of its former range making it impossible for re-	Strong	−−	Parker (1994)

		colonisation’.			
Eastern Cape Province, South Africa	1962–1967	‘Status uncertain due to confusion with Stanley’s Bustard *Neotis denhami* and Ludwig’s Bustard *Neotis ludwigii.* If most identifications are correct, kori has considerably weakened in status’.	Weak	−−	Skead (1967)
Eastern Cape Province, South Africa	1960s	‘Has probably declined in the eastern Cape’.	Weak	−	Clancey (1972)
North of Windhoek, Namibia	1960s	‘Status satisfactory in Northern Namibia, and there is no evidence for decline’.	Weak	=	Clancey (1972)
Botswana	1960s–1970	‘No evidence for decline’, author citing June 1970 pers. comm. with R.H.N. Smithers.	Weak	=	Clancey (1972)
Zimbabwe	1960s–1970	‘Regarded as holding its own’, author citing June 1970 pers. comm. with M.P.S. Irwin.	Weak	≈	Clancey (1972)
Free State Province, South Africa	1960s–1970s	‘Present status in province unclear’.	Weak	≈	Clancey (1972)
Somalia, Kenya and Tanzania	1940s–1950	‘In the wilder parts of Somalia, Northern Frontier Province and Turkana in Kenya and in Northern Tanganyika, still very plentiful’.	Weak	≈	Lynn-Allen (1951)
Ethiopia	1960s–1970	‘Formerly fairly common south of *Ardeotis arabs* range (the two almost entirely allopatric) in less arid areas’.	Strong	−	Ash (1989)
Somalia	1960s–1970	‘Previously fairly common in open bush country and grassy plains of the northwest, south to about 9º-N and east to 46 º-E, but no recent records’.	Strong	−−	Ash (1989)

Population trends

Although quantitative data suitable to examine whether population declines had occurred were not available for any range state, reported qualitative trends provided a strong indication of subregional and global-level declines in abundance. There was strong qualitative evidence from published statements of population declines within 12 of the 14 range states, both pre- and post-1970 (Tables 2.2, 2.3). Of 16 inferred pre-1970 trends from published statements, 11 were negative or strongly negative. Published subjective abundance indices and qualitative comments on trends together suggest that in some countries (e.g. South Africa and Zimbabwe) declines occurred from the early 1900s (Table 2.2).

Published statements suggest Kori population numbers continued to decline post-1970 in all six East African and six of the eight southern African range states; exceptions were Zambia and Angola (Table 2.3). However all six Zambian records (in all but one case singletons) were from 1997–1999 (Dowsett, 2009), so any apparent population increase may have been temporary. While only five records were available from Angola (Appendix 2.1), expert opinion suggested a larger population still existed in the country (W. R. J. Dean & P. Vaz Pinto pers. comm.), although abundance trends were unclear (Dean, 2000).

Twenty-nine responses were obtained from 55 questionnaires sent to in-country experts regarding post-1970 population and range-size trends; a 53% response rate. Responses spanned all range states, providing one (South Africa, Mozambique, Tanzania, Somalia, Sudan), two (Zimbabwe, Uganda), three (Angola, Ethiopia), four (Botswana, Kenya) and six (Namibia) respondents respectively. However ten respondents (34%), all with more than 20 years' fieldwork experience in their range states, did not comment on likely trends, seven reporting they had infrequently encountered Koris or had not noted sightings and thus were unable to judge trends; these were excluded from analyses. The remaining 19 survey responses providing information on Kori trends were all from fieldworkers with long experience in their respective countries (seven 1970s–2009; two 1980s–2009; six 1990s–2009; three 2000s–2009; one 1974–1981), and all but one were still involved in conservation in-country. Of these, 12 made national-level assessment (Angola, Namibia, Mozambique, Tanzania, Kenya, Uganda, Ethiopia and Somalia), with no disagreement where more than one country-level response was obtained (Angola, Kenya and Ethiopia). Seven respondents commented on trends at provincial or site-levels, mostly protected areas Appendix 2.4. Responses were subjective in most instances, but in South Africa they were supplemented by published data (Tarboton *et al*., 1987).

Expert opinion from the 12 range states assessed suggested that post-1970 Kori numbers have declined, or are at best unchanged; of the 12 respondents providing information on national-level Kori trends, four (33%) reported declines (two substantial, respondents themselves suggesting more than 50% decline; two slight), six considered trends uncertain, two reported no change and none reported increases. Half were unclear if there had been concomitant range-size changes, four suggested range contraction and two reported no change.

Published post-1970 Kori population estimates were available from only three range states, all in southern Africa (Table 2.3). However, all population numbers are best guesses and none of the sources provided underlying evidence; thus any future assessments of population trends against these estimates need to be done with caution.

Discussion

We have demonstrated that changes in abundance and range-size in unmonitored widespread species can be systematically evaluated without comparing occupancy patterns between atlases (e.g. Gibbons *et al*., 2007; Robertson *et al*., 2010) or field surveys (e.g. Riou *et al*., 2011). It was possible to calculate historical and recent Extent of Occurrence (EOO), and recent Area of Occupancy (AOO), based on national atlas data, incidental records and other published sources. Range boundaries were validated by inferring observer coverage from the distribution of co-occurring species. Although non-systematic records prior to the period of atlas compilation were sparse, by formally testing the distribution of such records against the 95% density kernel of more abundant recent records we were able to test whether range contraction had occurred. Systematic review of published sources provided strong qualitative evidence of declines in abundance, and localised reductions in range. Questionnaire responses provided further qualitative evidence of recent trends in abundance.

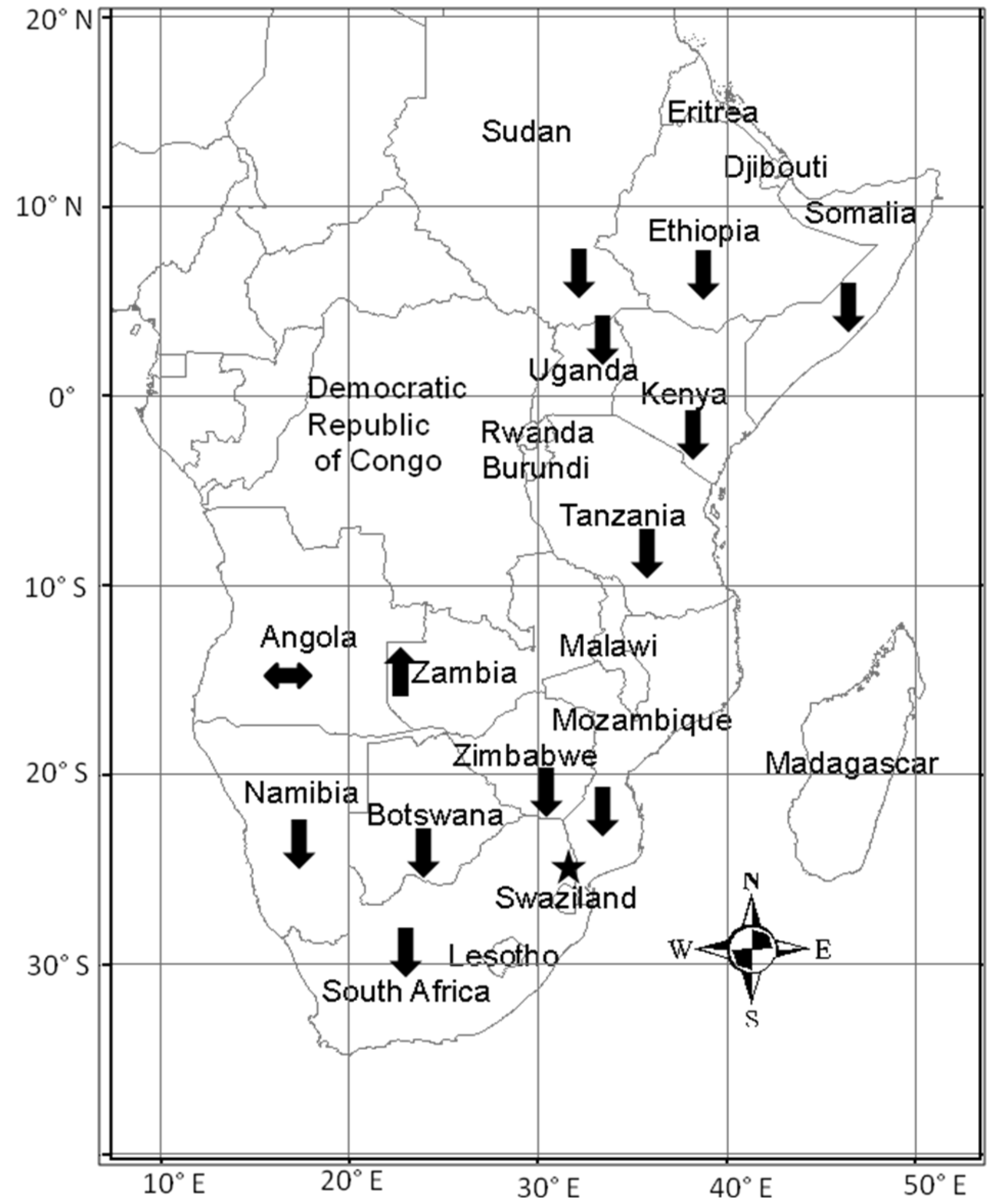

Figure 2.3. Kori Bustard *Ardeotis kori* population trends in each range state during 1970–2009, based on published sources and in-country expert opinion. ★ Strong evidence for possible local extinction; ⬇ strong qualitative evidence for population decline; ⬌ population trend unclear; ⬆ strong qualitative evidence for population increase. None of the range states has quantitative estimates of population decline.

Table 2.3. Post-1970 population estimates and trends for Kori Bustard *Ardeotis kori*, collated from published accounts in each range state.

Subspecies	Country	Population estimate (year)	Population trend (time-period)	Source
Ardeotis k. kori	Angola	none	unclear (1970s–2000)	Dean (2000)
	Botswana	none	decline (1990–2005)	Tyler (2005)
	Mozambique	<100[a] (1999)	decline (1970s–1999)	Parker (1999)
	Namibia	none	decline (1990s–2000)	T. Osborne & L. Osborne (unpublished data)
	South Africa	2000–5000 (2000)	decline (1980s–2000)	Anderson (2000)
	Swaziland	0 (1994)	decline, extinct in 1950s	Parker (1994)
	Zambia	none	range expansion; slight population increase (1997–present)	Dowsett (2009)
	Zimbabwe	10,700 (1980); 2000 (1989) 5000 (1990)	decline (1980s–1990)	Rockingham-Gill (1983); Mundy (1989); Dale (1990)
	Subregion	none		
A. k. struthiunculus	Ethiopia	none	decline (1980s–2009)	Ash & Atkins (2009)
	Kenya	none	decline (1970s–1989)	Lewis & Pomeroy (1989)
	Somalia	none	decline (1970s–1998)	Ash & Miskell (1998)
	Sudan	none	decline(1976–1989)	Nikolaus (1987)
	Tanzania	none	decline (1970s–present)	Baker *et al*. Tanzania Bird Atlas (in prep.)
	Uganda	none	decline, possibly locally extinct in 1970s [b]	Carswell *et al*. (2005)
	Subregion	none		
	Entire range	none		

[a] This estimate is for southern Mozambique, south of the Save River. Kori have only been reported from this region, thus this estimate is effectively a country estimate.

[b] However, there are recent (post-2000) reports from Kidepo National Park in north-east Uganda along the border with Sudan (H. Kemigisha & A. Byaruhanga pers. comm.)

Trends in Kori population and range size

Our analysis indicates the importance of data-screening and quality control as critical steps in evidence-based status assessment, particularly for widespread low-density species whose ranges straddle multiple countries. Verification of locality records revealed some misleading historical records from central Sudan, Eritrea and northern Ethiopia which inflated the true historical range of *A. k. struthiunculus*.

Although Kori populations declined greatly in both subregions during the period 1863–2009, overall range sizes (measured as EOO) did not, being moderately reduced in East Africa and largely unchanged in southern Africa. At the species scale, range contraction was 13% over more than 100 years, based on contrasts of pre- and post-1970 EOO. However, the continued contemporary occupation of the atlas-based range is difficult to gauge, owing to (1) the use of 1970s–80s data in post-1990 atlases and (2) sparse data since some earlier atlases (e.g. no information on Sudanese Kori post-1989). Our analysis was, therefore, unable to examine whether more recent range contractions may have also occurred. However, further range contraction is highly unlikely to have exceeded 30% (the weakest Red List threshold: IUCN, 2001) over the period 1965–2010 (approximately three generations for *Ardeotis* bustards: S. H. M. Butchart pers. comm.), given both the strong spatial similarity of post-1990 atlas records to records from the 1960s and 1970s and qualitative evidence from survey respondents suggesting no dramatic post-1980 distributional change. Consequently, solely on the basis of range contraction, the Kori's current listing as Least Concern (BirdLife International, 2008) is not inappropriate. Nevertheless, there is extensive qualitative evidence for a considerable overall population decline and profound change in the internal characteristics of the Kori's range, which has been ongoing since the 1900s. It is a source of substantial unease that this has occurred without being registered as a significant issue for the conservation of the species.

The causes of overall population declines and range losses in south-east South Africa, south-west Somalia, south-west Tanzania as well as south-west and northern Uganda are unknown. Hypothesised factors include persecution (Astley-Maberly, 1937; Porter, 1949; Herremans, 1998) and perceived impacts of rangeland degradation and shrub encroachment largely driven by livestock (Collar, 1996; Ash & Miskell, 1998; Herremans, 1998). However, these have not been investigated in any range states. Thus, in Chapter 3, I test the relative importance of bushmeat hunting (indexed as proximity to human settlement) and cattle-driven impacts (indexed as proximity to a livestock-watering borehole) in influencing the abundance or incidence of Kori Bustards and 20 other large-bodied vertebrates in the Kalahari, Botswana.

The apparent discrepancy in severity of range loss between the eastern and southern subspecies, as measured by historical and recent EOOs, is not an artefact of coarser atlas grid-square resolution in East Africa. Range loss was most distinct in south-west and northern Uganda, south-west Somalia and western Tanzania, where seemingly isolated subpopulations were extirpated. All East African extralimital historical records outside the current AOO were obtained either from national parks that remain popular with visitors, or within 50 km of settled areas, so recent Kori absence from these localities is unlikely to be attributable to lack of observation effort.

Influence of spatio-temporal sampling effort and data resolution

It is important to examine how robust the methodology was to different levels of search effort, sampling bias and spatial scale. Our approach overcame several statistical issues resulting from uneven spatial and temporal sampling effort within and across range states, which may otherwise compromise the analysis of occurrence records collated through search strategies of the type used in this study.

First, there was more sampling effort for Kori in protected than unprotected areas. At site level, this bias was reduced by subsuming all records within one calendar year into a single entry. At national level, where atlas data are available, grid-squares cover the whole country, and the 95% kernel was largely based on these extensive datasets. In countries without geo-referenced atlases (Angola and Zambia), fewer than 10 records were collated, so any bias towards protected areas was unlikely to influence subregional range estimates significantly.

Second, animal detectability and observer-favoured sampling sites vary with vegetation type and accessibility, increasing the potential for under-reporting in more wooded or harder-to-reach areas. However, the coarse spatial scale of analysis reduced finer-scale errors resulting from preferential sampling along roads or habitats offering better visibility.

Third, there were differences in sampling effort between the two time-periods, because effort increased greatly with time throughout the range (Fig. 2.1). However, the χ^2-test of the extent of pre- compared to post-1970 ranges used to evaluate evidence of range decline was robust, though conservative. Although the long time-periods used here compromised temporal resolution, they ensured that the recent range boundaries, against which decline was measured, were delineated based on the best available data. Our results are robust largely because kernel estimators are not sensitive to (1) different in-country sample sizes (robust if more than 30 data points are used), (2) range size or shape, and (3) the spatial resolution of input data (Kenward, 2001). Our use of kernel estimators is an improvement over methods based solely on minimum convex polygons, whose estimates can be largely biased by sample size and range shape (Burgman & Fox, 2003). However, sparse historical records (48 and 49 records for the East and southern subspecies respectively) meant that the test of whether more occurred outside the recent AOO than expected by chance had limited statistical power and was therefore highly conservative.

Fourth, however, at local scales our 95% kernels probably overestimated true recent AOO owing to the coarse spatial resolution used so that any increased perforation of continuously occupied range could not be detected. Moreover, our estimates of distributional limits and buffers around kernels are conservative and possibly underplay range contractions; for example, although the recent range limits in southern Africa are fairly robust, being based on extensive and systematic atlasing (e.g. Harrison *et al*., 1997; Parker 1999), we still buffered them by 85 km, equivalent to nearly two or more than three of some of the subregion’s atlas grid-squares (Appendix 2.1). Similarly, we rounded range estimates to 10,000 km^2 based on the coarsest atlas resolution (Sudan), although that country contributed only six occupancy records, and most countries had atlases with resolutions smaller than half that of the Sudanese atlas (Appendix 2.1).

We acknowledge that demonstrating long-term Kori decline required an extensive exercise in data-gathering and analysis. Such work is greatly intensified if different in-country experts are sought to validate records from range states or provide trend evidence for different subpopulations. Using only expert-interviews would reduce effort required to complete assessments, but such appraisals remain possible only for a few species, particularly those not prone to misidentifications in the field or subject to recent taxonomic revisions (e.g. Turvey *et al*., 2010; Ogada & Buij, 2011), and where the number of experts is not likely to be limited. Moreover, for species with ranges as large as the Kori's, expert-interviews alone cannot be used for range-wide quantitative assessments that permit fine-scale spatial analysis because the assumption that informants continuously 'surveyed' wildlife at multiple fine-scale localities throughout the geographic extent and the period of interest would less probably be met.

Conservation implications

Widespread low-density species may experience steady, pervasive and virtually undetected declines in abundance without showing obvious commensurate range collapse (Rodríguez, 2002; Turvey *et al*., 2010). There is, therefore, a compelling need to develop methods for objective range-wide status assessments of such species. While an important long-term goal is to build capacity for systematic monitoring based on repeat survey or atlas work (e.g. Telfer *et al*., 2002; Pollock, 2006), the conservation value of shorter-term assessments in the absence of such information is obvious. It is not appropriate to use studies that have only measured local abundance or relations between habitat and density to extrapolate range-wide (e.g. Tobias & Brightsmith, 2007) or even country-wide (e.g. Gros, 2002) population size or patterns of population trend or abundance. Problems with such approaches include variation in wildlife-habitat association (Whittingham *et al*., 2005), for example arising from patchily distributed conservation effort (Gray *et al*., 2009). Consequently, ecologists in developing countries may need to assess range-wide conservation status using incidental rather than systematic distributional or census data from localised scales. Within the caveats discussed our methodology may be especially valuable for key indicator species, and its transferability (for instance to flocking rather than solitary species such as Kori), needs to be investigated.

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Appendix 2.1

Number, source and period (pre or post-1970) of Kori Bustard Ardeotis kori *unique locality records (sightings, museum collections, hunting records and occupied atlas grid-squares) collated from published literature for each range state, and atlas characteristics.*

Subspecies	Country	No. locality records [a]			Atlas characteristics			Main non-atlas sources
		Atlas	Non-atlas [b]		Temporal resolution	Spatial resolution (km)	Source [c]	
			Pre-1970	Post-1970				
Ardeotis kori kori	Angola	-	3	2	-	-	-	10
	Botswana	122	7	68	Monthly surveys, 1989–1995	50 × 50	1	11, 12
	Mozambique	-	-	5	Monthly surveys, 15 of 1778 checklists from 1980–94, otherwise 1994–98	50 × 50	2	13, 14
	Namibia	415	14	5	Monthly surveys, 1989–95	25 × 25	1	15, 16, 17
	South Africa	438	22	56	Monthly surveys, 1989–95	25 × 25	1	17, 18, 19, 20, 21, 22
	Swaziland	2	-	-	Monthly surveys, 1985–91	12.5 × 12.5	3	none
	Zimbabwe	120	3	67	Monthly surveys, 1989–95	25 × 25	1	23, 24
	Zambia	-	-	6	opportunistic data 1997–2008	-	-	25
	Total	1097	49	209				
A. k. struthiunculus	Ethiopia	54	16	2	>70% data from 1969–77, opportunistic	50 × 50	4	26
	Kenya	84	14	89	Mostly 1970–84 opportunistic data	50 × 50	5	12, 27, 28
	Somalia	12	7	1	>70% data from 1978–81, opportunistic data	50 × 50	6	27, 28
	Sudan	5	1	-	Continuous 1976–84 field surveys by author	120 × 120	7	27, 28
	Tanzania	283	10	12	mid-1990s–2009, opportunistic	12.5 × 12.5	8	27, 28
	Uganda	3	-	-	1800s–1990 published literature, post-1990 opportunistic sight records	1–10 km diameter point data	9	27, 28
	Total:	441	48	104				

[a] Each record is a unique locality; comprising either all records at one site within one calendar year subsumed into a single entry, or the centre of an occupied atlas grid-square. South Africa had two post-1970 atlases: Brooke (1984, data collected 1970s–84) and Harrison *et al*. (1997; records from 1989–95), and a further 65 collated incidental records (spanning 1970–93); although 9 of these 65 records may also have been included in the atlases (six from 1970–81; three from 1992–93), thus *n* = 56 for 'post-1970 non-atlas' refers to occupied grids in Brooke (1984). South African records collected post-1995 (mostly as part of an ongoing atlasing project, www.sabap2.adu.org.za) are not included in our database.

[b] Large non-atlas sample sizes are available in some states due to more than one sighting report from the same locality over subsequent years (in www.worldbirds.org: Kenya and Botswana), summary of earlier atlas (South Africa: Brooke [1984]) or previous collation of *A. kori* records (Zimbabwe: Rockingham-Gill [1983]). Swaziland (*n* = 2) and Uganda (*n* = 3) records are reported in respective country atlases, but are pre-1970 records; our analysis includes them within the pre-1970 dataset.

[c] Sources: 1, Harrison *et al*. (1997); 2, Parker (1999); 3, Parker (1994); 4, Ash & Atkins (2009); 5, Lewis & Pomeroy (1989); 6, Ash & Miskell (1998); 7, Nikolaus (1987); 8, Barker (in prep.); 9, Carswell *et al*. (2005); 10, Dean (2000); 11, *Babbler*; 12, www.worldbirds.org; 13, Clancey (1971); 14, Clancey (1996); 15, *Madoqua*; 16, *Lanioturdus*; 17, *Ostrich*; 18, Brooke (1984); 19, *Bokmakierie*; 20, *Mirafra*; 21, *Laniarius*; 22, *Promerops*; 23, Rockingham-Gill (1983); 24, *Honeyguide*; 25, Dowsett *et al*. (2008); 26, *Walia*; 27, *Scopus*; 28, *East African Natural History Bulletin.*

Appendix 2.2.

Data quality – museum records, conflicts and East African atlases

Historical records commonly derive from museum specimens and narratives of hunting expeditions. All range states except Ethiopia are former colonies of only four European countries: Britain, Germany, Portugal and Italy, although colonial period differed. Degree of interest in natural history and thus data-collecting effort differed among colonial powers, being greatest in British and German colonies respectively, although these were spread widely across the continent. Collecting in-country is likely to have been biased towards more accessible areas, but resulting error was minimised by adopting a coarse-scale analysis.

Civil conflict and unrest restricted data collection during discrete periods in some range states: Sudan (1955–72, 1983–2005, Darfur 2003–10), Ethiopia (1974–91), Angola (1975–2002), Mozambique (1977–92), Uganda (1981–86) and Somalia (1991–present). Thus pre-1970 conflicts may contribute to under-estimation of the historical range in Sudan only, although this is not likely to be significant: Cave & MacDonald (1950, 1955) suggested a Kori range restricted to south-east Sudan, overlapping the contemporary range. In contrast, post-1970 conflicts could potentially have affected many contemporary range estimates. However, range states with post-1970 conflicts were generally still open to atlas data collection either because the conflict was short relative to atlas data periods (Uganda; five-year war, atlas data spans late 1800s–1990s: Carswell *et al*., 2005); or because most data were collected prior to (Ethiopia, Ash & Atkins, 2009; Somalia, Ash & Miskell, 1998) or after (Sudan: Nikolaus, 1987; Mozambique: Parker, 1999) conflicts, again ameliorated by long atlas data collection periods (Appendix 2.1, Fig. 2.1). In contrast, prolonged conflict in Angola precluded fieldwork and χ^2-tests of range changes with and without the Angola data are therefore presented.

To test the extent to which the Kori range boundaries in East Africa could be influenced by incomplete atlas survey coverage, for apparently unoccupied grid-squares that border occupied squares at the range margins, we quantified atlas-derived occupancy of ten conspicuous and widely-distributed species: Common Ostrich *Struthio camelus*, Bateleur *Terathopius ecaudatus*, Black-shouldered Kite *Elanus caeruleus*, Secretarybird *Sagittarius serpentarius*, White-backed Vulture *Gyps africanus*, Helmeted Guineafowl *Numida meleagris*, Crested Francolin *Francolinus sephaena*, Black-bellied Bustard *Lissotis melanogaster*, Little Bee-eater *Merops pusillus* and Lilac-breasted Roller *Coracias caudatus*. All co-occur with Kori in semi-arid scrub and savanna habitats (pers. obs.) and have a potential range encompassing the relevant grid-squares (Stevenson & Fanshawe, 2004).

Kori range boundaries defined by East African atlases are unlikely to be artefacts of incomplete survey coverage, because most of the co-occurring widely-distributed and conspicuous species were recorded from grid-squares bordering the outermost Kori-occupied grid-squares. In Sudan a mean 6 ± 4 SD (range 2–9) of the widely-distributed species were recorded in all four grid-squares adjoining the five Kori-occupied grid-squares. In Ethiopia widely-distributed species were recorded in 56 of 83 grid-squares around the 54 Kori-occupied grid-squares (mean 3 ± 3 SD species per grid-square, range 0–8). In Kenya widely-distributed species were recorded in 61 of 73 grid-squares adjoining 84 grid-squares occupied by Kori at the species range margin (mean 4 ± 3 SD, range 0–8), and the only region for which Kori range limit remained uncertain was bounded by 0°30'–1°30'N and eastwards of 40°E towards the Somalia border, an area approximately 15,000 km^2 (six 50-km grid-squares). No records for any Kenyan bird species were received from this area during atlas data collection (Lewis & Pomeroy, 1989). However, Bateleur and White-backed Vulture were recorded in adjoining areas in Somalia (Ash & Miskell, 1998). Therefore, because Kori was not recorded along the Somali border, the species' range limits in Kenya and Somalia are probably disjunct, and at worst its easternmost range limit in Kenya lay in the six 50-km grid-squares eastwards of our range boundary estimate, but within the Kenyan border. This area (15,000 km^2) is approximately 1.26% of the overall East African AOO estimate, thus the potential maximum error in estimating the true boundary in this part of the range is negligible.

Somalia had a total of 14 Kori-occupied grid-squares; Ash & Miskell (1998) show an additional two historically (pre-1970) occupied grid-squares in the south-west (Fig. 2.2a). The 14 grids were surrounded by a total of 20 adjoining grid-squares, nine surrounding the pre-1970 records in the south-west and 11 surrounding the north-west subpopulation. Widely-distributed species were reported from 8 of 9 grid-squares surrounding the south-west subpopulation (mean 4 ± 3 SD, range 0–8), and because Kori have not been reported in this region post-1970, that subpopulation is likely to be genuinely extirpated. Widely-distributed species were not reported from six grid-squares surrounding the north-west range limit, although the widely-distributed species were recorded in grid-squares 100 km east of the 46°E limit suggested by the atlas data. The other gaps around Kori-occupied grid-squares were also bounded by grid-squares occupied by widely-distributed species, 50 km away (grid-square resolution = 50 km). Consequently our contemporary Kori range boundary estimate in north-west Somalia may at worst have been underestimated by approximately 7500 km^2, about 0.63% of the estimated East Africa AOO.

In Tanzania, maps for most of the widely-distributed species were still incomplete (Baker *et al.*, in prep.), but where these were available (Secretarybird, Ostrich and Black-shouldered Kite) these species were recorded around the Kori range boundary west of Lake Victoria and eastwards of Serengeti National Park, suggesting depicted western and eastern Kori range limits were genuine. No widely-distributed species was recorded south-west of the Kori range in the Serengeti. While data on Kori historical range was incomplete, at least post-1950 it was unlikely to have extended into central Tanzania (south of Shinyanga Province: Reynolds, 1968). Kori were never recorded around Tabora: Reynolds (1968) traversed much of the region during 1959–1966 and recorded no Koris. Thus the contemporary southernmost range limits were most likely genuine.

Additional references

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Appendix 2.3.

Questionnaire sent to in-country experts to solicit opinions on trends in Kori Bustard population numbers and geographic range.

As part of a PhD study on Kori Bustard *Ardeotis kori*, supervised by Dr. Nigel Collar (BirdLife International) and Dr. Paul Dolman & Dr. Iain Lake (University of East Anglia), I would like to seek your assistance. I aim to assess the conservation status of wild Kori across all range states. I have reviewed existing distributional data, including sighting localities, peer-reviewed literature, and other documentary sources, to assess whether there is any evidence of range contraction, or fragmentation. However, there is scant published material by which to assess population trends. To assist in this, we seek your opinion. We appreciate very few quantitative data are likely available, but pooling expert opinion from across the bird's range should enable us gain a clearer idea of the bird's likely population trends in the recent past (1970–2009). The survey should take less than 10 minutes to complete. Thank you for your support.

Mr. Kabelo Senyatso (School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK. Please email questionnaire/questions, to k.senyatso@uea.ac.uk; or post to abovementioned address.

1. Respondent's name	
2. Email contact	
3. Country to which assessment applies	

4. Are you commenting on status throughout country?

☐	Yes	☐	No

If no, please list Districts/Provinces to which your assessments apply

5. Which time-period(s) does your assessment refer to?

☐	1970–2009	☐	1980–2009	☐	1990–2009	☐	2000–2009	☐	Other		to	
										Month/Year		*Month/Year*

6. Kori Bustard population trend over time-period? (if this is different among districts please provide details under no. 10)

☐	Large decrease	☐	No change	☐	Large increase
☐	Small decrease	☐	Small increase	☐	Unclear

7. Has the population trend been accompanied by any change in geographic range?

☐	Range contraction	☐	Range perforation	☐	No noticeable change	☐	Range increase	☐	Unclear

8. In your view, what factors explain the population trends and range patterns?

9. Data quality

☐	Personal experience	☐	View of long-term residents	☐	Published data (please cite in no. 10)

10. Any other comments, including names of other experts you recommend I contact?

Appendix 2.4

Summary data of responses to questionnaire sent to in-country experts to solicit opinions on post-1970 population trends.

Country [a]	No. of questionnaires sent out	No. of positive responses	Main characteristics of assessment (from positive responses)		
			Countrywide assessment	Sub-national assessment	Unable to comment on trends
Angola	3	3	3	0	0
Botswana	9	4	0	3	1
Mozambique	2	1	1	0	0
Namibia	8	5	1	1	3
South Africa	4	1	0	1	0
Zimbabwe	5	2	0	0	2
Southern Africa sub-total	31	16	5	5	6
Ethiopia	4	3	2	1	0
Kenya	9	4	2	1	1
Somalia	3	1	1	0	0
Sudan	2	1	0	0	1
Tanzania	3	2	1	0	1
Uganda	3	2	1	0	1
East Africa sub-total	24	13	7	2	4

[a] Swaziland and Zambia excluded because Kori is known to have gone locally extinct in Swaziland in pre-1970 (Parker, 1994), while for Zambia, the species has been recorded only six times (Dowsett, 2009) and thus inference of population trends is not possible.

Chapter Three

How well do Wildlife Management Areas manage wildlife?

Abstract

Wildlife Management Areas (WMAs) are promoted to achieve positive outcomes for both livelihoods and conservation in southern Africa, primarily through ecotourism and trophy hunting. However, the response of different functional groups of vertebrates to WMAs and whether WMAs abate livestock-driven impacts and illegal hunting (presumed key threats to wildlife in these landscapes), are poorly understood. Using data from 103 independent driven transects totalling 4030 km and spanning eight protected areas (PAs; area 64,000 km^2), 15 WMAs (72,000 km^2) and intervening unprotected areas (114,000 km^2) in Botswana's Kalahari ecoregion, this study examined the relative abundance among land-uses of seven vertebrate functional groups, comprising 21 species of medium- and large-bodied mammals and birds. WMAs enhanced the abundance of most functional groups, relative to unprotected areas, and appeared adequate to conserve medium-sized ungulates. In contrast, although less effective than comparable South African PAs, Kalahari PAs are crucial for conserving large-bodied ungulates. Abundance of large-bodied grazers, medium-bodied browsers, carnivores and raptors was greater in WMAs than in unprotected areas, with encounter rates in WMAs similar to (large-bodied grazers, medium-bodied browsers, carnivores), greater than (pale chanting goshawk), or lower than (large ground birds) those found in PAs. However, gemsbok (the largest legally huntable ungulate) had encounter rates within WMAs almost as low as in unprotected areas; contradicting a key tenet of the WMA model, that species generating the most revenue for local communities should be directly or preferentially conserved. Furthermore, scarcer species for which models could not be constructed were largely restricted to PAs: they either were not encountered in either WMAs or unprotected areas (zebra, eland, giraffe, leopard and lion), or were only rarely encountered in WMAs (greater kudu, wildebeest and bat-eared fox: PA encounter rates 6–7 times greater than WMAs). In contrast, galliforms (predominantly helmeted guineafowl) were most abundant in unprotected areas, and least abundant in WMAs. The relative importance of unregulated bushmeat extraction (indexed as proximity to human settlement) and cattle impacts (indexed as distance to borehole) as mechanisms underlying wildlife responses was examined in Generalised Linear Mixed Models that also controlled for habitat characteristics (Normalised

Difference Vegetation Index, pan proximity and altitude). Model-averaged parameter estimates and selection probabilities obtained by Multi Model Inference showed a strong negative effect of hunting (with lower abundance or incidence closer to settlements) for medium-bodied browsers, including a specific effect on steenbok, and for large ground birds, including specific effects on both black korhaan and red-crested korhaan. In contrast, no detrimental direct impacts of cattle were found, with no functional groups or species occurring at lower abundance or incidence closer to boreholes. WMAs clearly offer tangible benefits to many wildlife species in Botswana, greatly expanding and buffering the areal extent of conservation beyond strictly protected parks. However, stronger regulation of hunting quotas may further enhance these benefits within WMAs, while the largest bodied browsers and grazers appear to be severely depleted even within PAs.

Introduction

Protected areas (PAs) exist to conserve wildlife (Rodrigues *et al.*, 2004; Gaston *et al.*, 2008) and can mitigate anthropogenic threats to wildlife and habitats (Bruner *et al.*, 2001). However, pragmatic and ethical problems caused by excluding communities from land and resources, along with other livelihood impacts such as livestock depredation or crop damage by wildlife, require the development of alternative models (Naughton-Treves *et al.*, 2005). Efforts to engage local communities more fully in conservation by directly linking livelihoods to biological resources are increasingly common, with increased emphasis on co-management, empowerment and participatory approaches (Salafsky & Wollenberg, 2000; Naughton-Treves *et al.*, 2005). Recent global conservation area network expansion has primarily been through areas allowing consumptive use, not strictly protected categories (Naughton-Treves *et al.*, 2005), but the extent to which these approaches actually conserve biodiversity remains largely uninvestigated (Ferraro & Pattanayak, 2006; Gaston *et al.*, 2008). Unregulated bushmeat harvest is emerging as one of the most serious threats to the viability of wildlife populations, both inside and outside conservation areas (Fa *et al.*, 2002, 2005; Milner-Gulland & Bennett, 2003), so it is crucial to examine whether wildlife exploitation is mitigated by livelihood-based approaches to conservation in human-occupied areas.

In southern Africa, primarily in Botswana, Namibia, Zambia and Zimbabwe, community-based conservation has been attempted through Wildlife Management Areas (WMAs) based on trophy hunting and ecotourism (Du Toit, 2002; Child & Barnes, 2010; Naidoo *et al.*, 2011). WMAs have increased communities' wildlife-based income particularly when profit margins are large, for example where high-value species such as African elephant (*Loxodonta africana*) are included in hunting quotas (Taylor, 2009; Naidoo *et al.*, 2011). However, the degree to which WMAs mitigate threats to wildlife and the mechanisms by which this may occur are unknown. If WMAs promote conservation by strengthening the link between wildlife resources and livelihoods, giving incentives to curb illegal hunting, then species on which livelihood activities are directly based should be maintained following WMA designation. However, this predicates that communities' interests are best served by the conservation approach (with even marginalised sectors perceiving it as in their own interest to desist from illegal hunting), that viable institutions exist or can be created, that benefit-sharing mechanisms are transparent and that wildlife utilisation is based on appropriate biological assessments (Du Toit, 2002; Child & Barnes, 2010).

If WMAs also permit other livelihoods incompatible with or providing little incentive for conservation, then this could undermine WMAs' ecological aims. Notably livestock-rearing is allowed in WMAs, typically within specified buffers, despite postulations that livestock may compromise wildlife conservation in African savannas (du Toit & Cumming, 1999; Ogutu *et al*., 2005). Although differing wildlife abundances between PAs and unprotected areas have been interpreted as evidence of livestock impacts (Ogutu *et al*., 2005; Rannestad *et al*., 2006), these contrasts are confounded by other anthropogenic impacts such as bushmeat harvest. Relationships between cattle stocking rates and wildlife densities have never been investigated. Notwithstanding, several mechanisms have been proposed by which cattle may impact wildlife, including competition for forage or water (Sitters *et al*., 2009; Hibert *et al*., 2010) and indirect impacts through cattle-induced bush encroachment (du Toit & Cumming, 1999). At localised scales cattle can reduce grass forage and increase bush encroachment (Skarpe, 1990; Perkins, 1996; Roques *et al*., 2001), but it is unclear whether such effects are detrimental to large-scale wildlife conservation.

The aims of this study were threefold: first, to investigate the conservation effectiveness of WMAs relative to that of PAs and unprotected pastoral savanna landscapes in a large-scale intensively replicated study and to examine the response of differing functional groups (wildlife of similar diet and body size) and individual species of diurnal vertebrates to designation; second, to use the opportunity provided by replicated WMAs, PAs and unprotected areas to test the responses of wildlife to varying intensities of cattle and other anthropogenic impacts, particularly unregulated (and illegal) hunting; and third, to qualitatively contrast Kalahari PAs to previously sampled South African PAs, to enable us to place any differences in effectiveness between Kalahari PAs and WMAs in a wider regional context.

This study tested the conservation effectiveness of WMAs in Botswana's Kalahari ecoregion. This region is ideal for such a study because it contains multiple WMAs that cover more than 80,000 km^2, have been operational for more than 15 years, and are interspersed with both PAs and unprotected land. This reduces the confounding effects of latitudinal rainfall gradients and finer-scaled factors such as localised rains, terrain variation and anthropogenic habitat modification.

The conservation effectiveness of Kalahari WMAs has not previously been assessed systematically. Earlier studies (mammals: Wallgren *et al*., 2009b; birds: Herremans, 1998) suggested that wildlife may be more abundant in WMAs than in unprotected areas, but less so than in PAs. While these findings appear intuitively correct, both studies suffered shortcomings including: (a) low spatial replication within and across land-uses; (b) re-sampling within short time-periods the same transects in fenced-in areas but analysing as independent data despite a strong likelihood of re-counting the same individuals of sedentary species; (c) not accounting for potential differences in animal detectability among land-uses (Wallgren *et al*., 2009b); or (d) directional biases due to slower driving speed and increased search effort within PAs, relative to WMAs, and with least effort in unprotected areas (Herremans, 1998). Both Herremans (1998) and Wallgren *et al*. (2009b) suggested that a combination of cattle and hunting contributed to observed wildlife patterns, but neither tested these hypotheses. Similarly, Verlinden (1997) has suggested negative effects of cattle and unregulated bushmeat hunting on Kalahari wildlife, but did not test their relative importance. The relative importance of differing anthropogenic threats for different functional groups and individual species, and the extent to which WMAs may mitigate them, had not been investigated prior to this study.

Using data from 103 independent driven transects (total length 4030 km) that quantified wildlife abundance in eight replicate PAs, 15 WMAs and extensive contiguous unprotected areas, this study examined: (1) the relative abundance of different functional groups of large-bodied vertebrates among PAs, WMAs and unprotected areas; (2) differential responses of functional groups to WMA designation; (3) the relative importance of cattle stocking rate (indexed by distance to borehole), bushmeat hunting (indexed by proximity to human settlement), and habitat characteristics (independent of cattle effects) to different functional groups and individual species; and (4) whether the wildlife response to conservation designations and the anthropogenic threats support the notion that direct biodiversity–livelihoods linkages have resulted in effective wildlife conservation.

Methods

Study area

The study area (about 250,000 km^2: 20–24°S 22–26°E; Fig. 3.1) lies within a flat semi-arid region of the Kalahari Desert in central Botswana, characterised by fossil river valleys, pans and sandy soils, with predominantly wooded grasslands and dense bushland interspersed with low-growing shrubs (Weare & Yalala, 1971). Principally summer (October–March) rainfall varies from 300 mm y^{-1} in the south-west to 450 mm y^{-1} in the north-east (Nicholson & Farrar, 1994), and field-measured mean annual rainfall at the 11 rainfall stations with long-term data (spanning the period 1961–2003) had a coeffiecint of variation that ranged 0.28–0.43 (Parida & Moalafhi, 2008). Drought-resistant *Acacia* scrub increases south-westwards while woody plant density and diversity increases north-eastwards, where tree savanna and isolated stands of *Colophospermum mopane* dominate (Weare & Yalala, 1971). The study area is among the driest savannas in Africa, with a depauperate species richness for both plants and mammals (Shorrocks, 2007). With the exception of crested francolin, which is restricted to tree savannas that represent the south-westernmost edge of its geographic range in central Botswana (Harrison *et al*., 1997) all sampled species occurred throughout the study area (Kingdon, 1997).

Sampled PAs comprised three privately owned (Jwana Park, Orapa Park and Nata Sanctuary) and all five state-managed PAs in central Botswana (area 64,000 km^2), 15 WMAs (72,000 km^2) and intervening unprotected areas (114,000 km^2: Fig. 3.1). To reduce confounding geographic effects, analyses controlled for underlying habitat and rainfall gradients (see below and Table 3.1). All PAs were designated before 1980 and WMAs during the early 1990s; therefore any contemporary difference in wildlife abundance were considered to primarily to reflect differences in designation and management (following Urquiza-Haas *et al*., 2011).

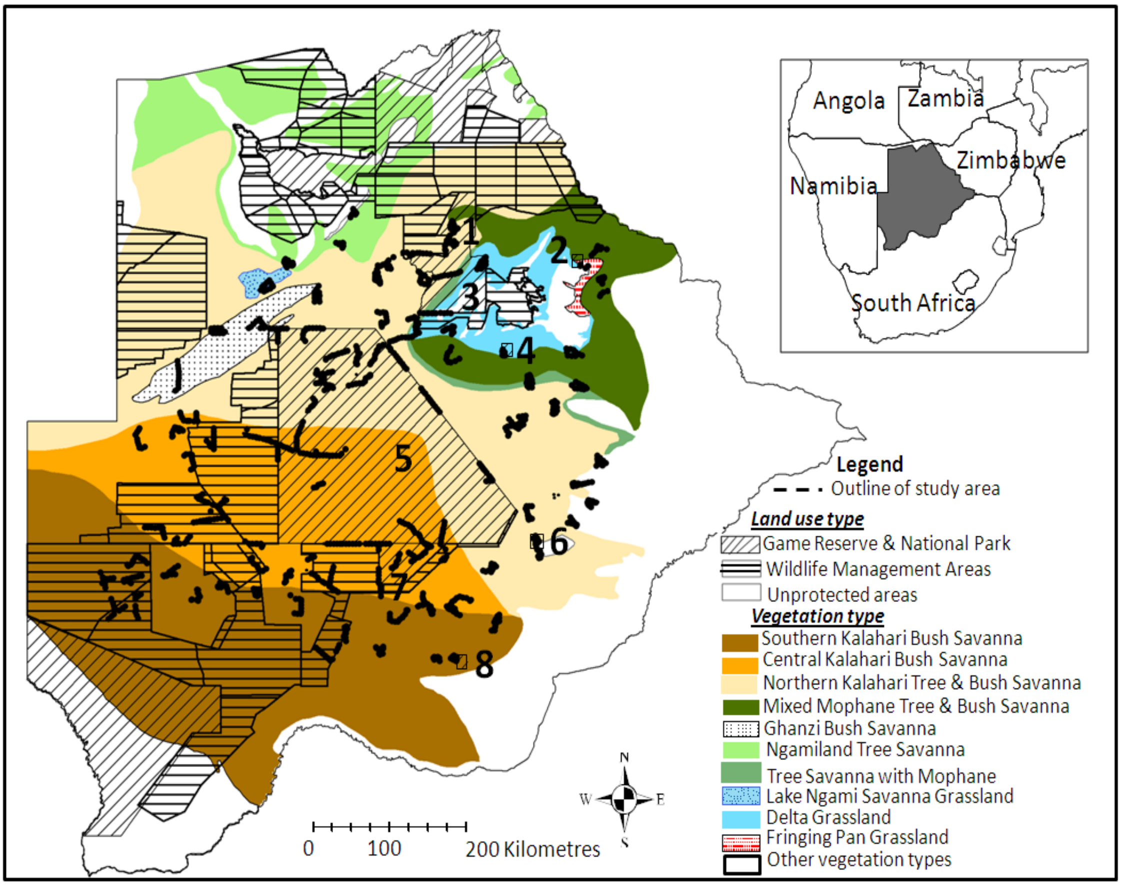

Figure 3.1. Location of the study area in the Kalahari, showing transect positions, land-use designation (Government of Botswana, 2001) and vegetation zones (following Weare & Yalala, 1971). Protected areas within the sampling extent are (1) Nxai National Park, (2) Nata Sanctuary, (3) Makgadikgadi National Park, (4) Orapa Game Park, (5) Central Kalahari Game Reserve, (6) Dithopo Game Ranch, (7) Khutse Game Reserve and (8) Jwana Game Park.

Hunting is prohibited in PAs. Within WMAs, trophy hunting of medium- and large-bodied ungulates and ostrich (Table 3.2) is regulated by communities under quotas issued by the national Department of Wildlife and National Parks (DWNP). In WMAs, areas within 20 km of settlements are zoned for livestock-rearing (hereafter, WMA livestock-rearing buffers). The remainder of the WMA (hereafter, WMA wildlife zones) is designated for either regulated hunting or wildlife viewing (Appendix 3.1); my own field count data of cattle confirmed that this species was absent from these wildlife zones (Appendix 3.2). Gamebird shooting under permit occurs in unprotected areas and WMAs. Illegal, largely subsistence hunting, of large ungulates speared from horseback and of smaller species caught with dogs or snaring, occurs across all land-use types (pers. obs.), but was hypothesised to be ubiquitous across unprotected areas, potentially reduced in WMAs and lowest in PAs due to both remoteness from settlement and law enforcement (Appendix 3.1).

Human settlements were absent from PAs and WMA wildlife zones, communities within them having been relocated at their establishment (Campbell, 1973; Twyman, 2001; Appendix 3.1). In WMA livestock-rearing buffers and unprotected areas, human activities are typically restricted to 20–40 km around villages (Chanda *et al.*, 2003). Livestock-rearing is important to livelihoods across unprotected areas and WMAs, while arable farming is negligible (Twyman, 2001; Chanda *et al.*, 2003; Chapter 1). Livestock are prohibited from PAs; all three private reserves and one state-managed PA were entirely fenced, while remaining PAs were fenced to exclude livestock along borders close to human settlements. Livestock-rearing, with herders and cattle staying at permanent bases (‘cattle posts’) throughout the year (see Chapter 1), primarily involved cattle, restricted to within 10 km of boreholes throughout the year (Perkins, 1996), occasionally with associated horses, donkeys, sheep and goats. Livestock-rearing was mostly on a subsistence and free-ranging basis; those commercial ranches occurring locally (typically not exceeding 16 km^2) were excluded from study because fencing minimised interaction between ranched cattle and wildlife.

Spatially replicated sampling across the gradient of PA, WMAs and unprotected areas (comprising locations at differing proximities to settlement and to boreholes) allowed us to examine responses to land-use designation, cattle density, and proximity to human settlement in order to examine mechanisms underlying observed patterns.

Survey methodology

A 500-km square centred on the Central Kalahari Game Reserve (CKGR) was subdivided into 25-km grid-squares, the basic sampling units. Replicate non-contiguous grid-squares were randomly selected for survey, stratified by land-use (PAs, WMAs and unprotected areas), with the constraint that they contained drivable tracks, because substratum structure prohibited off-road driving. Surveys were conducted over a single discrete period from 15 April to 8 July 2009, when most trees had shed leaves, to minimise seasonal variation in animal detectability. Within these survey design constraints, a total of 103 grid-squares were sampled (n = 33, 18 and 52 for PAs, WMAs and unprotected areas respectively). Unprotected areas received the greatest sampling effort because the largest variation in the primary predictor variables, cattle abundance and proximity to human settlement, was expected in this land-use type. Because of their similar size, the intention was to sample an equal number of grid-squares in PAs and WMAs, but this could not be achieved owing to the poor track network within WMAs. Consequently, the overall lower sampling intensity in WMAs meant that tests of whether more wildlife occurred in this than the other land-use types had limited statistical power and were therefore highly conservative, but unbiased. The poor track network within WMAs also meant that it was not possible to stratify WMA livestock-rearing and WMA wildlife zones *a priori* and in the field; but *post-hoc* stratification resulted in similar sampling effort (n = 98 and 94 4-km segments in WMA wildlife zones and WMA livestock-rearing buffer respectively), which were considered to introduce minimal bias (see below for justification of using 4-km sampling segments). To avoid confounding spatial and temporal effects, different land-uses or far-apart grid-squares within one land-use were surveyed within short time-periods; where possible a pair of grid-squares representing different land-uses was surveyed in one day.

Within each surveyed grid-square, characteristic medium- and large-bodied diurnal mammals, raptors, large ground birds and galliforms (Table 3.2) were surveyed along transects driven at 20 km/h following unpaved roads or tracks, after preliminary comparison of encounter rates and variance in density estimates with transects driven at 40 km/h. Although disturbance-sensitive species may avoid tracks, vehicle encounter rates were negligible across all land-use types (PAs 0.02 vehicles km^{-1} ± 0.10 SD; WMAs 0.06 vehicles km^{-1} ± 0.25; unprotected areas 0.04 vehicles km^{-1} ± 0.22, $F_{2,\,1108}$ = 3.013, P = 0.05) and so this was not considered a concern. All surveys were conducted by the same three observers, between 07:00–11:00 and 15:00–18:00, coinciding with peak activity times for the study species.

Within each grid-square a single uninterrupted 40-km DISTANCE transect (Buckland *et al*., 2001) was driven, along which animal abundance and local explanatory variables, including vegetation structure (woody vegetation canopy cover), were sampled simultaneously on contiguous 4-km segments; this scale was considered appropriate to capture gradients in cattle intensity and their impacts on vegetation close to and away from boreholes, following Perkins (1996). Segments were constrained to homogeneous canopy cover based on a 4-point ordinal score of openness (woody vegetation cover index, Table 3.1, this index was strongly correlated with canopy cover of shrubs and trees, Chapter 4); if a marked change in canopy cover occurred before 4 km elapsed then a new segment was begun, with the boundary recorded using a handheld GPS. Mean segment length was therefore less than 4 km and although slightly shorter in unprotected areas owing to greater heterogeneity was broadly similar across land-use types (PAs 3.7 km ± 1.0 SD; WMAs 3.8 km ± 0.9; unprotected areas 3.5 km ± 1.0, $F_{2,\,1108} = 6.564$, $P = 0.001$). Animal observations were recorded in four distance categories (Buckland *et al.*, 2001): 0–50, 50–100, 100–200 and >200 m, with individuals within 30 m of each other recorded as a single group. Large dispersed groups that spanned distance category boundaries were recorded according to the estimated geometric centre of the group, following Buckland *et al*. (2001). Canopy cover of woody vegetation, measured in variable radius sampling plots (Mueller-Dombois & Ellenberg, 1974) in one randomly selected segment within each of 91 transects (out of total 103 transects), differed among land-use types (Generalised Linear Model, GLM Wald $\chi_2^2 = 9.106$, $P = 0.011$), being lowest in PAs (9.63 percent cover ± 9.16 SD), intermediate in WMAs (14.76 percent ± 8.75), and greatest in unprotected areas (19.89 percent ± 11.52), but was not influenced by vegetation zone (GLM Wald $\chi_3^2 = 6.083$, $P = 0.108$; Chapter 4). Thus segments with poorest visibility were most common in unprotected areas. Consequently, it was not possible to simultaneously control for vegetation cover and varying detectability of wildlife while comparing encounter rates among land-use designations, the lowest common distance band within which animals were consistently detected irrespective of habitat was identified, and subsequent analyses were restricted to this band. Sighting records were therefore truncated to 100-m wide strip transects (simultaneously surveying 50 m either side of the vehicle), within which all animals were detected (Appendix 3.3).

Predictors of animal abundance

To test possible mechanisms driving observed wildlife abundance, the following predictors were considered: (1) land-use designation (PA, WMA, unprotected); (2) segment proximity to human settlement, considered a proxy for illegal hunting pressure following similar use of the index in other parts of Africa (e.g. Muchaal & Ngandjui, 1999; Brashares *et al*., 2001) and other tropical regions (e.g. Urquiza-Haas *et al*., 2009;

Latin America); (3) segment proximity to borehole (a robust proxy measure for cattle density: Appendix 3.2); three terrain variables: (4) pan proximity; (5) mean altitude and (6) altitudinal variance along segment; and (7) Normalised Difference Vegetation Index difference between the start and end of the wet season (flush NDVI) as a measure of segment-level cumulative rainfall during the preceding rainy season (see below). Predictors were obtained from remotely sensed data and statutory agencies (Table 3.1). Of the species for which species-specific models were developed, seasonal movement patterns in the Kalahari have been investigated for gemsbok (a large-bodied grazer) and springbok (a medium-bodied browser); neither undertakes large-scale movements (Verlinden, 1998).

For each segment, land-use classification was extracted, and for segments within WMAs or unprotected areas, distance to nearest PA was also calculated. Spatially referenced human settlement data obtained from the Botswana atlas (Government of Botswana, 2001) were incomplete, so were cross-validated against the complete but non-spatially referenced 2001 census data that provide all settlement names and associated population estimates (www.cso.gov.bw/images/stories/Census/population_town.pdf). All settlements with more than 200 people were mapped based on coordinates obtained from the Botswana atlas and the National Geospatial Intelligence Agency (Table 3.1); these sources do not map smaller settlements. For each segment, distance to the nearest borehole located within a WMA livestock-rearing buffer or unprotected area provided a measure of cattle density, validated by relating borehole data to independent cattle abundance estimates from aerial counts and to field-based cattle encounter rates (Appendix 3.2). The relationship between observed cattle encounter rate and segment distance to borehole was similar and consistent between unprotected areas and WMA livestock-rearing buffers (Appendix 3.2).

In arid and semi-arid tropical areas plant phenology and productivity are largely influenced by soil moisture (Nicholson & Farrar, 1994). However, measures of spatial variation in rainfall were not available owing to a lack of weather stations across much of the study area, so seasonal variation in NDVI (the difference between the start of the 2009 dry season [March] and the start of the 2008 wet season [October], hereafter ‘flush NDVI’) was considered in models of wildlife abundance, as a proxy for geographic and local differences in precipitation and therefore vegetation productivity (following Pettorelli *et al*., 2005). Larger positive values of flush NDVI indicate greater wet season productivity. Flush NDVI was not related to vegetation zone, localised density of woody vegetation or borehole proximity (Appendix 3.4), suggesting that the index primarily measured segment-specific rainfall. Both flush NDVI and borehole proximity were retained as independent measures in subsequent modelling of wildlife abundance.

Local landscape terrain measures (area-weighted mean altitude and altitudinal variance extracted for each 1 km-buffered segment: Table 3.1) were also considered as candidate variables that relate to local ecological variation between higher-elevation sand-dominated shrublands and lower-elevation grasslands. Because pans provide key foraging resources for some Kalahari wildlife (Verlinden, 1997; Wallgren *et al.*, 2009a), distance to the nearest pan mapped in the Botswana atlas was also considered as a candidate variable.

Statistical analysis

Wildlife responses were analysed for functional groups defined by body size and diet (large-bodied grazers, large-bodied browsers, medium-bodied browsers, carnivores, raptors, large ground birds and galliforms: Table 3.2) and individually for all species recorded in more than 25 segments. Two sets of models were considered. First, wildlife encounter rates were compared among land-use categories (PAs, WMAs, unprotected), controlling for regional variation in ecosystem considered as four regional vegetation classes (grasslands, short shrub savanna, fine-leaved tree savanna and broad-leaved tree savanna: Appendix 3.4). Second, the response of the wildlife species to cattle and hunting was examined by testing independent effects of segment proximity to borehole and to settlement (both square-root transformed because effects were predicted to decrease non-linearly), in models that controlled for any significant effects of landscape productivity (flush NDVI), pan proximity and terrain.

Table 3.1. Explanatory variables examined as determinants of wildlife abundance in the Kalahari, their spatial scale and data source. All variables extracted for each 4-km segment.

Variable	**Units**	**Mean**	**SD**	**Min**	**Max**	**Description**
Land-use designation						
PA, WMA or unprotected area	Nominal	-	-	-	-	Botswana atlas (Government of Botswana, 2001; 1-km^2 resolution polygons).
Distance between WMA-segment start-point and PA boundary	km	68	40	0.01	156	Derived.
Anthropogenic threats						
Hunting (distance to nearest settlement)	km	29	26	0.24	122	All settlements with more than 200 people (mapped point localities, 1-km^2 resolution, Botswana atlas; additional coordinates from www.geonames.nga.mil/ggmagaz/geonames4.asp).
Cattle-induced impacts (distance to nearest livestock-watering borehole outside PA or WMA wildlife zone)	km	13	16	0.08	101	Borehole GPS points (correct to less than 10 m; Government of Botswana, Geological Surveys Department, unpublished data).

Ecological and environmental variation						
Vegetation zone	Nominal scale 1–4	-	-	-	-	Ten vegetation types (Weare & Yalala, 1971) pooled into four broad classes: grasslands; shrub savanna; fine-leaved tree savanna; broad-leaved tree savanna, see Appendix 3.4 for details (1-km^2 resolution).
Flush NDVI: mean March 2009 minus mean October 2008 NDVI values	Index potentially ranges −2 to +2	0.51	0.08	0.03	0.52	10-day composites, based on min and max NDVI over 10-day period (October 2008 and March 2009; from the VEGETATION programme, www.free.vgt.vito.be; 1-km^2 resolution raster data) overlain on vector layer of segments buffered by 1-km, and area-weighted mean NDVI calculated based on the extent of overlap between NDVI dataset and the straight line connecting the segment's start and end points. Flush NDVI potentially ranges from −2 to +2 because raw NDVI ranges −1 to +1.
Mean altitude	m, a.s.l.	1043	93	900	1254	Mean segment altitude (800-m grid-square resolution polygons; mean altitude error: ±1.13 m (scrub habitats). NASA, www.asterweb.jpl.nasa.gov/gdem.asp).
Altitudinal variance	m	13	45	0	699	Based on differences between the mean altitude along a segment, and the larger of the highest or lowest points along that segment.
Distance to nearest pan	km	6.18	6.56	0	45	Distance from segment-start point to nearest mapped pan larger than 1 km^2 (1-km^2 resolution polygons; Botswana atlas).
Woody vegetation cover	Ordinal scale 1–4 (most to least dense)	-	-	1	4	Field measure of vegetation openness and perpendicular distance to which wildlife readily detected along segments: <30 m, 30–80 m, 80–150 m, >150 m.

Wildlife counts per segment were modelled using Generalised Linear Mixed Models (GLMMs; Bolker *et al.*, 2009), within an information-theoretic approach (Burnham & Anderson, 2002), including segment length as an offset variable and grid-square as a random effect to account for sampling multiple segments within each transect. Non-flocking species were modelled as count data (Poisson error, log link function), producing models with minimal over-dispersion (deviance/df ≤ 1.5). For flocking birds, herding ungulates and any functional group that included a congregatory species (large-bodied grazers, medium-bodied browsers, large ground birds and galliforms) models considered incidence per segment (0/1, with binomial error and a logit link function), due to overdispersion of count data (deviance/df ≥ 10) in Poisson models that was not resolved by modelling square-root tranformed counts rounded to integers, or by use of quasi-Poisson models. GLMMs were constructed within R v2.11.1 (R Development Core Team, 2008) using the glmer function of the lme4 package, which calculates parameter estimates based on Laplace approximations to compute true likelihood and generate robust Akaike Information Criterion (AIC) values, unlike GLMMs based on penalised quasi-likelihood (Bolker *et al.*, 2009).

The abundance (or incidence) of functional groups and individual species was compared among the three levels of land-use designation, by comparing the strength of support for four *a priori* models:

Model 1, effects of PAs and WMAs are similar (sharing a single parameter), and differ from those of unprotected areas. Land-use modelled with 2 levels: (PA + WMA); unprotected.
Model 2, each land-use has a unique effect. Three levels: PA; WMA; unprotected.
Model 3, WMA and unprotected areas effects are similar (sharing a single parameter), and differ from PA effects. Two levels: PA; (WMA + unprotected).
Model 4, null model; land-use effects are similar (land-use variable excluded).

Models within two AIC-units of the best-supported model were considered to have similar support, ΔAIC 4–7 much less support, and ΔAIC >10 little support (Burnham & Anderson, 2002). Model support was further considered by calculating Akaike weights and evidence ratios, following Burnham & Anderson (2002).

Next, wildlife responses to settlement proximity, borehole proximity, flush NDVI, and terrain variables were examined by Multi Model Inference (Burnham & Anderson, 2002), using a reduced dataset comprising only segments in WMAs and unprotected areas. In the complete dataset, strong positive correlations between segment proximity to settlement and nearest borehole ($r = 0.811$, $n = 1109$, $P < 0.0001$) resulted from a strong correlation among segments that were simultaneously distant from settlements and boreholes, and located within PAs ($r = 0.822$, $n = 352$, $P < 0.0001$). Outside PAs, settlement and borehole proximity were not strongly related (unprotected areas: $r = 0.333$, $n = 565$; WMA livestock-rearing buffer: $r = 0.374$, $n = 94$; WMA wildlife zone: $r = 0.429$, $n = 98$), allowing independent examination of their effects. Within this reduced non-PA dataset, no other predictor pairs were strongly correlated ($-0.106 < r < 0.195$, $n = 757$ segments). Prior to examining effects of anthropogenic variables, candidate terrain variables were filtered by highly conservative backward elimination from the full model of all test and candidate effects, retaining those for which $P \leq 0.1$ for subsequent multi-model inference. The ‘dredge’ function within the MuMIn R package was then used to develop all possible combinations of retained candidate terrain variables (pan proximity, altitude mean, altitude variance), flush NDVI and test variables (distance to borehole, distance to settlement), while segment length and grid-square were included into all models as an offset variable and a random factor respectively. There was no *a priori* ecological reason to consider interaction terms, so none was modelled. Model-averaged parameter estimates, standard errors and confidence intervals were calculated using Akaike weights of all models within the 95% confidence model set (cumulative Akaike weight >0.95) following Burnham & Anderson (2002). The selection probability of each predictor was estimated by summing Akaike weights of all models in the confidence model set containing that predictor.

Protected area proximity may potentially buffer wildlife trends in surrounding areas through source–sink dynamics (Gaston *et al*., 2008). Whether wildlife abundance within WMAs was affected by overspill from PAs was, therefore, examined using GLMMs that considered distance between segment and nearest PA boundary (square-root transformed) as a fixed effect, grid-square as a random effect, segment length as an offset variable, and settlement proximity (square-root transformed, to account for decreased likelihood of illegal hunting farther from settlements). Outside PAs, distance to PA boundary was only weakly related to distance to nearest borehole, similarly for WMAs ($r = –0.220$) and unprotected areas ($r = –0.232$); relationships between distance to PA boundary and human settlement were also weak and similar (WMAs: $r = -0.123$, unprotected $r = -0.166$), so independent effects of PA proximity could be tested.

Raw encounter rates (animals km^{-2}, assuming ESW of 136 m, obtained from DISTANCE analysis pooling all sight records of the six species regardless of tree cover index and distance categories [i.e. 0–50, 50–100, 100–200 and >200 m], but with truncation of the 10% most distal records) of large-bodied grazers and browsers in Kalahari PAs were compared to those from sampled South African PAs. Choice of sampled South African PAs included deliberate inclusion of Kruger National Park because it is the largest South African PA and presumably similarly susceptible to census bias due to wildlife movement within a large PA, as suspected for the large Kalahari PAs. The published literature was searched (using Google Scholar and Web of Science) for a single study that tabulated recent wildlife abundance at multiple PAs spanning similar vegetation and rainfall as the Kalahari PAs, as well as an example of a small fenced PA to enable contrasts with the three completely fenced Kalahari PAs.

Spatial autocorrelation in model residuals was examined by Moran's I, based on Euclidian distances between segments. All spatial analyses were conducted in ArcGIS 9.2 (ESRI ArcMap 1999–2006).

Results

A total 4722 individuals from 21 vertebrate species, 2174 in PAs, 975 in WMAs and 1573 in unprotected areas were recorded. Encounter rate varied greatly among species (Table 3.2, Fig. 3.2), from those that were only recorded in a single segment (zebra, leopard and lion) to at least one record in 199 segments for northern black korhaan (Table 3.2). Ten species (Table 3.2) were recorded in fewer than 10 segments; these were included within functional groups, but species-specific models were not constructed. Species-specific GLMMs testing the effects of land-use and the relative importance of management-influenced variables were developed for the remaining 11 species (Table 3.2), although for gemsbok models testing anthropogenic variables were not constructed because it was encountered in only five non-PA segments. For large-bodied browsers sample sizes were too small to allow any statistical model to be fitted, either for constituent species or for the pooled functional group.

None of the GLMM residuals were spatially autocorrelated (Moran's I ≤ 0.012, $P \geq 0.384$ for all models).

Effects of land-use designation on functional groups and species-specific encounter rate

Encounter rates of functional groups differed among land-use types (Fig. 3.2), however, different functional groups and species showed contrasting responses. There was strong evidence that WMAs provided positive effects for numerous functional groups and species that had lower abundance in unprotected areas. For these, either Model 1 (that abundance was similar between PA and WMA, but different in unprotected areas) and/or Model 2 (that land-use designation gave unique effects, with WMAs again better than unprotected areas but not as good as PAs) was the most strongly supported, receiving much greater support than either Model 3 (similar abundance between WMAs and unprotected areas, differing from PAs) or Model 4 (null model; no effect of designation). Large-bodied grazers, medium-bodied browsers, overall abundance of carnivores, specific abundance of black-backed jackal, and abundance of raptors (specifically pale chanting goshawk) all shared this pattern (Table 3.3), with estimates of land-use effects (produced for Model 2) confirming the ranking as PA ≥ WMA > unprotected. However, patterns for individual species within these functional groups were not always consistent. For example, although overall abundance of large-bodied grazers did not differ between PAs and WMAs, there was nevertheless strong evidence that the probability of encountering gemsbok was lower in WMAs than in PAs, with Model 3 (PA > WMA ≈ unprotected) the best-supported model. For gemsbok, although there was also moderate support for Model 2 (ΔAIC < 1.5), suggesting incidence in WMAs may have been intermediate between PAs and unprotected areas, encounter rate in PAs was 33-times that in WMAs (Fig. 3.2). Species-specific models could not be constructed for the infrequently encountered large-bodied grazers (wildebeest, hartebeest and zebra); however none of these was recorded from unprotected areas and most had encounter rates 6–7-times greater in PAs than in WMAs (Table 3.2). Conversely, despite strong evidence that overall encounter rates of medium-bodied browsers were similar in WMAs and PAs, apparent abundance of steenbok was three times greater in WMAs than in PAs (Fig. 3.2), with Model 2 the best-supported (ΔAIC ≈ 2 compared to Model 1, Table 3.3). In contrast, springbok had similar abundance in WMAs and PAs, with Model 1 best-supported (ΔAIC ≈ 2 compared to Model 2; Table 3.3, Fig. 3.2).

Although overall abundance of carnivores was similar between PAs and WMAs, with Model 1 receiving strongest support (ΔAIC ≈ 2 compared to Model 2, Table 3.3), this pattern was strongly influenced by the frequently encountered jackal. In contrast, although not considered in species-specific models, the infrequently encountered carnivores were only seen in PAs (lion, leopard) or were rarely encountered in WMAs (bat-eared fox) and consistently absent from unprotected areas (Table 3.2). Raptors (comprising pale chanting goshawk only) were twice as abundant in WMAs as in PAs, and least abundant in unprotected areas, which supported approximately 20% of the WMA abundance (Fig. 3.2). However, although Model 2 was the best-supported model, indicating different abundance between PAs and WMAs, Model 1 (PA ≈ WMA) also received moderate support (ΔAIC≈1.0, Table 3.3); thus it can only be concluded that the species’s abundance was lower in unprotected areas than in either conservation area.

Table 3.2. Species and functional groups considered, showing body weights, hunting quota or game status and total number of segments on which species were recorded. For each land-use (Protected Areas, PAs, *n* = 352; Wildlife Management Areas, WMAs, *n* = 192; unprotected areas, *n* = 565) the mean encounter rate per 100 km (± SE) of animals in 100 m-wide 4-km long strip transect segments is presented, and in parentheses the total number of individuals sighted and largest number of individuals recorded on an individual segment.

Functional groups and representative species	Body weight (kg)[a]	Sociality[b]	Hunt vulnerability[c]	segment with record	Mean segment length (km ± SD), total survey effort (km)		
					PA	WMA	unprotected areas
					$\bar{x}$ 3.69 ± 1.0	3.81 ± 0.88	3.54 ± 1.01
					Σ 1298	732	1998
					Wildlife encounter rate, individuals/100 km		
Large-bodied browsers [d]					**3.24 ± 1.52**	**0.13 ± 0.13**	**0.49 ± 0.23**
Giraffe *Giraffa camelopardalis angolensis*	450–1930	H	HNQ	2	1.78 ± 1.26 (25; 13)	0 (0; 0)	0 (0; 0)
Eland *Taurotragus oryx*	460–700	H	HNQ	3	0.61 ± 0.49 (9; 7)	0 (0; 0)	0 (0; 0)
Greater Kudu *Tragelaphus strepsiceros*	180–250	H	HQ	9	0.86 ± 0.72 (12; 10)	0.13 ± 0.13 (1; 1)	0.49 ± 0.23 (11; 3)
Large-bodied grazers [e]					**5.52 ± 1.53**	**2.68 ± 1.268**	**0.18 ± 0.14**
Gemsbok *Oryx gazella*	210–240	H	HQ	27	4.39 ± 1.32 (58; 15)	0.13 ± 0.13 (1; 1)	0.18 ± 0.14 (4; 3)
Wildebeest *Connochaetes taurinus*	180–250	H	HQ	4	0.90 ± 0.77 (13; 11)	0.13 ± 0.13 (1; 1)	0 (0; 0)
Red Haartebeest *Alcelaphus caama*	120–150	H	HQ	7	0.09 ± 0.09 (1; 1)	2.42 ± 1.24 (19; 7)	0 (0; 0)
Plains Zebra *Equus quagga burchellii*	175–320	H	HNQ	1	0.14 ± 0.14 (2; 2)	0 (0; 0)	0 (0; 0)
Medium-bodied browsers [f]					**79.97 ± 35.80**	**87.71 ± 35.72**	**10.49 ± 6.24**
Steenbok *Raphicerus campestris*	7–16	S	HQ	138	4.82 ± 0.79 (59; 4)	13.99 ± 2.38 (99; 6)	3.00 ± 0.53 (55; 3)
Springbok *Antidorcas marsupialis*	20–59	H	HQ	54	75.15 ± 35.81 (1012; 468)	73.72 ± 35.75 (539;197)	7.49 ± 6.22 (193;153)
Carnivores [g]					**2.44 ± 0.66**	**1.85 ± 0.70**	**0.45 ± 0.19**

Black-backed Jackal *Canis mesomelas*	6–10	S	HQ, NG	28	1.17 ± 0.35 (16; 2)	1.46 ± 0.59 (9; 2)	0.45 ± 0.19 (9; 2)
Bat-eared fox *Otocyon megalotis*	3–5	H	HQ, NG	6	1.13 ± 0.56 (9; 3)	0.38 ± 0.38 (3; 3)	0 (0; 0)
Leopard *Panthera pardus*	20–90	S	HNQ, NG	1	0.07 ± 0.07 (1; 1)	0 (0; 0)	0 (0; 0)
Lion *Panthera leo*	110–225	H	HNQ, NG	1	0.07 ± 0.07 (1; 1)	0 (0; 0)	0 (0; 0)
Raptors [h]					**4.30 ± 0.66**	**8.27 ± 1.39**	**1.90 ± 0.39**
Pale chanting goshawk *Melierax canorus*	0.7–0.8	S	HNQ, NG	115	4.16 ± 0.64 (57; 4)	8.27 ± 1.39 (58; 4)	1.75 ± 1.29 (35; 3)
Secretarybird *Sagittarius serpentarius*	3–4	S	HNQ, NG	3	0.14 ± 0.14 (2; 2)	0 (0; 0)	0.10 ± 0.10 (2;1)
Large-bodied ground birds [i]					**39.25 ± 3.83**	**24.56 ± 3.47**	**16.33 ± 2.02**
Ostrich *Struthio camelus*	90–130	H	HQ	28	2.18 ± 0.86 (28; 9)	3.37± 1.11 (27; 5)	2.82± 1.42 (65; 25)
Kori Bustard *Ardeotis kori*	6–12	S	HNQ	27	1.46 ± 0.02 (10; 2)	1.09 ± 0.003 (7,2)	0.55 ± 0.007 (11; 4)
Northern black korhaan *Eupodotis afraoides*	0.7–0.8	S	HNQ	199	27.94 ± 3.51 (355; 21)	13.89 ± 2.88 (109; 12)	6.39 ± 1.12 (123; 10)
Red-crested korhaan *Eupodotis ruficrista*	0.6–0.8	S	HNQ	183	7.89 ± 1.19 (89; 5)	6.24 ± 1.19 (47; 5)	6.65 ± 0.83 (128; 5)
Galliforms [j]					**32.64 ± 9.39**	**6.15 ± 4.83**	**47.90 ± 11.05**
Crested francolin *Francolinus sephaena*	0.2–0.4	H	HQ	28	1.36 ± 1.02 (11; 6)	1.40 ± 0.91 (12; 7)	3.86 ± 1.21 (83; 21)
Helmeted guineafowl *Numida meleagris*	1.1–1.6	H	HQ	46	31.28 ± 9.34 (387; 53)	4.76 ± 4.76 (42; 42)	44.11 ± 10.97 (854; 80)

[a] Taxonomy, bodyweights and Extent of Occurrence (EOO) range maps follow Kingdon (1997) for mammals; Hockey *et al*. (2005) for birds. Based on EOO range estimates, all 21 species occur throughout the sampling extent, except crested francolin, which is restricted to tree savannas.

[b] S, singletons; H, herding/social group

[c] HQ, legally hunted in WMAs on quota issued by Department of Wildlife and National Parks; HNQ, no legal hunting quota, but liable to poaching or indiscriminate snares; NG, non-game species whose meat is generally not consumed by humans nor fed to pets, otherwise considered edible.

[d,e,f,g,h,i,j] Row statistics based on pooled data for species listed below each functional group heading.

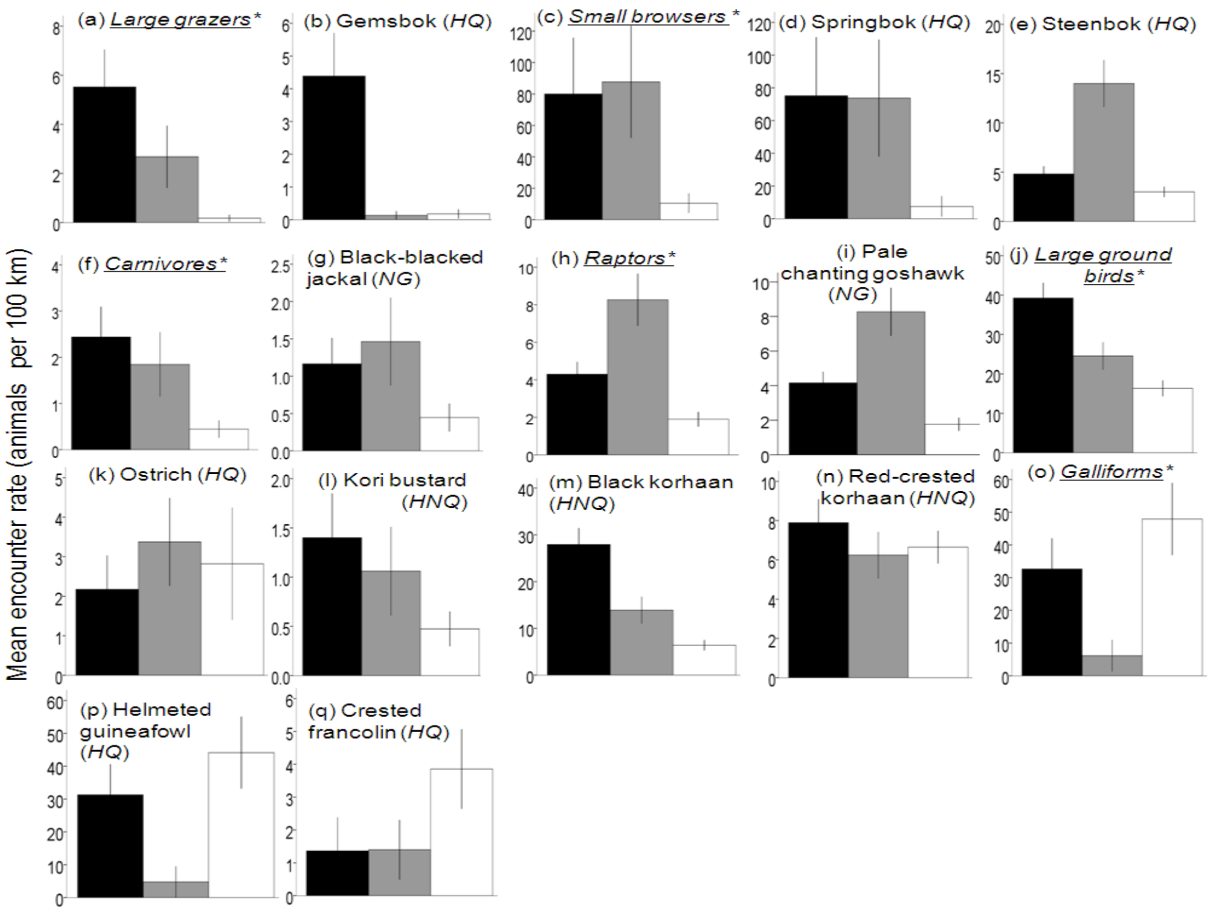

Figure 3.2. Mean encounter rate per 100 km (± SE) of species recorded in at least 25 segments and of functional groups in 100 m-wide 4-km long strip transect segments in protected areas (black bars, *n* = 352), Wildlife Management Areas (grey bars, *n* = 192) and unprotected areas (white bars, *n* = 565). See Table 3.2 for details on hunting vulnerability (HQ, HNQ, NG).

While all of the preceding groups were clearly or marginally more abundant in conservation areas than in unprotected areas, the pooled abundance of galliforms was substantially greater in unprotected areas. This group was dominated by the frequently encountered helmeted guineafowl (Fig. 3.2); both this species and the aggregate group showed incidence in PAs that approached those in unprotected areas, but a considerably lower incidence in WMAs. In contrast, there was no evidence that crested francolin (which was scarce overall) differed in abundance among land-uses (Table 3.3) despite a trend towards greater abundance in unprotected areas relative to both PA and WMAs (Fig. 3.2).

For four species (steenbok, pale chanting goshawk, black korhaan and red-crested korhaan) recorded in more than 30 segments within WMAs, it was possible to test whether abundance within WMAs was related to PA proximity. Abundance of steenbok was marginally greater closer to PAs (GLMM PA proximity 0.19 ± 0.09 SE, $P = 0.04$, controlling for proximity to settlement 0.27 ± 0.12, $P = 0.03$, $n = 192$); such effects were not found for the three remaining species (pale chanting goshawk, PA proximity 0.02 ± 0.05, $P = 0.67$, settlement −0.18 ± 0.11, $P = 0.11$; black korhaan, PA proximity −0.17 ± 0.10, $P = 0.10$, settlement 0.72 ± 0.17, $P < 0.001$; red-crested korhaan, PA proximity 0.04 ± 0.10, $P = 0.73$, settlement 0.19 ± 0.18, $P = 0.28$; $n = 192$ in all cases).

Table 3.3. Wildlife species response to Protected Area (PA), Widlife Management Area (WMA) and unprotected areas, controlling for vegetation zone in Generalised Linear Mixed Models, including grid-square (*n* = 103) as a random effect and segment length (*n* = 1109) as an offset. Parameter estimate (mean ± SE) are shown for models testing unique effects of each land-use category (M2) to illustrate direction of effect for the conservation areas relative to unprotected area. The Log-likelihood (Log(*L*)), AIC of best-supported model, AIC differences from the best model (ΔAIC), Akaike weights (ω) and evidence ratios (ω_1/ω_j) for the four *a priori* models [a] testing for differences in the effects of land-use designation are also shown. Functional wildlife groups as in Table 3.2.

Response Variable	Model [a]	Log(*L*)	AIC	ΔAIC	ω	ω_1/ω_j	Land-use		
							β ± SE		
							PA	WMA	Unprotected area
Large-bodied grazers	M1	−144.721	301.441	0	0.626	1.000			
	M2	−144.251		1.061	0.368	1.700	3.63 ± 1.16	3.03 ± 1.26	0
	M3	−149.533		9.625	0.0005	123.008			
	M4	−158.378		25.316	0.000002	314236.134			
Gemsbok	M1	−110.967		4.801	0.057	11.030			
	M2	−108.280		1.428	0.310	2.042	3.39 ±1.16	1.15 ±1.65	0
	M3	−108.566	229.133	0	0.633	1.000			
	M4	−119.642		20.151	0.00003	23750.290			
Medium−bodied browsers	M1	−482.368	976.735	0	0.604	1.000			
	M2	−481.795		0.855	0.394	1.534	1.10 ± 0.34	1.58 ± 0.42	0
	M3	−488.503		12.271	0.002	461.924			
	M4	−490.745		14.754	0.0004	1599.026			
Steenbok [b]	M1	−418.112		1.993	0.263	2.709			
	M2	−416.116	846.232	0	0.714	1.000	0.45 ± 1.44	1.22 ± 0.31	0
	M3	−421.853		9.475	0.006	114.148			
	M4	−421.936		7.640	0.015	45.604			

Springbok	M1	−169.521	351.0411	0	0.646	1.000			
	M2	−169.496		1.951	0.244	2.653	2.59 ± 1.41	2.87 ± 1.74	0
	M3	−171.875		4.708	0.061	10.529			
	M4	−173.109		5.177	0.049	13.310			
Carnivore [b]	M1	−180.112	372.224	0	0.649	1.000			
	M2	−180.096		1.969	0.243	2.676	1.30 ± 0.54	1.19 ± 0.67	0
	M3	−181.903		3.583	0.108	5.998			
	M4	−184.172		6.121	0.030	21.338			
Black-backed jackal [b]	M1	−125.512	263.023	0	0.361	1.000			
	M2	−125.511		1.998	0.133	2.716	0.70 ± 0.58	0.73 ± 0.70	0
	M3	−126.142		1.259	0.192	1.877			
	M4	−126.654		0.285	0.313	1.153			
Pale chanting goshawk (*Raptors*)[b]	M1	−333.555		1.040	0.372	1.682			
	M2	−332.035	678.070	0	0.627	1.000	0.80 ± 0.31	1.42 ± 0.36	0
	M3	−340.296		14.521	0.0004	1422.968			
	M4	−340.989		13.909	0.0006	1047.593			
Large ground birds	M1	−683.902		4.611	0.067	10.029			
	M2	−681.548		1.905	0.258	2.592	1.01 ± 0.29	0.12 ± 0.37	0
	M3	−681.596	1375.192	0	0.670	1.000			
	M4	−687.441		9.691	0.005	127.167			
Ostrich	M1	−125.859	263.718	0	0.364	1.000			
	M2	−125.103		0.488	0.285	1.276	0.48 ± 0.64	1.30 ± 0.69	0
	M3	−127.200		2.683	0.096	3.825			
	M4	−127.209		0.701	0.256	1.420			
Kori bustard [b]	M1	−129.049		0.485	0.269	1.274			
	M2	−128.897		2.182	0.115	2.977	0.83 ± 0.68	0.39 ± 0.82	0
	M3	−129.028		0.442	0.274	1.247			
	M4	−129.806	269.613	0	0.342	1.000			
Black korhaan[b]	M1	−782.326	1576.652	0	0.470	1.000			
	M2	−781.948		1.245	0.252	1.864	1.44 ± 0.47	0.87 ± 0.62	0

	M3	−782.922		1.191	0.259	1.814			
	M4	−786.604		6.557	0.018	26.536			
Red-crested korhaan [b]	M1	−525.701		1.439	0.212	2.053			
	M2	−524.855		1.747	0.182	2.395	−0.02 ± 0.26	−0.48 ± 0.33	0
	M3	−525.913		1.864	0.171	2.540			
	M4	−525.981	1061.962	0	0.435	1.000			
Galliforms	M1	−248.436		1.292	0.309	1.908			
	M2	−246.790	507.580	0	0.589	1.000	−0.56 ± 0.43	−1.89 ± 0.78	0
	M3	−250.717		5.853	0.032	18.661			
	M4	−250.904		4.228	0.071	8.283			
Helmeted guineafowl	M1	−187.015		2.634	0.196	3.732			
	M2	−184.698	383.396	0	0.732	1.000	−0.53 ± 0.43	−2.57 ± 1.27	0
	M3	−189.189		6.982	0.022	32.817			
	M4	−189.391		5.386	0.050	14.775			
Crested francolin	M1	−114.561		0.676	0.293	1.402			
	M2	−114.522		2.599	0.112	3.668	−0.88 ± 1.20	−1.26 ± 1.71	0
	M3	−115.027		1.609	0.184	2.235			
	M4	−115.223	240.446	0	0.411	1.000			

[a] Four *a priori* models tested M1: [PA≈WMA]≠unprotected areas; M2: PA≠WMA≠unprotected areas; M3: PA≠ [WMA≈unprotected areas]; M4, null model: PA=WMA=unprotected areas.

[b] Species or functional group modelled using count data (with Poisson error and log link); all other species and groups modelled as presence/absence (with binomial error and a logit link). For functional groups, if any of the members was a congregatory species, logistic regression was used.

Effects of anthropogenic factors on functional groups and individual species

The relative importance of illegal hunting (indexed as proximity to human settlement) and cattle impacts (indexed as distance to borehole) as mechanisms underlying wildlife responses to land-use were examined in GLMMs that controlled for potentially important aspects of habitat (flush NDVI, pan proximity and altitude). Strength of evidence for anthropogenic effects was assessed by examining selection probabilities and the confidence intervals of model-averaged parameter estimates obtained by Multi Model Inference.

There was a strong negative effect of hunting (with strong support for lower abundance or incidence closer to settlements) for aggregate medium-bodied browsers, including a specific effect on steenbok (Table 3.4), and also for large-bodied ground birds, including specific effects on both black korhaan and red-crested korhaan, although with no effect on either ostrich or kori bustard. In contrast, no support was found for a negative impact of hunting on large-bodied grazers, carnivores, raptors or galliforms, with confidence intervals spanning zero.

No evidence of any detrimental direct impact of cattle was found, with no functional groups or species occurring at lower abundance or incidence closer to boreholes. For red-crested korhaan, there was some evidence that abundance increased closer to boreholes, with a negative parameter estimate for distance to borehole and a 95% CI that only marginally spanned zero. This is compatible with greater shrub cover in the vicinity of livestock-watering areas (Perkins, 1996; see also Chapter 4), which would enhance habitat quality for this scrub-associated species (Harrison *et al.*, 1997).

Aggregate abundance of medium-bodied browsers and large ground birds was also strongly affected by local habitat. Pooled abundance of medium-bodied browsers and the specific abundance of steenbok and springbok were greater in areas with lower values of flush NDVI (Table 3.4). Encounter rates for large ground birds were greater closer to pans; encounter rates for black korhaan also increased with lower flush NDVI and altitude, while that of red-crested korhaan increased with increasing flush NDVI and closer to pans (Table S4).

Kalahari PAs supported much lower abundances (generally at least an order of magnitude less, Table 3.5) of large-bodied grazers and browsers for which species-specific models were not developed (giraffe, eland, kudu, wildebeest, hartebeest and zebra) than observed in South African PAs.

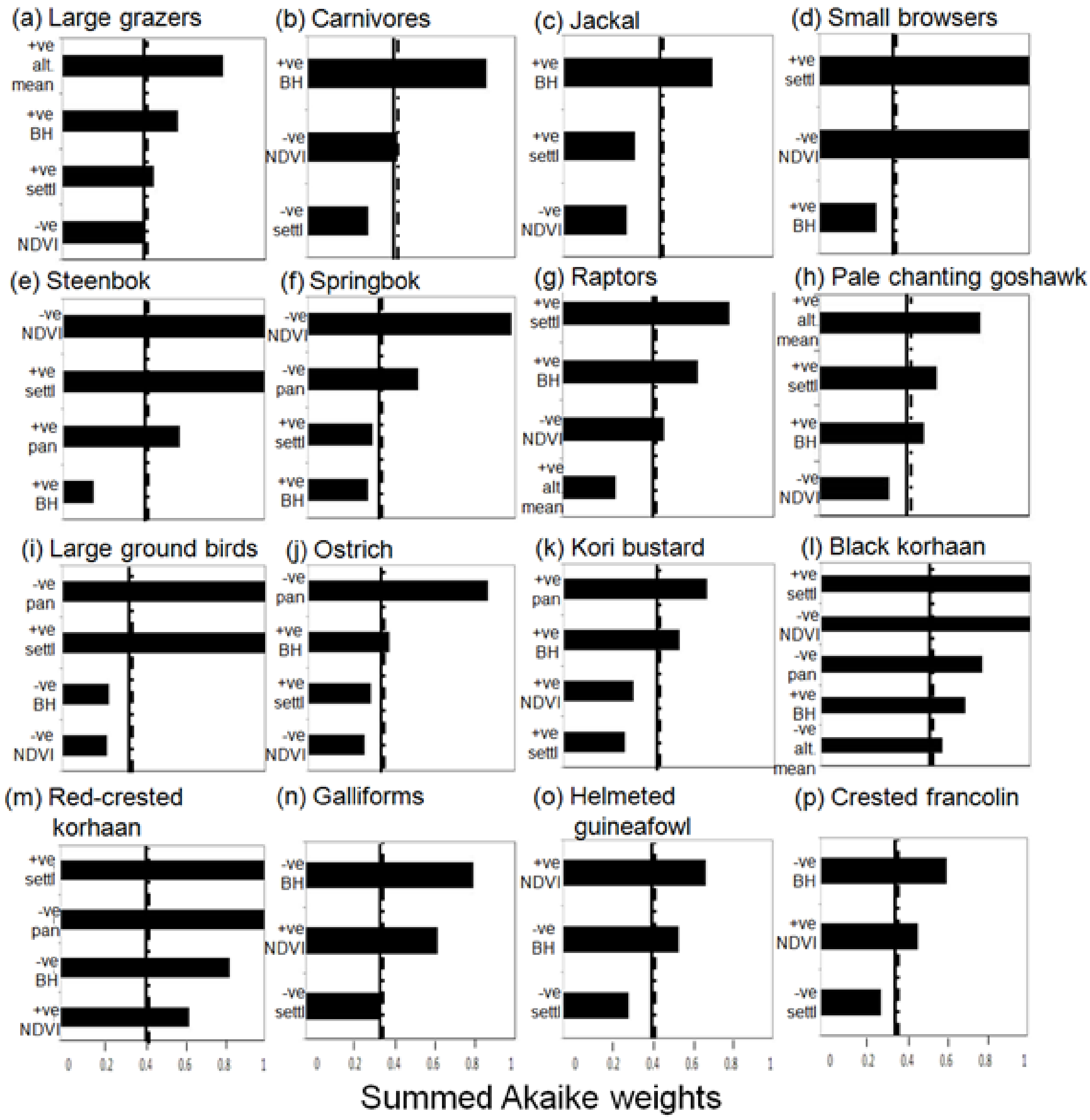

Figure 3.3. Ranking of variables in the best-supported models accounting for cumulative Akaike weights ≥0.95 (Table 3.4). –ve and +ve indicate direction of effect on wildlife abundance. settl, settlement proximity; BH, borehole proximity; NDVI, flush Normalised Difference Vegetation Index; pan, pan proximity; alt.mean, mean segment altitude. Null variable (—— mean selection probability; ▬ ▬ ▬ 95th percentile, 100 replicates; see *Statistical analysis* section of Chapter 4 for how the null variable and its 95th percentile are calculated). Selection probabilities greater than the null variable and its 95th percentile represent significant effects.

Table 3.4. Effects of anthropogenic impacts (hunting, indexed as proximity to settlement and cattle density, indexed as proximity to borehole) and flush NDVI (change in NDVI over the wet season, a proxy for segment-specific rainfall) for wildlife functional groups and species, assessed by multi-model inference across candidate models that also included combinations of potentially important terrain and ecological variables (listed under Model). Model-averaged parameter estimates are shown, with lower and upper confidence intervals in parentheses; parameters for which confidence limits do not span zero are shown in bold. See Fig. 3.3 for selection probabilities and Table S4 for highest ranked models, number of predictors, AICc of best-fitting model, AICc differences, model Akaike weights and cumulative Akaike weights.

Response Variable	segments with ≥1 record	Model[b]	Averaged-model β (confidence interval)		
			Settlement proximity	Borehole proximity	Flush NDVI
Large-bodied grazers	9	int+alt.mean	0.19 (−0.38, 0.76)	0.28 (−0.42, 0.98)	−2.20 (−9.10, 4.69)
Medium-bodied browsers	109	int	**0.36 (0.13, 0.59)**	−0.003 (−0.09, 0.08)	**−6.85 (−10.70, −2.96)**
Steenbok	93	int+distpan	**0.34 (0.14, 0.53)**	−0.003 (−0.05, 0.04)	**−6.04 (−9.05, −3.02)**
Springbok	19	Int−distpan	0.07 (−0.25, 0.39)	0.05 (−0.25, 0.35)	**−15.00 (−25.80, −4.16)**
Carnivore[a]	19	int	0.01 (−0.16, 0.18)	0.35 (−0.20, 0.89)	−1.83 (−7.50, 3.83)
Jackal[a]	16	int	0.04 (−0.20, 0.27)	0.29 (−0.28, 0.86)	−0.26 (−3.05, 2.52)
Pale chanting goshawk[a] (*Raptor*)	69	int−alt.mean	0.11 (−0.14, 0.34)	0.07 (−0.17, 0.37)	−0.66 (−3.09, 1.77)
Large ground birds	211	int−distpan	**0.35 (0.19, 0.51)**	−0.01 (−0.09, 0.06)	−0.14 (−1.00, 0.72)
Ostrich	19	int−distpan	0.05 (−0.16, 0.26)	0.08 (−0.22, 0.37)	−0.26 (−2.51, 1.99)
Kori bustard[a]	14	int+distpan	0.03 (−0.17, 0.23)	0.22 (−0.34, 0.78)	1.05 (−3.61, 5.71)
Black korhaan[a]	91	int−alt.mean−distpan	**0.59 (0.34, 0.84)**	0.15 (−0.12, 0.42)	**−4.88 (−8.13, −1.62)**
Red-crested korhaan[a]	119	int−distpan	**0.43 (0.23, 0.62)**	−0.20 (−0.46, 0.05)	1.84 (−1.95, 5.63)
Galliforms	48	int	−0.08 (−0.35, 0.19)	−0.24 (−0.74, 0.27)	4.02 (−3.80, 11.80)
Helmeted guineafowl	30	int	−0.03 (−0.20, 0.13)	−0.19 (−0.68, 0.31)	3.81 (−4.20, 11.80)
Crested francolin	23	int	−0.05 (−0.35, 0.24)	−0.42 (−1.39, 0.56)	3.24 (−6.80, 13.30)

[a] Modelled using count data; otherwise as presence/absence. Among functional groups, large-bodied grazers, medium-bodied browsers, large ground birds and galliforms modelled using logistic regression because one of the group members was congregatory (see main text).

[b] int, intercept; distpan, distance to nearest pan; alt.mean, mean segment altitude; alt.var, altitude variance along segment. +ve or –ve prefix shows direct of effect for the habitat variables.

Table 3.5. Raw encounter rates (animals km^{-2}) of large-bodied grazers and browsers in Kalahari protected areas (PAs) relative to those from sampled South African PAs (considering from one to four parks for each species), with abundance estimates derived from driven transects. Also shown are estimates for Shamwari Game Reserve (walked transects), Kruger National Park (Smit *et al*., 2007; aerial counts) and five other PAs reviewed by Hayward *et al*. (2007, aerial counts).

Species	Density (animals km^{-2})					
	Driven transects			Walked transects	Aerial counts	Aerial counts
	Eight Kalahari PAs (this study)	1 to 3 PAs, MLR, PRR, PNP	Sabi-Sand Wildtuin	SGR	1 to 5 PAs, including KNP, MZNP, Addo, Nyathi, Darlington	Kruger National Park
	$\bar{x}$ ± SD (*n* = 352 segments)	Hayward *et al.* (2007) [a] $\bar{x}$ (range)	Ben-Shahar (1995) $\bar{x}$ (range)	Hayward *et al.* (2007) [a] $\bar{x}$ (range)	Hayward *et al.* (2007) [a] $\bar{x}$ (range)	Smit *et al.* (2007) [n] $\bar{x}$ (range)
Giraffe	0.075 ± 0.768	0.39 [b]		0.74 (0.13–0.96)	-	0.24 (0.23–0.25)
Eland	0.026 ± 0.302	1.24 [c]		0.56 (0.37–0.66)	0.89 (0.19–1.43) [i]	0.03 (0.02–0.05)
Kudu	0.021 ± 0.336	1.17 (0.53–2.13) [d]		4.80 (4.27–5.26)	2.17 (0.50–8.44), [j]	0.29 (0.15–0.43)
Wildebeest	0.253 ± 2.277	4.63 (1.67–8.53) [e]	55 (10–160) [h]	0.65 (0.29–0.93)	1.49 (0.68–1.99) [k]	0.69 (0.63–0.72)
Hartebeest	0.009 ± 0.139	3.63 (2.43–5.33) [f]		0.72 (0.60–0.84)	1.30 (0.11–2.43) [l]	-
Zebra	0.004 ± 0.067	2.40 (0.33–5.73) [g]	12 (0–60) [h]	0.55 (0.33–0.74)	0.20 (0.04–0.43) [m]	1.53 (1.43–1.60)

[a] Survey timing: Shamwari Game Reserve (SGR: all species sampled annually 2000–2004 inclusive); Karoo National Park (KNP: 2002–2004); Mountain Zebra National Park (MZNP: 2002–2004); Addo Elephant National Park (Addo: 2002–2004), Nyathi and Darlington (different sections of Addo, both fully fenced and separate from Addo Main Camp, 2004); Madjuma Lion Reserve (MLR, sampled 1997 and 1998); Phinda Resource Reserve (PRR: 1995); Pilanesberg National Park (PNP: 1997)

[b] One estimate: PRR.

[c] One estimate,: PNP

[d] Three estimates, two PAs: MLR, PRR

[e]. Three estimates, two PAs: MLR, PRR

[f] Three estimates, two parks: MLR, PNP.

[g] Four estimates, three parks: MLR, PRR, PNP.

[h] Sabi-Sand Wildtuin (540 km^2), bordering Kruger National Park, South Africa; 52 abundance estimates, 13 monthly driven surveys May 1998–June 1999, in four different habitat types

[i] Ten estimates, five PAs: KNP, MZNP, Addo, Nyathi, Darlington

[j] Eleven estimates, five PAs: KNP, MZNP, Addo, Nyathi, Darlington

[k] Four estimates, three PAs: KNP, Nyathi, Darlington

[l] Eleven estimates, five PAs: KNP, MZNP, Addo, Nyathi, Darlington

[m] Ten estimates, four PAs: KNP, MZNP, Addo, Nyathi

[n] Mean (and range) of aerial census counts during 1987–1993.

Discussion

Designating WMAs has provided clear conservation benefits for many functional groups and species. Positive WMA effects were observed for large-bodied grazers, medium-bodied browsers, carnivores and large ground birds. Abundance of large-bodied grazers and large ground birds was greatest in PAs, intermediate in WMAs and lowest in unprotected areas, while abundance of medium-bodied browsers was greatest in WMAs, intermediate in PAs and lowest in unprotected areas. However, of the legally huntable species, WMAs appeared to offer marginal benefit for steenbok, while the infrequently encountered large-bodied browsers, although not modelled, were rarely seen outside of PAs; therefore WMAs appear best-suited for conserving medium-sized ungulates while PAs remain crucial for conserving large-bodied herbivores. Galliforms were least frequently encountered in WMAs, and were more abundant in unprotected areas than in either conservation designations, perhaps reflecting differences in ecology, resources or the abundance of competitors and predators.

There was strong evidence that hunting depressed abundance or incidence of several functional groups and individual species. Conversely, and contrary to frequent opinion (Verlinden, 1997; Herremans, 1998; Wallgren *et al.*, 2009b), no evidence of any direct impact of cattle on wildlife abundance was observed. The clear implication here is that, if hunting pressure can be alleviated or at least regulated, WMAs offer positive conservation benefits for characteristic Kalahari wildlife.

Contrasts of Kalahari wildlife encounter rates to those of other southern African savannas

Before commenting on the performance of WMAs relative to PAs and unprotected areas, it is important to first assess how effective Kalahari PAs are at conserving wildlife. Although offering some benefits to large-bodied herbivores relative to unprotected areas, Kalahari PAs supported much lower abundances of large-bodied grazers and browsers for which species-specific models were not developed (giraffe, eland, kudu, wildebeest, hartebeest and zebra) than observed in South African PAs; because raw encounter rates measured in this study were an order of magnitude less than obtained by similar driven transect methodology or other census methods across ecologically comparable PAs in South Africa (Table 3.5). Caveats include the possibility that wildlife in South African PAs may be more habituated to vehicles (e.g. Ben-Shahar, 1995), that transects may have preferentially sampled habitats where visibility was greater or ungulate density higher (as may occur in pans) or that greater rainfall or more mineral-rich soils in South African parks may support greater carrying capacity; for example much of Kruger National Park receives a mean 400–600 mm y^{-1} of rainfall, up to 25% greater rainfall than much of central Botswana. However, given comparable landscapes (thickets, grasslands and savanna habitats) and variable size for PAs reported by Hayward *et al.* (2007: ranging 70–3410 km^2), these are not likely to be consistent biases. The unavoidable conclusion is that densities of the large-bodied grazers and browsers have been depleted within Kalahari PAs. Park guards in Kalahari PAs are few and restricted to PA gates, and only occasionally undertake anti-poaching patrols. In contrast, most South African PAs are fenced, which restricts unauthorised access, and receive a greater degree of anti-poaching patrols (e.g. Hayward *et al.*, 2007) than occurs in the Kalahari.

Aerial counts by DWNP in the Kalahari ecosystem suggested that large-bodied herbivores (both browsers and grazers), particularly migratory species, declined drastically between 1979/1980 and 2004 (Fynn & Bonyongo, 2010). Wildebeest and hartebeest experienced >90% declines and zebra 75% declines, although some species fared better, with giraffe and eland apparently unchanged and a 20% increase for gemsbok (Fynn & Bonyongo, 2010). Although population crashes were presumed to have been primarily drought-induced in the early 1980s (Spinage & Matlhare, 1992; Fynn & Bonyongo, 2010) reasons for the lack of subsequent recovery are unclear, particularly for species such as wildebeest, hartebeest and zebra. In contrast, in the Serengeti wildebeest populations increased sixfold in 14 years following rinderpest disappearance in 1963 (Sinclair, 1995). While aerial census methodology is reported to have remained consistent, the possibility that the large estimates (approximately 300,000 animals each for wildebeest and hartebeest during the 1979/1980 counts; Fynn & Bonyongo, 2010) may have been overestimated owing to the difficulty of censusing animals that congregate in large herds (Buckland *et al.*, 2001) cannot be excluded. Moreover, although it has been argued that the lower abundance in 2004 than in 1979/1980 was due to fencing along the northern border of the CKGR, restricting access to the Okavango river system and Lake Xau north of the PA (Fynn & Bonyongo, 2010), this remains debatable.

First, whereas Fynn & Bonyongo (2010) argue but provide no evidence that fencing severed movements of animals tracking forage resources, Williamson *et al*. (1998) showed that movements were in search of water, because migrating animals left abundant forage inside CKGR for localities with limited forage but plentiful surface water. Large numbers of some species died in the early 1980s owing to the fence, directly entangled or as a result of thirst and starvation, with an estimated 52,000 (95% CI: 28,000–76,000) wildebeest killed in 1983 (Williamson & Mbano, 1988). However, since the mid-1980s wildlife in the CKGR has been supplied with water from boreholes, with no significant change to grass species composition or habitat degradation reported around these watering points after 10 years of use (Makhabu *et al*., 2002), so that forage and water may not be limiting factors within CKGR.

Second, sampling was intensive on both sides of the fence, but low large-bodied herbivore encounter rates were observed on PAs either side of the fence, and in adjoining WMAs and unprotected areas. Furthermore, because the west and south of the CKGR are unfenced, migratory species should be able to move between their dry and wet season foraging grounds inside and outside PAs; Verlinden (1998) showed that eland, wildebeest and hartebeest had their dry season ranges restricted to PAs, and the wet season centred on neighbouring WMAs. Consequently, one would expect much greater wildlife abundance inside PAs than outside, because wildlife were sampled during the dry season, but, because the large-bodied herbivore encounter rates were only marginally greater in PAs than in WMAs and unprotected areas, this suggests that the Kalahari PAs are failing to effectively conserve this group even within park boundaries. Because the abundance of lions and leopards—the largest carnivores in the Kalahari capable of killing many of the large-bodied herbivores—was also low within PAs (although this may partly be because the felids are more active at night), predation is unlikely to explain the low large-bodied herbivore abundance. Consequently, the low encounter rates for the large-bodied herbivores is suggestive of unregulated hunting, independently, or jointly with Allee effects, as an issue limiting the effectiveness of Kalahari PAs and impeding population recovery since the 1980s decline.

Wildlife response to land-use designation

The mean distance between sampled WMA segments and PAs was 68 km ± 40 SD and, because most WMAs abut PAs, greater wildlife abundance was expected in WMA wildlife zones (especially closer to PAs) as these areas should be exposed only to legal hunting. However, for species benefiting from WMAs abundance was not enhanced by PA proximity, although a marginal relationship was found for steenbok (non-significant after Bonferroni correction for multiple tests). The lack of any relationship between PA proximity and wildlife encounter rate suggested anthropogenic threats are not restricted to the WMA livestock-rearing buffer and may persist even within WMA wildlife zones.

Steenbok were more frequently encountered in WMAs than in either PAs or unprotected areas. This may reflect density compensation, following population crashes of large-bodied herbivores, as observed in other systems where mid-sized taxa compensate for reduced abundance of large-bodied taxa with similar dietary requirements (e.g. Peres & Dolman, 2000).

Abundance of pale chanting goshawk was greater in WMAs than in PAs, but encounter rates within WMAs did not vary with distance to park boundary or human settlement. Because this species prefers drier areas (Harrison *et al*., 1997, Fig. 3.3), the difference between PA and WMA encounter rates may be due to a combination of greater representation of WMAs in the drier south-west of the sampling extent, and more open woody vegetation cover in that area, permitting more efficient hunting; the species hunts from a perch, rather than on the wing (Herremans & Herremans-Tonnoeyr, 2000). Wallgren *et al*. (2009b) found that although small mammal (≤0.2 kg) trapping frequency was highest in PAs, abundance, species richness and diversity were not different across PAs, WMAs and unprotected areas (except inside cattle ranches), which suggests that variations in habitat structure rather than food availability may account for the observed abundance patterns of raptors feeding on these small mammals, such as pale chanting goshawk.

Declining encounter rates for large-bodied grazers across the site protection spectrum perhaps reflects their status as the preferred target for both legal and illegal hunting (Verlinden, 1997; Verlinden *et al*., 1998); thus cumulative offtake was probably greatest in unprotected areas, reduced in WMAs, and lowest in PAs. Although DWNP undertake aerial surveys on which WMA hunting quotas are ideally based, counts are often PA-restricted (DWNP, unpublished data); the poor geographic coverage and time-lag between sampling and quota-setting possibly leads to both spatial and numerical mismatches between quotas and true abundance in WMAs. Additionally, perhaps because large-bodied ungulates generate greater revenue (Du Toit, 2002; Naidoo *et al.*, 2009) there is political and financial pressure on DWNP to allocate large trophy hunting quotas, despite a lack of scientific basis, so as to entice communities to adopt more pro-conservation attitudes as per WMA assumptions.

In Kalahari WMAs, gemsbok constitutes the second largest proportion (by number) of huntable species, representing ≥15% of all quotas for 11 of the 15 sampled WMAs during 2007–2009 (second to ostrich, which constituted ≥35%: DWNP, unpublished data). As the largest legal ungulate quarry, extremely popular with hunters (Verlinden, 1997), gemsbok should generate the largest revenue per animal. However, scant evidence was found that WMAs benefit gemsbok and the species’s low encounter rate in WMAs suggests that either legally permitted offtake is unsustainable or unregulated hunting persists. This is a cause for concern given the species’s importance to the economic viability of WMAs. Because overall gemsbok numbers are thought to have increased in the Kalahari since the 1980s (Fynn & Bonyongo, 2010), as these animals are largely restricted to PAs this suggests WMAs have lower positive effects compared to strict parks.

The causes of the paradoxically greater abundance of galliforms (principally helmeted guineafowl) in unprotected areas and apparent lower abundance in WMAs relative to PAs, are unclear, but there are at least two plausible mechanisms independent of hunting by humans, a widely assumed direct threat to galliforms (e.g. Herremans, 1998). First, galliforms associate with heavily wooded habitats (Harrison *et al.*, 1997), which were most prevalent in unprotected areas, largely driven by cattle-driven effects up to 10 km around boreholes (Chapter 4). Second, as results from this study and earlier published work (e.g. Herremans, 1998) suggest, raptors have greater encounter rates in conservation areas, and the increased incidence of raptor predation in these land-uses may account for reduced galliform encounter rates. Therefore, availability of food resources and/or predator release may override effects of hunting by humans on these *r*-selected species, and consequently, galliform hunting quotas need to consider these potential ecological trade-offs.

Furthermore, robust census methodologies are critical, as for instance contrasts of sighting records based on unsystematic surveys across land-use types (Herremans,

1998) had suggested galliforms were least abundant in unprotected areas; in contrast, results from this study highlight the importance of using standardised and narrow strip transects because wildlife density in unprotected areas may otherwise be underestimated, as likely to have happened in Herremans (1998), owing to the poor visibility which effectively results in narrower sampling strips within these landscapes relative to land-use types with less woody vegetation cover.

Effects of human settlement and borehole proximity

Previous work in the Kalahari (Verlinden, 1997; Herremans, 1998; Verlinden *et al.*, 1998; Wallgren *et al.*, 2009b) hypothesised that key mechanisms driving wildlife population declines were poaching and cattle-grazing, although their relative importance was not tested. At the large spatial scale considered here, results from this study suggest that unregulated hunting is a genuine threat while cattle-grazing is not. Hunting effects may in part be greater owing to the greater distance over which this threat operates. Transhumance is not practised in the study area, and cattle are restricted to within 10 km around boreholes (Perkins, 1996). Moreover, the proportion of WMAs and unprotected areas that is within 10 km of a borehole is approximately 10% and 70% respectively, suggesting a small spatial extent over which cattle-grazing may affect wildlife in WMAs (see Chapter 4). In contrast, hunters on horseback can travel much farther than 10 km.

Further evidence that hunting effects were more important than cattle-driven effects came from contrasts of model support for wildlife abundance across the three land-use types. The hypothesis that the effects of PAs and WMAs were similar (Model 1) should have had strong support for more species and groups, if indeed illegal hunting was much reduced in WMAs. This was expected because, for most sampled WMAs, the WMA wildlife zone areal extent was at least three times greater than the livestock-rearing buffer (mean WMA area 4117 km^2 ± 3835 SD, n = 15; in contrast, assuming a 20 km WMA livestock-rearing buffer gives an area of approximately 1257 km^2), so that much of the WMA wildlife zone areal extent was far from human settlements. Furthermore, human population density in WMA wildlife zones was negligible (Appendix 3.1). However, the low encounter rate of legally hunted species in WMA wildlife zones suggests that subsistence hunting persisted. Thus WMAs appear to underperform in abating the impacts of illegal hunting.

However, the extent to which hunting may be a threat is not universal for functional groups and may be species-dependent; for example, the larger-bodied ostrich and kori bustard were less affected by this threat than the smaller-bodied black and red-crested korhaans. This may be due to several factors, e.g. korhaans skulk when approached rather than fly off and thus may be easier to kill, ostriches may outrun hunters, ostrich and kori are less likely to be killed by catapult shots or caught in snares (most of which are improvised motion-triggered contraptions made from strings or twigs: pers. obs.), and may also be less hunted due to their stronger legal protection (kori hunting is prohibited, ostrich only huntable by permit, while no strict regulation exists for the smaller korhaans).

Of the 11 species for which species-specific models could be developed, four (gemsbok, ostrich, steenbok and springbok) are huntable trophy species in WMAs, but their ecology suggests even legal offtake needs to be managed cautiously. Gemsbok was infrequently encountered in WMAs and its hunting therefore seemed unsustainable. While steenbok benefited most from WMAs, springbok and ostrich had similar encounter rates in WMAs and PAs. But outside PAs, for steenbok, springbok and ostrich, habitat variables (flush NDVI and pan proximity) showed strong selection probabilities, suggesting that the abundance of these species was strongly determined by landscape features, rather than the two main threats (cattle-grazing and bushmeat hunting) that WMAs aim to curb. Findings from this study suggest an urgent need to incorporate an improved understanding of the ecology and demographics of trophy species into quota-setting mechanisms.

Conservation implications

Within Botswana, PAs comprise 17% and WMAs 22% of the national land area. WMAs offer tangible benefits to many wildlife species in the study area, greatly expanding and buffering the areal extent of conservation areas. However, findings from this study highlight the importance of assessing WMA ecological viability, and of strictly regulated hunting quotas that are based on ecological rather than economic considerations. This is probably more important in those semi-arid areas such as the

Kalahari that lack mega-herbivores that provide much greater revenue per animal (e.g. Naidoo *et al*., 2009). Paradoxically, while WMAs in semi-arid areas have low carrying capacity, high quotas of trophy ungulates are needed to ensure their economic viability owing to the lack of high-value species; for instance during 2007–2009, a mean 97 ± 23 SD animals per annum of 14 species were availed for trophy hunting in each of nine WMAs (mean WMA area 3861 km^2 ± 3787 SD) sampled during this study (DWNP, unpublished data).

A key assumption of the WMA model is that increased income from trophy hunting decreases illegal hunting (Du Toit, 2002; Child & Barnes, 2010). However, results from this study suggest that illegal hunting may persist in both WMAs and the poorly protected Kalahari PAs. Identification of co-occurring economic activities at WMA level, against which wildlife use and species-specific responses could be compared, would help clarify the value of wildlife to livelihoods, and identify factors optimising WMA effectiveness. If the contribution of trophy hunting to livelihoods is minor, there may be little incentive to cease illegal hunting, and the WMA model may be inadequate to curb wildlife declines. Results from this study highlight the importance of testing the assumptions behind these alternatives to strictly protected landscapes, and show that although WMAs have important tangible benefits for wildlife conservation they cannot replace PAs.

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Appendix 3.1

Wildlife Management Areas (WMAs): Institutional organisation and density of human populations and boreholes relative to protected areas and unprotected pastoral lands

The WMAs were established primarily for wildlife conservation, and secondarily for sustainable wildlife utilisation for economic returns (Rozemeijer, 2009). The Botswana government's Department of Wildlife and National Parks (DWNP) supported communities in forming a legally constituted community trust, to which WMA management was devolved (Twyman, 2001). Trusts have an elected management committee that develops benefit-sharing protocols, and land-use and management plans that guide zoning within WMAs. Annually, after DWNP issue WMA-specific hunting quotas, the management committee decide how much trophy hunters should be charged for the huntable species. Part of the revenues from hunting and tourism are directly paid to households, and the remainder invested in community projects selected by the management committee.

Protected areas are occasionally patrolled by DWNP personnel. In contrast, within WMAs, DWNP staff only attend to reported incidents of unregulated hunting or problem wildlife animals (e.g. carnivores depredating livestock) that stray near human settlements; large dangerous predators are captured and released in parks, but are shot if this is not possible (C. Taolo, DWNP, pers. comm.), but it is unclear what impact such offtake has on overall carnivore abundance and land-use specific population trends. None of the WMAs have regular community-led patrols, although community members ('wildlife escorts') accompany hunters during sanctioned trophy hunts. Thus the level of enforcement is lower in WMAs than in PAs. No coordinated or regular anti-poaching patrols are undertaken in unprotected areas; however, DWNP personnel may again attend to incidents of livestock depredation, whose frequency is variable, although in a part of this study's sampled area, lions and leopards killed at least ten cattle, goats or sheep per month over the period October 1999–September 2002 (Schiess-Meier *et al*., 2007).

Since designation, none of the PAs have had human settlements within their boundaries, except for nomadic non-pastoralist San communities in the Central Kalahari Game Reserve (CKGR), totalling a maximum of five communities each numbering fewer than 150 people when the park was created in 1961 (Campbell, 1973; Tanaka, 1976). Presently, these communities number 10–50 people each (C. Taolo, pers. comm.), following large-scale relocation of San from the CKGR since the mid-1990s (e.g. Taylor, 2003).

One of the study's predictions was that WMAs presently experience lower cattle grazing and human population pressure than unprotected areas. Current human population density, based on the 2001 census estimates (www.cso.gov.bw/images/stories/Census/population_town.pdf) of only settlements with more than 200 people as these could be accurately mapped using coordinates obtained from the Botswana atlas (Government of Botswana, 2001) and from the National Geospatial Intelligence Agency, (www.geonames.nga.mil/ggmagaz/geonames4.asp), were compared among WMAs and unprotected areas. Comparisons of borehole density exclude boreholes inside PAs and within WMA wildlife zones (see Appendix 3.2 for justifications). Human population and borehole density were both calculated within all WMA livestock-rearing buffers and unprotected area shapefile polygons that intersect sampled 25-km grid-squares. This was achieved by first calculating land-use-specific surface areas in each 625 km^2 grid-square with at least one sampled segment. Within each 625 km^2 grid-square, land-use specific human and borehole density was then calculated, based on population estimates of settlements and number of boreholes that intersect the land-use-specific polygons, respectively. Overall land-use density estimates were obtained by averaging across all polygons designated as either WMA livestock-rearing buffer or unprotected area. Density estimates are based on measures extracted for each 625 km^2 grid-squares rather than across the entire land-use-specific polygons, because human activities are restricted to 20–40 km around settlements (Chanda *et al*., 2003). Contemporary human population and borehole density within WMA livestock-rearing buffers are approximately 10% of that across unprotected areas (Table S1).

Although the lack of historical records and the undated borehole dataset precluded confirmation that these densities were always lower in WMAs, there is strong circumstantial evidence to suggest this. Most boreholes in the Kalahari were drilled after national independence in 1966 (Perkins, 1996) primarily through government grants and livestock development schemes, such as the Tribal Land Grazing Policy (TGLP) of 1975 that also promoted demarcation and fencing of ranches (Twyman, 2001). Government-financed borehole drilling continued through the 1980s, but dropped when TGLP was discontinued in 1991 (Perkins, 1996). On the other hand, discussions to create WMAs began as early as 1983 (Cooke, 1985), and WMAs were first officially mentioned as an alternative land-use type in the 1986 Fauna Conservation Act (Twyman, 2001). When they were designated, WMAs excluded ranched areas. Moreover, with minimal government grants for borehole drilling in unfenced communal areas post-1990 (Perkins, 1996), it is unlikely that the greater borehole density in unprotected areas (Table S1) was due to a recent increase in the number of boreholes drilled in this land use, relative to WMAs.

Thus, the assumption that WMAs were preferentially located in areas with lower cattle density and have always had lower borehole and human density is not unrealistic.

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Table S1. Mean (± SD) of human population and borehole density across protected areas (PAs), Wildlife Management Area (WMA) wildlife zones (WMA wildlife zone), WMA livestock-rearing buffers and unprotected areas.

Variable	PA	WMA wildlife zone	WMA livestock-rearing buffers	Unprotected area	F	*df*	*P*
Borehole density (boreholes km^{-2}) [a]	0 ± 0	0 ± 0	0.003 ± 0.006	0.016 ± 0.018	34.706	273	<0.0001
Human population density (persons km^{-2}) [b]	0 ± 0	0 ± 0	0.092 ± 0.258	0.998 ± 2.407	9.458	273	<0.0001

[a] All pairwise comparisons significantly different (Tukey HSD, $P < 0.05$), except between PA and WMA wildlife zone ($P = 1.000$), between PA and WMA livestock-rearing buffer ($P = 0.515$) and between WMA wildlife zone and WMA livestock-rearing buffers ($P = 0.527$).

[b] All pairwise comparisons significantly different (Tukey HSD, $P < 0.05$), except between PA and WMA wildlife zone ($P = 1.000$), between PA and WMA livestock-rearing buffer ($P = 0.989$) and between WMA wildlife zone and WMA livestock-rearing buffers ($P = 0.989$).

Appendix 3.2

Validation of borehole proximity as a measure of cattle density: relation with field-based estimates of cattle abundance

During field surveys cattle were encountered within a PA and within a WMA wildlife zone in only two segments in each land-use type, resulting in similarly low encounter rate (mean within PAs 0.006 animals km^{-1} ± 0.10 SD; WMA wildlife zone 0.01 animals km^{-1} ± 0.15, $t_{448} = 0.711$, $P = 0.477$). Cattle encounter rates were an order of magnitude greater within WMA livestock-rearing buffer segments (within ≤20 km of settlements: 0.73 animals km^{-1} ± 2.88 SD), although encounter rates were then two-fold greater in unprotected areas (1.47 animals km^{-1} ± 6.01 SD). However, although encounter rates during driven transects sampled those cattle visible in the immediate vicinity of the transect segment on that day, they have large sampling error variance and do not provide a full picture of the prevailing cattle density per segment. Consequently, a dataset of borehole locations was used, because cattle are restricted to within a few kilometres of these watering points (Perkins, 1996) that therefore predict the spatial distribution of cattle averaged over longer time periods.

A spatially referenced borehole dataset (Botswana government: Geological Surveys Department, unpublished data) included both privately owned boreholes outside PAs, predominantly used for watering cattle, and government-owned boreholes provisioning wildlife inside PAs or human settlements throughout the study area. Because interest was on boreholes used for cattle-rearing, all government-owned boreholes were excluded from analysis. Furthermore, because cattle were effectively absent from WMA wildlife zones (as demonstrated by encounter rates from field surveys, see above), private boreholes located in these zones were also excluded from analysis. Therefore for each transect segment, the distance of the segment start point to the nearest private borehole located either in a WMA livestock-rearing buffer or in unprotected areas was extracted. Segment mid-points often could not be established because many of the tracks along which counts were made were unmapped.

At the landscape level (25-km grid-square), the following metrics were compared: (1) cattle aerial counts obtained from the Department of Wildlife and National Parks (for methodology see Verlinden, 1997; the most recent and comprehensive data available were from the dry season, June–September 2003: mean

3.4 livestock unit km^{-2} ± 3.9 SD, range: 0–17.8 livestock unit km^{-2}), (2) field counts of cattle per 40-km long 100-wide strip transects along which wildlife were sampled (mean 1.75 cattle km^{-1} ± 2.97 SD, range: 0–13 cattle km^{-1}, for 40-km transects) and (3) density of boreholes per 25-km grid-square (mean 0.02 boreholes km^{-2} ± 0.02 SD, range: 0–0.11 boreholes km^{-2}). All three measures were significantly positively related ($r > 0.4$, $P < 0.0001$; Fig. S1), validating use of borehole data as a measure of cattle density. At the segment level (overall mean segment length 3.61 km ± 0.99 SD, $n = 757$, non-PA segments only), field counts of cattle were negatively related to the segment distance to the nearest borehole (Fig. S1d). To test whether proximity to borehole acts similarly as a proxy of cattle density in different land-use designations, comparisons were made of the relation between segment-level cattle encounter rates obtained during transect surveys (cattle km^{-1}, integer of square-root transformed value) and square-root transformed distance to nearest borehole (km), among those segments located in unprotected areas, those within WMA livestock-rearing buffers (within 20 km of settlements), and those within WMA wildlife zones. Both the density of cattle close to boreholes, and the rate at which this declined with increasing distance from the nearest borehole, were similar between unprotected areas (Generalised Linear Mixed Model incorporating grid-square as a random effect with Poisson error and log link function: unprotected area constant −3.880 ± 0.206 SE; coefficient of distance to borehole: −0.248 ± 0.073) and WMA livestock-rearing buffers (constant −4.287 ± 0.567, $t_{657} = 0.733$, $P = 0.464$; borehole −0.503 ± 0.178, $t_{657} = 1.325$, $P = 0.186$). Thus borehole proximity acted as a similar proxy for cattle density in both land management types. In contrast, in WMA wildlife zones both the intercept and borehole coefficient were close to zero, confirming negligible presence of cattle (GLMM constant −18.391 ± 19.008, $z = -0.968$, $P = 0.333$; borehole −18.391 ± 19.008, $z = 0.269$, $P = 0.788$).

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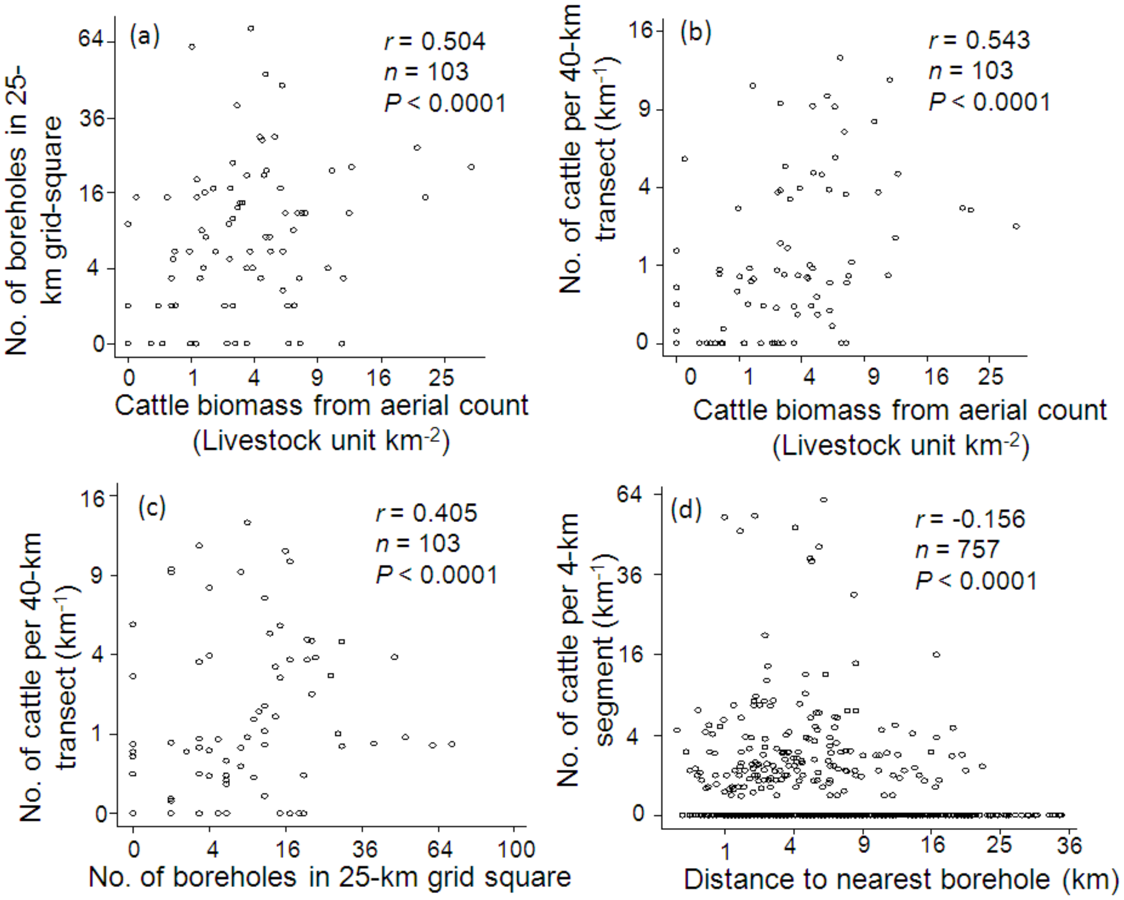

Figure S1. Relationships between (a) number of boreholes in 25-km grid-squares, (b) field count of cattle in 100-m wide 40-km long strip transects, and cattle biomass as estimated from June–September 2003 aerial census;(c) field count of cattle per 40-km transect and borehole density per 25-km grid-square, and (d) field count of cattle per c.4-km segment and segment proximity to the nearest borehole (considering only segments in WMAs and unprotected areas). Correlations were performed on square-root transformed data; plots show untransformed data. Boreholes in parks and in WMA wildlife zones were excluded in calculating both borehole density and segment proximity to borehole.

Appendix 3.3

Detectability of wildlife in relation to land-use specific density of woody vegetation

To examine how detectability of characteristic species varied among segments with different density and canopy cover of woody vegetation, the Effective Strip Width (ESW) estimated in DISTANCE analysis (Buckland *et al*., 2001) was compared among models in which the detection function was stratified by woody vegetation canopy index (Table 3.1). The ESW estimates for individual species (following truncation of the 10% most distal records) had large confidence intervals due to low encounter rates; therefore, data for similar-sized species were pooled and truncated at 200 m to improve the fit of detection functions. The ESW for cattle was used to test for detection bias of wild large-bodied ungulates (giraffe, eland, kudu, gemsbok, wildebeest, hartebeest and zebra) and ostrich because even after pooling the total number of large-bodied ungulates and ostrich, sightings were less than the 40 records recommended by Buckland *et al*. (2001), and thus inadequate for DISTANCE analysis for some of the woody vegetation canopy cover index scores (<30 m, 14 groups; 30–80 m, 23 groups; 80–150 m, 21 groups; >150 m, 147 groups).

The ESW was greater than 50 m for large and medium bodied size classes regardless of the woody cover index (Table S2). Thus for analysis of wildlife responses to land-use designation and anthropogenic factors, all data were truncated at 50 m and analysed surveys as 100-m wide strip transects. Within these strip transects, there was no detection bias for large-bodied ungulates, bustards and ostrich (Table S2) between segments with denser or more open cover of woody vegetation. However, abundance estimates for medium-sized mammals may have been underestimated by up to 24% in densely wooded strata, for which the estimated ESW was only 38 m (confidence interval: 14–106 m; Table S2). More densely wooded segments were predominantly found in unprotected areas (Chapter 4) relative to WMAs and PAs. Therefore, because medium-bodied browsers' apparent encounter rates in WMAs (the land-use favoured by this group, see main text) were at least four times greater than in unprotected areas (Fig. 3.2c, main text), a 30% underestimation of abundance in the unprotected area would make the reported patterns conservative. Similarly, the smallest-bodied species considered (galliforms) were most frequently encountered in unprotected areas (Fig. 3.2o, main text), thus reported results are again conservative. Conversely, jackal encounter rates in unprotected areas were at least half (relative to PA) or one-third (relative to WMA) those of conservation areas (Fig. 3.2g, main text), thus the lower abundance in unprotected areas may be partly attributable to vegetation-mediated encounter rates, inflating the observed difference in density.

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Table S2. Effective Strip Width (m) for different animal size-classes sampled in 1109 transect segments in Protected Areas, Wildlife Management Areas and unprotected areas. For each group, data (truncated at 200 m) are pooled across land-use types, with detection function and encounter rate stratified by woody vegetation canopy cover index (Table 3.1). Ninety-five percent confidence intervals in parentheses, *n* = number of groups recorded.

Taxa [a]		Relative woody vegetation canopy cover (visibility strata)			
		<30 m (253 segments)	30–80 m (291)	80–150 m (232)	>150 m (333)
Cattle		59 (47–75)	66 (52–84)	65 (49–88)	73 (59–90)
	n	185	172	121	99
Steenbok, jackal		38 (14–106)	35 (21–61)	47 (41–53)	57 (48–68)
	n	29	67	85	93
Kori bustard, black korhaan, red-crested korhaan		57 (47–71)	56 (48–67)	55 (48–64)	43 (0–16,863)
	n	67	97	104	493
Pale chanting goshawk		44 (30–64)	62 (46–83)	48 (38–61)	63 (50–79)
	n	17	48	46	77

[a] Size-classes: (i) cattle (large-bodied ungulates), (ii) steenbok and jackal (medium-sized mammals), (iii) three bustard species (large ground birds) and (iv) pale chanting (perching birds). Cattle data used owing to inadequate sample sizes for large-bodied wild ungulates, and suffices as evidence that similar-sized wildlife ungulates are detectable without bias regardless of vegetation density. Pale chanting goshawk was the only large perching bird for which a large sample size was available.

Appendix 3.4

Vegetation zones and Normalised Difference Vegetation Index (NDVI)

Segment-specific NDVI scores were extracted as area-weighted means computed using the extent of overlap between the 1-km^2 resolution NDVI raster dataset and the straight line connecting the segment's start and end points, buffered by 1-km. Area-weighted means were calculated using the Polygon-in-Polygon Analysis function in Hawth's Tool ArcGIS Extension.

Segment-level NDVI provided a proxy for the effects of cumulative localised rainfall on flush vegetation development (difference in accumulated biomass) between the start of the wet season in October 2008 and the end of the wet season in March 2009. It was important to investigate whether NDVI also represented geographical variation in woody cover between vegetation zones, local variation in habitat structure as measured by the index of woody vegetation canopy cover, or localised cattle impacts close to boreholes (as may be expected if NDVI is influenced by bush cover).

Thus, the relationship between NDVI and vegetation zone was examined, after combining a total of ten finer vegetation types (Weare & Yalala, 1971) mapped in the Botswana atlas into four broad vegetation zone classes based on similarities in physiognomy (Fig. S2): (1) Grassland landscapes (Lake Ngami Savanna Grassland; Fringing Pan Grassland, Delta Grassland, all on fluvisols), (2) Short shrub savanna (Southern Kalahari Bush Savanna; Central Kalahari Bush Savanna, both on arenosols), (3) fine-leaved tree savanna (Northern Kalahari Tree and Bush Savanna; Ghanzi Bush Savanna, on arenosols and luvisols respectively), and (4) broad-leaved tree savanna (Ngamiland Tree Savanna; Tree Savanna with Mophane; Mixed Mophane Tree and Bush Savanna, on various soils). The NDVI marginally increased along this gradient of increasing woody vegetation biomass, being generally greater in tree savanna (classes 3 and 4) than in shrub savanna or grassland vegetation zones (Table S3, Fig. S2). However, the relationship between NDVI and vegetation zone was non-significant, with stronger support for the intercept-only model (Table S3). There was considerable variation in NDVI scores among segments within the same vegetation zone (Fig. S2). Contrary to expectation, however, NDVI was not related to local woody vegetation cover (as indexed by the woody canopy cover metric) or to borehole proximity, as again the intercept-only model received the strongest support (Table S3). Therefore, segment-specific NDVI was considered to primarily represent localised rain showers; local thundershowers are a common phenomenon in the study area (Nicholson & Farrar, 1994). Furthermore, NDVI can be considered as independent of proximity to borehole in GLMMs exploring wildlife responses.

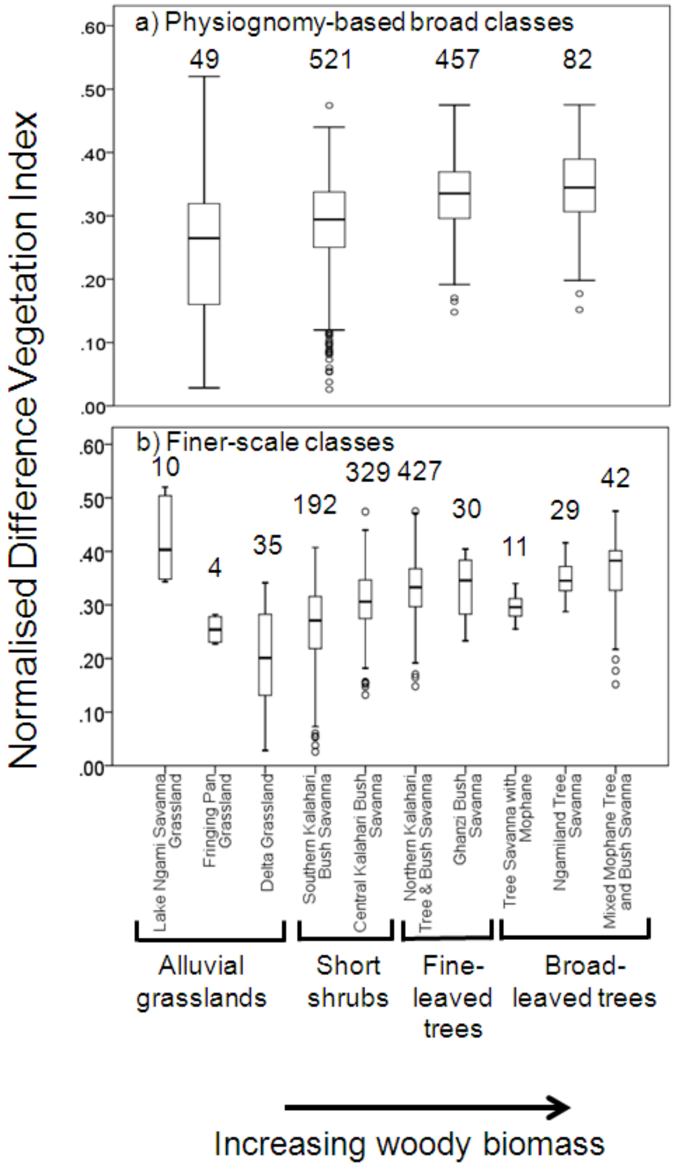

Figure S2. Relationships between (a) physiognomy-based broad vegetation classes, (b) finer-class vegetation zones, and flush Normalised Difference Vegetation Index (NDVI) for 1109 individual 4-km segments. Mean NDVI scores were not statistically different across the vegetation zones (Table S3). Marks outside boxplots are outliers; numbers are sample sizes. Finer-class vegetation zones based on Weare & Yalala (1971), whose classification relies on species composition; the classification into four groups in this study was based on physiognomy.

Table S3. Segment-level Flush Normalised Difference Vegetation Index (NDVI) compared in relation to vegetation zone (grasslands, short shrub savanna, fine-leaved tree savanna and broad-leaved tree savanna), segment-level woody vegetation canopy cover index (Table 3.1) and borehole proximity, based on relative performance and parameter estimates of Generalised Linear Mixed Models (Normal error, identity link) that included grid-square as a random factor. Models consider either (a) effects of vegetation zone and woody vegetation canopy cover index (analysed across all land-use types) or (b) vegetation zone, local density of woody vegetation and also proximity to borehole, for only those segments within Wildlife Management Areas and unprotected areas.

Model	Model predictors [a]	β ± SE	t-value	Log-likelihood	AIC	ΔAIC
a) Effects of vegetation zone and woody vegetation canopy cover index (n = 1109 segments within n = 103 grid-squares)						
1	*int*			1909.695	−3813.39	0
2	*int + veg zone*			1908.718		+7.953
	int	0.26 ± 0.03	9.522			
	grasslands	0				
	short shrub savanna	0.03 ± 0.03	0.943			
	fine-leaved tree savanna	0.07 ± 0.03	2.437			
	broad-leaved tree savanna	0.08 ± 0.03	2.333			
3	*int +woody veg cover*			1902.154		+21.082
	int	0.31 ± 0.007	44.706			
	<30 m visibility	0				
	30–80 m visibility	−0.004 ± 0.004	−0.966			
	80–150 m visibility	0.009 ± 0.004	2.066			

	>150 m visibility	−0.0007 ± 0.004	−0.173			
4	*int + veg + woody veg cover*			1900.962		+29.465
b) Effects of vegetation zone, woody vegetation canopy cover index and borehole proximity (*n* = 757 segments, *n* = 70 grid-squares)						
5	*int*			1250.489	−2494.977	0
6	*int + veg zone*			1250.095		+6.787
7	*int + BH*			1246.400		+10.176
	int	0.31 ± 0.01	31.043			
	BH	−0.003 ± 0.002	−1.540			
8	*int + veg zone + BH*			1245.829		+17.318
9	*int + woody veg cover*			1243.424		+20.128
10	*int + veg zone + woody veg cover*			1242.670		+27.638
11	*int + veg zone + woody veg cover + BH*			1238.327		+38.323

[a] int, intercept; BH, borehole proximity; veg, vegetation zone (relative to grassland as a reference category); woody veg cover, woody vegetation canopy cover index.

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Appendix 3.5

Table S4. The most important predictor variables driving wildlife species abundance. Shown are the highest ranked models (that account for cumulative Akaike weight ≥0.95), averaged model parameter estimates and lower and upper confidence intervals (in parenthesis, calculated using unconditional standard errors) based on predictor importance within the highest ranked models, as well as the number of predictors (*K*), AICc, AICc differences (ΔAICc) among ranked models, Akaike weights (ω) and cumulative Akaike weights (Σω). See Table 3.3 for model specification, error structures used and criteria for inclusion of habitat variables (distance to pan, altitude mean and altitude variance) in a model.

	Model selection						Averaged-model β (lower CI–upper CI)			
Response	Model	K	AICc	ΔAICc	ω	Σ ω	Model[a]	Settlement proximity	Borehole proximity	NDVI
Large-bodied grazers	BH+Alt.mean	4	92.76	0.00	0.19	0.19	int+alt.mean	0.19	0.28	−2.20
	Settl+NDVI+Alt.mean	5		0.91	0.12	0.30		(−0.38–0.76)	(−0.42–0.98)	(−9.10–4.69)
	Settl+ Alt.mean	4		0.96	0.11	0.42				
	BH+Settl+ Alt.mean	5		1.26	0.10	0.52				
	BH+NDVI+Alt.mean	5		1.61	0.08	0.60				
	NDVI+Alt.mean	4		1.90	0.07	0.67				
	Alt.mean	3		1.94	0.07	0.74				
	BH+Settl+NDVI+Alt.mean	6		2.51	0.05	0.80				
	BH	3		2.54	0.05	0.85				
	Settl+NDVI	4		3.08	0.04	0.89				
	BH+NDVI	4		3.62	0.03	0.92				
	NDVI	3		3.64	0.03	0.95				
	Settl	3		3.86	0.03	0.98				
	BH+Settl	4		4.05	0.02	1.00				
Medium−bodied browsers	Settl+NDVI	4	556.11	0.00	0.73	0.73	int	0.36	−0.003	−6.85
	BH+Settl+NDVI	5		2.02	0.27	1.00		(0.13–0.59)	(−0.09–0.08)	(−10.70–−2.96)
Steenbok	Settl+NDVI+Pan	5	521.45	0.00	0.42	0.42	int+distpan	0.34	−0.003	−6.04
	Settl+NDVI	5		0.02	0.42	0.84		(0.14–0.53)	(−0.05–0.04)	(−9.05–−3.02)
	BH+Pan+Settl+NDVI	6		2.02	0.16	1.00				
Springbok	Pan+NDVI	4	138.70	0.00	0.24	0.24	Int−distpan	0.07	0.05	−15.00

	NDVI	3		0.18	0.22	0.45		(−0.25–0.39)	(−0.25–0.35)	(−25.80–−4.16)
	Pan+Settl+NDVI	5		1.33	0.12	0.57				
	Settl+NDVI	4		1.49	0.11	0.69				
	BH+Pan+NDVI	5		1.55	0.11	0.80				
	BH+NDVI	4		1.76	0.10	0.89				
	BH+Pan+Settl+NDVI	6		3.29	0.05	0.94				
	BH+Settl+NDVI	5		3.45	0.04	0.98				
	Pan	3		5.27	0.02	1.00				
Carnivore	BH	3	158.43	0.00	0.37	0.37	int	0.01	0.35	−1.83
	BH+NDVI	4		1.13	0.21	0.58		(−0.16–0.18)	(−0.20–0.89)	(−7.50–3.83)
	BH+Settl	4		2.00	0.14	0.72				
	NDVI	3		2.17	0.13	0.85				
	BH+Settl+NDVI	5		3.15	0.08	0.93				
	Settl+NDVI	4		3.16	0.07	1.00				
Jackal	BH	3	140.65	0.00	0.41	0.41	int	0.04	0.29	−0.26
	BH+Settl	4		2.02	0.15	0.56		(−0.20–0.27)	(−0.28–0.86)	(−3.05–2.52)
	BH+NDVI	4		2.02	0.15	0.71				
	Settl	3		2.20	0.14	0.85				
	NDVI	4		2.93	0.10	0.95				
	Settl+NDVI	3		4.00	0.05	1.00				
Pale chanting goshawk (*Raptor*)	alt.mean+Settl	4	430.92	0.00	0.17	0.17	int−alt.mean	0.10	0.10	−0.66
	alt.mean+BH	4		0.71	0.12	0.29		(−0.14–0.34)	(−0.17–0.37)	(−3.09–1.77)
	alt.mean+Settl+NDVI	5		0.74	0.12	0.41				
	alt.mean	3		1.20	0.10	0.51				
	alt.mean+BH+Settl	5		1.42	0.09	0.60				
	Settl	3		1.67	0.08	0.68				
	alt.mean+BH+NDVI	5		2.06	0.06	0.74				
	alt.mean+NDVI	4		2.07	0.06	0.80				
	BH	3		2.29	0.06	0.86				
	Settl+NDVI	4		2.41	0.05	0.91				
	alt.mean+BH+Settl+NDVI	6		2.46	0.05	0.96				
	BH+Settl	4		2.92	0.04	1.00				
Large ground birds	Settl+Pan	4	845.34	0.00	0.55	0.55	int−distpan	0.35	−0.01	−0.14
	BH+Settl+Pan	5		1.72	0.23	0.78		(0.19–0.51)	(−0.09–0.06)	(−1.00–0.72)
	Settl+NDVI+Pan	5		1.83	0.22	1.00				
Ostrich	Pan	3	169.56	0.00	0.28	0.28	int−distpan	0.05	0.08	−0.26
	BH+Pan	4		0.86	0.18	0.46		(−0.16–0.26)	(−0.22–0.37)	(−2.51–1.99)
	Settl+Pan	4		1.12	0.16	0.61				
	NDVI+Pan	4		1.89	0.11	0.72				

	BH+Settl+Pan	5		2.68	0.07	0.79				
	BH+NDVI+Pan	5		3.01	0.06	0.86				
	Settl+NDVI+Pan	5		4.42	0.03	0.89				
	BH	3		4.70	0.03	0.91				
	BH+Pan+Settl+NDVI	6		4.79	0.03	0.94				
	Settl	3		4.79	0.03	0.96				
	NDVI	3		4.85	0.02	0.99				
	BH+NDVI	4		6.26	0.01	1.00				
Kori Bustard	Pan	3	144.25	0.00	0.18	0.18	int+distpan	0.03	0.22	1.05
	BH+Pan	4		0.07	0.17	0.34		(−0.17–0.23)	(−0.34–0.78)	(−3.61–5.71)
	BH+NDVI+Pan	5		1.38	0.09	0.43				
	Settl+Pan	4		1.52	0.08	0.51				
	NDVI+Pan	4		1.78	0.07	0.59				
	BH	3		1.84	0.07	0.66				
	BH+Settl+Pan	5		2.09	0.06	0.72				
	Settl	3		2.22	0.06	0.78				
	BH+NDVI	4		2.74	0.04	0.82				
	NDVI	3		2.89	0.04	0.86				
	Settl+NDVI+Pan	5		3.34	0.03	0.89				
	BH+Settl+NDVI+Pan	6		3.39	0.03	0.93				
	BH+Settl	4		3.57	0.03	0.96				
	Settl+NDVI	4		3.79	0.03	0.98				
	BH+Settl+NDVI	5		4.62	0.02	1.00				
Black Korhaan	BH+Settl+NDVI+Pan+Alt.mean	7	664.49	0.00	0.29	0.29	int−alt.mean −distpan	0.59	0.15	−4.88
	BH+Settl+NDVI+Pan	6		0.42	0.23	0.52		(0.34–0.84)	(−0.12–0.42)	(−8.13–−1.62)
	Settl+NDVI+Alt.mean+Pan	6		1.54	0.13	0.65				
	Settl+NDVI+Pan	5		1.77	0.12	0.77				
	Alt.mean+BH+Settl+NDVI	6		2.07	0.10	0.87				
	BH+Settl+NDVI	5		2.88	0.07	0.94				
	Alt.mean+Settl+NDVI	5		3.46	0.05	0.99				
Red-crested Korhaan	BH+Settl+NDVI+Pan	6	615.99	0.00	0.51	0.51	int−distpan	0.43	−0.20	1.84
	Settl+BH+Pan	5		0.91	0.32	0.83		(0.23–0.62)	(−0.46–0.05)	(−1.95–5.63)
	Settl+NDVI+Pan	5		2.54	0.13	0.96				
	Settl+Pan	4		4.88	0.04	1.00				
Galliforms	BH+NDVI	4	327.85	0.00	0.27	0.27	int	−0.08	−0.24	4.02
	BH	3		1.10	0.16	0.42		(−0.35–0.19)	(−0.74–0.27)	(−3.80–11.80)
	Settl+NDVI	4		1.11	0.15	0.58				
	BH+Settl+NDVI	5		1.26	0.14	0.72				
	NDVI	3		1.39	0.13	0.86				

	BH+Settl	4		2.39	0.08	0.94				
	Settl	3		2.92	0.06	1.00				
Helmeted Guineafowl	NDVI	3	247.93	0.00	0.33	0.33	int	−0.03	−0.19	3.81
	BH+NDVI	4		1.30	0.17	0.51		(−0.20–0.13)	(−0.68–0.31)	(−4.20–11.80)
	Settl+NDVI	4		1.31	0.17	0.68				
	BH	3		1.71	0.14	0.82				
	Settl	3		2.27	0.11	0.93				
	BH+NDVI+Settl	5		3.02	0.07	1.00				
Crested Francolin	BH	3	174.37	0.00	0.27	0.27	int	−0.05	−0.42	3.24
	BH+NDVI	4		0.27	0.23	0.50		(−0.35–0.24)	(−1.39–0.56)	(−6.80–13.30)
	NDVI	3		1.21	0.15	0.65				
	BH+Settl	4		1.81	0.11	0.75				
	BH+Settl+NDVI	5		2.19	0.09	0.84				
	Settl	3		2.31	0.08	0.93				
	Settl+NDVI	4		2.60	0.07	1.00				

[a] Additional parameters: int, intercept; distpan, distance to nearest pan; alt.mean, mean segment altitude; alt.var, altitude variance along segment. +ve or – ve prefix shows direct of effect for the habitat variables

Chapter Four

Wildlife Management Areas mitigate cattle-induced landscape-scale increased bush cover

Abstract

Although bush encroachment is recognised as a major change to the structure and functioning of African savannas, its causes remain debated, particularly the role of cattle. The juxtaposition of eight protected areas (PAs, 64,000 km^2, cattle excluded), 15 Wildlife Management Areas (WMAs, 72,000 km^2, separate zones for cattle-rearing and for wildlife), and unprotected areas (114,000 km^2, cattle-rearing unregulated) in Botswana's Kalahari Desert allowed us to examine the response of woody and herbaceous vegetation to gradients of cattle density. An index of woody vegetation cover was estimated for each of 1109 4-km long segments, sampled over 103 independent 25-km grid-squares. The relative influence of cattle density (indexed as borehole proximity), pan proximity, mean altitude, altitudinal variance along segment (all three influence soil properties), vegetation zone and flush Normalised Difference Vegetation Index (NDVI) on the index of woody vegetation cover was examined using Generalised Linear Mixed Models, within an information-theoretic and multi-model inference framework. Additionally, field measures of vegetation structure were compared across 91 independent sampling points spanning PAs, WMAs and unprotected areas. In unprotected areas, shrub density was 300% greater, overall canopy cover of woody vegetation 40% greater, canopy cover of encroaching *Dichrostachys cinerea* and *Acacia mellifera* 200–800% greater, and non-grass herbaceous cover 250% greater than in PAs and WMAs, which had similar cover. Canopy cover of shrubs <2 m in height and of *Grewia flava*, as well as grass cover and point frequency of grass bases, did not differ among land-use types. In contrast, the index of woody vegetation cover decreased along the gradient unprotected areas > PAs ≥ WMA livestock-rearing buffer ≥ WMA wildlife zone, with similar tree cover between WMA livestock-rearing and wildlife zones, and between WMA livestock-rearing zones and PAs. The WMA wildlife zones successfully excluded cattle. Outside PAs, proximity to borehole was the most important predictor of woody vegetation cover (selection probability, 0.992), with greater woody vegetation cover within 10 km of boreholes. Other strongly supported predictors were positive effects of NDVI (0.838), and positive effects of pan proximity (0.598), vegetation zone (reflecting greater woody biomass: selection probability 0.520), and mean altitude (0.478). Borehole effects did not differ between vegetation zones, with the interaction between borehole proximity and vegetation zone not supported (selection probability 0.130, compared to a random null variate: mean 0.270, upper 95th percentile 0.309). No effect of altitudinal variation was found (selection probability

0.266). Results suggest that on an ecoregion scale cattle are more important drivers of increased bush cover than suggested by continent-wide assessments, and that PAs and WMAs mitigate such cattle-induced vegetation structure changes. Based on the efficacy of zoning within WMAs to mitigate increased bush cover, results suggest that zoning of boreholes and cattle-rearing, coupled with habitat management where feasible, may help mitigate rangeland degradation and improve sustainability of cattle-based livelihoods within unprotected areas.

Introduction

Bush encroachment, the increased density and canopy cover of indigenous woody vegetation and concomitant reduction in grass cover over time (Asner *et al*., 2004), is recognised as a rangeland degradation problem across semi-arid regions globally (Eldrige *et al*., 2011). This shrub dominance is particularly important in sub-Saharan Africa, where semi-arid savannas cover more than 50% of the land area (Du Toit & Cumming, 1999). Changes in the grass-tree balance affect ecosystem functioning through reduced fire frequency and intensity (Illius & O'Connor, 1999; van de Langevelde *et al*., 2003) and have cascading effects on faunal assemblages, plant communities and soil properties (Eldrige *et al*., 2011). Fire, herbivory, rainfall and nutrient availability are thought to have the largest influence on the grass-tree balance (Sankaran *et al*., 2004), but studies investigating their relative importance have mostly been at small spatial scales, in single (Prins & Van der Jeugd, 1993; Staver *et al*., 2009) or non-replicated abutting land-use types (Roques *et al*., 2001; Wigley *et al*., 2010), reducing the ability to generalise to landscape or ecoregional scales. A recent synthesis (Sankaran *et al*., 2008), using data from 161 sites across Africa, concluded that rainfall was the most important driver of site-specific woody vegetation canopy cover, particularly in areas with a mean precipitation between 200–700 mm y^{-1}; fire return interval, soil phosphorus, soil nitrogen, soil clay content, elephant biomass, browser biomass, and grazer biomass respectively had decreasing effects. However, sites considered by Sankaran *et al*. (2008) had excluded human use for more than ten years; therefore the relative importance of potential causative factors across extensive human-occupied savannas (as opposed to parks) remains poorly understood.

Livestock grazing, primarily of cattle, is often regarded as an important driver of landscape-scale bush encroachment (van Vegten, 1984; Du Toit & Cumming, 1999, Riginos & Young, 2007), although alternative views exist (e.g. Ward, 2005; Wigley *et al*., 2010). It is important to determine the extent to which cattle may cause widespread bush encroachment because, as cattle-rearing is a dominant economic activity across many African savannas, any measures to regulate it need to be ecologically, economically, and socio-politically justifiable (Abel & Blaikie, 1989). Although advocated primarily to achieve synergistic goals of wildlife management and livelihood improvement (Du Toit, 2002; Child & Barnes, 2010), Wildlife Management Areas (WMAs) regulate cattle by designating separate zones for livestock-rearing and for wildlife (hereafter, WMA livestock-rearing buffers and WMA wildlife zones, respectively). Whether this zonation also offers a tool to mitigate cattle-grazing impacts remains uninvestigated. The juxtaposition of WMAs abutting unprotected pastoral areas and protected areas (PAs) also offers an experimental opportunity to examine the response of woody vegetation to gradients of cattle density.

At localised scales, some understanding exists of the role cattle grazing plays in driving bush encroachment (e.g. Mace, 1991; Illius & O'Connor, 1999; Oba *et al*., 2000; Roques *et al*., 2001). Robust evidence exists that cattle reduce grass forage and increase tree cover, based on exclosure experiments (Skarpe, 1990, 1992), fence-line contrasts of sites with different stocking density (Roques *et al*., 2001), and vegetation conditions at frequently used sites, such as boreholes, relative to infrequently used sites (Perkins, 1996). However, lack of replication spatially and across different stocking densities precludes generalisation, so that presumed impacts of a given stocking rate are not transferable in space. Hypothesised mechanisms through which cattle cause bush encroachment are that the cattle’s preferential removal of grass allows trees to access more water and nutrients (the competition-based model: Sankaran *et al*., 2004), disrupting the grass-tree equilibrium (Skarpe, 1990). Ward (2005) suggests that this is more likely if grazing coincided with frequent and plentiful rains, which favours tree seedling germination and survival relative to grasses. Alternatively, it has been suggested through demographic-bottleneck models (Sankaran *et al*., 2004) that grass removal by cattle or other grazing herbivores reduces fuel-loads, with subsequent reduced fire impacts allowing increased woody vegetation recruitment and growth (van de Langevelde *et al*., 2003; Staver *et al*., 2009). Both models have some empirical support, but evidence increasingly supports the conclusion that disturbance-mediated (fire and herbivory) factors are more important than competition for resources (water and nutrients: Roques *et al*., 2001; Sankaran *et al*., 2004).

Using Botswana’s Kalahari ecoregion as a case study, the study’s first aim was to quantify associations between cattle density and degree of bush cover across replicate localities differing in cattle abundance, land-use, vegetation type, rainfall and terrain features (elevation and distance to pan). In the absence of concurrent locality-specific time-series dataset of the extent of bush cover and cattle stocking density, this study uses extensively spatially replicated estimates of the contemporary extent of bush cover across WMAs and unprotected landscapes that were historically subjected to the same land use (unprotected), to infer the relative importance of potential predictors of the observed bush cover, following Sankaran *et al*. (2005, 2008). By inference, if cattle are a key determinant of landscape-scale increased bush cover even after accounting for confounding climatic, land-use, vegetation and terrain habitat variables, then the hitherto suggestions that cattle-grazing can significantly influence landscape-scale bush encroachment (e.g. Du Toit & Cumming, 1999) would be supported. The second aim was to test if WMAs are effective at spatially restricting cattle-rearing, with the expectation that if they did, then cattle encounter rates should be greater within the livestock-rearing buffer and negligible in the wildlife zone. The third aim was to quantify the extent to which WMAs mitigate cattle-induced vegetation impacts as judged by vegetation conditions (shrub density, woody vegetation canopy cover, canopy cover of encroaching species and measures of herbaceous vegetation) in these landscapes compared to those of PAs and unprotected areas, and use the outcome to comment on options to mitigate rangeland degradation more generally. Botswana’s PAs successfully exclude livestock (e.g. Wallgren *et al.*, 2009), so it was hypothesised that if cattle are an important driver of bush cover extent, and WMAs effectively spatially restrict cattle, then bush cover should be greatest in unprotected areas, reduced in WMAs and lowest in PAs.

The extent to which bush encroachment affects cattle productivity is debatable (Abel & Blaikie, 1989; Illius & O'Connor, 1999; Angassa & Oba, 2008). However, a recent meta-analysis of 244 studies worldwide showed that although the extent to which bush encroachment affects savanna structure and functioning (e.g. vascular plant species-richness, soil pH or soil moisture) is context-specific, grass cover consistently decreased in bush encroached areas (Eldridge *et al.*, 2011). In this study, it was therefore assumed that Kalahari livestock-owners, who predominantly keep cattle (a grazer), would prefer savannas with more extensive grasslands than areas with greater bush cover.

The study was conducted across a 250,000 km^2 region spanning eight PAs, 15 WMAs and intervening unprotected areas, lying across four broad vegetation zones spanning a 300–450 mm y^{-1} rainfall gradient. A total 103 independent 25-km grid-squares were sampled, within which transects were driven (total length 4030 km) and an index of woody vegetation cover estimated for each of 1109 segments (mean length = 3.63 km). In addition field-based measures of vegetation structure were taken at 91 independent points.

Methods

Study site

The sampling extent was the area described in Chapter 3 (20–24°S 22–26°E; Fig. 4.1). Vegetation is predominantly wooded grasslands and dense bushland, interspersed with low-growing shrubs, mainly *Grewia flava*, *G. flavescens*, *Dichrostachys cinerea* and *Ziziphus mucronata*, and grass swards dominated by *Aristida* spp., *Eragrostis* spp., *Schmidtia* spp., *Antephora pubescens* and *Heteropogon contortus* (Weare & Yalala, 1971).

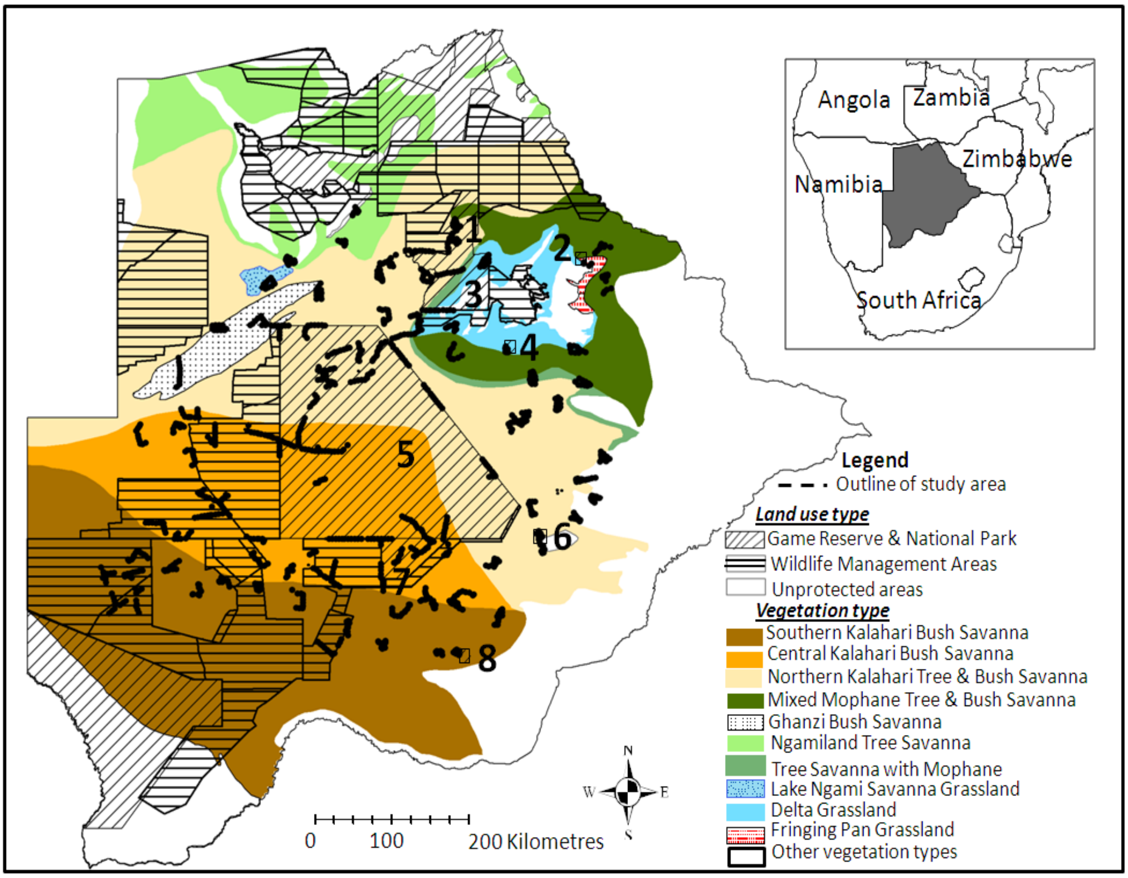

Figure 4.1. Location of the study area in the Kalahari, showing positions of driven transects, land-use types (Government of Botswana, 2001) and vegetation zones (Weare & Yalala, 1971). Protected areas within the sampling extent are (1) Nxai National Park, (2) Nata Sanctuary, (3) Makgadikgadi National Park, (4) Orapa Game Park, (5) Central Kalahari Game Reserve, (6) Dithopo Game Ranch, (7) Khutse Game Reserve and (8) Jwana Game Park.

Sampling grid layout

The sampling extent covered three privately owned parks (Jwana Park, Orapa Park and Nata Sanctuary) and all five state-managed PAs in central Botswana (total area 64,000 km^2), 15 WMAs (72,000 km^2), and intervening unprotected areas (114,000 km^2). A 500-km square centred on the Central Kalahari Game Reserve was subdivided into 25-km grid-squares, the basic sampling units. Replicate and non-contiguous grid-squares, stratified by land-use (PAs, WMAs and unprotected areas), were sampled for cattle abundance and vegetation measures; some of the analyses pool WMA livestock-rearing buffers and WMA wildlife zones while others separate them (see below). Unprotected areas received the greatest sampling effort because the largest variation in the primary predictor variable, cattle abundance, was expected in this land-use type. The original plan to sample an equal number of grid-squares in PAs and WMAs, but this could not be achieved owing to the poor track network within WMAs. Sampling was restricted to grids with tracks, because substratum structure prohibited off-road driving. A total 103 grid-squares were surveyed (33, 18 and 52 in PAs, WMAs and unprotected areas respectively), between 15 April and 8 July 2009, within the dry season (spanning April–September: Nicholson & Farrar, 1994).

Historical land-use in WMAs and PAs

As WMAs were preferentially established in regions of low human density and thus of lower cattle density during the 1990s (Appendix 3.1), the current condition of savanna vegetation within these areas cannot solely be attributed to contemporary management; but reflects a combination of historical processes as well as effects of recent zoning. However, time-periods since designation of PAs (≥30 years) and WMAs (≥15 years: Appendix 3.1) were nevertheless considered adequate for land-use-specific effects to become apparent.

To test whether WMAs effectively restricted cattle to livestock-rearing buffers (typically within 20 km of WMA settlements), the mean number of cattle encountered along 4-km long 100-m strip transect segments in PAs, WMA wildlife zones, WMA livestock-rearing buffers and unprotected areas, were compared.

Habitat measures

Vegetation measures were obtained within each grid-square using 40-km driven transects. Along each transect an index of woody vegetation cover was measured, and related to local explanatory variables, within consecutive 4-km segments. This scale was considered appropriate to capture gradients in cattle impacts close to and away from boreholes, following Perkins (1996). To ensure homogeneity within segments, if contrasting vegetation physiognomy was encountered before 4-km elapsed, a new segment was begun, with the boundary recorded using a handheld GPS. Mean segment length was slightly shorter in unprotected areas owing to greater landscape heterogeneity (PAs 3.7 km ± 1.0 SD; WMAs 3.8 km ± 0.9; unprotected areas 3.5 km ± 1.0; $F_{2,\ 1108} = 6.564$, $P = 0.001$). For each segment, the predominant level of woody vegetation cover was assessed according to the relative openness and ease of visibility, using four ordinal categories: (1) very open (visibility >150 m); (2) open (80–150 m); (3) partly closed (30–80 m); (4) closed (≤30 m) vegetation, hereafter referred to as the index of woody vegetation cover.

To obtain field-based measures of vegetation characteristics from each land-use type woody vegetation and undergrowth structure were sampled at the midpoint of one randomly selected segment, within each of 91 transects, stratified by land-use type. These data, supplemented by similar field measures obtained from a further 51 transect segments (non-independent, with some replicate segments within individual transects), were also used to calibrate and ground-truth the index of woody vegetation cover. At each of these 142 sampling locations, the following variables were measured:

1. grass frequency over one hundred equally spaced points along a 100-m transect (this was sampled directly away and at least 60–70 m from vehicle tracks);
2. GPS coordinates;
3. land form (pan or non-pan);
4. recent evidence of grazing/browsing incidence by medium- or large-bodied herbivores (combining wild ungulates and domestic livestock), recording visible signs (single-set tracks, dung or pellet groups, tallying presence in a 10-m × 10-m quadrat) on a four-point ordinal scale as: 0, 1–5, 6–10 or ≥10;
5. visual estimate of percentage ground cover (in 5% increments) of bare ground, grass cover and non-grass herbaceous vegetation;

6. canopy cover of all shrubs between 0.5 m and 2 m in height (to obtain a metric of woody biomass relatively easily accessible as browse forage to most herbivores, but also because shrubs ≤2 m directly affected ease of detecting sampled animals);
7. canopy cover of three key invasive shrub species (*Acacia mellifera*, *Dichrostachys cinerea* and *Grewia flava*) in degraded Kalahari rangelands (van Vegten, 1984; Skarpe, 1990);
8. canopy cover of all shrubs and trees ≥0.5 m (to obtain a metric to relate site-specific total woody biomass to Normalised Difference Vegetation Index, NDVI); and
9. density of all shrubs between 0.5 m and 2 m in height (to obtain a metric of abundance of relatively easily accessible browse resources, but also because shrubs of this height are more likely to directly affect the ease with which animals can move through a given habitat patch).

Variables 2–5 were measured at the 100-m transect end-point; variables 6–9 were measured within variable radius sampling plots (Mueller-Dombois & Ellenberg, 1974) centred on the 10-m quadrats. The placement of the quadrats was such that two of the sides laid parallel to the vehicle track. Canopy cover measures were estimated using Bitterlich gauges (Mueller-Dombois & Ellenberg, 1974; Friedel & Chewings, 1988), with three observers standing at the same spot independently estimating canopy cover and their estimates averaged per sampling point. Bitterlich gauges are hand-held ‘T-shaped’ wooden apparatus (in this study, gauges with a crosspiece of 10 cm and a holding stick of length 50 cm were used). To use, an observer stands at the same place and in turn sights each tree along the holding stick, assessing whether its canopy cover is equal to or greater than the crosspiece. Each gauge has a percentage factor defined by the crosswire: holding stick ratio (with the dimensions of the gauges used in this study, the percentage factor was 1%, meaning that any canopy cover that was equal to or greater than the crosswire was equivalent to 1% cover; see Mueller-Dombois & Ellenberg [1974] for the theory and mathematical justification). Care is required for instance when estimating canopy cover of shrubs whose view is partially obscured by vegetation between the observer and shrub of interest; secondly, especially at high shrub cover, it is important to distinguish individual shrubs, particularly for species that grow in clumps (e.g. *Acacia mellifera*). These challenges cannot be completely eliminated, but after extensive trialling to ensure standardisation of measures by the field-team, these potential biases were considered negligible. Preliminary fieldwork tested the efficacy of Bitterlich gauges for the study site, recording error that was less than 15% of the mean, without directional bias, for canopy cover values of 10–30%; error was assessed relative to independent cover measures by a range ecologist (M. Flyman) who was not part of the research team and also used a Bitterlich gauge of different dimensions to that used in this study. For the infrequent cases (<5% of all canopy cover estimates) when cover was outside this range, it was estimated visually in 5% increments (35, 40 or 45%, maximum).

Shrub density was estimated as the mean of four point-centred quadrat measures (Mueller-Dombois & Ellenberg, 1974),with one taken from each corner of the 10-m quadrats, using a rangefinder for distances greater than 10 m and visual estimates for shorter distances; for shrubs farther than 1000 m (14 out of 91 points, mostly in pans), distances were recorded as 1000 m. Mean inter-shrub distance was consistently less than 10 m across all land-use types (PAs 3.7 m ± 3.0 SD; WMAs 4.3 m ± 3.8; unprotected areas 2.4 m ± 2.0; $F_{2,\,1115} = 46.799$, $P < 0.0001$); thus measures from the four quadrat corners do not represent replicate measures of the same individual trees.

The index of woody vegetation cover was strongly correlated with canopy cover of all shrubs and trees (Fig. 4.2) and was therefore considered a robust proxy measure for shrub cover that could be collected with relative ease from a large number of replicate locations. The index of woody vegetation cover did not exhibit any spatial pattern across the sampling extent (Moran’s I = 0.258, $P = 0.610$); therefore vegetation measures from sampled points could be related directly to the distribution of land-use types (Appendix 4.1).

Model predictors

Segment scale woody vegetation cover index was related to the following predictors: (1) land-use designation (PA, WMA livestock-rearing buffer, WMA wildlife zone, unprotected); (2) segment proximity to borehole (a robust proxy measure for cattle density: see below); (3) proximity to mineral-rich pans; (4) mean altitude; (5) altitudinal variance along segment (estimated from Digital Elevation Models and hypothesised to affect segment-specific soil properties; see below); (6) Normalised Difference Vegetation Index (NDVI) between early and late rainy season, to provide a measure of local variation in rainfall (see below); (7) vegetation zone (four classes; see Table 4.1); and (8) an interaction between borehole proximity and vegetation zone (to test whether cattle effects varied across vegetation zones). All tests were based on square-root-transformed distance to borehole, because effects were expected to decrease non-linearly with distance. Predictors were obtained from remotely sensed data and statutory agencies (Table 4.1).

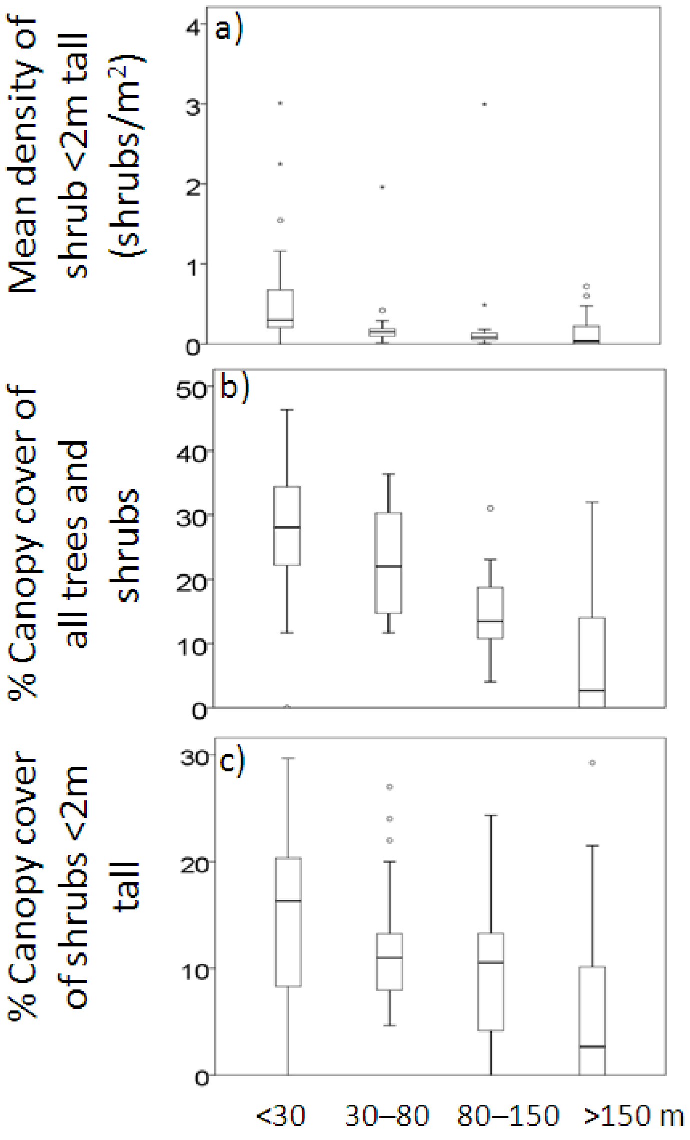

Figure 4.2. Relationships between (a) shrub density ($r_s = 0.432$, $P < 0.001$), (b) canopy cover of all shrubs and trees ($r_s = 0.565$, $P < 0.001$), (c) canopy cover of shrubs <2 m tall ($r_s = 0.418$, $P < 0.001$), and an ordinal index of segment-level woody vegetation cover for 142 individual 4-km segments. Canopy cover was estimated at one sampling point per segment, while the index of woody vegetation cover was a composite assessment of perpendicular sighting distance along the segment, measured on a four-point ordinal scale, ≤30, 30–80, 80–150 and >150 m.

Table 4.1. Explanatory variables considered as causal factors of greater landscape-scale bush cover in the Kalahari, showing spatial scale and data source. All variables extracted for each 4-km segment.

Variable	Units	Mean	SD	Min	Max	Description
Land-use designation						
PA, WMA or unprotected	Nominal scale 1–3	-	-	-	-	Botswana atlas (1-km^2 resolution).
Cattle impacts						
Distance to nearest borehole outside PA or WMA wildlife zone	km	13	16	0.08	101	Measured relative to borehole GPS points (correct to less than 10 m) from Geological Surveys Department, Botswana.
Ecological and environmental variation						
Vegetation zone	Ordinal scale 1–4	-	-	-	-	Ten vegetation zones (Weare & Yalala, 1971, Botswana atlas, 1-km^2 resolution) pooled into four classes: grasslands (Lake Ngami Savanna Grassland; Fringing Pan Grassland; Delta Grassland, all on fluvisols), short shrubs (Southern Kalahari Bush Savanna; Central Kalahari Bush Savanna, both on arenosols), tall fine-leaved trees (Northern Kalahari Tree and Bush Savanna; Ghanzi Bush Savanna, on arenosols and luvisols respectively) and tall broad-leaved trees (Ngamiland Tree Savanna; Tree Savanna with Mophane; Mixed Mophane Tree and Bush Savanna, on various soils). In GLMMs, analysed as ordered factor: grasslands < short shrubs < tall fine-leaved trees < tall broad-leaved trees, based on estimated woody biomass gradient in vegetation zones.
Flush NDVI: mean NDVI March 2009	Index potentially	0.51	0.08	0.03	0.52	Composites raster layer based on min and max NDVI over 10-day period (from the VEGETATION programme, www.free.vgt.vito.be; 1-km^2 resolution raster data) overlain

minus mean NDVI October 2008	ranges −2 to +2					on vector layer of segments buffered by 1-km, and area-weighted mean NDVI calculated based on the extent of overlap between NDVI raster dataset and the straight line connecting the segment's start and end points. Flush NDVI potentially ranges from −2 to +2 because raw NDVI ranges −1 to +1.
Mean altitude	m a.s.l.	1043	93	900	1254	Mean altitude of segment (800-m grid-square polygon resolution; mean altitude error: ±1.13 m (scrub habitats), NASA, www.asterweb.jpl.nasa.gov/gdem.asp).
Altitudinal variance	m	13	45	0	699	Based on differences between the mean altitude along a segment, and the larger of the highest or lowest points along that segment.
Distance to nearest pan	km	6.18	6.56	0	45	Measured relative to nearest mapped pan ≥1 km^2 (Botswana atlas, 1-km^2 resolution polygons).

Analysis used proximity to the nearest borehole outside PAs and WMA wildlife zones as a proxy for cattle density; borehole density was correlated with independent data for cattle encounter rates along transect segments and the relationship between observed cattle density and borehole proximity was similar between unprotected areas and WMA livestock-rearing buffers, so that its use as a proxy across both was validated (Appendix 3.2 in Chapter 3).

In arid savannas such as the Kalahari, soil moisture drives plant phenology and productivity (Nicholson & Farrar, 1994). However, the lack of weather stations in the study area precluded use of spatially referenced rainfall measures. NDVI was hypothesised to be a good proxy for differences in precipitation and therefore localised vegetation productivity, following Pettorelli *et al*. (2005). Differences in mean October 2008 NDVI and mean March 2009 NDVI ('flush NDVI') were used as a proxy for differential segment-level rainfall between the start and end of the wet season, because for the Kalahari these months show the largest variation in NDVI (Nicholson & Farrar, 1994). In Generalised Linear Mixed Models (GLMMs) of segment-specific NDVI (considering n = 757 non-PA segments, modelled with normal error, identity link) that included grid-square as a random factor (n = 70) to account for non-independence of segments along a single transect, the intercept-only model was best-supported, relative to poorly supported models that attempted to relate NDVI separately to vegetation zone (ΔAIC +6.787), localised habitat structure (index of woody vegetation cover, ΔAIC +20.128), or borehole proximity (ΔAIC +10.176). Therefore NDVI was considered to overwhelmingly represent the influence of localised rainfall events on flush vegetation productivity, rather than geographic gradients or local response to shrub density. Local thunderstorms are a common phenomenon in the otherwise arid Kalahari (Nicholson & Farrar, 1994).

Finer-scale variation in vegetation between higher-elevation sand-dominated shrublands and lower-elevation grasslands is not captured by the coarse-scale vegetation zones. Therefore area-weighted mean altitude and altitudinal variance along each 1-km-buffered transect segment were considered as candidate variables in models; altitude variation may lead to deposits of nutrient-rich or clay soils in valleys between sandy ridges and hills (Table 4.1). While pan soils tend to be more mineral-rich and with high clay content, favouring grasses over woody vegetation (Sankaran *et al*., 2008), it was hypothesised that cattle-rearing communities may have preferentially settled near pans due to resource availability (grasslands, salt licks and sometimes standing water) potentially increasing the likelihood for cattle-induced increased bush cover in these areas. Therefore, distance to the nearest mapped pan in the Botswana atlas (Table 4.1) was considered an explanatory variable for correlates of bush cover extent.

Statistical analysis

Three sets of models were considered. First, the effects of land-use designation on field-based measures of vegetation structure (shrub and tree canopy cover, shrub density, canopy cover of encroacher species and herbaceous vegetation) were modelled using Generalised Linear Models (GLMs, with a Negative Binomial error term and a log link function) that controlled for vegetation zone; for these tests tall broad-leaved trees and grassland landscapes were pooled, as were WMA livestock-rearing buffers and wildlife zones, to increase sample sizes. The small sample size for vegetation measures in pans ($n = 13$, none in WMAs) precluded contrasts of vegetation characteristics among land-use types for this habitat; therefore analysis of vegetation structure across land-use types was restricted to non-pan locations.

Second, the index of woody vegetation cover was compared among land-use types (PAs, WMA wildlife zone, WMA livestock-rearing buffer, unprotected area) using GLMMs that included grid-square as a random effect. Although the index of woody vegetation cover was recorded on an ordinal scale (as visibility bands: 1, very open >150 m; 2, open 80-150 m; 3, partly closed 30-90 m; 4, closed <30 m) it was nonetheless modelled as a numeric count (1–4; with Poisson error term and a log link function) because parameter estimates and Akaike Information Criterion (AIC) inference based on count data and Poisson error are more robust than models of ordinal responses, within freely available statistical packages and the GLMM modelling framework (Bolker *et al*., 2009). GLMMs were fitted using the glmer function within the R package lme4, which calculates parameter estimates based on Laplace approximations (Bolker *et al*., 2009).

Third, having examined the effects of land-use designation on the index of woody vegetation cover, the relative effects of variables representing possible underlying mechanisms for greater bush cover (borehole proximity, pan proximity, mean altitude, altitudinal variance, flush NDVI and vegetation zone) were then examined within an information-theoretic multi-model inference approach (Burnham & Anderson, 2002) using a reduced dataset comprising only segments in WMAs and unprotected areas because cattle were absent from PAs. Outside PAs ($n = 757$ segments), no predictors were strongly correlated ($-0.106 < r < 0.195$). The ‘dredge’ function within the MuMIn R package was used to develop all possible combinations of candidate variables and to calculate AICc-values and model Akaike weights. Model-averaged parameter estimates, unconditional standard errors and confidence intervals were calculated based on the 95% model set (for which the cumulative Akaike weights were ≥0.95) following Burnham & Anderson (2002). Selection probabilities of candidate variables (summed for models in the 95% set) were compared to the mean and 95th percentile of the frequency distribution of selection probabilities of 1000 iterations of a random normally distributed null variable (selected from the range 0–1) included with other variables in the multi-model inference procedure, following Boughey *et al*. (2011).

Spatial autocorrelation in the index of woody vegetation cover and in GLMM residuals was examined using Moran’s I, based on Euclidian distances between all segments.

The R software package (vers. 2.11.1; R Development Core Team, 2008) and ArcGIS 9.2 (ESRI ArcMap 1999–2006) were used for all statistical and GIS analyses respectively.

Results

Influence of land-use on vegetation structure

The segment-scale index of woody vegetation cover (*n* = 1109) differed among land-use types (Fig. 4.3). Index values were greatest in unprotected areas (GLMM *unprotected area* mean index = 1.03 ± 0.09 SE) and broadly similar among other land-uses (*PA* 0.71 ± 0.10; *WMA livestock-rearing buffer* 0.61 ± 0.12; *WMA wildlife zone* 0.53 ± 0.11; all pairwise comparisons significant, Tukey HSD, $P < 0.05$, except WMA livestock-rearing buffers *versus* WMA wildlife zone, $P = 0.666$; WMA livestock-rearing buffers *versus* PAs, $P = 0.644$). Controlling for land-use, the index of woody vegetation cover was unaffected by vegetation zone (GLMM *vegetation zone* z-value = −0.28, $P = 0.782$).

Field-based measures of woody vegetation structure at the 78 non-pan sampling points differed among land-uses. Most measures were similar between PAs and WMAs (with wildlife zone and livestock-rearing buffer pooled), but differed significantly in unprotected areas (Fig. 4.4). In unprotected areas, shrub density was 300% greater (Fig. 4.4f), canopy cover of all shrubs and trees 40% greater (Fig. 4.4b), and canopy cover of the encroaching shrubs *Dichrostachys cinerea* (Fig. 4.4c) and *Acacia mellifera* (Fig. 4.4d) 200–800% greater, relative to PAs and WMAs across which cover was similar. *D. cinerea* was not recorded in WMAs. In contrast, canopy cover of all shrubs <2 m and of *Grewia flava* did not differ among land-use types (Fig. 4.4a, 4.4e).

Non-grass herbaceous cover was similar between WMAs and PAs but 250% greater at sampling points in unprotected areas (Fig. 4.4h). In contrast, the point frequency of grass bases (Fig. 4.4g) and grass cover (Fig. 4.4i) did not differ among land-use types. Contrary to expectation, the extent of bare ground was greatest in WMAs (Fig. 4.4j), 150% greater than at sampling points in unprotected sites, for which extent of bare ground did not differ from PAs.

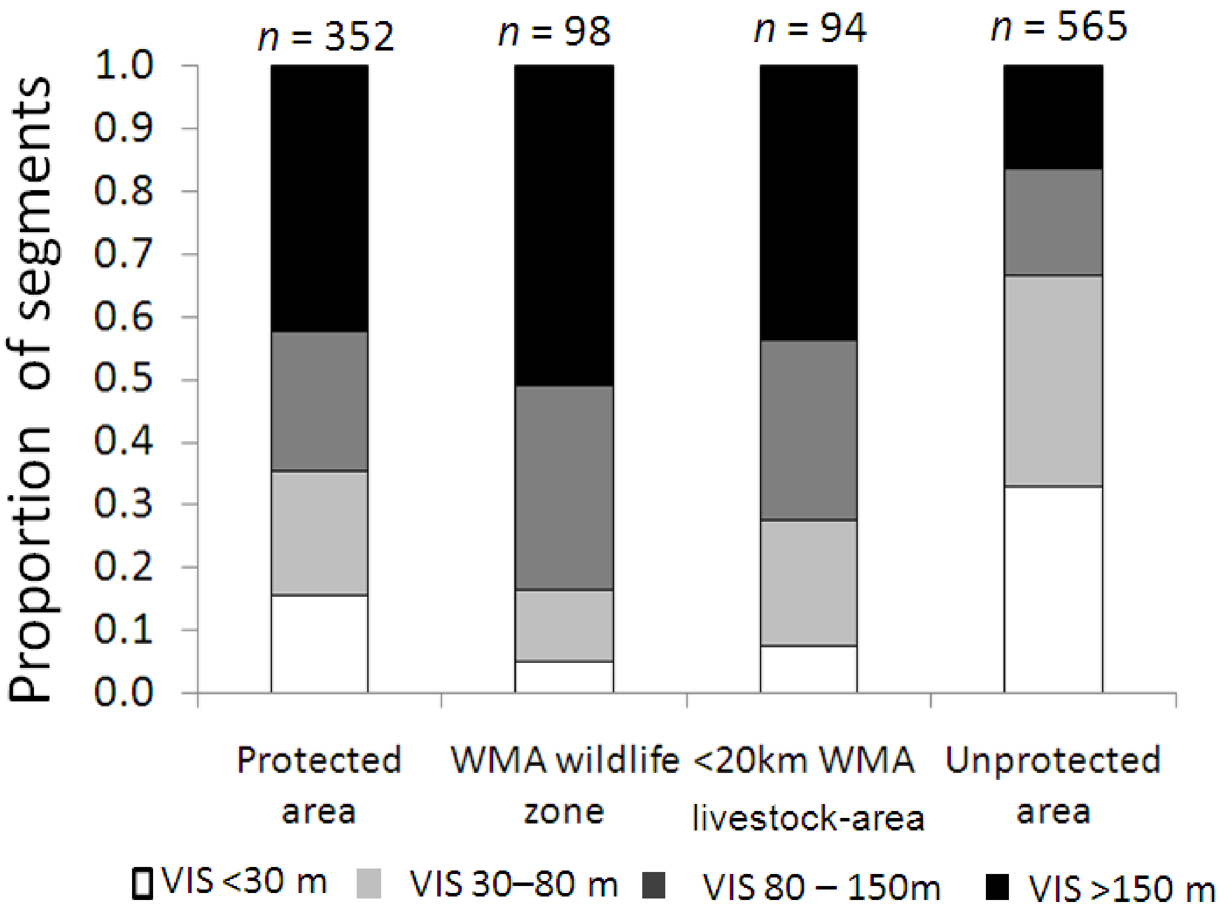

Figure 4.3. Proportion of segments with different scores of woody vegetation cover in each of the land-use categories: PA, WMA wildlife zone, WMA livestock-rearing buffer, unprotected area.

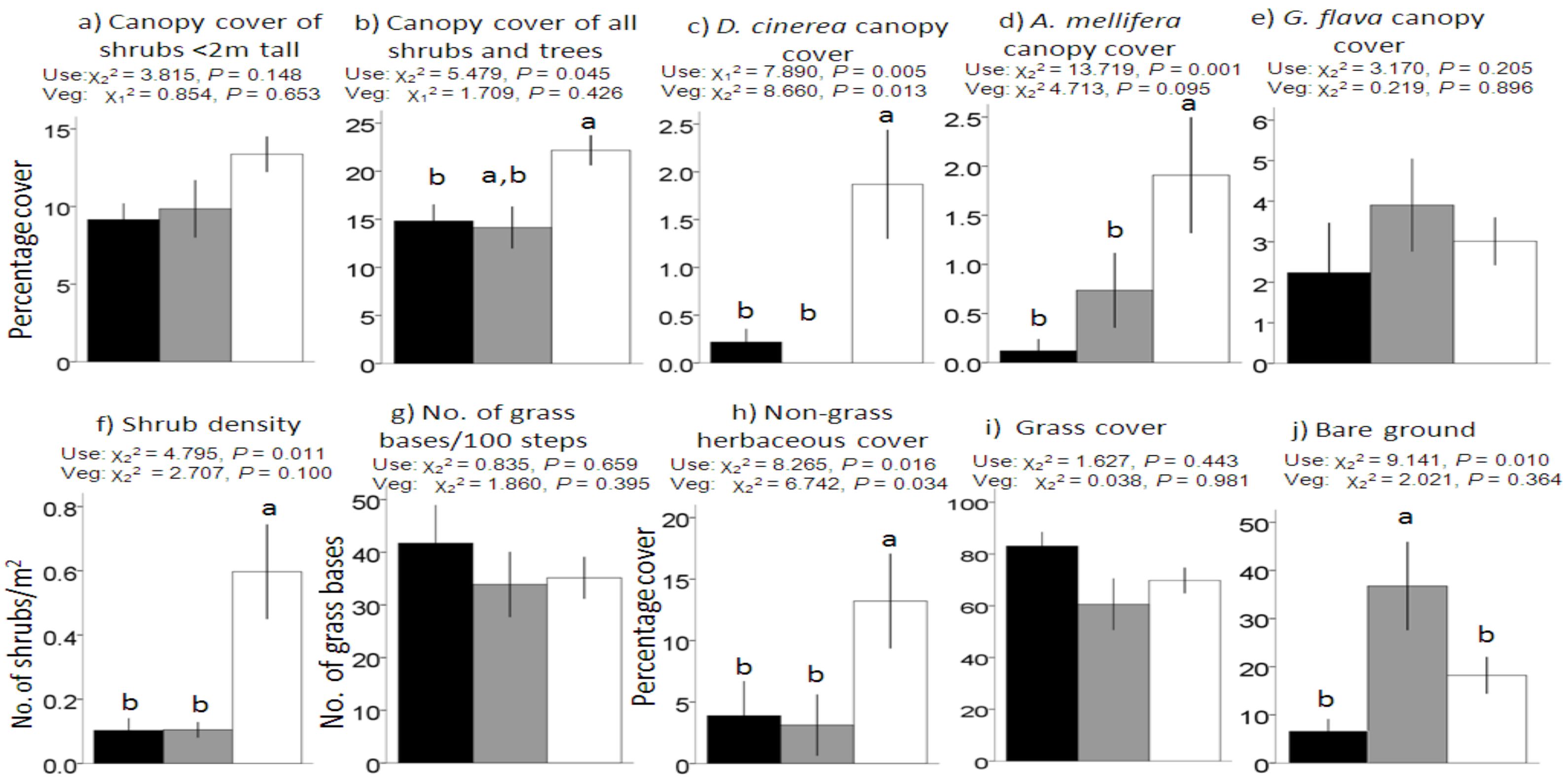

Figure 4.4. Mean (± SE) field-measured vegetation structure at non-pan sampling points in protected areas (n = 19, black bars), Wildlife Management Areas (n = 18, grey bars) and unprotected areas; (n = 42, white bars). Canopy cover of (a) shrubs <2 m tall, (b) all shrubs and trees, (c) *Dichrostachys cinerea*, (d) *Acacia mellifera* and (e) *Grewia flava* was estimated using Bitterlich gauges, shrub density estimated using point-centred quadrats, mean grass bases estimated using the point transect method, and herbaceous cover and bare cover estimated visually in 10-m grid-squares at each sampling point. Results of Generalised Linear Models show Wald χ^2 tests for land-use (Use) and vegetation zone (Veg). Significantly different estimated marginal means have different superscript letters (Sequential Sidak multiple comparison test, $P < 0.05$).

Cattle and wild herbivore presence across land-use types

There was no evidence of herbivore droppings or hoof marks at 60%, 50% and 17% of sampled quadrats in PAs, WMAs and unprotected areas respectively (*n* = 91), suggesting that overall domestic livestock incidence in unprotected areas was much greater than wildlife incidence in PAs. Because herbivore markings were sampled away from tracks this index is not susceptible to differential avoidance of tracks by livestock relative to wild herbivores. In contrast, 15%, 17% and 24% of sampling points in PAs, WMAs and unprotected areas respectively showed signs of intensive use (Fig. 4.5).

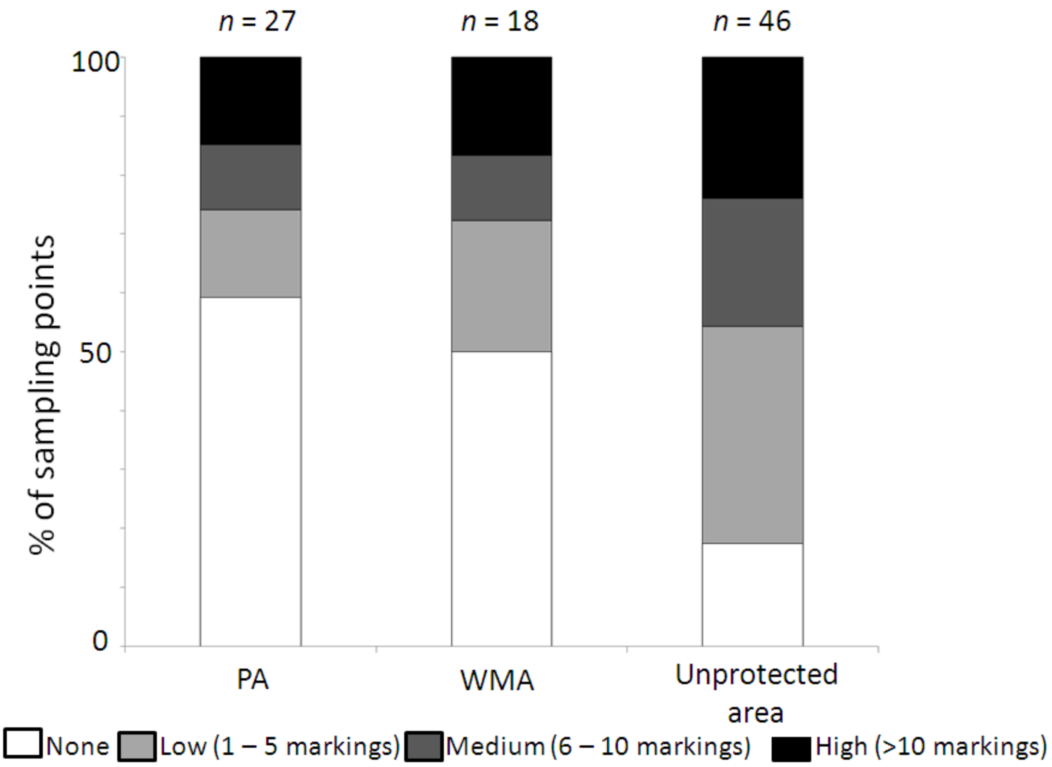

Figure 4.5. Grazing and browsing intensity (marks per 10-m grid-square sampling point) in protected areas (PAs), Wildlife Management Areas (WMA) and unprotected areas.

Cattle encounter rates during field surveys differed among the land-use types, with lower encounter rates within the WMA wildlife zone than in WMA livestock-rearing buffers and unprotected areas (Fig. 4.6). Cattle were encountered within a PA and within a WMA wildlife zone on only two occasions (mean encounter rates PAs 0.006 animals km^{-1} ± 0.10 SD; WMA wildlife zone 0.01 animals km^{-1} ± 0.15, t_{448} = 0.711, *P* = 0.477). Encounter rates were an order of magnitude greater in WMA livestock-rearing buffers (0.73 animals km^{-1} ± 2.88 SD) than in WMA wildlife zones, while encounter rate in unprotected areas (1.51 animals km^{-1} ± 6.28) was twice that in WMA livestock-rearing buffers. Encounter rates were significantly greater in unprotected areas (Fig. 4.6).

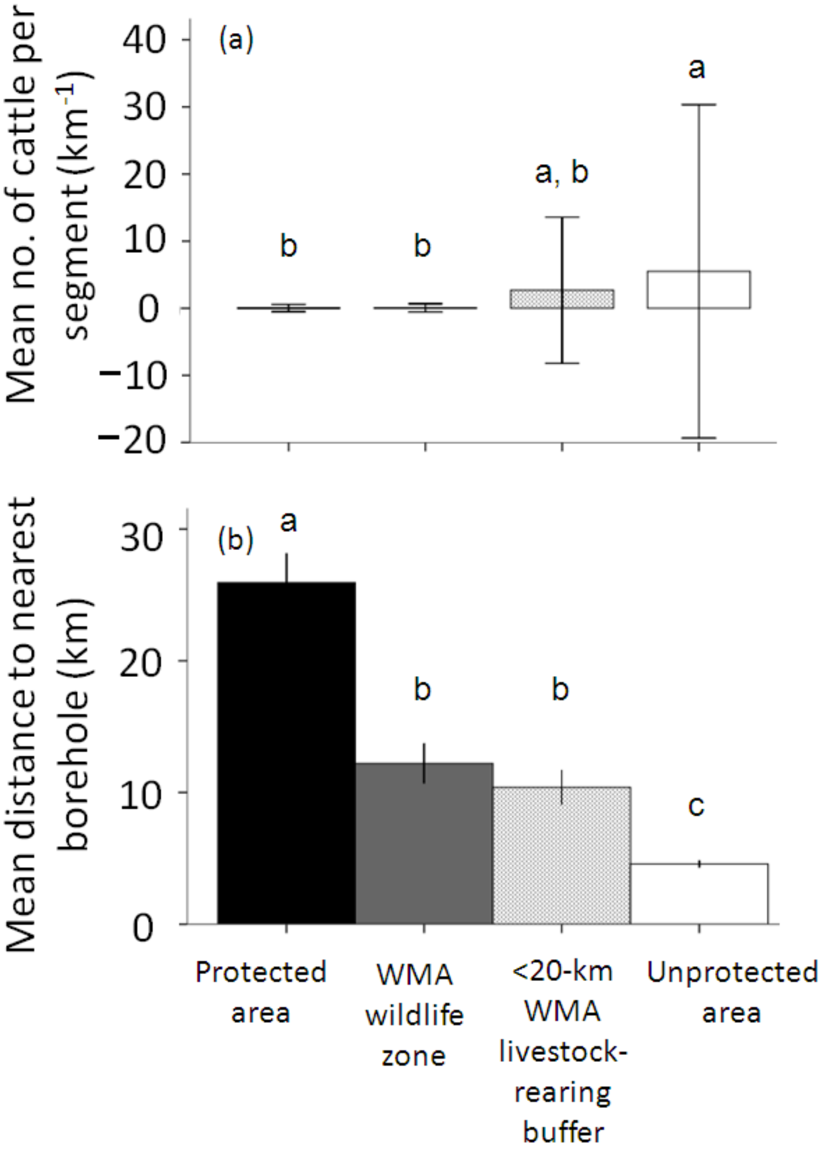

Figure 4.6. Relationships between (a) mean cattle count per 4-km segment (animals km^{-1} ± SD; $F_{3,1108} = 9.328$, $P < 0.0001$) and (b) mean distance to the nearest livestock-watering borehole for sampled 4-km segments (km ± SD; $F_{3,1108} = 209.428$, $P < 0.0001$) in protected areas ($n = 352$), WMA wildlife zone ($n = 98$), WMA livestock-rearing buffers ($n = 94$), and unprotected areas ($n = 565$). Significantly different estimated marginal means across land-use types have different superscript letters (Tukey HSD $P < 0.05$).

Relative importance of borehole proximity, flush NDVI and terrain variables in driving greater bush cover

Borehole proximity was the most important predictor of the segment-scale index of woody vegetation cover (Fig. 4.7; selection probability 0.992) with borehole effects most pronounced within 10 km of boreholes (Fig. 4.8b). Woody vegetation cover decreased farther from boreholes (Fig. 4.7, Fig. 4.8a), but increased with increasing NDVI, at greater distance to pan and at higher mean altitude (selection probabilities 0.838, 0.598 and 0.478 respectively: Table 4.2, Fig. 4.7). Woody vegetation cover index was also greater in the more mesic vegetation zones with inherently greater woody biomass (selection probability 0.520: Fig. 4.7). Effects of altitudinal variance and a potential interaction between borehole proximity and vegetation zone were not supported, with similar or lower selection probabilities (0.266 and 0.130 respectively) than a random null variate (mean 0.270, upper 95th percentile 0.309). No single model received overwhelming support. The best-supported model had an Akaike weight of 0.09, with eight other models within two AIC-units and with 34 models within the 95% confidence model set (Table 4.2). However, all eight models within two ΔAIC-units of the best-supported model included borehole proximity and NDVI, again emphasising the importance of these factors (Table 4.2). The GLMM normalised residuals of the parameter-averaged model testing the relative importance of borehole proximity, NDVI and terrain variables on the tree cover index were not spatially autocorrelated (Moran’s I = −0.00611, $P = 0.977$).

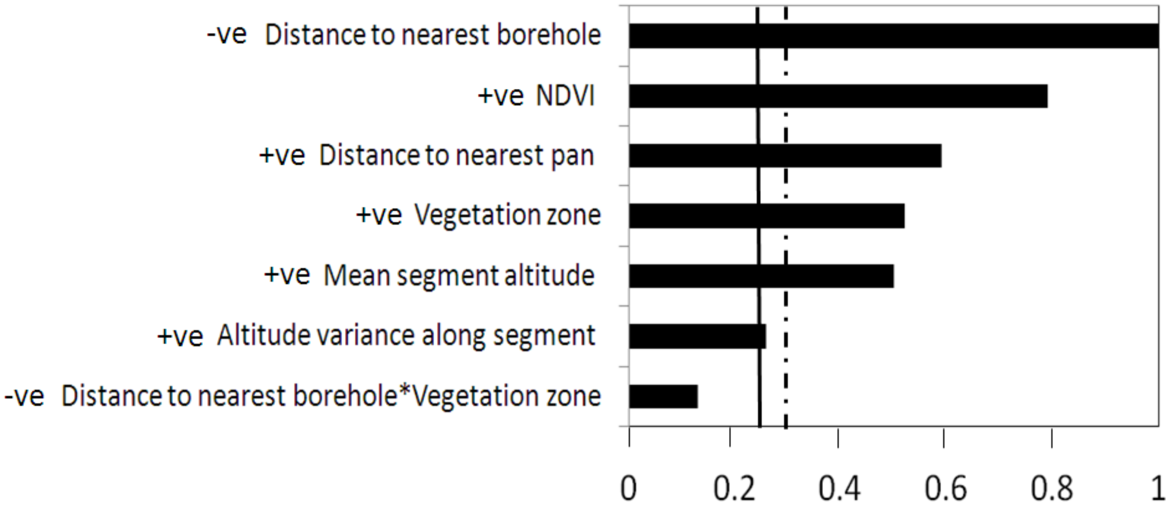

Figure 4.7. Selection probabilities of variables in the best-supported models accounting for cumulative Akaike weights ≥0.95 of the averaged best model (Table 4.2) for key drivers of greater bush cover. –ve and +ve indicate direction of effect on woody vegetation canopy cover cover index (1 = very open, 2 = open, 3 = partly closed, 4 = closed). Null variable (——— mean selection probability, 0.270; ▬ ▬ ▬ 95th percentile, 0.309; 1000 replicates, see main text).

Discussion

Of the factors considered in this study, cattle density had the strongest effect on contemporary levels of woody vegetation cover across the Kalahari. Findings from this study suggest that the impacts on vegetation of livestock-watering boreholes and associated high cattle stocking rates are not restricted to fenced-in areas, but can occur across large-scale communal pastoral areas. Although lower cattle encounter rates in the livestock-rearing buffers of WMAs relative to unprotected areas may partly reflect a historical legacy of preferential placement of WMAs in sparsely populated areas, zonation within WMAs has been effective at spatially restricting and mediating impacts of cattle on vegetation. Thus, cattle zonation can mitigate cattle-induced increases in bush cover.

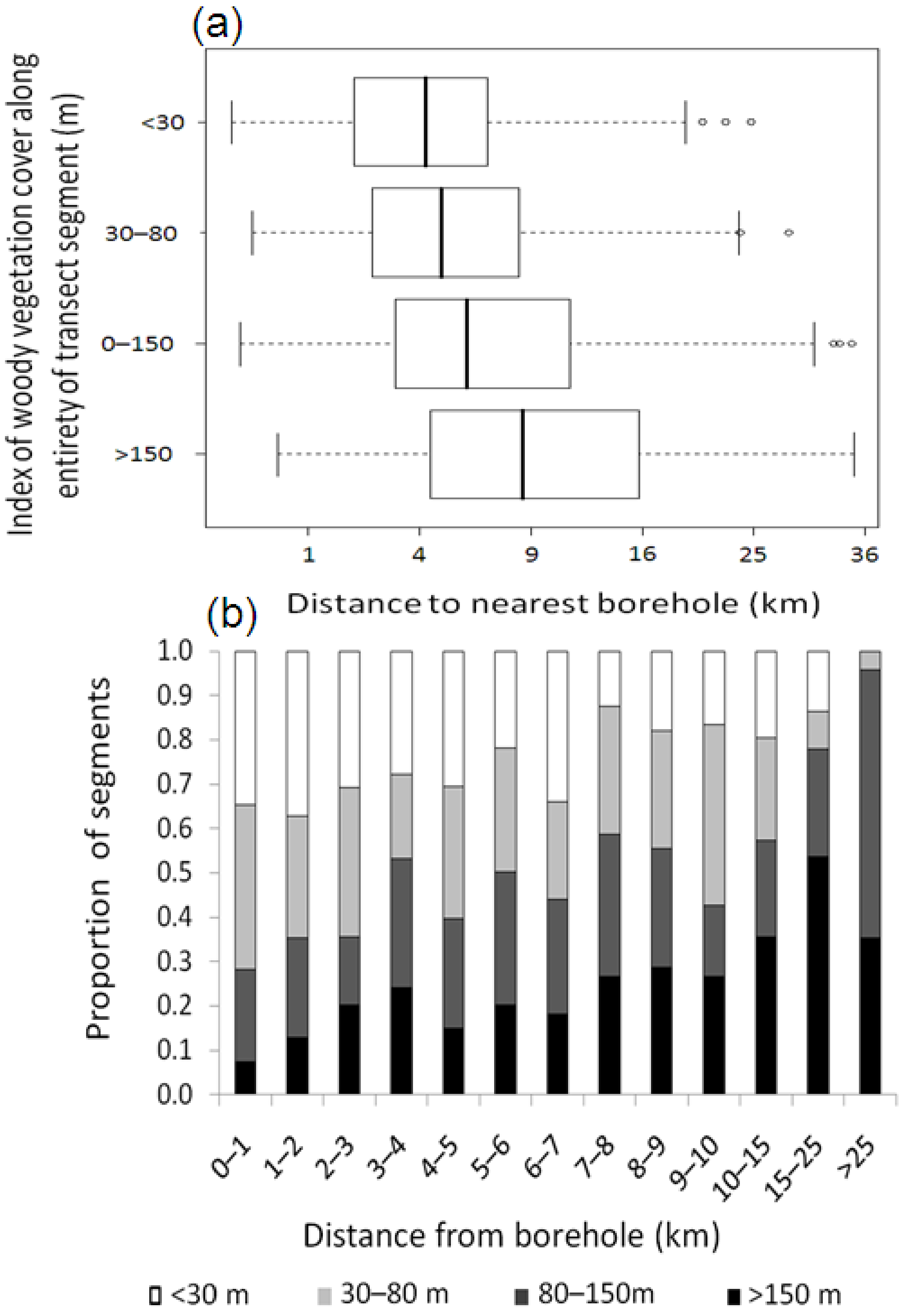

Figure 4.8. Relationships between an index of woody vegetation cover (shorter sighting distances imply closed canopy cover) and distance to the nearest livestock-watering borehole for Wildlife Management Area and unprotected area segments only. (a) $r_s = -0.298$, $n = 757$, $P<0.0001$, (b) n = 184, 154, 221 and 198 for index of woody vegetation cover <30 m, 30–80 m, 80–150 m and >150 m respectively.

Table 4.2. The most important predictor variables driving woody vegetation canopy cover index in Wildlife Management Areas and unprotected areas segments only, calculated using Generalised Linear Mixed Models, incorporating a Poisson error term with a log link function, and including grid-square as a random effect (*n* = 70). The highest rank models (accounting for cumulative Akaike weight ≥ 0.95), and averaged-model parameter estimates (± SE) and confidence intervals (CIs) of candidate variables based on this confidence set ($\Sigma\omega_i \geq 0.95$) are shown, as well as AICc of best-supported model, AICc differences (ΔAICc), model Akaike weights (ω) and cumulative Akaike weights (Σω).

Model	Borehole proximity	NDVI	Pan proximity	Vegetation zone	Mean altitude	Altitude variance	Borehole /vegetation interaction	AIC	ΔAICc	ω	Σω
1	■	■	■					331.4	0	0.09	0.09
2	■	■	■		■				0.28	0.08	0.17
3	■	■							0.71	0.06	0.23
4	■	■			■				0.78	0.06	0.29
5	■	■	■	■	■				0.79	0.06	0.35
6	■	■	■	■					0.95	0.06	0.41
7	■	■		■	■				1.11	0.05	0.46
8	■	■		■					1.53	0.04	0.5
9	■	■	■			■			1.82	0.04	0.54
10	■	■	■		■	■			2.25	0.03	0.57
11	■	■				■			2.57	0.02	0.59
12	■		■						2.66	0.02	0.61
13	■		■	■	■				2.68	0.02	0.63
14	■		■	■					2.75	0.02	0.65
15	■	■	■	■		■			2.76	0.02	0.67
16	■	■	■	■	■	■			2.77	0.02	0.69
17	■	■			■	■			2.77	0.02	0.71
18	■	■	■	■	■		■		2.84	0.02	0.73
19	■	■	■	■			■		2.99	0.02	0.75
20	■	■		■	■	■			3.12	0.02	0.77

21	▨	▨		▨	▨		▨	3.15	0.02	0.79
22	▨		▨		▨			3.16	0.02	0.81
23	▨	▨		▨		▨		3.38	0.02	0.83
24	▨	▨		▨			▨	3.56	0.02	0.85
25	▨			▨	▨			3.7	0.01	0.86
26	▨			▨				4.03	0.01	0.87
27	▨							4.19	0.01	0.88
28	▨		▨			▨		4.5	0.01	0.89
29	▨				▨			4.5	0.01	0.9
30	▨		▨	▨	▨		▨	4.55	0.01	0.91
31	▨		▨	▨		▨		4.57	0.01	0.92
32	▨		▨	▨			▨	4.59	0.01	0.93
33	▨		▨	▨	▨	▨		4.67	0.01	0.94
34	▨	▨	▨	▨		▨	▨	4.8	0.01	0.95
35	▨	▨	▨	▨	▨	▨	▨	4.82	0.01	0.96

Model average	Borehole proximity	NDVI	Pan proximity	Vegetation zone	Mean altitude	Altitude variance	Borehole/ Vegetation interaction	Constant
$\beta\times10^{-1}$	−0.80	7.24	0.04	0.30	0.0002	0.0005	−0.0005	5.60
SE	0.03	0.52	0.005	0.05	0.0003	0.0002	0.005	0.38
CIs	−0.14–−0.02	−0.29–1.73	−0.006–0.01	−0.06–0.12	−0.0004–0.0009	−0.0003–0.0004	−0.01–0.009	−0.19–1.31

Can cattle-grazing induce greater bush cover at landscape-scales?

Whether cattle-grazing can induce increased bush cover at landscape scales has been debated (Ward, 2005; Wigley *et al*., 2010), partly owing to the absence of empirical measures of bush cover along a gradient of cattle densities. However, outside Kalahari PAs, transect segments with greater woody vegetation canopy cover were nearer boreholes than can be explained by chance. Therefore, within an ecoregion with consistently low rainfall (300–450 mm y^{-1}), grazers may be a more important driver of bush cover than suggested by continent-wide syntheses (Sankaran *et al*., 2005, 2008). In these studies grazer biomass had negligible effects and mean annual precipitation was the primary determinant of maximum woody cover (Sankaran *et al*., 2005) as well as actual site-specific cover (Sankaran *et al*., 2008).

Similar to Roques *et al*. (2001), results from this study provide evidence that the relative importance of determinants of woody canopy cover is largely influenced by the historical legacy of land-use (e.g. heavier grazing in WMA wildlife areas before designation as livestock-free zones) and more contemporary stocking rates (e.g. lower stocking rates in WMAs overall, relative to unprotected areas). But, effects are also scale-dependent, possibly largely influenced by the spatial scales at which the landscape heterogeneity occurs. Within a landscape, the scale-dependency has at least three components: (1) the distance to which the cattle impacts are manifest around boreholes; (2) terrain characteristics such as pan proximity and altitude, which may influence distances over which the cattle forage, and (3) the mean and variance in prevailing rains across the sampling extent, which may influence patchiness and spatial heterogeneity of resources, particularly where isolated rain showers may be prevalent such as in the study area. Study findings also provide some support for hypotheses that herbivore-induced increases in bush cover may be more pronounced on sandy soils away from the nutrient-rich clayey soils (Sankaran *et al*., 2008), and at higher elevations, presumably with less fertile soils. Strong support for the positive effects of flush seasonal differences in NDVI is consistent with rainfall being an important variable in regulating woody cover across large spatial scales (Sankaran *et al*., 2008).

Lessons for bush encroachment mitigation in communal rangelands

Cattle encounter rates in WMA wildlife zones were negligible; this study presents the first evidence that WMAs restrict cattle. However, this effect of the WMA buffers is aided by the lack of surface water in the Kalahari, which confines cattle-rearing to the vicinity of boreholes (Perkins, 1996). Boreholes historically operating within the wildlife zones of WMAs are now defunct. Thus, at a landscape scale, cattle effects in the Kalahari are a collection of localised disturbance points, and are most pronounced within 10 km of functional cattle-watering boreholes. In the study area the proportion of WMAs and unprotected area extent falling within 10 km of a borehole is approximately 10% and 70% respectively. Thus the impacts of cattle on bush cover can be expected to be particularly pervasive in non-protected areas. Because of the very low wildlife encounter rate in unprotected areas (see Chapter 3), the contribution of the wild ungulates to the ‘distance to borehole’ and bush cover is considered negligible. Findings from this study suggest that if a large proportion of the communally managed unprotected area is close to a borehole, then aggregations of the localised habitat changes around boreholes could have implications for broad-scale vegetation dynamics. Thus, although seemingly localised, borehole impacts have significant influence on surrounding vegetation; for instance, despite the uneven spread in sampled segments with respect to land-use, rainfall, soil types and vegetation zones, there was no spatial autocorrelation among neighbouring segments, suggesting very strong pressure from boreholes on local vegetation structure. Consequently, in regions which rely predominantly on boreholes to water cattle, extensive cattle-rearing in communal areas can still lead to widespread increased bush cover and range degradation, possibly through the same mechanisms that have been identified in small exclosures, where preferential grass removal by cattle or other grazers reduced fire frequency and intensity, favouring bush encroachment (Roques *et al*., 2001; van de Langevelde *et al*., 2003; Staver *et al*., 2009).

Study findings suggest that strict regulation of borehole placement is critical to ensuring long-term sustainability of communal rangelands and cattle-based livelihoods, because borehole presence increases the likelihood of increased woody vegetation cover through long-term confinement of cattle pressure. The efficacy of the WMA buffers and restriction of cattle grazing impacts to within 10 km of boreholes suggest that zonation of communal unprotected lands to designate a borehole-free zone that all livestock-owners in a village can use to graze cattle, or ensuring large inter-borehole spacing, may abate further range-wide degradation. One option to regulate borehole spacing is for joint committees of livestock-owners and government officials to assess new application for borehole sinking, with the decision to grant permission guided largely by the prevailing stocking rates, rather than as done presently where only the physical inter-borehole distance but not stocking density is considered (Field, 1978). This model, however, demands for a greater role of livestock-owners' associations in managing their rangelands, rather than at present where rangelands are largely managed by the state. However, the creation of borehole-free grazing areas would require that the juxtaposition of existing boreholes has left large undrilled areas (perhaps because borehole placement followed dry riverbeds rather than being random across the landscape). Where there is presently high borehole density, perhaps compensation could be availed to entice livestock-owners to decommission their boreholes and relocate to mutually agreed (by the state and livestock-owners associations) localities, as was done when WMAs were created. All these policy options could prove controversial, but also predicate that there exist secure communal land tenure and credible livestock-owners syndicates to guide for example buffer demarcations, permissible stocking rates and any rotational grazing that may be imposed to ensure all of the grazing reserve is utilised to avoid localised overgrazing; these conditions (e.g. existence of cattle-keepers associations), are met to differing levels across the Kalahari.

Importantly, harmonized use of the grazing zones with other user groups is crucial. For instance, whether the WMA livestock-rearing buffers impinge on other livelihood activities, and what the community perceptions are about the demarcations, is unknown. However, antagonistic attitudes, primarily caused by restrictions on use and harvesting of non-timber forest products such as thatching grass and wild fruits, have been reported in some Kalahari WMAs (Twyman, 2001). Many rural people probably also collect firewood, poles and bushes for making kraals from outside the WMA livestock-rearing buffers. It is unlikely that such subsistence collection promotes bush encroachment or significantly affects vegetation structural integrity because the use is often localised and relates to exploitation of individual species. Thus, the current restriction of human utilisation of vegetation resources to the WMA livestock-rearing buffers probably produces unwarranted antagonistic attitudes between the state and communities (Twyman, 2001).

Reconciling the different use-values of savanna landscapes may be even more problematic in communal unprotected grazing lands. Because choice of domestic livestock and stocking levels is unregulated (Abel & Blaikie, 1989), while public perception of deliberate use of fire is different for each user group and may change with time (e.g. Angassa & Oba, 2008), investigations into how to achieve livelihood compromises that permit low grazing pressure and frequent fires—whose joint effects can reduce bush encroachment (Roques *et al*., 2001, van de Langevelde *et al*., 2003)—in unprotected areas, are an urgent priority. Whether fire frequency and intensity vary across the land use types is unknown, as is the differential influence of fire on vegetation conditions in PAs, WMAs and unprotected areas; for example, PAs may suffer more extensive fires due to remoteness and a lack of human resources to control those fires, while unprotected areas and WMA livestock-rearing zones may suffer more frequent fires due to greater human use and thus increased chances of deliberate fires in these landscapes. Within Botswana, there is presently no policy for regulated use of fire to manage vegetation. But within unprotected areas, habitat management, particularly the use of fire, may be more pragmatic in landscapes that already have too many boreholes in close proximity, precluding mutually agreed decommissioning of some boreholes or designation of borehole-free grazing zones.

Influence of predictor interaction and data resolution on observed patterns

It was possible to develop a proxy for bush cover, and validate it with field-measures. Relating this proxy to possible causative factors within an information-theoretic framework enabled us quantify the relative predictor importance without assuming their interactive effects or other relationships. Thus, without explicit models of the mechanism through which cattle may be driving greater bush cover, this study nonetheless demonstrates a very strong positive association between increased cattle density and greater woody vegetation canopy cover in human-modified landscapes of the Kalahari.

Field-based vegetation measures suggest rangeland degradation was most pronounced in unprotected areas, reduced in WMAs and lowest in PAs, as per the study's expectations. In contrast, the woody cover index suggests bush cover was greatest in unprotected areas, reduced in PAs and lowest in WMAs. While this seemingly contradicts the expectation of greater bush cover in WMAs than in PAs, decreasing woody vegetation canopy cover index along the gradient unprotected area > PA ≥ WMA livestock-rearing buffers ≥ WMA wildlife zone lends support to the hypothesised links between a positive relationship between grazer biomass and the woody vegetation cover index. The greatest grazer abundance was expected in unprotected areas (due to high densities of cattle). On the other hand, PAs support greater ungulate abundance than WMA wildlife zones (Chapter 3). The inference therefore is that PAs probably support marginally greater herbivore abundance than the pooled livestock and wildlife abundance within WMA livestock-rearing buffers, suggesting that the coarse canopy cover index is robust. Moreover, it is plausible that PAs support greater abundance of browsers than WMAs, animals which could diminish the extent of woody vegetation cover at greater rates within PAs relative to WMAs; this would minimise the contrast in woody vegetation cover between PAs and WMAs, but as the overall patterns of PA woody cover being greater than woody cover in WMAs have been retained, the results suggest disparity in bush cover between these land-uses is genuinely very large. Consequently, study findings are robust, but conservative; land-use contrasts would probably be more pronounced with finer-resolution vegetation measures. First, a coarse index of woody vegetation cover, estimated over a 4-km segment, was used. Second, vegetation contrasts across land-use types were based on structural measures rather than species composition or proxies for plant quality, which are more sensitive to tests of vegetation differences (Illius & O'Connor, 1999). Thus, for instance, because grass was not categorised by quality or palatability, contrasts based on the point frequency of grass bases and mean grass cover did not differ among land-use types, although poor quality and less palatable grasses were probably more prevalent in the intensely grazed unprotected areas (e.g. Abel & Blaikie, 1989). However, greater cover of the encroacher species *Dichrostachys cinerea* and *Acacia mellifera*, greater shrub density, and greater cover of non-grass herbaceous plants in unprotected areas relative to the conservation areas were all indicative of more range degradation in the unprotected landscapes (van Vegten 1984; Skarpe 1990), reaffirming patterns suggested by the woody vegetation canopy cover index. Notwithstanding, WMAs had a much greater extent of bare ground. While this would ordinarily be interpreted as a sign of range degradation and perhaps greater soil erosion potential (e.g. Illius & O'Connor, 1999; Asner *et al*., 2004), within our sampling extent, this may partly be due to at least two factors that could operate independently of herbivore-grazing pressure. First, most sampled WMAs were in the drier south-west Botswana, and the lower rainfall (and therefore reduced plant-accessible soil moisture) in this region may intrinsically explain the low basal cover relative to other land-uses; for instance, a countrywide vegetation sampling transect running from south-west to north-east Botswana recorded the lowest percentage cover of both live and dead herbaceous vegetation in south-west Botswana (Ringrose *et al*., 1998). Secondly, much of south-west Botswana is underlain by deep sandy-textured arenosols (Government of Botswana, 2001), and due to this soil type the vegetation predominantly comprises tufted grass and isolated rather than continuous herbaceous stands (e.g. Skarpe, 1986), which may account for the greater extent of bare ground at sampling points, most of which were within WMAs.

Conservation and management implications

Both PAs and WMAs are effective models to mitigate cattle-induced increases in bush cover, relative to unprotected areas. The evidence from WMAs suggests that savanna ecosystem structure with greater grass cover than woody vegetation (presumably preferred by cattle owners) within communal grazing areas could be maintained through cattle zoning, but further investigations are required. To assure minimal cattle-induced increases in bush cover a recommendation from this study is that rangeland management should not focus only on stocking rates, but consider the spatial distribution of boreholes. With growing human populations resulting in increasingly sedentary cattle-rearing and greater reliance on livestock-watering boreholes across African savannas (Du Toit & Cumming, 1999), coupled with changing perceptions on possible mitigation measures of bush encroachment (Angassa & Oba, 2008), improved understanding of the best means to minimise adverse bush encroachment impacts on agricultural productivity and conservation goals remains crucial. New approaches are required.

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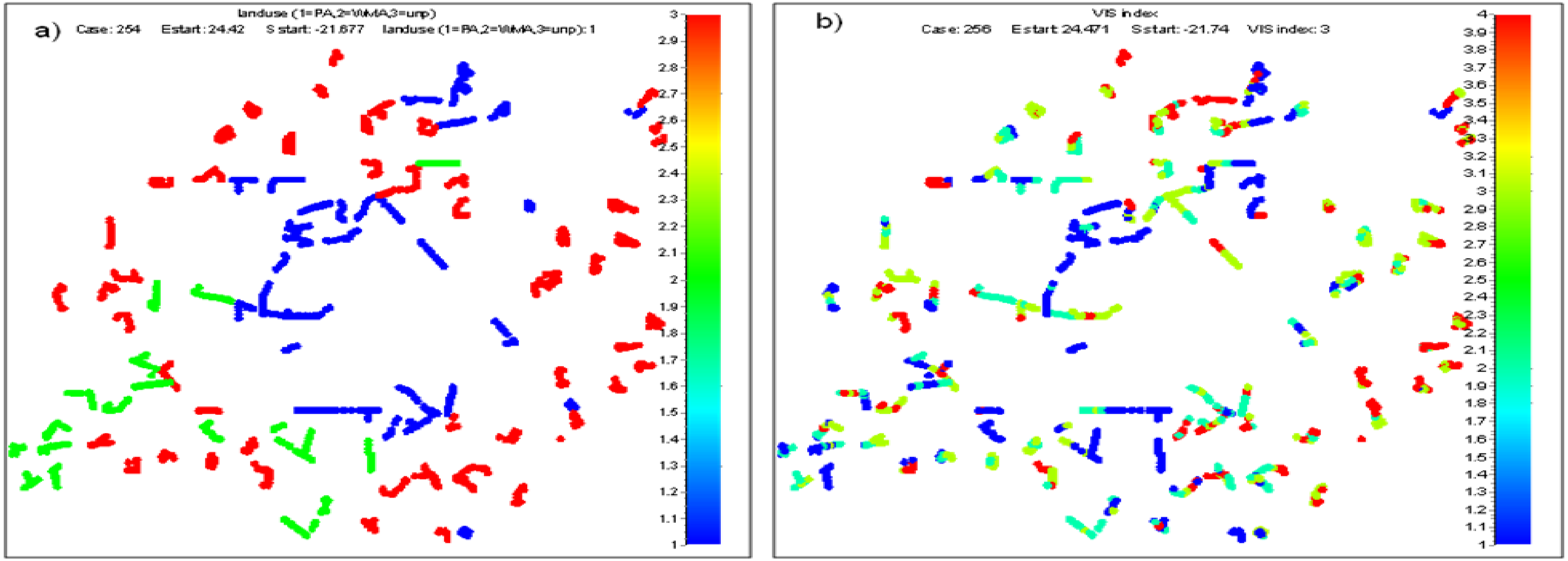
Appendix 4.1

Spatial distribution of transect segments, categorised by land-use type and by woody vegetation canopy cover index.



(a) Geographic spread of transects categorised by land-use, (b) distribution of woody vegetation canopy cover index (ordinal scale: 1 = very open, 2 = open, 3 = partly closed, 4 = closed). There were significant differences in *x*,*y* coordinates for segments from the three land-uses (*x*-coords $F_{2,1108} = 153.759$, $P < 0.0001$; *y*-coords $F_{2,1108} = 77.997$, $P < 0.0001$). All pairwise comparisons different (Tukey's HSD, $P < 0.0001$) for *y*-coordinates, and for all of *x*-coordinates except between PAs and unprotected areas ($P = 0.981$). Despite uneven distribution of transects relative to land-use (and rainfall), and while woody vegetation canopy index differs between land-use types (Fig. 4.3), there was no spatial autocorrelation in the woody vegetation canopy cover index at the landscape-scale (Moran's I = 0.258, $P = 0.610$). Thus, site-specific landscape correlates and borehole proximity are key explanatory factors of observed segment-level woody vegetation canopy cover ($n = 1109$ segments).

Chapter Five

Resource-rich pan habitats regulate seasonal movements and home range dynamics in female Kori Bustard *Ardeotis kori*

Abstract

Knowledge of what determines annual movement patterns, home range size and site-fidelity is fundamental to the design of species conservation programmes. However, this information is unavailable for most bird species, particularly in dryland Africa. Drylands experience large spatial and temporal variation in food resources, forcing some species or populations to adopt patterns of movement or home range use that lessen the negative impacts of the stochastic resource availability. Using data from satellite transmitters deployed on six Kori Bustard *Ardeotis kori* in Botswana's Central Kalahari Game Reserve during December 2008–March 2011, this study investigated the effects of season (wet, dry) on home range size, site-fidelity and association with pan (low-lying areas on mineral-rich clay soils) and non-pan habitats (upland sandy soils). Home range estimates were variable across individuals and for individual birds sampled over multiple periods of the same season. Across all birds, the largest home range over the entire sampling period (1580 km^2, Minimum Convex Polygon, MCP; 1619 km^2, 95% kernel; 302 km^2, 50% kernel) was respectively 13 times, 38 times, or 50 times greater than the smallest (122 km^2, MCP; 43 km^2, 95% kernel; 6 km^2, 50% kernel). The mean home range (measured over the entire sampling period for each individual) for the six birds was 528 km^2 ± 574 SD (MCP), while 95% and 50% kernel estimates were 420 km^2 ± 238 and 77 km^2 ± 112, respectively. Across all birds, seasonal home range size did not differ between wet (n = 12) and dry (n = 7) seasons based on MCP (wet 278 km^2 ± 396 SD, dry 79 km^2 ± 44, $t_{16} = 1.619$, $P = 0.125$) and 95% kernels (wet 356 km^2 ± 628, dry 118 km^2 ± 144, $t_{16} = 1.673$, $P = 0.114$), but 50% kernels were marginally larger in the wet than the dry season (wet 65 km^2 ± 120, dry 24 km^2 ± 33, $t_{16} = 1.930$, $P = 0.072$), controlled for individual birds and number of telemetry fixes. However, differences in seasonal home range extent were up to an order of magnitude for some individuals; where this occurred, the wet season home range was consistently larger than the dry season home range. Birds were sedentary and did not exhibit any migratory tendencies. There was strong site-fidelity, with dry season home ranges largely confined within the boundaries of the wet season ranges, and with similar overlap of the MCP, 95% kernel and 50% kernel and regardless of the seasonal pairs (wet–wet, wet–dry, dry–wet, dry–dry) considered. Only one bird had a multi-modal home range, with seasonal home ranges separated by up to 30 km. Pan

habitats were not used more than expected by chance during the wet season or during the entire sampling period, given relative availability within the 95% kernel home ranges of individuals. However, during the dry season birds were more often located within pans than expected by chance (Wilks $\Lambda = 0.545$, $t_5 = -2.0436$, $P = 0.056$). Findings suggest that food resource affects Kori movement patterns, home range size and site-fidelity, although sample sizes were modest. Improved understanding of habitat preference and use, disaggregated by sex and age, would enhance knowledge on the abiotic and biotic factors that may underlie the mechanisms accounting for the observed sedentary lifestyle, and establish whether Kori are likely to be sedentary throughout much of their geographic range.

Introduction

Over 41% of the world's land surface comprises drylands (Reynolds *et al*., 2007), characterised by an annual mean potential evapotranspiration at least 1.5 times greater than the annual mean precipitation (Safriel *et al*., 2005), and discontinuous vegetation cover with more productive patches largely restricted to watercourses. Four dryland subtypes of increasing aridity are recognised: dry sub-humid (predominant biome: woodland), semi-arid (semi-desert), arid (desert), hyper-arid (desert: Safriel *et al*., 2005); all four can occur in savannas. The vegetation-patch patterns and erratic rains that drive the phenology of these ecosystems (e.g. Beatley, 1974) result in spatial and temporal variation in food resources for vertebrates, especially of seeds, fruits and invertebrates. In semi-arid and arid ecosystems in the tropics, many bird species undertake nomadic movements, as a mechanism to cope with this intermittent food supply (Dean, 2004); nomadism entails moving from one area to another and staying only long enough to utilise resources there and possibly breed before moving to another locality (Newton, 2008). In Africa and Asia, nomadic species are primarily sandgrouse (Pteroclididae), larks (Alaudidae) and sparrows, weavers and finches (Passeridae), while honeyeaters (Meliphagidae), parrots (Psittacidae) and crows (Corvidae) comprise the majority of Australia's nomadic species (Dean, 2004). Nomadic species are predominantly seed-eaters (Dean, 2004), but other trophic groups are also frequently nomadic, including insectivores and raptors that prey on the smaller-bodied birds that congregate to exploit opportunistic food resources, or on small mammals whose abundance increases in response to plentiful resources (Newton, 2008). An understanding of the extent and ecological correlates of movement patterns, home range size, and site-fidelity is lacking for many tropical bird species. These knowledge gaps may compromise the effectiveness of conservation planning for species exposed to particular threats during extensive movements.

Bustards (Otididae) are the largest-bodied flying birds in the semi-arid and arid tropical regions of Africa, Eurasia and Australia. The basic ecology of many bustards, especially African species, is unknown. For example, while widely recognised as omnivores (Collar, 1996), for most species the relative importance of various food items is unknown, making it difficult to gauge the extent to which bustards may move in response to rainfall-driven pulses in food resources. Although nomadism is more influenced by diet than phylogeny (Newton, 2008), the positive relationship between the *per capita* energy cost of walking and body weight (Schmidt-Nielsen, 1972) suggests that the large-bodied bustards, which (like all Otididae) are strictly terrestrial, may more likely exhibit the alternative of a resident strategy rather than opportunistic nomadism, as long as occupied patches provide the minimum resources to meet basic energy needs throughout periods of resource scarcity. That even large-bodied bustards are capable of long distance migration if breeding habitats are unsuitable during winter periods is exemplified by the Great Bustard *Otis tarda* which migrates across much of its European range (Streich *et al*., 2006). The largest bustards are of the *Ardeotis* genus (*A. arabs, A. australis, A. nigriceps*, *A. kori*) with body weights ranging 4–12 kg (Collar, 1996). Three of these bustards are thought to undertake long-distance nomadic movements in the non-breeding season: *A. arabs* (Nikolaus, 1987), *A. australis* (Ziembicki & Woinarski, 2007) and *A. nigriceps* (Dutta *et al*., 2010). However, only Ziembicki & Woinarski (2007) provide quantitative and objective evidence of large-scale distribution and abundance changes synchronised with rainfall, based on mail surveys with landholders from much of the species’s range. In contrast, evidence of nomadism for *A. arabs* (Nikolaus, 1987) and *A. nigriceps* (Dutta *et al*., 2010) is based on apparent seasonal reduction in numbers at localised sites, mostly small parks. The extent to which these apparent reductions are attributable to seasonal changes in habitat use, decreased visibility when breeding season mating displays cease, variable observer effort or changes in detectability due to changed vegetation conditions at the same localities, is unknown.

Kori Bustard *A. kori* has an extensive geographic range spanning much of southern and East Africa, although its numbers show evidence of decline (Senyatso *et al*., in review; Chapter 2). Kori movements are poorly understood (Collar, 1996). It has been suggested that the species undertakes long-distance movements in response to rainfall or food supply (Collar *et al*., 1986; Collar, 1996), largely based on anecdotes. For example, Nikolaus (1987) remarked that birds in south-east Sudan were local migrants that embarked on distinct seasonal movements, inferred from opportunistic sight reports in only some months of the year. Similarly, Britton (1980) opined that in Kenya Kori were probably resident, but with apparent visits to Tsavo East National Park by some birds interpreted as evidence for regular movements. Furthermore, apparent increases in Kori abundance on the eastern end of its range in South Africa were taken to suggest large-scale eastward movements during the non-breeding season

(Snow, 1978); however, most of these records are now thought to have been misidentified Denham's Bustard *Neotis denhami* (Harrison *et al*., 1997). Based on atlas records from the former Transvaal Province in South Africa, Tarboton *et al*. (1987) suggested Koris undertake nomadic movements, as judged by their presence at some localities only after rains. By contrast, a widely held viewpoint in southern Africa is that Koris have no regular movements, based on Southern Africa Bird Atlas Project seasonality maps (SABAP; Harrison *et al*., 1997), where changes in the proportion of monthly records reporting a species across eight geographic zones in southern Africa were assumed to indicate movement across those zones. Moreover, Young *et al.* (2003), based on bi-annual coordinated counts across farmlands in South Africa, also suggested Kori do not undertake systematic movements. The latter two studies, however, were limited by small sample sizes and data pooled across large geographic areas within which seasonal movements might go undetected owing to the coarse spatial resolution. Moreover, Young *et al*. (2003) did not correct for observer effort, and both studies assessed movement based on population-level presence/absence trends, which may mask movements by individual birds.

In contrast Osborne & Osborne (1999), reported seemingly nomadic and dispersive movements in Namibia, based on radio-telemetry and vehicle-based surveys. Even so, their results may be biased, owing to limitations of relocating birds in an area with a poor road network when radio transmitters are used (although they occasionally used aircrafts to search some parts of their study area). Osborne & Osborne (1999) also reported that home range sizes based on Minimum Convex Polygons (MCPs) were larger in the dry than the wet season; however this may also be biased because MCP-based home ranges are sensitive to sample sizes (Laver & Kelly, 2008), and the low number of re-locations by Osborne & Osborne (1999) may not have been sufficient to reach asymptotes for Kori home ranges. Their home range estimates were typically based on 20–50 locational fixes for the entire year, for example, a mean 28 locations per bird for the period 1997–1998 (range: 11–55, *n* = 10 birds: Osborne & Osborne 1999).

Satellite telemetry, which provides unbiased estimates of movement and home range extent, was used to study Koris in Botswana's Central Kalahari Game Reserve using, with three main aims. The first was to determine home range size during both the wet (breeding) and dry (non-breeding) seasons; the hypothesis was that during the wet season, when food resources are plentiful, Koris should have less extensive movements and thus smaller home ranges. The second aim was to test for site-fidelity, and establish whether Koris undertake long-distance seasonal movements between breeding and non-breeding areas. The third aim was to examine the influence of pan habitats on seasonal movement patterns and home range use. Pans, which are low-lying areas on nutrient-rich clay soils where moisture is retained longest, and which often therefore hold extensive grasslands, are key resource areas for many Kalahari ungulates (Wallgren *et al.*, 2009), with recent work suggesting that greater Kori numbers are also recorded nearer these habitats (Chapter 3). It was therefore hypothesised that pans may provide patches with largely predictable and less fluctuating food resources compared to higher-elevation sand-dominated shrublands, and that Kori with home ranges near or overlapping pans may become restricted to these habitats during periods of low resource availability (particularly during the dry season).

The specific questions were: (1) How large are Kori home ranges and does the size change through the year?; (2) How much site-fidelity is there in Kori?; (3) Do Kori undertake long-distance seasonal or nomadic movements?; and (4) To what extent do Kori associate with pan habitats within their home ranges and is this season-dependent?

Methods

Study area

The study area, calculated as the MCP enclosing all locational fixes, covered 3029 km^2 of the Central Kalahari Game Reserve (CKGR, 21–24°S 22–26°E; Fig. 5.1), within the Kalahari Desert, Botswana. The study site was located within the semi-arid Northern Kalahari Tree and Bush Savanna vegetation zone (Weare & Yalala, 1971), between the 350 mm y^{-1} and 450 mm y^{-1} rainfall isohytes, with predominantly summer (October–March) rainfall (Nicholson & Farrar, 1994, Fig. 5.2). The woody savanna comprises tall trees, predominantly *Lonchocarpus nelsii*, *Terminalia serecia*, *Acacia erioloba* and *A. mellifera*, interspersed with low-growing shrubs, mainly *Grewia flava* and *G. flavescens*, and on pan edges *Cataphractes alexandri*. Predominant grasses are *Aristida* spp., *Eragrostis* spp. and *Schmidtia* spp. (Weare & Yalala, 1971). Within this broad vegetation zone four habitat types were recognised (following Makhabu *et al.*, 2002): fossil river valley and pan habitat predominantly comprising grasslands on low-elevation clay soils; gently undulating dune and interdunal (valleys between dunes) habitats, both comprising mosaics of woodland, shrublands and grasslands on sandy soils; and plain habitats comprising mixed shrubs and grasslands with few large trees on mainly loamy soils.

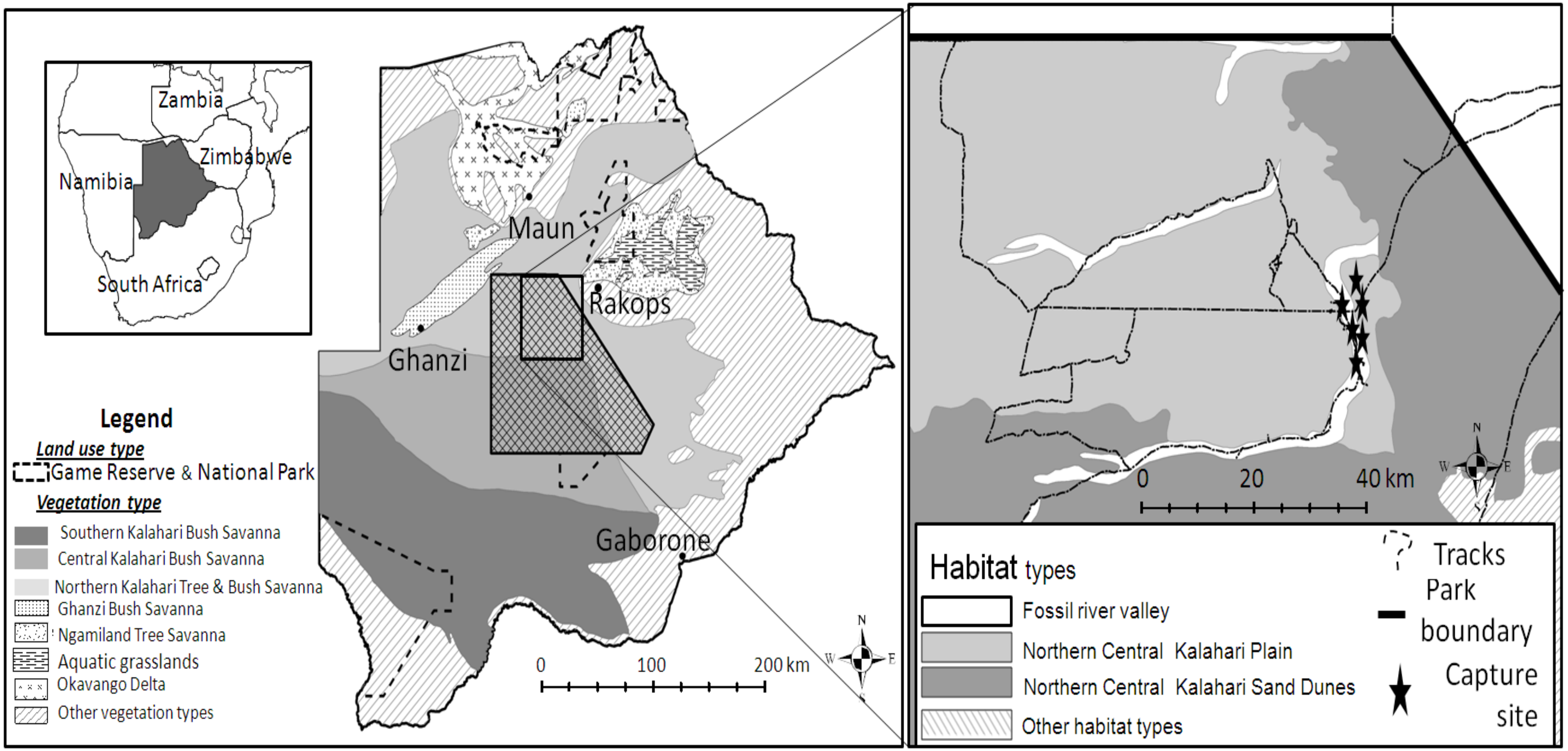
Hunting has been prohibited since the park (55,000 km^2) was established in 1961 (Campbell, 1973), and the nearest human settlement was at least 40 km from the study area. CKGR is thought to support a large population of Kori (Tyler & Bishop, 1998), but quantitative estimates are unavailable. However, driven DISTANCE surveys in December 2008–March 2009, covering 1211 km of line transects, recorded a total of 245 birds, 86% of them on pans, 11% in dune and interdunal and 3% in plain habitats, with estimated densities of 1.71 Kori km^{-2} ± 0.42 SE on pans and 0.24 Kori km^{-2} ± 0.10 in dune habitats, while observations from plains were too few to draw any biologically meaningful density estimate (Senyatso *et al*., unpublished data).

Trapping and satellite tracking

Birds (six females, two males) were caught during 8–11 December 2008 (four birds) and 4–6 August 2009 (four birds, Table 5.1), using vehicles to herd them into 100 m × 3 m mono-filament gillnets hung on trees, following methods used elsewhere on Kori (Osborne & Osborne, 1999) and Bengal Florican *Houbaropsis bengalensis* (Gray *et al*., 2009). Birds were fitted with back-pack harness-mounted satellite Platform Transmitter Terminals (PTTs), four with 105-g battery-powered GPS PTTs (Microwave Telemetry, USA) programmed to take one locational fix at 10:00 h GMT every day and four with 65-g solar-powered GPS PTTs (North Star Telemetry, USA) programmed to take one fix every four hours. The initial decision to collect one fix per day was borne out of the need to maximise battery life. But, as these PTTs provided sporadic high resolution location fixes (see below), for the second batch, solar-powered PTTs were preferred, and a sampling regime that allowed a reading every four hours was employed so as to increase the likelihood of a dataset with a large number of location fixes. The PTTs weighed less than 2% of the Kori body weights, and were therefore considered to have negligible negative effects. Birds were released within 20 minutes of capture, and no capture-related myopathy, a common problem with captured bustards (Marco *et al*., 2006), was recorded. However, two birds died within two months of capture, a male and female: the male bird was shot, based on assessment of recovered PTT (C. Bykowsky, Microwave Telemetry, pers. comm.), while the female bird was a presumed mortality rather than transmitter failure because the PTT transmitted from a stationary point for several weeks, although the PTT was never recovered. These two birds are excluded from subsequent analysis owing to too few locational fixes.

Locational fixes were obtained via satellites managed by the Argos CLS service (Argos, 2011). A total 4770 locations were retained for analysis, comprising GPS fixes (error <26 m), and Argos fixes (determined by satellite Doppler shift) of class 3 (error <250 m) and class 2 (error 250–500 m: Argos, 2011). Analysed data included Argos class 1 (error 500–1500 m) records for three birds, 84381 (64/138 records), 84382 (21/139 records) and 84383 (83/159 records), to ensure a minimum sample size of 15 location fixes per season; these records introduced minimal bias because for each bird they were all within an MCP delineated by the finer-scale records. In addition to removing from the dataset location fixes with large spatial error (classes 0, A and B: errors exceed 1500 m or unquantified, Argos, 2011), analyses also excluded (applicable to North Star PTTs only) location fixes obtained between 21:00 h and 05:00 h (GMT+2) when the birds were roosting and stationary, to avoid biasing home range estimates towards these spatially non-independent points. Thus all fixes analysed relate to diurnal activity. To filter potential spatially duplicated records in the remaining dataset, for each bird all location fixes within 30 minutes of each other were examined, and one random record (among those with the least spatial error) was retained. Thirty minutes was deemed sufficient for a Kori to have walked more than 1.5 km from a particular point, a distance exceeding the coarsest spatial error of the Argos fixes used, so records were considered spatially independent, following Rooney *et al*. (1998). However, the time interval required to achieve two non-autocorrelated successive locational fixes (Swihart & Slade, 1985) was neither statistically tested nor considered in this analysis because temporal autocorrelation does not affect home range estimators (De Solla *et al*., 1999; Kie *et al*., 2010), unlike spatial autocorrelation where duplicate or extremely close location fixes may result in non-convergence during the selection of smoothing factors, particularly for Least-Squares Cross Validation (Rodgers & Kie, 2010).

Figure 5.1. Location of the Central Kalahari Game Reserve within Botswana and predominant habitat types within parts of the reserve where Kori Bustards were caught, tagged and released.



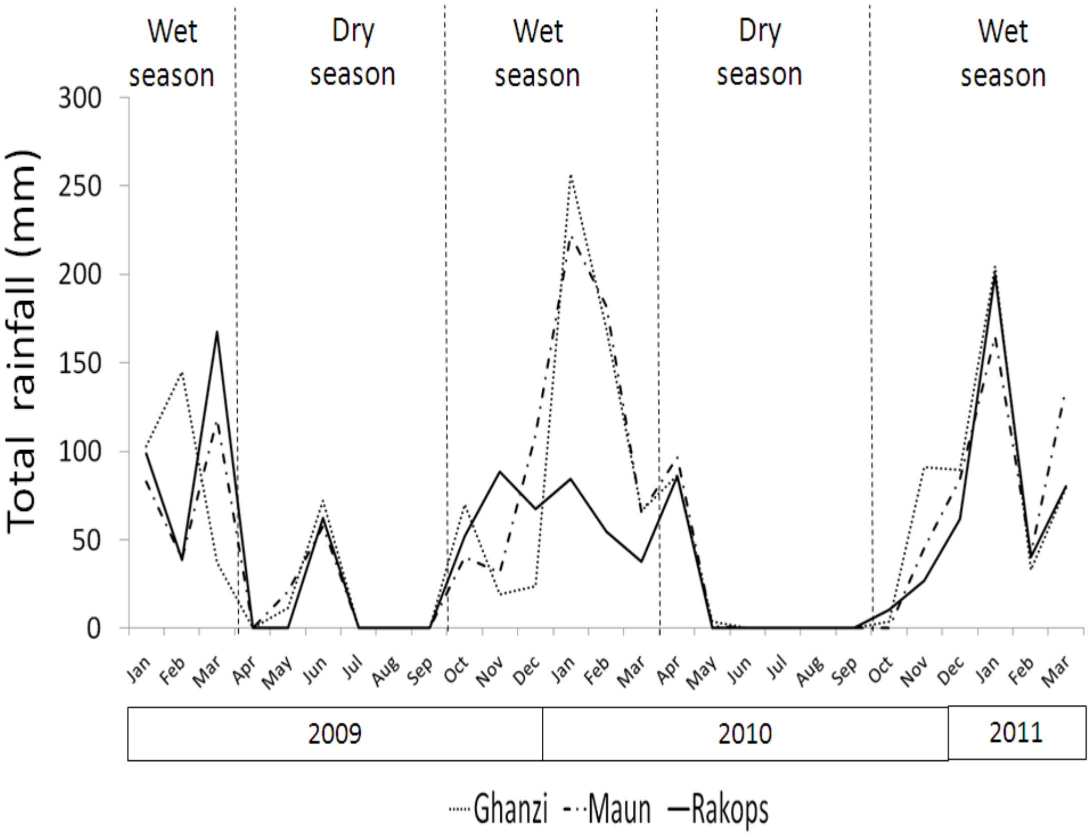


Figure 5.2. Mean monthly rainfall in the vicinity of the study site, measured at Rakops (50 km NE), Maun (110 km NW) and Ghanzi (200 km SW) of study site (see Fig. 5.1).

Home range estimates

Location fixes were separated into wet seasons (October–March, corresponding to the Kori breeding season in southern Africa, Allan & Osborne, 2005) and dry seasons (April–September, non-breeding; Fig. 5.2), hypothesised to correspond to high and low resource availability respectively. Individual home ranges were estimated for each bird per season (hereafter ‘seasonal home ranges’) and for the entirety of the sampling period. Using simulations, Seaman *et al*. (1999) recommend that a minimum 30–50 location fixes be utilised to obtain stable kernel-based home range, and because each of the six Kori considered had much greater total number of location fixes (median = 434, range: 139–1812, Table 5.1), available sample sizes were considered adequate to obtain stable home ranges over the entire sampling period. For each bird, season-specific home ranges were estimated for each season with more than 15 location fixes in that season, following Hingrat *et al.* (2004); a strong correlation between home range size and number of telemetry fixes can bias estimates if sample sizes are limited (Seaman *et al.*, 1999; Laver & Kelly, 2008), but results from linear mixed models that related home range size to season, corrected for individual bird and number of telemetry fixes (see below) confirmed that using as few as 19 fixes per season (minimum seasonal sample size: Table 5.1) was not a concern in this study. To estimate home range size, three measures used in other bustard studies (e.g. Hingrat *et al.*, 2004; Gray *et al.*, 2009) were adopted to facilitate future comparisons: 100% MCPs, 95% kernel and 50% kernel (core) home range.

Minimum Convex Polygons were constructed; although these have been criticised as an inaccurate measure of home range size (Laver & Kelly, 2008), MCP home ranges provide a measure of the maximum area over which a Kori may range, an important parameter for conservation planning. Home range kernels were modelled based on bivariate normal fixed-kernels, 100-m grid-cells, and with *x*, *y* data standardised to unit variances, using HOME RANGE TOOLS for ARCGIS (version 1.1; Rodgers & Kie, 2010). Selecting a smoothing factor (Kenward, 2001) by Least Squares Cross-Validation (h_{lscv}) underestimated home ranges owing to over-smoothing and delineation of perforated home ranges (with several intermittent contours rather than a single one), or convergence to the reference smoothing factor (h_{ref}). Therefore h_{ref} was used for all home range estimates, because this smoothing factor gave similar or better home range fit—based on extent of home range perforation—than proportions of h_{ref} following an *ad hoc* approach that tested values from 0.2 to 0.95 times h_{ref} in increments of 0.05 (Rodgers & Kie, 2010). Using a single smoothing factor rather than multiple factors also facilitates comparisons with other studies, as per Laver & Kelly's (2008) recommendations.

Home range overlap, seasonal movements and site-fidelity

Whether Kori undertook seasonal movements was examined by calculating the extent of each bird's home range overlap between consecutive wet and dry season (wet-to-dry and dry-to-wet transitions considered separately) for MCP, 95% and 50% kernel home range estimates. Static interactions—areal overlaps that do not account for the probability of use within a home range (Powell, 2000)— were used, because the primary interest was testing whether separate wet and dry season home ranges exist.

Table 5.1. Sex and age of tracked Kori Bustard, satellite transmitter identity (PTT ID), transmitter type, deployment date, tracking life and number of location fixes obtained.

PTT ID	Transmitter [b]	Date released	Sex	Age	Tracking duration (months)	No. of fixes per seasons tracked [c]				
						2009		2009/10	2010	2010/11
						Wet 1	Dry 1	Wet 2	Dry 2	Wet 3
84381 [a]	MT	8 Dec 2008	F	Subadult	11	37	53	48	–	–
84382 [a]	MT	8 Dec 2008	M	Subadult	10	72	59	8	–	–
84383	MT	9 Dec 2008	F	Adult	23	22	27	46	19	45
84384 [a]	MT	11 Dec 2008	M	Adult	1	4	–	–	–	–
84385 [a]	NS	5 Aug 2009	F	Adult	19	–	–	584	357	871
84386 [a]	NS	4 Aug 2009	F	Adult	2	–	–	15	7	–
84884	NS	5 Aug 2009	F	Subadult	16	–	–	603	395	789
84885 [a]	NS	6 Aug 2009	F	Adult	15	–	–	262	202	245

[a] Mortality, none of the PTTs lost are assumed due to battery failure.

[b] MT: Microwave Telemetry 105 g battery-powered GPS transmitter; NS, North Star 65 g solar-powered.

[c] Seasons based on total monthly rainfall, see Fig. 5.2.

Home range overlap, expressed in terms of overlap area relative to either dry season range or wet season range, was asymmetrical and therefore expressed as the mean percentage overlap between the two seasons. To obtain a pooled index across all birds, a mean overlap value was calculated by summing all overlap percentages within the period of interest, and dividing that sum by $2k$, where k is the number of wet–dry season pairs, following Kenward (2001). This index of overlap quantifies intra-annual seasonal site-fidelity (Powell, 2000). Inter-annual site-fidelity between successive wet–wet or dry–dry seasons were also examined, using the same approach described above.

Habitat associations

For analysis of habitat association, dune, interdunal and plains habitat were pooled as ‘non-pan habitat’ (due to their similar vegetation physiognomy) and their use compared to use of pans (hypothesised to be preferred). Habitat boundaries were based on maps from the Botswana atlas, which utilised 1-km^2 resolution polygons (Government of Botswana, 2001); as the habitat map resolution was greater than the tracking resolution, and habitats were contiguous blocks rather than isolated patches (Fig. 5.1), it was considered that the mapping resolution introduced minimal bias in tests of habitat preference. Location fixes that were near the pan/non-pan habitat boundaries were included in analyses, to avoid too small sample sizes for birds 84381, 84382 and 84383, whose datasets were largely based on Argos fixes (at best error <250 m). Moreover, because pan habitats were narrow and elongated strips (at places only 1 km wide, Fig. 5.1) exclusion of points near habitat boundaries may have underestimated use of pan habitats. Therefore all fixes were used, accepting that ability to detect differential use of pans may be reduced by location error, but that this error would be unbiased.

Habitat association was examined by compositional analysis (Aebischer *et al.*, 1993) which, for pairs of habitats, considers the log ratio of differences in usage to differences in availability. The proportions of location fixes obtained within pan or non-pan habitats relative to the proportional extent of these habitats within the 95% kernel of pooled telemetry data across all seasons for that individual were examined, corresponding to Johnson’s (1980) third-level of preference assessment, separately for three time-periods: entire sampling period, wet season and dry season. For the seasonal contrasts, location fixes from multiple repeat seasons were pooled. It was not possible to test habitat association by examining home range placement within the overall study area (second-level of preference assessment: Johnson 1980) and whether home ranges were preferentially located in pans, because all birds were caught in pan habitats owing to the ease of catching Kori in these landscapes.

Compositional analysis was conducted in Microsoft EXCEL and the COMPOS ANALYSIS version 6.2 standard software add-on (Smith, 2005). Where habitat use was zero, the zero was substituted by 0.01, which was an order of magnitude less than the smallest non-zero value, following Aebischer *et al*. (1993). One thousand iterations of randomised data were drawn, with Student's *t* used to examine if preferences differed significantly from zero, testing significance at the 0.05 level. Significant departures from random use of pan versus non-pan habitat were tested using Wilks's Lambda.

Statistical analysis

Mean wet and dry home range extents for MCPs, 95% kernel and 50% kernels were compared using linear mixed models performed on log-transformed areas (to achieve homogeneity of variance); whether differences in the number of fixes affected seasonal home range sizes was tested by considering season (wet, dry) and number of fixes as fixed effects, and individual bird as a random effect. ArcGIS version 9.3 was used for geospatial analysis and SPSS version 16.0 for statistical analysis. Data are presented as mean ± SD.

Results

Based on data pooled across the entire sampling period for each bird, the mean MCP area for the six Kori was 528 km^2 (± 574 SD), while the mean of the 95% kernels was slightly less at 420 km^2 (± 238 SD) but was strongly correlated with MCP extent (r = 0.91, P = 0.007). Mean extent of 50% kernel home ranges was 77 km^2 (± 112 SD), just 19% (± 5 SD, n = 19 seasonal home range estimates) of the 95% kernel home range extent, suggesting that birds spent half of their time in a small part of their home range. However, home range estimates varied greatly among individuals (Table 5.2, Fig. 5.3), with one individual having over the entire sampling period a home range of 1580 km^2

(MCP), estimated as 1619 km^2 using 95% kernel, which were 13 and 38 times greater respectively than the individual with the smallest home range extent (122 km^2 and 43 km^2).

Wet season home ranges were marginally larger than dry season home ranges (Table 2). The number of fixes did not affect home range estimates or seasonal contrasts for MCPs (Table 2b). In contrast, the number of telemetry fixes per season affected area estimates of both 95% and 50% kernels (Table 2b); the negative parameter estimates for this covariate, suggesting that smaller home ranges were obtained as the number of telemetry points increased, was due to the better performance of the solar transmitters because they more often gave GPS location fixes rather than the less precise Argos fixes. Moreover, these more accurate GPS fixes were collected more regularly (multiple fixes per day) relative to the battery-powered PTTs (which often did not produce a location fix with less than 1,500 m error for several days). Controlling for these effects, differences between home range extent in the wet and dry seasons were still non-significant (Table 2).

Although an individuals’ home range in the wet and dry season could differ in extent by an order of magnitude, there was no consistent or significant difference in home range extent between wet and dry season, for either MCP, 95% kernel or core home ranges (Table 5.2). Dry season home ranges were largely confined within the boundaries of wet season ranges, except for one bird with a large multi-modal home range (Fig. 5.4).

Tracked birds showed considerable home range fidelity, both for consecutive seasons (dry–wet and wet–dry) and intra-annual contrasts of repeat seasons (wet–wet and dry–dry; Table 5.3). Percentage seasonal overlap of the 50% kernel was marginally larger than that for the 95% kernel and MCP regardless of the season pairs (wet–wet, wet–dry, dry–wet, dry–dry) considered. The extent of overlap when transitioning from dry-to-wet was 5–10% greater than that of wet-to-dry (Table 5.3), regardless of the home range estimate considered. Intra-annual overlap (between two consecutive seasons) was similar to inter-annual overlap for a consistent season.

Table 5.2. Wet (October–March) and dry (April–September) season and entire sampling period home range sizes (km^2) based on Minimum Convex Polygons (MCP), 95% kernel and 50% kernel: (a) for individual birds, in parentheses is the number of wet and dry seasons over which the bird's location fixes were obtained, and each row summarises a seasonal home range estimate. See Table 5.1 for the number of location fixes for each season, (b) mean (± SD) home range size averaged across the six birds, $n = 12$ wet and seven dry season home range estimates, with linear mixed models (based on log-transformed seasonal home range size) used to examine the effect of season (fixed factor) on home range size, controlling for number of telemetry fixes (covariate) and individual bird (random factor); table shows *t-test* contrasts of wet versus dry season; subscripts show parameter estimates (± SE) of model constant and covariate, in all cases calculated relative to dry season, whose parameters were set to zero.

a)

Bird	MCP			95% kernel			50% kernel		
	Entire sampling period	Wet	Dry	Entire sampling period	Wet	Dry	Entire sampling period	Wet	Dry
84381 (2,1)	1580	139	62	1619	283	70	302	49	12
		1355			2271			434	
84382 (1,1)	117	94	69	185	85	68	45	14	9
84383 (3,2)	315	44	78	318	102	183	67	22	43
		152	149		332	421		77	92
		245			450			100	
84385 (2,1)	801	180	123	291	56	46	29	15	6
		799			517			39	
84884 (2,1)	234	117	52	43	15	13	6	3	2
		110			57			12	
84885 (2,1)	122	42	18	62	36	28	12	6	8
		65			64			13	

b)

MCP [a]				95% kernel [b]				50% kernel [c]			
Wet	Dry	t_{16}	P	Wet	Dry	t_{16}	P	Wet	Dry	t_{16}	P
278 ± 396	79 ± 44	1.619	0.125	356 ± 628	118 ± 144	1.673	0.114	65 ± 120	24 ± 33	1.930	0.072

[a] Constant 1.793 ± 0.168, $t_{16} = 10.686$, $P < 0.0001$; number of fixes 0.0002 ± 0.0004, $t_{16} = 0.498$, $P = 0.625$.

[b] Constant 1.969 ± 0.214, $t_{16} = 9.183$, $P < 0.0001$; number of fixes −0.0009 ± 0.0005, $t_{16} = -1.882$, $P = 0.078$.

[c] Constant 1.259 ± 0.202, $t_{16} = 6.221$, $P < 0.0001$; number of fixes −0.0011 ± 0.0004, $t_{16} = -2.402$, $P = 0.029$.

Table 5.3. Home range fidelity, showing mean percentage (± SD) overlap of home range (Minimum Convex Polygon, 95% kernel, 50% kernel) based on static volume of overlap between consecutive seasons (wet-dry or dry-wet) and inter-annual overlap for consistent season (wet-wet and dry-dry). See main text for computation details. In parenthesis are the minimum–maximum of the raw seasonal overlap.

Home range estimate	Seasonal contrasts			
	Wet-dry	Dry-wet	Wet-wet	Dry-dry
MCP	55 ± 32	58 ± 31	58 ± 29	62 ± 28
	(0,100)	(4,100)	(7,100)	(43,82)
95% kernel	59 ± 33	63 ± 30	62 ± 29	66 ± 38
	(0,91)	(9,100)	(8,100)	(41,93)
50% kernel	66 ± 36	70 ± 33	71 ± 31	73 ± 38
	(0,100)	(3,100)	(2,100)	(47,100)
Birds	6	5	5	1
Seasonal pairs	7	6	7	1

Birds showed no preference for pan habitat during the entire sampling period or for the wet season, relative to availability within their 95% kernel home ranges (Wilks Λ = 0.975, t_5 = 0.356, P = 0.698; Wilks Λ = 0.916, t_5 = 0.676, P = 0.469, respectively). In contrast, during the dry season, location fixes tended to fall within pan habitats more often than expected by chance given relative areal extent (Wilks Λ = 0.545, t_5 = −2.0436, P = 0.056).

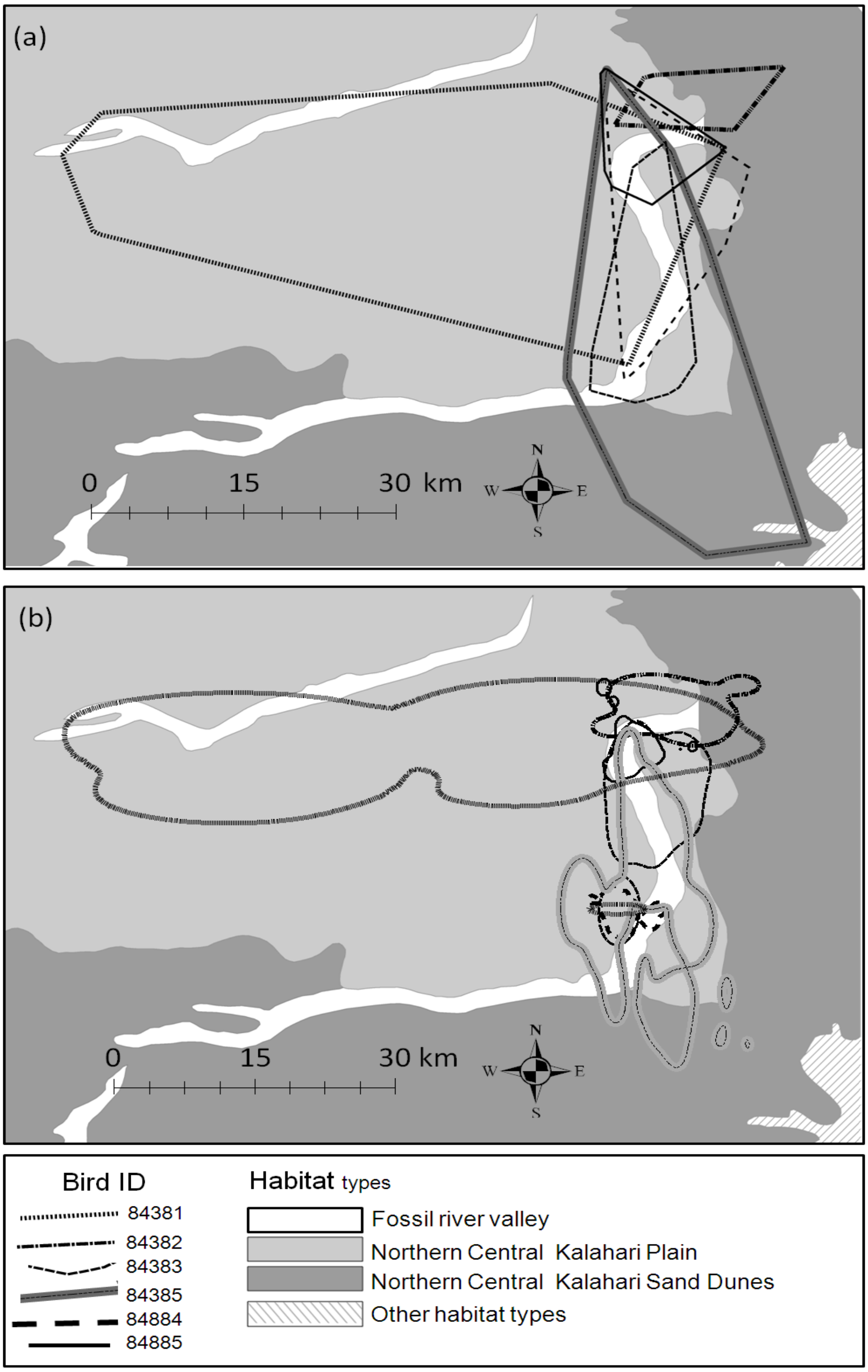


Figure 5.3. Location and overlap of home ranges (a) Minimum Convex Polygons, (b) 95% kernel, for six Kori Bustards in the Central Kalahari Game Reserve, also showing the extent of overlap with the three habitat types within the study area. Home range estimates based on all locational fixes detailed in Table 5.1.

Figure 5.4. Wet (October–March) and dry (April–September) season home range overlap (95% and 50% kernels; h_{ref}, bivariate normal fixed-kernels, 100-m grid-cells, x, y data standardised to unit variances). Sample sizes of repeat wet or dry seasons and number of location fixes per season vary across individuals; see Table 5.2 for sampling periods and total number of location fixes. Note different scales for (a)–(c) and (d)–(e).

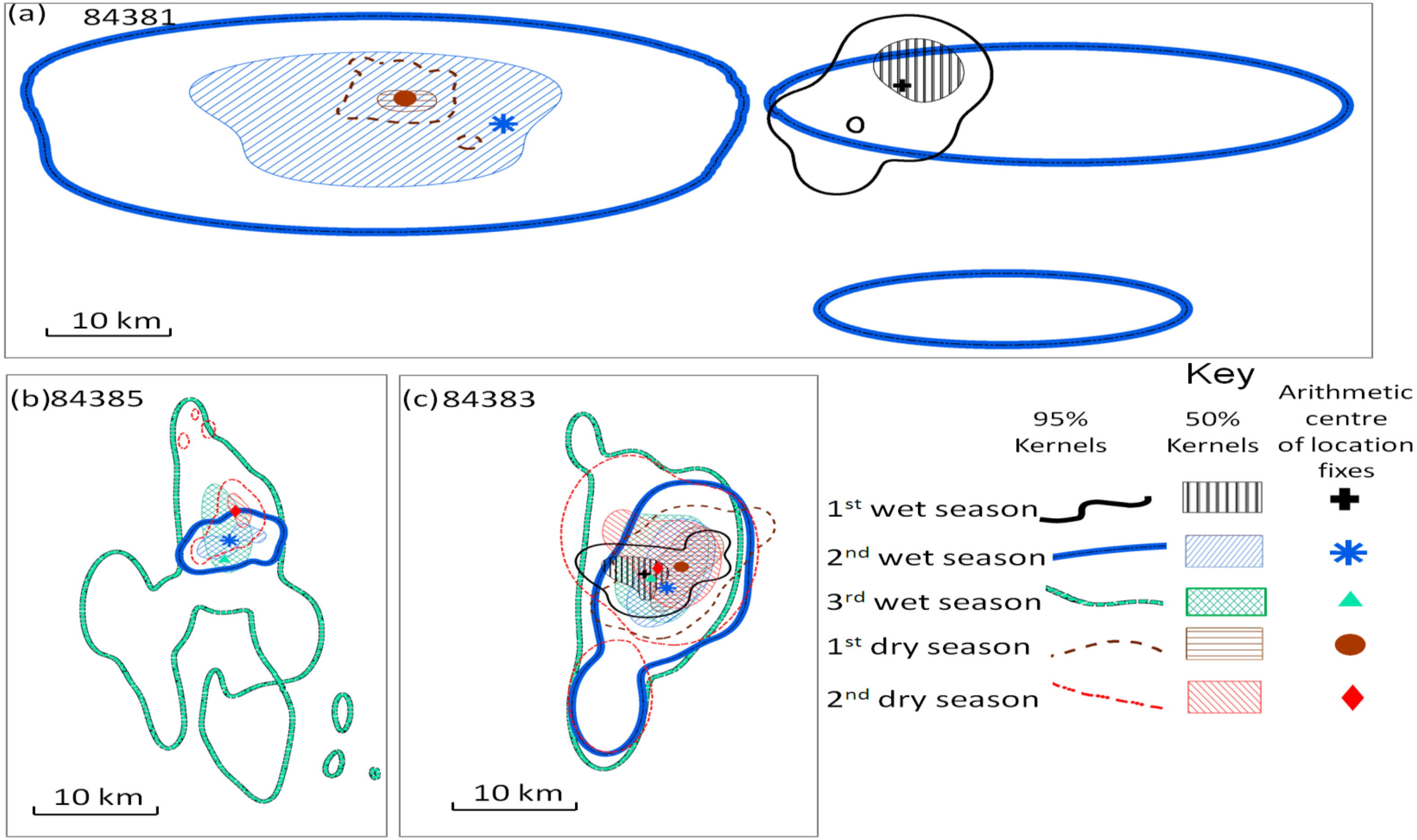
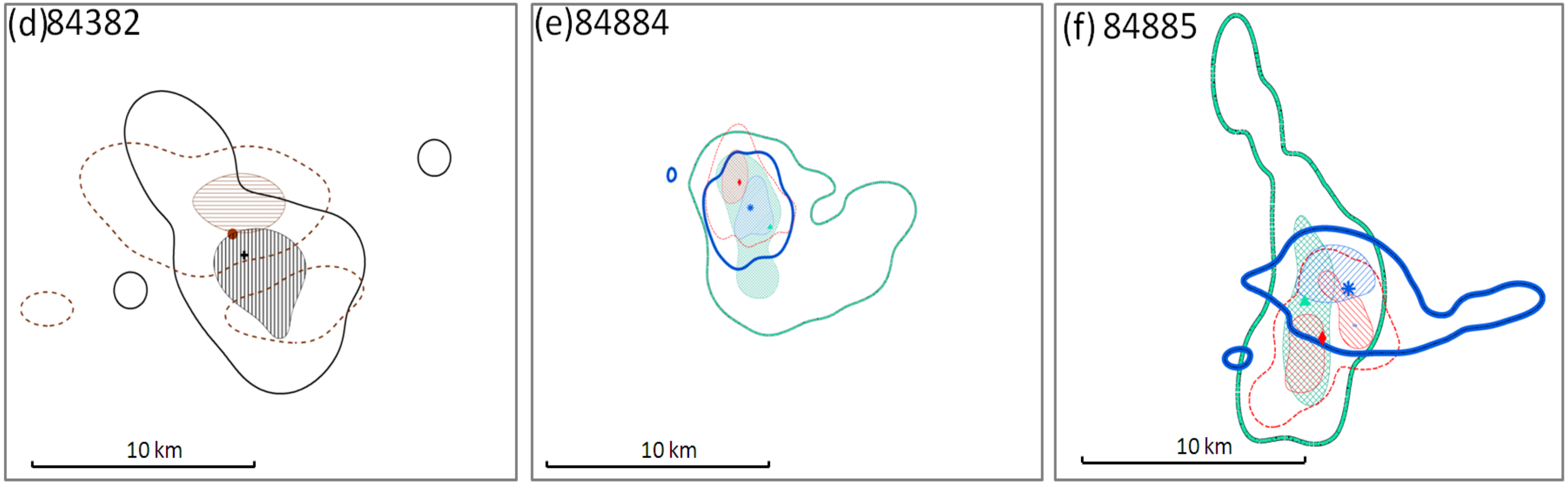


Figure 5.4 (continued).



Discussion

Kori home ranges sizes were variable between and within individuals, with strong site-fidelity and dry season home ranges largely nested within the wet season home range. During the dry season, telemetry locations were positively associated with pans. Findings suggest that the species adopts a strategy whereby the home range expands and contracts, rather than seasonally moving between spatially isolated patches, supporting the hypothesis that these large-bodied bustards may be sedentary rather than nomadic or migratory.

Home range size, overlap and seasonal movements

Previous research on Kori movement patterns and home range dynamics has been limited, with the extent of movements inferred from apparent patterns in seasonal abundance (e.g. Snow, 1978; Britton, 1980; Nikolaus, 1987; Harrison *et al*., 1997). The view widely reflected in the literature (Snow, 1978; Britton, 1980; Nikolaus, 1987) that Koris make long-distance seasonal movements was not supported by findings from this study, which indicated that within the Central Kalahari Game Reserve movements can be restricted, with birds exhibiting strong site-fidelity and largely overlapping wet and dry season home ranges.

The mean MCP, 95% kernel and 50% kernel home range estimates for birds tracked continuously for a minimum six months were 528 km^2, 420 km^2 and 77 km^2 respectively. These estimates are broadly similar to findings in Namibia's Etosha National Park, where Osborne & Osborne (1999) reported mean MCP-based home ranges spanning 2–413 km^2 for 10 females tracked during 1997/1998. In that study, while females with chicks had the smallest ranges, those without moved up to 100 km from their release site during the non-breeding season, and males moved 'several hundred kilometres' from the breeding areas (MCPs: 45–6718 km^2 for six males in 1997/1998: Osborne & Osborne, 1999); examples of birds that utilised similar-sized home ranges at localities separated by nearly 100 km (3 of 8 females) suggested that Kori undertook nomadic movements. Moreover, sex-specific and breeding-status differences in home range size and extent of movements imply that movements were strongly driven by the breeding cycle, because differences in mean rainfall in Etosha and in CKGR appear unlikely to explain differences in movement patterns between these regions; the long-term (1954–2001) mean annual total rainfall in Etosha, and during 1997/1998, exceeded 200 mm y^{-1} (ranging 279–436 mm y^{-1}, de Beer *et al*., 2006), while during this study the total rainfall was consistently below this level. This suggests that within Etosha, because birds retained similar-sized home ranges in different parts of the reserve, the separate home ranges could both meet energy demands and that long-distance movements between these seasonal ranges may have been breeding-related.

By contrast, and with the strong proviso that sampled birds in this study consisted of females of unknown age and breeding status and one immature male, results suggest strong food resource-driven effects on home range size and site-fidelity, which could operate independently of breeding status. Dry season home ranges, which largely formed the core of the more extensive wet season home ranges, were associated with pan habitats, at least in female Koris. Owing to their greater soil water-retention capabilities and more fertile soils (Wallgren *et al*., 2009), pans presumably hold higher levels of food resources and are subject to less marked fluctuations in such resources than dunes, interdunal and plain habitats. Because there is a positive relationship between patch residence time and energy availability (Stephens & Krebs, 1986), longer residence times can be expected in habitats that provide the basic energy requirements with minimal search effort. Therefore the greater proportion of telemetry fixes on pans in the dry season was considered to indicate greater food availability in these landscapes than non-pan habitats. Preferential use of pan habitats during the dry season, when food resources are limited, supports the hypothesis that forage resource availability determines home range size and placement of the home range core.

On the other hand, habitat use by bustards may be influenced by the distribution of conspecifics (e.g. Osborne *et al*., 2007). Effects of Kori socialisation on patch selection and use are unknown, but as the species is assumed to have a lek-based breeding system (Morales *et al*., 2001; Allan & Osborne, 2005), it is likely that the most pronounced use of conspecifics as cues would occur when birds aggregate in leks during the breeding season (September–March: Allan & Osborne, 2005), which coincides with the period designated as the wet season in this study. If birds congregated on CKGR pans and remained restricted to these areas owing to breeding-mediated behaviours, then wet season home ranges should have been smaller than those for the dry season, in contrast to the hypothesis of larger home ranges during the non-breeding season (Osborne &

Osborne, 1999). Moreover, because leks are presumably on open areas (Astley-Maberly, 1937; Osborne & Osborne, 1999), the vegetation physiognomy of pans make them more likely candidates for lek sites, in contrast to dunes and plains; however, the lack of any selection for pans during the wet season (which would support the hypothesis of their use as leks) in this study could be because tracked birds were mostly non-breeding females, or that lekking may not be entirely restricted to pans. The study's findings suggest that the apparently greater propensity for nomadism in Namibia (Osborne & Osborne, 1999) probably reflects the fact that lekking areas and localities providing food resources during the dry season may be spatially separated. In contrast, CKGR pans may serve the dual roles of a wet season lekking area and a key source of food in the dry season.

Tracked birds in the CKGR were sedentary, but ranged over larger areas in the wet than in the dry season, with the small-scale movements presumably in response to resource availability. Therefore, although broadly in agreement with Harrison *et al*. (1997) and Young *et al*. (2003)'s findings of no regular seasonal movements, the coarse-scale of analysis in these studies may have masked genuine localised seasonal movements or seasonal contractions and expansions of range albeit with the range core largely overlapping the dry season home range. However, in both the wet and dry season, the mean home range size (MCP or 95% kernels) for the six Kori were an order of magnitude less than the 50-km (Botswana) or 25-km atlas grid-squares (South Africa, Namibia, Zimbabwe: Harrison *et al*., 1997). Moreover, Harrison *et al*.'s (1997) assessment of whether regular movement exist was based on data pooled within eight SABAP zones each spanning at least 8°-longitude × 5°-latitude, an area exceeding 440 000 km^2 and representing more than 270 times the size of the largest home range recorded in this study, even after pooling all data from the sampling period for each individual. Even then, most of the SABAP grid-squares were poorly sampled; for instance, 34% of the grid-squares in Botswana (n = 203) were visited fewer than four times in eight years (Penry, 1994). Findings from this study suggest that Kori conservation assessments, particularly correlates of movement, require datasets that are at finer scale than that collated by Harrison *et al*. (1997), presently the most extensive dataset on bird species distribution on the subcontinent.

Results for bird 84381 suggest that small home ranges may not be universal, and some Kori may be more nomadic than others. It is unclear why this subadult female was the only bird that had a multi-modal home range and ranged more extensively over the study area, but several plausible guesses can be made. Although this bird was caught and released on pan habitat, all its 37 location fixes from the first wet season were in non-pan habitats; however, there is no evidence of nesting (which could have been inferred from clustered location fixes) in the non-pan habitats that are presumably used for nests (Allan & Osborne, 2005). However, during the subsequent dry season, it migrated to near pan habitats at least four times the distance from the nearest pan where it was originally caught. Because other tagged birds stayed within the pan habitats in which they were caught, food was probably not limiting, and so perhaps bird 84381 associated with other untagged birds whose dry season range was centred on the far-off pans; but this assumption cannot be tested until Kori socialisation is better understood. Because female Kori are generally not aggressive to each other, and may often associate in feeding groups (pers. obs.), it is unlikely that intra-specific competition would limit home range size. Similarly, as the only large-bodied bustard in the study area and in central Botswana, it is unlikely that home range sizes were limited by competition with other Otididae. However, sample sizes in this study were too small to investigate any sex- or age-dependent factors that may account for differential nomadic behaviours, and this remains an urgent research priority, including ascertaining the role that the species's mating system may have in influencing seasonal home range size.

Applicability to low-density and widespread species in arid environments

It is important to acknowledge several design constraints that may limit direct transferability of the results to other widely distributed wildlife species in arid environments.

First, sample sizes were modest, and having the birds' home range largely overlap each other in a small geographic area further reduced the statistical power to generalise Kori habitat preferences, in contrast to home ranges spread across replicate localities within which Koris were randomly caught. However, the sample size of six birds met the minimum threshold for conducting Compositional Analysis (Aebischer *et al.*, 1993). In contrast, the lack of spatial replication of where Koris were captured precluded testing home range placement in relation to available habitat types within the CKGR. Consequently, although the study demonstrates the importance of pan habitats in the dry season, further research is required to establish if home range size, seasonal overlap and seasonal movement patterns would be similar if birds had home range cores centred on dune and plain habitats.

Second, it is unclear if the type, seasonal abundance and spatial distribution of potential food resources across the different habitat types within the study area are affected to the same extent by rainfall; how Kori would respond to such spatio-temporal resource variation in unknown. This study's finding of a wet season home range larger than a dry season home range, contrary to expectation, is possibly linked to the differential habitat response to rainfall, which would affect the constituent vegetation and invertebrates of those habitats in particular ways; thus for example there may be particular food resources (either plants or animals) that the Kori tracks across the larger landscapes following rainfalls. In contrast, in the dry season, diet may be restricted to or dominated by the food items available on the pans. Better understanding of the bird's diet and whether this changes seasonally is crucial.

Third, interspecific relationships between Kori and co-occurring species, particularly predators, are unknown. If predation risk varies seasonally, then Kori movement patterns and seasonal home range use may be strongly coupled with these co-occurring species. For instance, there is probably a direct positive relationship between lion *Panthera leo* density and bustard mortality attributable to these carnivores: in 3134 hr of observation and 1443 km traversed following lion prides in Etosha National Park, lions made hunting attempts on 93% of all prey species encountered, including all six Kori encountered (Stander, 1992). Consequently Kori seasonal home range use may reflect a balance of localities that provide food, breeding opportunities and minimal predation risk.

Conservation and management implications

Findings suggest that pans are an important habitat type that may be critical for Koris particularly during the dry season, as is the case for the larger mammals in the Kalahari (e.g. Wallgren *et al*., 2009). It is plausible that the home range size, overlap and extent of long-distance movements (e.g. Osborne & Osborne, 1999) may in part be influenced by the proximity of pans.

Moreover, the extent and pattern of home range overlap, with a large wet season centred on that from the dry season, provides strong circumstantial evidence for food-regulated home ranges dynamics, at least for females. Consequently, if conservation areas do not provide adequate areal extent of habitats and forage resources, movements may be more extensive and possibly increase mortality risk owing for instance to collision with anthropogenic structures, to which Koris are vulnerable (Martin & Shaw, 2010).

Nevertheless, the highly right-skewed distribution of home range sizes, with most birds having small home ranges and only one bird undertaking seemingly exploratory movements in an MCP exceeding 1500 km^2, suggests it may be possible to target Kori conservation at a few strategic localities spanning only a modest spatial extent, perhaps targeting pan habitats within the landscape.

Even so, the small home ranges and high site-fidelity suggest that the species may not be an ideal flagship for the conservation of extensive grasslands, as is widely promoted (e.g. Kemp & Begg, 2001); as an alternative, perhaps equally distinctive and widely distributed species such as secretarybird *Sagittarius serpentarius* may serve as more suitable alternatives, although their range-wide conservation status, movement patterns, home range size and main threats, which are largely unstudied (e.g. Boshoff & Allan, 1997), would need to be determined. As for Kori, the species is probably most responsive to finer-scale habitat conditions, and presumed threats from widespread rangeland degradation, including cattle-induced bush encroachment (e.g. Herremans, 1998) may have been overestimated. Improved understanding of habitat preference and use, disaggregated by sex and age, would enhance knowledge of the abiotic and biotic factors that that may underlie the mechanisms accounting for the observed sedentary lifestyle, and establish more clearly just how sedentary Koris are likely to be. Such knowledge would help identify the factors that may account for population and range decline (Senyatso *et al.*, in review, Chapter 2) across the species's geographic range.

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Chapter Six

Lessons learnt and options for the way forward in conserving widespread low-density species

Synthesis & conservation implications

General findings

This study had five main aims: (a) to test if high cattle grazing pressure is associated with greater landscape-scale bush cover; (b) to examine the relative importance of cattle grazing and unregulated hunting as threats to a suite of savanna wildlife species; (c) to investigate the conservation effectiveness of PAs and WMAs in the Kalahari, based on the abundance of wildlife species in these management areas relative to unprotected landscapes; (d) to test a new methodology to assess the range-wide conservation status of a widely distributed low-density species despite a lack of quantitative and long-term population monitoring data; and (e) to test the extent to which home range size and placement of a savanna-inhabiting large ground bird are affected by season and habitat type.

These research objectives were largely achieved, with the thesis examining the conservation status of case study species at continent-wide (Kori Bustard) and landscape scales (21 medium- and large-bodied vertebrates in central Botswana), as well as study localised home range dynamics (Kori Bustard). These assessments, across a wide range of temporal (one season, Chapter 3; 2–3 wet and dry seasons, Chapter 5; 146 years, Chapter 2) and spatial scales (3,000 km^2, Chapter 5; 250,000 km^2, Chapters 3 and 4; 4,060,000 km^2, Chapter 2), afford a unique opportunity to make a significant contribution towards understanding the conservation ecology of wide-ranging low-density wildlife species. The study confirms the decline of Kori Bustard populations across its entire Africa range but without a proportionate loss of that range (although range-extent loss was greater in East Africa, Chapter 2), and documents what by comparison with similar savanna systems elsewhere appear to be low encounter rates of other medium- and large-bodied vertebrates across the Kalahari, including within strictly protected areas (PAs; Chapter 3).

Causal factors for the decline in Kori numbers and range extent across Africa are poorly understood, but persecution (Astley-Maberly, 1937; Porter, 1949) and impacts of rangeland degradation and shrub encroachment (Collar, 1996; Ash & Miskell, 1998; Herremans, 1998) have been suggested. Findings from central Botswana (Chapter 3) suggest that threats due to hunting (indexed as proximity to human settlement) are genuine, but the perceived threat from cattle-induced increases in bush cover (as indexed by distance to borehole) may be overestimated. Encounter rate of Kori not showing any response to the local density of cattle, lends support to the finding that bushmeat offtake is a more important threat than the negative impacts of cattle (Chapter 3). These results support a stronger influence on Africa-wide Kori trends from hunting (e.g. Astley-Maberly, 1937) than from livestock-induced habitat modification (e.g. Ash & Miskell, 1998).

At least female Kori in central Botswana were sedentary, contrary to the expectation of a tendency for extensive migratory movements to track the presumably stochastic resources within the arid Kalahari. Because WMAs are meant to buffer PAs by providing connectivity for migration between PAs (Rozemeijer, 2009), the implication then is that these sites are unlikely to offer long-term protection for the species, particularly as bushmeat offtake still persists. However, the sedentary nature of Kori also makes them less susceptible to extensive offtake; but this predicates that large populations persist in PAs. However, I acknowledge that data from the Kalahari are not directly transferable to the entire geographic range because (a) birds were preferentially caught in pan habitats, while (b) the roles of Kori sex and age and of co-occurring species in influencing Kori home range placement and size are unknown.

This study represents the first time that the independent correlates of bushmeat hunting and cattle-grazing have been tested in an African savanna. The stronger effect of hunting both for Kori and for other large-bodied vertebrates in the Kalahari, with no perceptible cattle-driven impacts, suggests that the greater conservationist preoccupation with livestock-rearing (Prins, 1992; Du Toit & Cumming, 1999) than with unregulated hunting (Milner-Gulland & Bennett, 2003) in African savannas may be misplaced. The two main mechanisms through which cattle are hypothesised to impact wildlife are direct competition for forage and water, and habitat modification through bush encroachment (Du Toit & Cumming, 1999). The present study demonstrates that high cattle densities are associated with greater woody vegetation cover at landscape scales (Chapter 4), and that Wildlife Management Areas (WMAs) buffers restrict cattle from WMA wildlife zones (Chapter 3). However, no evidence of detrimental effects of cattle was found for any of the species examined. Therefore, the finding of a much lower abundance of large-bodied vertebrates in WMAs (including within wildlife zones) than in PAs suggests that bushmeat offtake may also be the more important of the two threats in other African savannas, where researchers have only qualitatively commented on their relative importance (e.g. Homewood *et al*., 2001;

Fynn & Bonyongo, 2010; Craigie *et al*., 2010). Cattle-grazing has very probably been perceived as the greater threat because previous studies contrasting wildlife abundance in areas with and without cattle, and attributing any differences in wildlife abundance to cattle (e.g. Ogutu *et al*., 2005; Rannestad *et al*., 2006), were confounded by bushmeat offtake.

The findings of this study (Chapter 4) on the vegetation response to variable stocking density across the gradient of unprotected areas, WMAs and PAs are consistent with other work where greater stocking density directly increased the abundance of non-grass herbaceous vegetation, shrub density and canopy cover of a few encroacher species (e.g. van Vegten, 1984; Skarpe, 1990; Asner *et al*., 2004). Reduced grass cover reduces fuel loads, reducing fire intensity and frequency, which facilitates woody vegetation invasion and with effects reinforced through positive feedback mechanisms (Roques *et al*., 2001; Sankaran *et al*., 2004; Staver *et al*., 2009). These structural changes to savannas may possibly narrow dietary options for wildlife species, but could be expected to favour browsers such as steenbok (e.g. Du Toit, 1993) over grazers. However, all browser species considered (and with species-specific models for springbok and steenbok) showed stronger negative association with human settlements and none showed a positive association with borehole proximity. The implication then is that while greater bush cover outside PAs may have been favourable for wild browsers, the negative effects of unregulated hunting are greater.

Africa's savannas may be losing its currently widespread species, many of which may reach very low numbers without triggering any conservation alert, particularly if their population decline is decoupled from range extent loss. The lack of any strong contrasts between wildlife encounter rates inside and outside PAs for most of the species, coupled with the generally poor performance of Kalahari PAs relative to South African PAs (Chapter 3), suggests that current conservation approaches in Botswana where single PAs (or IBA: Fishpool & Evans, 2001) are managed on their own rather than as a network of conservation sites (albeit of varying protection status) is inadequate to ensure long-term conservation of the country's currently widespread wildlife. In the short (several years) to medium (few decades) term, population declines may be apparent only for large-bodied species that aggregate in large mobile groups, such as are evidenced by population crashes of wildebeest in the Kalahari (Chapter 3) and elsewhere on the continent, e.g. Kruger National Park (Fynn & Bonyongo, 2010) and Serengeti (Sinclair, 1995; Homewood *et al*., 2001). However, even then, declines across a single PA and its neighbouring unprotected areas are unlikely to trigger any global conservation attention, owing to the assumption that adequate numbers may persist elsewhere (Gaston & Fuller, 2008). However, the slow decline of the Kori Bustard range extent, 8% (southern Africa) and 21% loss (East Africa) in nearly 150 years, despite an extensive reduction in population numbers (Chapter 2), shows that the phenomenon of widespread species undergoing dramatic population declines while maintaining more or less intact range extent may be more widespread than suggested by the few studies that report this to date (e.g. Rodríguez, 2002; Turvey *et al*., 2010; Ogada & Buij, 2011). This is particularly worrying because the lack of systematic biodiversity monitoring across much of the continent (Chapter 2) means declines are not likely to be detected or trigger any alert.

Community-managed conservation areas are primarily created to expand the areal extent over which Africa’s wildlife enjoy pro-conservation attitudes. But, in the Kalahari WMAs do not appear adequate to curb the pervasive impacts of unregulated hunting (Chapter 3), and findings from this study raise several conceptual and practical concerns about this conservation model.

First, without any investment in anti-poaching patrols or internal community policing, it is unclear how this model of participatory wildlife management can deter or apprehend people involved in unregulated hunting. The extent to which Kalahari WMAs self-regulate and guard against resource exploitation appears weak because there does not seem to be any institutional means to prevent such individuals from receiving income from trophy hunting and tourism and concurrently carrying on with unregulated hunting. Any decision to desist from hunting is unlikely to be made out of fear of punishment, and although free will or peer pressure may be important the incentives for either appear lacking. This contrasts with the Zambian model, where significant investments were made in mitigating unregulated hunting by recruiting community members as wildlife scouts (Lewis *et al*., 1990). The assumption that strengthened linkage between livelihoods and resources will translate into improved resource conservation (Salafsky & Wollenberg, 2000) was not supported by this study, and direct investment in anti-poaching efforts within WMAs may be a requisite for effectively conserving wildlife species.

Second, there appears to be a strong mismatch between hunting quotas and sustainable offtake. Thus, although gemsbok encounter rates in WMAs were as low as in unprotected areas, this species was still the second most numerous on the hunting quota issued to 11 of the 15 sampled WMAs during 2007–2009 (DWNP, unpublished data), while the smaller ungulates that responded positively to WMA designation made a small proportion of the quota. Perhaps owing to the perceived better taste of gemsbok meat than that of other large Kalahari ungulates (e.g. Verlinden, 1997), quotas for the species are set deliberately high to meet the culinary needs of communities and hunters. This raises the question of which considerations take precedence—social, economic or ecological—when WMA hunting quotas are drawn. Additionally, given the lack of systematic wildlife monitoring outside African PAs (Chapter 2), to what extent should community members participate in setting the quotas, as they may have particular traditional ecological knowledge that can help track population trends? Expert opinion has been shown to improve conservation assessment of huntable mammals (e.g. Irvine *et al*., 2009). Some successful localised community-based wildlife monitoring schemes exist in southern Africa, such as in Namibia where community members undertake driven or walked transects, with the data used to provide indices of species abundance outside PAs (Naidoo *et al*., 2011). But, the extent to which such monitoring systems work for widespread low-density species is unclear, and challenges are likely to include: (a) selection of sampling units that minimise bias (such as counts made at particular distances from settlements, or at sites known to be frequented by certain species); (b) obtaining adequate sample samples from localised surveys to inform trends at landscape scales; (c) creating incentives for sustained monitoring; and (d) ensuring reported trends are genuine, and not meant to mislead the quota issuing authority into issuing unsustainable trophy hunting quota. Ecologically informed practical guidelines on sustainable wildlife offtake limits at WMA- and national-level, building on theoretical models such as proposed by Du Toit (2002) are, at any rate, crucial.

Although they are not as effective as PAs at conserving large-bodied vertebrates, Kalahari WMAs mitigate cattle-induced increases in bush cover. However, owing to the context-specific impacts of increased bush cover on savanna structure and functioning (Eldridge *et al*., 2011) it is unclear whether this mitigation of greater bush cover delivers any ecosystem-wide benefits in the Kalahari. Nowhere in southern Africa is habitat conservation explicitly included in WMA management plans, a circumstance which possibly undermines the true contribution these landscapes could make to livelihoods.

Nonetheless, given global trends in land-use and management (Sala *et al*., 2000), it is highly probable that if the extent of Kalahari WMAs is maintained, these sites will make a significant positive contribution towards wildlife and habitat conservation over the next 50 years or so. For instance, across much of Africa there has been significant expansion of the cattle-rearing frontier, aided in part by cheaper borehole drilling technology (e.g. Perkins & Thomas, 1993; Sinclair, 1995). At the same time, arable farming, primarily with land parcelled into small crop fields, has expanded into extensive pastoral and rangeland areas formerly used by wildlife outside parks (e.g. Homewood *et al*., 2001). Moreover, there is often strong political pressure to privatise land for cattle ranches (Abel & Blaikie, 1989; Perkins & Thomas, 1993). Three main findings from this study suggest that WMAs offer a viable approach to assure the entire Kalahari is not transformed into pastoral lands, which would support far less wildlife, based on wildlife encounter rates observed in unprotected areas in contrast to those from WMAs (Chapter 3). First, this thesis demonstrates that cattle density is positively associated with woody vegetation cover. Second, however, cattle-grazing impacts and greater woody vegetation cover are restricted to within 10 km of boreholes. Third, WMAs buffers can successfully restrict cattle, preventing cattle from within WMAs and from neighbouring unprotected areas reaching WMA wildlife zones. Although the extent to which WMA governance structures empower local communities in broader land-use decision-making processes was not studied in this study, experiences from elsewhere in southern Africa (e.g. CAMPFIRE; Child & Barnes, 2010) suggest that if communities managing WMAs derive sufficient economic returns from sustainable wildlife utilisation, they form an important pro-conservation constituency that can contest the expansion of human encroachment into wildlife areas. Particularly in the Kalahari, the expansion of cattle-rearing is more likely to be a greater threat than the expansion of arable farming, owing to the aridity of the landscape. Based on findings from this study, and predicated on Kalahari WMAs being perceived as beneficial by WMA communities, it is probable that WMAs may help spatially restrict the spread of the cattle-rearing frontier. But this assumes that WMA managers maintain authority over or can influence where new boreholes are drilled, and can themselves regulate stocking rates within WMA livestock-rearing buffers.

The aforementioned long-term future scenario assumes that the areal extent of strict PAs will remain unchanged, or that any degazettement of conservation areas would be of WMAs, although WMAs (along with other extractive/multi-use reserves) are forecast to expand over the next few years in place of strict PAs (Naughton-Treves *et al*., 2005). On the other hand, because PAs support greater wildlife abundance than

WMAs particularly for the large-bodied vertebrates that generate the most income for trophy hunting and tourism, if PAs are preferentially degazetted, WMA viability is likely to be greatly compromised. Although there is presently no evidence that populations of large-bodied vertebrates in WMAs are sustained by leakage from PAs, that these species are largely restricted to PAs suggests that if PAs were lost, Kalahari's large vertebrates could suffer drastic population crashes particularly if unregulated bushmeat offtake persists within WMAs and unprotected areas. Thus, although not perfect, PAs remain an essential component of wildlife conservation in African savannas.

Future directions

This study has improved understanding of the conservation ecology of widespread low-density species, and the role of PAs and WMAs in abating threats to these species. However, future studies could improve on several aspects, particularly ascertaining the assumptions made in this study.

First, the study uses a proxy for hunting pressure (proximity to human settlement), which needs to be tested quantitatively, as done in other parts of Africa (e.g. Muchaal & Ngandjui, 1999; Brashares *et al*., 2001). Due to a lack of bushmeat markets where direct observations could be made of species hunted (for example, as done in some countries in Central and West Africa: e.g. Brashares *et al*., 2001; Ogada & Buij, 2011), in Botswana, community focus groups and interviews could be used to establish the levels of hunting actually taking place in unprotected areas and WMA livestock-rearing buffer zones, as well as the mode of hunting and species targeted. Because hunting is prohibited within parks, one option to investigate the extent of unregulated hunting within these landscapes is through regular systematic searches for evidence of hunting (such as used bullet shells or snares, e.g. Muchaal & Ngandjui, 1999). Relationships between collated metrics of hunting pressure and human settlement could then be established.

Second, one of this study's limitation was the lack of baseline data on the vegetation condition across the land-use types so that temporal trends in extent of bush cover, and thus the degree of bush encroachment, could be directly quantified and related to stocking rates. Consequently, historical analysis of indicators of rangeland change with particular focus on shrubs and WMAs and unprotected areas is a priority. Data can come from aerial photographs (e.g. Wigley *et al*., 2010) or remote sensing (e.g. Homewood *et al*., 2001). However, a challenge may be obtaining locality-specific cattle and wildlife stocking rates to which vegetation conditions could be related to (e.g. Roques *et al*., 2001), because this data would probably be only available for ranched areas (e.g. Perkins & Thomas, 1993). Therefore, perhaps this research would be more robust if restricted to village-level assessment (rather than finer-scale segments as in this study), as historical village-level livestock estimates may be more readily available (e.g. Moleele & Perkins, 1998).

Third, although the study demonstrates that the WMA buffers do restrict cattle, the extent to which the buffers are adhered to for other livelihood activities (such as fuelwood collection) is unclear. Moreover, it has never been determined whether these demarcations compromise or improve the conservation of wildlife on which WMA trophy hunting and tourism depends. For example, because the WMA buffers may hinder other livelihood activities (for instance if they severed historical or future transhumance routes for WMA and non-WMA cattle owners), this may create antagonistic attitudes towards wildlife and WMAs.

Fourth, an important research aim is to ascertain perceptions of the communities within WMAs to the conservation approach, and whether they perceive themselves as benefiting from it. Additionally, if benefits are considered inadequate, perhaps WMA communities and their supporting agencies could explore possibilities for linking the conservation approach to innovate funding mechanisms, such as Payments for Ecological Services, although research to demonstrate what measurable conservation outcomes are being achieved would be required so that payments could be linked to the conservation of the resource.

Fifth, it remains unclear how large-bodied wildlife species, on which WMA financial and socio-political viability depends, influence or respond to changes in the woody vegetation cover and its cascading effects on the quality, quantity and composition of their food resource. This has important implications more generally, as conservationists need to demonstrate that bush encroachment does negatively affect biodiversity conservation and wider ecosystem benefits.

Lastly, the role of human culture and beliefs in influencing Kori Bustard trends across Africa and species-specific responses of large vertebrates in the Kalahari may be important. For example, in some tribes such as the Bushmen (Basarwa) in central

Botswana, only the elderly are allowed to eat Kori, while younger people are required to be ‘treated’ first as it is believed they would otherwise experience mental disorders (Sugawara, 2001). Similarly, Rockingham-Gill (1983) suggested that in the early 1980s, Zimbabwe’s Matebeleland region probably had more Kori because local tribes there did not hunt or eat the species, which they regarded as ‘magical’, unlike tribes in the Mashonaland region. In Tanzania, Magige *et al*. (2009) compared perceptions and extent of Kori poaching between the Maasai (east of Serengeti National Park) and Ikoma, Natta and Kurya tribes to the west of the park: the Maasai did not hunt Kori nor use any of its body parts, and although 90% (n = 59) of respondents from the Ikoma, Natta and Kurya tribes reported no use of the bird’s body parts, 10% had eaten it.

Study findings highlight the need for conservation assessments of widespread low-density species to consider range-wide as well as site-specific concerns. This is crucial because if only site-specific assessments are made, incorrect policy and management decisions could be made about whether these species are effectively conserved by PAs or community-managed areas, and whether anthropogenic impacts such as cattle-grazing and unregulated hunting have pervasive or site-specific impacts.

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