

**ECOLOGY OF THE GREAT INDIAN BUSTARD (*ARDEOTIS NIGRICEPS*) IN
KACHCHH, GUJARAT WITH REFERENCE TO RESOURCE SELECTION IN AN
AGRO-PASTORAL LANDSCAPE**

**THESIS
SUBMITTED TO THE
FOREST RESEARCH INSTITUTE UNIVERSITY
DEHRADUN, UTTARAKHAND
For
THE AWARD OF THE DEGREE OF
DOCTOR OF PHILOSOPHY IN FORESTRY
(WILDLIFE SCIENCES)**



**By
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2012

DECLARATION

I hereby declare that the dissertation "Ecology of the Great Indian Bustard (*Ardeotis nigriceps*) in Kachchh, Gujarat with reference to resource selection in an agro-pastoral landscape" is original research conducted by me under the supervision of Dr. Yadvendradev V. Jhala of the Wildlife Institute of India and Dr. Asad R. Rahmani of the Bombay Natural History Society. The thesis has been submitted to the Forest Research Institute University for the award of the degree of Doctor of Philosophy in Forestry (Wildlife Science), and has not formed the basis for the award of any other degree. It embodies my own work and observations, and in that respect the investigation appears to advance knowledge on the subject.

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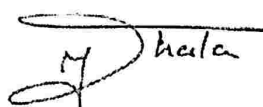
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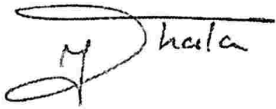


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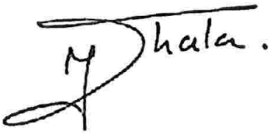
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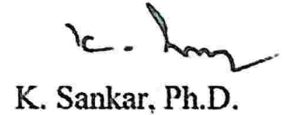
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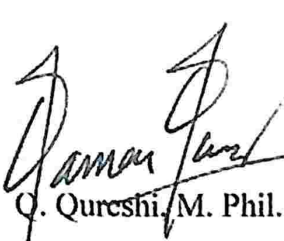
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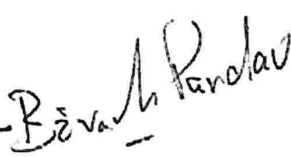
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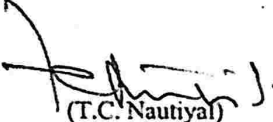
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Running out of time? The great Indian bustard *Ardeotis nigriceps*—status, viability, and conservation strategies

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Abstract The endemic great Indian bustard (GIB) is evolutionarily trapped between open nesting and *k*-selection that endangers its persistence under prevailing levels of habitat loss and hunting. A global population of about 300 birds is further fragmented into eight populations in the states of Rajasthan (shared with Pakistan), Maharashtra, Andhra Pradesh, Gujarat, Karnataka, and Madhya Pradesh in India. The largest population of 100–125 birds exists in Jaisalmer, Barmer, and Bikaner districts of Rajasthan. Remaining populations number less than 35 birds each. Prevalent GIB conservation strategies use legislation to (a) secure traditional breeding areas by declaring small Protected Areas (PA) or (b) protect vast areas with varied human land uses. The vagrant nature of GIB reduces the benevolent effect of small PAs, while large reserves alienate people by curbing legitimate subsistence rights through strict legislation. These factors along with ill-informed habitat management challenge the current PA approach, even causing local extinctions. Population viability analysis shows that GIB populations of ≤ 35 birds can persist only under unrealistic conditions of first year mortality $\leq 40\%$,

and no human caused mortality of adult birds. Even the largest population (≥ 100 birds) is sensitive to additional loss of adult birds to human causes. With current levels of hunting in Pakistan, extinction is a real threat. A landscape conservation strategy using conservation/community reserve concept that includes controlled traditional land uses with GIB-friendly infrastructural development is needed. The declining rate of GIB populations calls for immediate commencement of *ex situ* conservation breeding programs.

Keywords Endangered · Environmental stochasticity · *Ex situ* conservation · Grassland · Poaching · Population viability analysis

Current status

The family Otididae is an obligate grassland taxa highly specialized with *k*-selected traits and an open nesting system (Lack 1954), rendering them vulnerable to extinction when faced with environmental changes or direct threats. The endangered great Indian bustard (GIB, *Ardeotis nigriceps*) faces serious threat of extinction from habitat conversion to agriculture, infrastructural development, and hunting (Rahmani 1989; IUCN 2008). The population, which was roughly estimated in 1969 at about 1,260 individuals (Dharmakumarsinhji 1971) ranging over the western half of India, dwindled down to about 745 individuals by 1978 (Dharmakumarsinhji 1978a). Around 600 individuals survived at the turn of this millennium (BirdLife International 2001), and currently 300–350 (Rahmani 2006) are left, restricted to fragmented pockets in six states of India (Fig. 1).

In Rajasthan, the Desert National Park in the districts of Jaisalmer and Barmer along with the agro-pastoral land-

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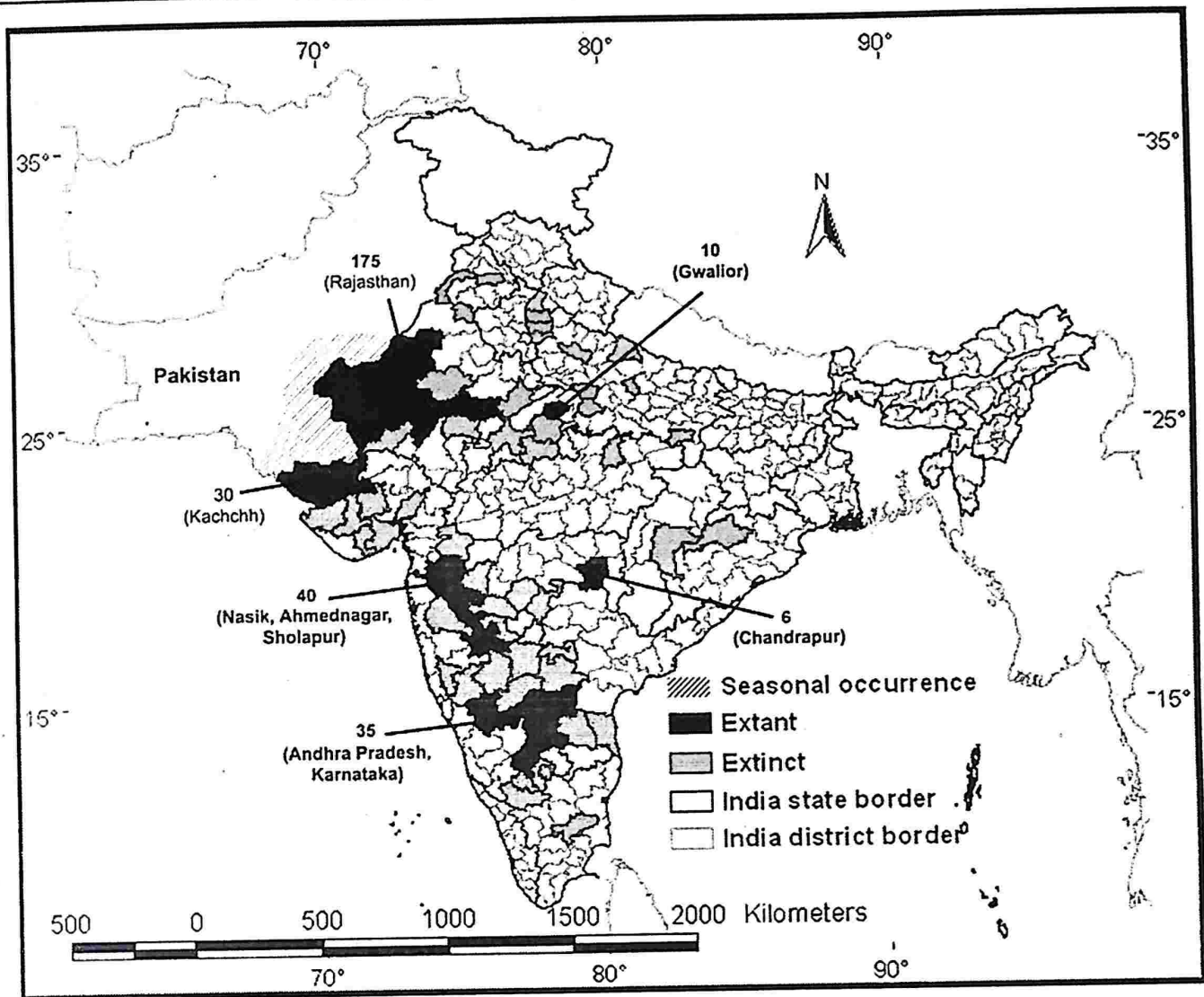


Fig. 1 Current (2008) and historical distribution of great Indian bustard within districts of India and occurrence of summer visitors in Pakistan. The numbers are the estimated maximum populations

scapes of Bikaner holds the largest global population of the GIB currently numbering between 100 and 125 birds, along with another 25–50 birds in Ajmer, Pali, and Tonk districts (Rahmani 2006). All other populations number less than 35 birds each (BirdLife International 2001). These populations are located within the states of (a) Maharashtra, at the Bustard Sanctuary of Sholapur and Ahmednagar districts having 30–35 birds, Nasik district having five to eight birds, and Chandrapur district having four to six birds (Thosar et al. 2007); (b) Andhra Pradesh, at Rollapadu Sanctuary of Kurnool district and its adjoining areas of Anantpur district having about 30 birds (Rao and Javed 2005; Rahmani 2006); (c) Gujarat, in Abdasa tehsil of Kachchh district having 25–30 birds (Singh 2001); (d) Karnataka, where the population status is poorly known, but few birds (2–4) have recently been reported from Sirguppa tehsil of Bellary district (Ahiraj 2008); and (e) Madhya Pradesh, where the GIB population has faced a stark decline (Rahmani 2006) and numbers in Gwalior district are likely to be less than 10 birds. The Rajasthan and Kachchh populations are probably shared with eastern

Pakistan where sporadic, seasonal occurrences of 15–20 bird sightings have been recorded (Khan et al. 2008).

The last two decades have seen a drastic reduction in the range occupancy and population size of the GIB in India (Fig. 1). For instance, within the state of Gujarat, GIB was recorded from Surendranagar, Jamnagar, Bhavnagar, Rajkot, Kheda, Amreli, and Kachchh districts (Rahmani 1989; Rahmani and Manakadan 1990), but currently a single population survives in Kachchh with rare transients reported in Bhavnagar, Jamnagar, and Surendranagar districts. Similar trends are reported across the GIB range (Fig. 1).

Ecological requirements of the species

Bustards originated 77 million years ago in Africa and speciated over discreet ranges of the Old World grasslands (Johnsgard 1991). They have subsequently coevolved with wild ungulates and depend on grazers to maintain a suitable habitat structure. Since the last thousand years, community of wild grazers has been steadily replaced by domestic

livestock in most of the bustards' range outside Africa (Skarpe 1991). GIB flocks vagrantly use wide, sparse grass-scrub landscapes with low intensity cultivation (Rahmani 1989) in the non-breeding season. They have a broad omnivorous diet chiefly consisting of fruits like *Zizyphus*, insects like grasshopper and beetle, reptiles, and seasonally available food crops like ground nut and millet (Rahmani 1989). During mid-summer and monsoon, they congregate at traditional areas to breed and avoid human disturbance (Rahmani 1989; Johnsgard 1991). Organized in a polygynous exploded lek mating system, dominant males show site fidelity to their display stations. This behavior has been recognized as one of the crucial factors in designing conservation strategies for the species (Rahmani and Manakadan 1986; Rahmani 1989; Johnsgard 1994).

Prevalent conservation strategies

Natural resource conservation is guided by two dichotomous approaches: sustainable use (IUCN 1991) regulated by traditional institutions (Gadgil 1992) or preservationism through complete cessation of resource extraction (Kramer et al. 1997). Alerted by naturalists about the decline of GIB and the need to conserve grassland resources (Tyabji 1952; Ali and Ripley 1969; Dharmakumarsinhji 1978b), State Governments of India declared eight bustard Sanctuaries in post-1980s, with a belief that establishment of "Protected Areas" (PAs) might hold the best hope for saving the species (Rahmani and Manakadan 1987). Most of these PAs were either too small, targeting traditional breeding patches following the preservationist approach (Kramer et al. 1997), or very large, covering entire agro-pastoral landscape inclusive even of large townships. Within these reserves, the recommendation was to maintain small, scattered (>100 to <500 ha) refuges with large buffers (Rahmani 1989) that should preferably be traditional breeding spots and protected during the breeding season (Rahmani 1989; Chauhan 2006) to exclude cattle. Refuges were recommended to be managed so as to provide habitat requirements for crucial activities such as lekking, nesting, chick rearing, and foraging (Rahmani 1989), and could be rotated over the PA through ≥ 5 -year periods (Chauhan 2006).

Limitations of current conservation strategies

The prevalent legal system in the 1980s–1990s governing PAs was not sufficiently flexible to permit implementation of even these simple recommendations. While declaration, many GIB Sanctuaries were inclusive of, or surrounded by privately owned lands, exemplified by Karera Bustard Sanctuary in Madhya Pradesh and the Bustard Sanctuary

of Maharashtra which included the township of Sholapur. Due to enhanced protection and restricted livestock grazing in the Karera Bustard Sanctuary (202 km²), the residing small blackbuck population exploded resulting in crop depredation in adjoining private agricultural lands. Blackbuck being a Schedule I species [Wildlife (Protection) Act 1972] could not be hunted. This antagonized local agro-pastoral communities (Rahmani 2003) resulting in a backlash by the communities that caused the local extinction of GIB and reduction of blackbuck population through poaching. In another case, the Bustard Sanctuary of Maharashtra which covers an area of 8,496 km² has faced rapid industrialization and increase in human population during the last 30 years. There is also a shift in agricultural practices from monsoonal crops such as *Sorghum* and millet to sugarcane and grapes—crops not suitable to bustards resulting in severe habitat loss for GIB. The remaining suitable habitat consists of small and scattered grassland patches protected under the Drought Prone Areas Programme. The total aggregate area of these scattered patches is not more than 400 km², the biggest patch being near a village called Nannaj, about 20 km north of Sholapur town. Traditionally, grasslands and scrub have been considered as "wasteland" and the Forest Department policy, until recently, has been to convert them to "forests" with plantation of fuel/fodder shrub/tree species, even exotics like *Prosopis juliflora*, *Gliricidium*, and *Eucalyptus* spp., under social forestry and compensatory afforestation schemes [Indian Forest Act 1927; Forest (Conservation) Act 1980] resulting in further loss of GIB habitat. The large expanse of this Sanctuary (much of it being non-GIB habitat) has restricted private land owners therein to use their lands freely and profitably, as the stringent Indian legislation is extremely restrictive about land use in legally gazetted Protected Areas [Wildlife (Protection) Act 1972]. This again has generated bitterness among the local populace. Currently, the government of Maharashtra is proposing to rationalize the boundary of this Sanctuary to accommodate the concerns of private land owners. The cumulative impact of all these land-use policies and attitude changes is that there is a declining population of GIB in the Bustard Sanctuary of Maharashtra.

On the other end of large Sanctuaries lie some extremely small conservation areas targeting lekking or nesting patches as in Sonkhaliya (17 km²) in Rajasthan, Gaga-Bhatiya (2 km²) and Lala-Naliya (17 km²) in Gujarat, and Rollapadu (6 km²) in Andhra Pradesh. Some of these GIB refuges have been subjected to well-intended but ill-informed management interventions such as development of large water bodies, network of roads, delineation of "reserve grasslands" through trenching-cum-mounding and plantation. Such managerial practices have resulted in severe habitat alteration (Pande and Pathak 2005) and are considered to have caused

local extinction of the species from Ranibennur and Gaga-Bhatia Sanctuaries, and decreased usage of Lala Sanctuary.

Since both these strategies, (a) creation of large PAs inclusive of private lands and (b) implementation of "minimum conservation area for breeding", have failed to address all the ecological requirements of the species and achieve the objective of GIB conservation, the decline in density (estimated 20–29%, see BirdLife International 2001) and range (estimated 90%, see Rahmani 2001) of the species have continued unabated. Hence, the prevalent conservation strategies need to be re-evaluated and rectified.

Population viability assessment

To understand the interactions between the inherent k -selected demographic traits of GIB with environmental stochasticity, habitat management, anthropogenic influences, and their effects on the viability of different size GIB populations, we conducted a population viability analysis (PVA) (Boyce 1992) using published demographic parameters of GIB and related species (Ena et al. 1986; Rahmani 1989; Alonso and Alonso 1992; Johnsgard 1994; del Hoyo et al. 1996; Combreau et al. 2000; Morales et al. 2001; Osborne and Osborne 2001; Hallager and Boylan 2004; Rao and Javed 2005; see Table 1). We used the program *VORTEX* version 9.72 (Lacy

et al. 2007) and ran 500 iterations for each of the following scenarios. We considered (a) the best case scenario where the initial population was 100 birds mimicking the Rajasthan population, (b) a scenario with the initial population of 40 birds, and (c) initial population of 25 birds representing most other populations, and (d) a scenario where the initial population was 10 birds mimicking the remaining few small, scattered populations. Since some of the life-history parameters were ill-known, we built "optimistic" and "pessimistic" models for each scenario to estimate extinction probabilities in 20, 50, and 100 years, using different combinations of first and second year mortality rates, carrying capacities, adult harvests, and catastrophic drought incidences occurring once in 5 (20%) years or 10 (10%) years (Fig. 2, also see supporting material—Appendix S1). During a catastrophe year, the survival and fecundity were reduced by 10% and 80%, respectively. GIB, though legally protected as a Schedule I species under Wildlife (Protection) Act (1972), has been a prized game bird and is occasionally poached. Poaching and accidental deaths due to human causes were simulated as "harvest" of one bird of either sex in alternate years from the modeled population (Fig. 2, also see models 1–113 in supporting material—Appendix S1 and Table 1 for PVA model inputs).

We found that populations of 10 individuals were in imminent risk of extinction (Fig. 2a, also see models 1–25

Table 1 Details of input parameters in population viability analysis models

PVA input parameters	Values and range
Initial population size	(a) 10, (b) 25, (c) 40, (d) 100
Reproductive system and rate	
Age of first offspring	3 years (♀) and 4 years (♂)
Max. age of reproduction	20 years
Max. no of progeny/year	1
Sex ratio at birth	1♀:1♂
% Adult ♀ breeding/year	50±10 ^a
% ♂ in breeding pool	25
Mortality rate	
1st year	30±6% 40±8% & 50±10%
2nd year	10±2% and 18±4% (♀) and 16±3% and 22±4.5% (♂)
Adults	5±1% (♀) and 8±1.5% (♂)
Catastrophe	
Frequency	(a) 10% and (b) 20% of years
Severity	Fecundity reduced by 80% and survival reduced by 10%
Harvest	(a) nil and (b) 1 adult ♂ and 1 adult ♀ in 2 years

^a Estimated as the mean ratio of breeding (nesting/chick rearing) females to total females in various populations obtained from published literature (1, 2) and field observations during current study. Average sex ratio was used to calculate number of females in cases where there was no separate mention of female and male birds in the population. Literature from where PVA input parameters were obtained: Ena et al. 1986; Rahmani 1989 (1); Alonso and Alonso 1992; Johnsgard 1994; del Hoyo et al. 1996; Combreau et al. 2000; Morales et al. 2001; Osborne and Osborne 2001; Hallager and Boylan 2004; Rao and Javed 2005 (2); Dutta and Jhala, unpublished data

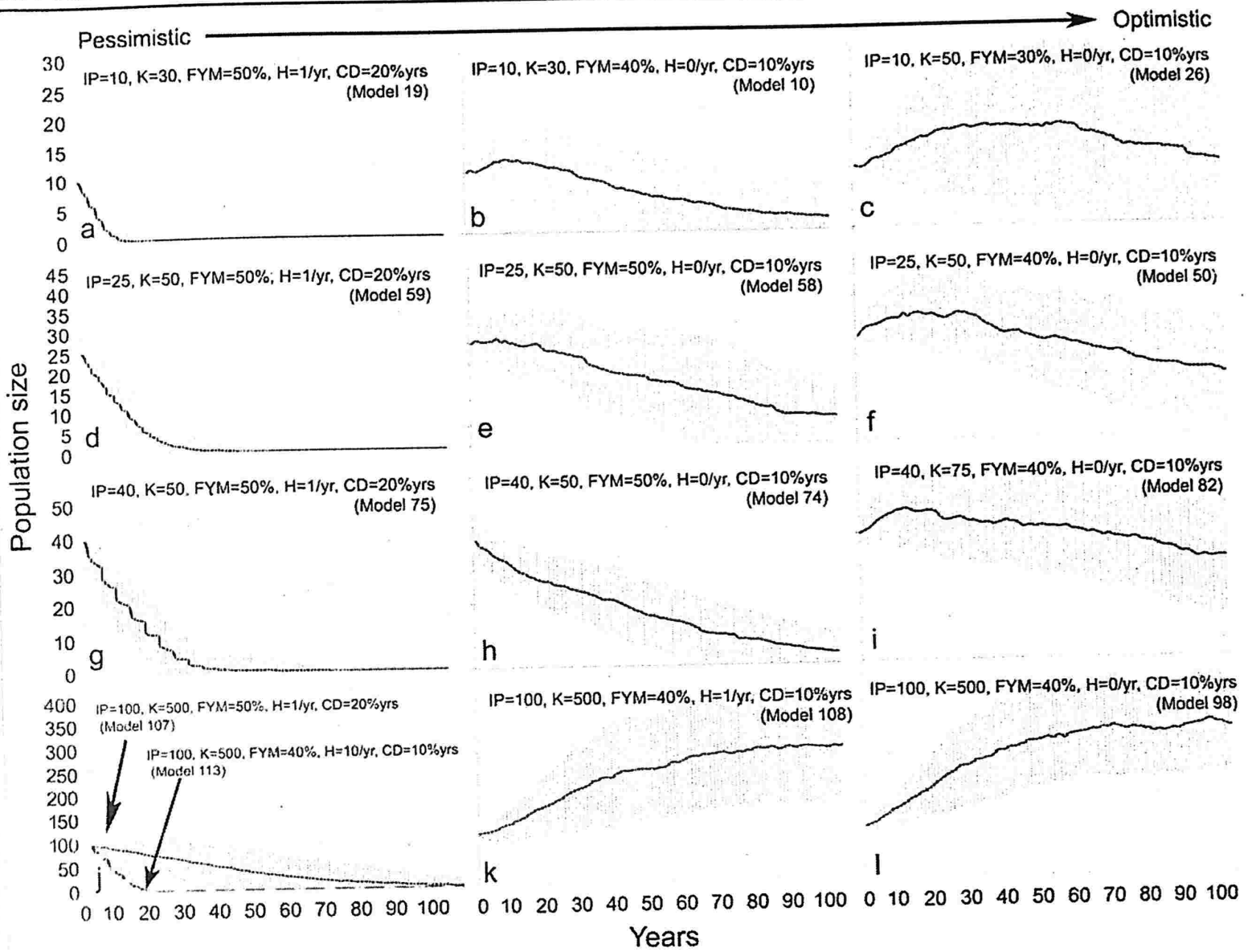


Fig. 2 Population viability analysis model predictions for GIB populations of initial sizes (IP) 10 (first horizontal panel—a, b, c), 25 (second horizontal panel—d, e, f), 40 (third horizontal panel—g, h, i), and 100 birds (fourth horizontal panel—j, k, l), under pessimistic (left vertical panel—a, d, g, j) and optimistic scenarios

(right vertical panel—c, f, i, l) of various combinations of potential carrying capacity (K), first year mortality rate (FYM), human caused adult bird loss (H), and catastrophic drought incidence (CD) during the next 100 years

and 27–48 in supporting material—Appendix S1) facing a likely extinction probability of 10% in 20 years, with 43% population trajectories becoming extinct within 50 years and 80% extinction probability in 100 years (Fig. 2b, also see model 10 in supporting material—Appendix S1). These populations had low chance of persistence (62% survival probability in 100 years) even under most optimistic (but unrealistic) conditions when first year mortality was below 30%, second year mortality was 10% for females and 16% for males, potential carrying capacity was ≥ 50 individuals, human caused adult loss was totally controlled, and catastrophe was less frequent (Fig. 2c, also see model 26 in supporting material—Appendix S1).

Populations of 25 individuals also showed high risks of extinction (67–100% extinction probability in 100 years, see Fig. 2d, also see models 49, 51–53, and 54–64 in supporting material—Appendix S1). Under realistic con-

ditions, these populations faced extinction probability of 16% in 50 years (Fig. 2e, also see model 58 in supporting material—Appendix S1). These populations could only persist (70% survival probability in 100 years) under optimistic (but unrealistic) conditions when first year mortality was below 40%, second year mortality was 10% for females and 16% for males, potential carrying capacity was ≥ 50 individuals, human caused adult loss was totally controlled, and catastrophe was less frequent (Fig. 2f, also see model 50 in supporting material—Appendix S1).

Populations of 40 individuals had fair chances of persistence (>80% survival probability in 100 years, see Fig. 2i, also see models 82 and 86 in supporting material—Appendix S1) provided first year mortality was $\leq 40%$, potential carrying capacity was ≥ 75 birds, and catastrophe was less frequent. However, when we assumed a pessimistic situation of higher nesting and fledgling mortality (50%) along with low

carrying capacity (50 birds) and more frequent catastrophes, extinction probabilities in 100 years jumped to 37%, 63% and 84%, respectively (Fig. 2h, also see models 74, 89 and 90 in supporting material—Appendix S1). Poaching or accidental additional death of one adult every year threatened these populations (extinction probability 6–37% in 20 years) with 99–100% population trajectories facing extinction within 100 years (Fig. 2g, also see models 67, 68, 71, 72, 75, 76, 79, 80, 83, 84, 87, 88, 91, 92, 95, and 96 in supporting material—Appendix S1).

The population of 100 individuals had a high probability of persistence (>70%) for the next 100 years even under realistic nesting and fledgling mortality ($\geq 40\%$), higher second year mortality rate, and more frequent catastrophe (Fig. 2i, also see models 97, 98, 100–102, 104, 106, and 110 in supporting material—Appendix S1). But persistence of even this “large” population was sensitive to loss of an additional adult bird every year to human causes (extinction probability 50–100% in 100 years, see Fig. 2j and k, also see models 99, 103, 107, 108, 111, and 112 in supporting material—Appendix S1).

Sensitivity analysis is often used to assess the relative importance of parameters in model-based inference (McCarthy et al. 1995; Heinsohn et al. 2004). Some of our parameter estimates were obtained from related species and some others were not known with reasonable certainty. The number of adult females in the breeding pool each year, second year mortality, frequency of catastrophes, and potential carrying capacity were examples of parameters which were fuzzily estimated from literature. We include these along with first year and adult mortality in our sensitivity analysis, wherein each of the parameters was altered by 10% of its original value, and the PVA models rerun to assess its effect on persistence of the GIB population for 50 years.

Sensitivity analysis revealed that persistence was most sensitive to proportion of females breeding each year (Table 2). This was followed by juvenile and adult mortality as the next most sensitive parameters. The PVA was not sensitive to 10% changes in second year mortality, potential carrying capacity and frequency of catastrophes with population persistence changing marginally by less than 9%.

Of the above three most sensitive parameters, we had reasonably reliable data on adult and juvenile mortalities. However, proportion of breeding females in the population was not as reliable and was based on anecdotal reports (Rahmani 1989; Rao and Javed 2005) and field data for only 2 years in Kachchh (Dutta and Jhala unpublished data). An incorrect estimation of this parameter would change our PVA results numerically, but our inferences on conservation actions would largely remain unaffected. An underestimation of 10% of the proportion of females in the breeding pool would overestimate the probability of extinction by 30–70%, while an overestimate of 10% of

proportion of females in the breeding pool would underestimate the extinction probability by 31–46%. Similarly, 10% decrease in first year mortality would increase population persistence by 34% and 10% increase in the same would reduce population persistence by 55%, while 10% decrease in adult mortality would increase population persistence by 21% and 10% increase in the same would reduce population persistence by 18%. Interestingly, changes in the potential carrying capacity did not alter model results, suggesting that GIB were restricted not by habitat availability but more by direct threats to their survival (Table 2). This model outcome could be misinterpreted to suggest that ample habitat was available for GIB populations. However, this is not true since crucial habitat requirements for lekking and nesting that are not reflected in the potential carrying capacity would act by limiting breeding success, and survival of juveniles as well as that of adult birds. The potential carrying capacity reflects the size of bustard habitat and food availability which were probably not limiting.

Effects of environmental stochasticity on breeding area use by GIB: a case study

Spatial variation in precipitation at local scales of a few square kilometers is a common phenomenon in arid landscapes where GIB occur. In the Abdasa tehsil (one tenth of a district) of district Kachchh, grasslands interspersed with scrub and crop fields stretch along the coastline for nearly 45 km forming a continuum of ca. 200 km² of prime GIB habitat between Virachia (23.25°N, 69.11°E) and Lala (23.18°, 68.76°E) villages. In this habitat, a 17-km² patch has been proposed as Naliya Bustard Sanctuary. This patch has been the traditional lekking and nesting area for the GIB population of Abdasa. Typical breeding habitat of GIB occurs in undisturbed grasslands (at least 2–3 km away from the nearest village) characterized by a mosaic of less grazed ($6.5_{\text{Mean}} \pm 0.6_{\text{SE}}$ livestock sign 10 m⁻¹) and relatively tall grass ($45_{\text{Mean}} \pm 2_{\text{SE}}$ cm height) preferred by nesting females (13 nest sites sampled), interspersed with well-grazed ($13.3_{\text{Mean}} \pm 3.8_{\text{SE}}$ livestock sign 10 m⁻¹) and short grass ($17_{\text{Mean}} \pm 2_{\text{SE}}$ cm height) preferred by displaying males (12 display sites sampled) (Dutta and Jhala unpublished data). Although males of this species show site fidelity to display arenas in traditional lekking grounds (Rahmani 1989), our observations suggest that site fidelity can at times be compromised as a consequence of local spatial shift in rainfall provided such typical breeding habitats are available in adjoining patches. Intensive monitoring between 2007 and 2009 revealed that during 2008, GIB did not form their traditional lek in Naliya grassland patch but instead showed a shift in display stations with sporadic displays spread over

Table 2 Sensitivity testing of population viability analysis wherein parameters estimated with less certainty and/or parameters of critical importance were modified by 10% of original values to assess the corresponding percentage change in population extinction over next 50 years [% Δ P(E)50] for initial populations (IP) of 10, 25, 40, and 100 birds

Modified parameter	Change (%)	IP	% Δ P(E)50	
Percentage adult female in breeding pool each year	-10	10	57	
	+10		-31	
	-10	25	54	
	+10		-44	
	-10	40	30	
	+10		-38	
	-10	100	69	
	+10		-46	
	First year mortality	-10	10	-14
		+10		24
		-10	25	-23
		+10		36
		-10	40	-38
		+10		34
-10		100	-62	
+10			126	
Adult mortality		-10	10	-21
		+10		17
	-10	25	-15	
	+10		21	
	-10	40	-11	
	+10		11	
	-10	100	-38	
	+10		23	
Second year mortality	-10	10	-12	
	+10		10	
	-10	25	-5	
	+10		10	
	-10	40	-4	
	+10		6	
	-10	100	-18	
	+10		5	
	Frequency of catastrophes	-10	10	-10
		+10		0
-10		25	-5	
+10			5	
-10		40	-9	
+10			6	
-10		100	-13	
+10			15	
Carrying capacity		-10	10	5
		+10		10
	-10	25	8	
	+10		-5	
	-10	40	-11	
	+10		2	
	-10	100	18	
	+10		-13	

a much wider area (Kanauthia Daun) to the east of and outside the proposed Sanctuary (Fig. 3). The probable reason for this shift was low rainfall in the traditional breeding area (Naliya Daun) in relation to Kanauthia Daun about 12 km east. We indexed this difference in precipitation by the geometric mean ratio of green to dry vegetation cover and found a 4-fold difference between Naliya ($2.6_{\text{Mean}} \pm 0.64_{\text{SE}}$) and Kanauthia ($11.3_{\text{Mean}} \pm 0.89_{\text{SE}}$). This plasticity in behavior of GIB is a likely response to the inherent nature of semi-arid stochastic systems they inhabit. In the non-breeding season, GIB disperse to cover an area of several thousand square kilometers of semi-arid grassland–scrub–agricultural landscape in Kachchh (Dutta, Jhala, and Sharma unpublished data). Thus, a strategy of only declaring small “traditional” breeding areas as preserves may not suffice for conserving the species.

Conservation implications

Results of PVA models have shown that GIB populations are extremely sensitive to removal of adult birds. Even the largest population can plummet to extinction with a constant

additional loss of one adult to human causes each year. Historically, GIB have been hunted as game bird (Hume and Marshall 1878; Ali 1927; Rahmani 1989) and continue to be hunted in neighboring Pakistan (Khan et al. 2008). Low intensity poaching still persists within India as well. The western Rajasthan and Kachchh populations are probably shared with Cholistan desert and Sindh of Pakistan, where 49 birds were hunted out of 63 that were sighted over a period of 4 years (Khan et al. 2008). Given the life history traits of GIB, this level of removal is unsustainable and threatens the extinction of the largest global western Indian population within next 15–20 years (Fig. 2j, also see PVA model 113 in supporting material—Appendix S1). Increasing unfriendly infrastructural development within the GIB habitats intensifies chances of fatal bird strikes against high-tension electric wires, fast-moving vehicles, and other structures like wind-power generators. Conservation strategies must try to minimize loss of adult birds from poaching and other human causes like infrastructural development.

The PVA models also show that $\geq 50\%$ nesting and fledgling mortalities can jeopardize the persistence of GIB populations substantially. GIB are known to abandon nests

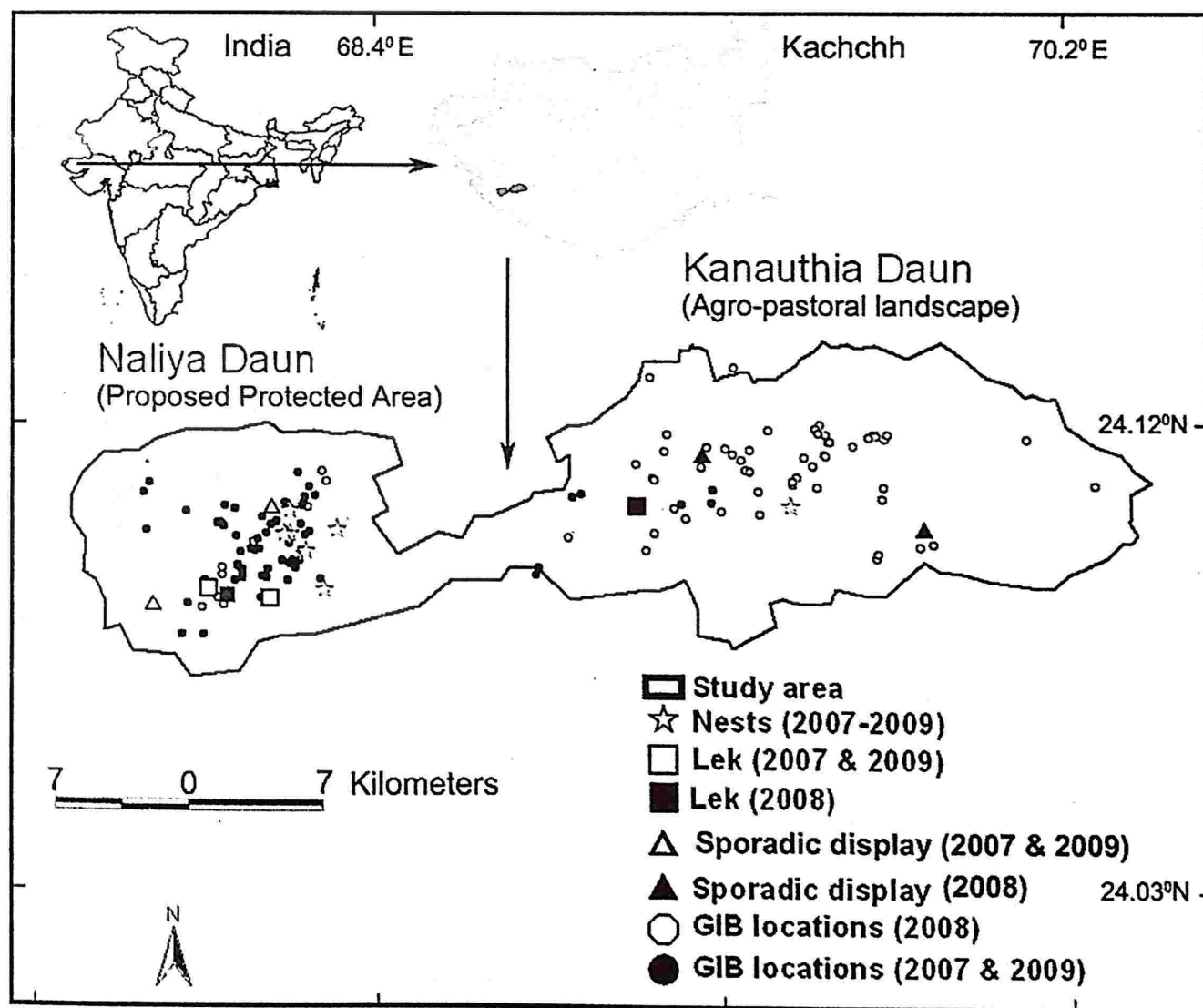


Fig. 3 Great Indian bustard breeding habitat in Kachchh showing variation in spatial use during breeding seasons of 2007–2009

due to human disturbance (Rao and Javed 2005). Since this species is extremely site-specific restricted area breeders, it is possible to enhance nesting and fledging success by creating disturbance-free zones during the breeding season. In populations of less than 30 birds, additional efforts may be needed to actively control predators (feral dogs, feral cats, jackals, and foxes) from these sites prior to and during the breeding season. Such predator control though controversial is essential and doable within these small breeding areas. Also, predator control within these small areas of a few square kilometers will not affect their populations adversely since they occur at reasonably moderate densities across the GIB landscapes. We believe that removal of significant source of mortality during the nesting and fledging stages (most vulnerable stage in the life history of GIB), along with supplementation of adult birds from a captive bred stock, may reverse the extinction trajectory of these small (≤ 30) populations.

GIB requires a landscape level conservation policy. Its habitat occurs in areas where human-induced changes in the landscape are most rapid due to intensive agriculture and industrialization, making it difficult to create protected areas that encompass GIB landscapes. Moreover, some form of traditional land uses like dry farming and controlled grazing are beneficial to GIB. Thus, its conservation is not entirely incompatible with some forms of human use of the landscape which requires minimal infrastructural development. The new categories of PAs introduced in Indian legislation such as (a) Conservation Reserve, (b) Community Reserve, and (c) Ecologically Sensitive/Fragile Area [Section 31A of Wildlife (Protection) Amendment Act 2002 (2003); Section 5 of Environment (Protection) Act 1986] can better protect bustards and their habitats on lands having government/private mixed ownerships (also see Gray et al. 2007). Such procedures will not require land acquisition or people displacement but will allow sustainable use of larger areas with participation from local communities and essential intervention of the Government (Rahmani 2006). GIB-friendly grassland management regime will benefit local communities in the long run as it will enhance productivity for livestock and prevent overgrazing. A major threat today to bustard habitat is not so much from pastoral use of GIB landscape but rather its conversion to other land uses such as intensive agriculture and industry, along with their associated infrastructural developments. Such land use changes rarely benefit local communities, and therefore it will be relatively easy to bring in reforms which are both economically beneficial for local people, as well as being GIB friendly. Appropriate incentive-driven legislation and policy reforms have to be implemented in collaboration with local NGOs to achieve this dual goal.

Although the bird requires strict protection measures, its wide-ranging nature makes implementation of protection difficult without public support (Rahmani 2003). Publicity

and awareness campaigns should ensue to generate support among the local populace like the ones undertaken by the Bombay Natural History Society in Rajasthan and Maharashtra (Rahmani 2006). A profitable and equitable mechanism to share revenues generated from eco-tourism with local communities (Narain et al. 2005) may go a long way in harnessing support for GIB conservation.

In spite of all these measures, owing to the extinction-prone, *k*-selected nature of the species and threat from hunting, GIB is in urgent need for *ex situ* conservation and subsequent supplementation of existing small *in situ* populations. Although a few unscientific attempts to breed GIB in captivity have failed in the past (Putman 1976; Sankhala 1977; Rahmani 1986), scientific execution of conservation breeding is possible (Collar 1983) along the lines of successful breeding programs of houbara *Chlamydotis undulata* (Lawrence et al. 2008), great bustard *Otis tarda* (Great Bustard Group 2006–2007), and kori bustard *Ardeotis kori* (A.R. Rahmani personal observation). Within India, like many other developing countries, there is migration of rural people to urban centers in search of better livelihood and in response to better economies (Okpara 1983; Gugler 1988). This is likely to reduce human pressures on the GIB habitat in the future. At such times in the future, it may be possible to restore GIB to their former range from captive stock. There are discussions in the Indian conservation circles and the Government to reintroduce the cheetah *Acinonyx jubatus* in India (Ranjitsinh and Jhala 2010). This would require consolidating large protected habitats which would be beneficial for GIB as well as other endangered fauna of the arid and semi-arid regions. If we fail to act now in promoting both *in situ* and *ex situ* measures for conserving the GIB, we are likely to witness the extinction of this species within a span of generations.

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Executive summary

1. Concerns for global species extinction and conservation concerns have resulted in a new eclectic crisis science, *conservation biology*, which studies and mitigates human impacts on biodiversity. India exemplifies a typical developing economy, growing fast to take advantages of global markets at the cost of environmental degradation. Due to increasing anthropogenic pressures, previously undisturbed *unprotected* semiarid landscapes of India are fast vanishing. The Great Indian Bustard (*Ardeotis nigriceps*, GIB) is an obligate grassland bird endemic to this region, with a global population of only about 300 birds. It is Critically Endangered (IUCN 2011) due to extremely slow life-history traits compounded with prevailing levels of habitat loss and hunting. Existing conservation strategies fail to address all ecological requirements of GIB, requiring urgent re-evaluation. Despite good natural history studies, there has been little research in this direction. I have attempted to fill this void by reporting crucial information such as species' status, resource selection, behavioural aspects and sociocological contexts, to reformulate viable bustard conservation strategies. I have conducted this study during 2007–11 in SW Kachchh (Gujarat, India) that harbours one of the eight extant GIB populations in 1000 km² landscape of Abdasa and Mandvi tehsils. Herein, 160 km² agro-grass-scrub mosaic forms the core bustard usage, inclusive of the traditional breeding patch (Naliya), also a proposed Sanctuary. Rann, a saline marshland, has separated this region from mainland since last 900 years, preserving its traditional livelihoods and wilderness. In response to the semiarid stochastic climate, local people in past have adopted a flexible agro-pastoral-trading economy, characterized by cycles of agricultural abandonment in drought years and intensification in wet years. However, policy changes and technological advancements during the last 5–10 years have facilitated intensive agricultural expansion and industrialization, catalyzing long-term socioecological shifts. The study examines their effects on GIB, the flagship of grassland fauna and a conservation-dependent species.
2. Information on population status and trend are central to ecological studies and crucial in objective assessment of conservation management, but are scanty for this species. To fill this void, I estimated density and occupancy of birds in the landscape and core areas by systematic seasonal transects. While density declined from $0.092_{\text{Mean}} \pm 0.052_{\text{SE}}$ km⁻² (2007–08) to 0.048 ± 0.025 km⁻² (2010–11) at an annual exponential rate of -0.33 ± 0.13 ; occupancy declined

from 0.15 ± 0.07 (2007–08) to 0.06 ± 0.03 (2010–11). The core area, harbouring 11 times higher year-round density than remaining landscape, also experienced decline in use across years, primarily during breeding season. Population exhibited female skewed adult sex ratio (0.33 males/female), and twofold increase in typical flock size from breeding to non-breeding season. Based on power analysis, five alternate year surveys to estimate bird density from $\geq 25\%$ landscape-area in summer and winter, and $\geq 40\%$ core area in summer had acceptable statistical power (80%) to detect 10% population changes per year. Contiguous *unprotected* habitats in immediate neighbourhood of the traditional breeding area should be immediately conserved to partly accommodate the non-breeding requirements of GIB.

3. Habitat selection is the hierarchical choice of space in response to environmental factors, and is frequently studied to guide conservation management. The GIB inhabits open habitats, but its space use is not comprehensively known, impeding mitigation of disruptive landuses. I tested hypothesized species' habitat responses, examining the influence of scale, season and life-history activities. At the macro-scale, I modeled seasonal population indices in 16 km^2 grids from transect surveys with habitat predictors by regression technique. Breeding use was restricted, mostly influenced by proximity to traditional breeding area, grassland cover in grid and adjoining matrix, terrain flatness (all positive) and disturbances (negative). Non-breeding use was relatively vast, being high in productive grids with short fruiting *Zizyphus* shrubs and grassland dominated matrix for easy access. At the micro-scale, I estimated Resource Selection Functions of daily use (foraging, resting and roosting) by logistic regression on used vs. available habitat samples, while that of breeding use (display and nesting) by discrete choice analysis of paired used vs. alternative habitat samples. Habitat envelopes differed between activities: 1) nesting females preferred moderately tall than short or tall scrubby vegetation and avoided livestock grazing; 2) displaying males and roosting birds preferred sparse vegetation; and 3) foraging birds preferred agro-grass mix and naturally available fruit resources. Breeding season density at the macro-scale was higher in areas that accommodated diverse habitat envelopes for daily use at the micro-scale, indicating that large contiguous heterogeneous patches should be conserved. Results highlighted detrimental effects of current landuses (intensive cultivation, infrastructure and tall plantation) on GIB habitat, and provided site

specific habitat management recommendations based on resource selection probability maps in the context of Kachchh.

4. In view of recent impetus on application of behavioural studies in fixing conservation problems *vis-à-vis* scanty quantitative information on GIB behaviour, I studied select aspects to enhance such understanding. I described birds' activity time budgets segregated by gender, season and day periods from instantaneous and scan samples. This exercise shed light on context specific trade-offs faced by birds in allocating time between behavioural acts to meet opposing ends. Conspecifics can influence behavior and survival of the gregarious GIB, while anthropogenic degradation of patch quality can reduce flock size. So I examined the possible functions of flocking, and found that it reduced individual vigilance, although weakly, and increased flock vigilance, enabling better detection of threats. But the time thus saved did not translate into increased pecking rate. However birds showed maximum tendency to flock in winter, when resources were moderately abundant but patchy, indicating that information-sharing could be another adaptive function of flocking. Flocking might also facilitate social learning, as preening was found to be synchronous among flock members. Bustards exhibit the rare exploded lek polygynous mating system with elaborate displays. I studied breeding space use through intensive search of the core area, observing that male arenas were strategically placed at relatively high and steady long-term female usage, wherein male occupancy corresponded with female usage across seasons. Such experiential selection of arenas implied that their destruction could set in *Allee* effects under such low bird densities, and should be considered as the most serious conservation problem. I examined proximate correlates of courtship release by mixed effect models, and found that courtship rate was influenced by female density (positive), disturbance (negative), and weather (highest in bright and cloudy weather). I analyzed courtship structure by decomposing observations into component postures objectively scored based on deviations from the 'normal' posture, and observed that courtship structural composition varied with arena environmental conditions, such as female density and weather.
5. I studied feeding habits of GIB, where I estimated a) food use from fecal pellets, correcting for published digestibility differences of food items; b) abundance of natural food items from belt transects; and c) order of food preference by Johnson's (1980) use vs. availability rank

comparison. Annual diet was composed of 17 food items, chiefly beetles and grasshoppers > *Zizyphus* and other fruits > *Sesame* and other crops. Seasonal diet breadths were similar but shifted from predominantly herbivorous in winter (71% dry weight of plant matter) to insectivorous in summer and monsoon (72% insects). Natural food biomass in environment was composed of lizards > grasshoppers > fruits, varying considerably between seasons. Beetles followed by *Zizyphus* and grasshoppers were the most preferred natural food items.

6. The GIB requires vast landscapes to accommodate entire life-cycle requirements, but creating landscape-size PA is not practical in this densely populated country. So the only conservation model is through sustainable coexistence with humans that requires comprehensive understanding of local socioecological perspectives. I tested if grazing pressure influenced grass height and GIB use by tracking livestock herds, vegetation sampling, and bird surveys. Grass height, but not GIB use, was negatively correlated with stocking density in 4 km² grids, indicating that grazing should be regulated to balance conservation and livelihood benefits. I assessed socioeconomy, herd ecology, attitude, threats and institutional arrangements of resident pastoralists from 22 villages through questionnaire survey. Data revealed that pastoralists earned two-thirds of their annual income from grassland resources, and agro-pastoralist livelihood provided better socioeconomics than just pastoralism. However, pastoralists represented only 6% of village households, and the remaining 94% population had negligible economic stakes although significant cultural stakes on grassland resources. Pastoralists were clearly not an economically or politically powerful community; their livelihoods on common resources were threatened by intensive agricultural encroachment. Natural cover in village grazing areas, and therefore livestock energetics, was negatively correlated to human population density. Pastoralists exhibited very low levels of problem reporting/protesting tendency, fidelity to occupation, exclusion of resources from other users, and ability to enforce land tenure rules, all implying weak institutions. Such small unevenly distributed stakes, weak institutions, and external economic forces could have led to open access of these grassland resources. But village groups with relatively strong institutions reported less threat from landuse conversions. Although traditional agro-pastoralism is compatible with bustard conservation, under current scenario it is unlikely that communities' institutional social mechanisms can achieve those conservation objectives. Hence managers should try to consolidate pastoralists' resources and livelihoods by strict enforcement of legal

land tenure rules and external aide such as veterinary support and Agro-environmental incentive schemes.

7. Population viability analysis shows that GIB populations of ≤ 35 birds can persist only under unrealistic conditions of first year mortality $\leq 40\%$, and no human caused mortality of adult birds. Even the largest population (≥ 100 birds) is sensitive to additional loss of adult birds to human causes. With current levels of hunting in Pakistan, extinction is a real threat. Conservation strategy should immediately secure traditional core areas by creating sacrosanct breeding refuges, where loss of birds from hunting and fatal accidents should be minimized. A landscape conservation strategy is needed in priority areas identified by biotelemetry research, where research informed habitat management, traditional land uses, and GIB-friendly infrastructural development should be implemented. The declining rate of GIB populations calls for immediate commencement of *ex situ* conservation breeding programs.

Chapter 1. Introduction

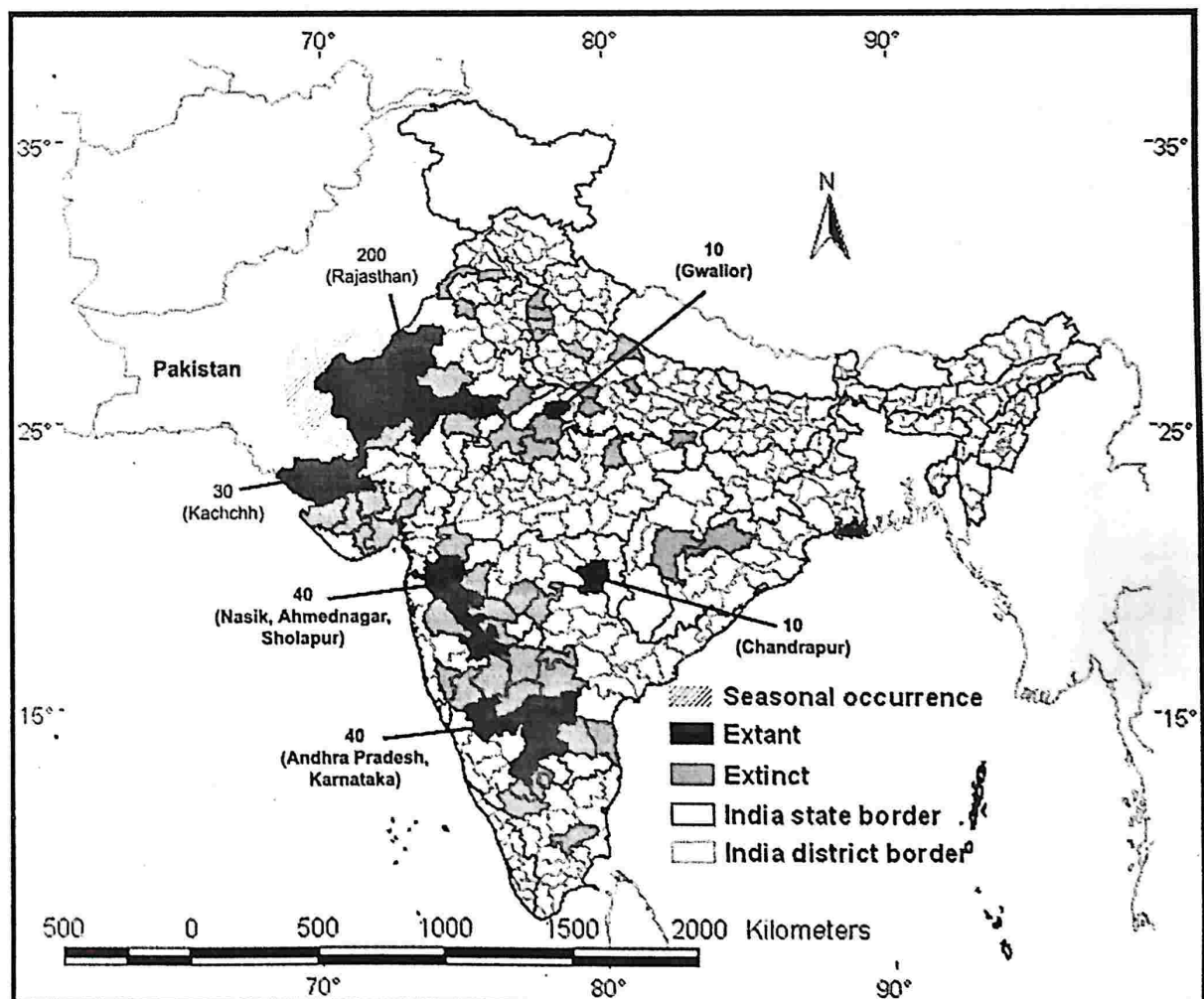
Globally, species' extinction and concern for their conservation are co-occurring at unprecedented intensities (Morrison et al. 2007, Isaac et al. 2008). They have influenced the emergence of an eclectic crisis science, *conservation biology* (Soulé 1985). It combines principles of ecology, population biology, genetics, social sciences etc. to study impacts of human activities on wildlife (Caro 2007), thereafter applying this knowledge for preservation of biological diversity. In essence, this discipline is tied up with its component sciences like war is related to political science (Soulé 1985). India exemplifies a typical developing economy, which is growing fast to take advantage of global markets, but disrupting its environment and human development in the process. Its human population has quadrupled in the last 150 years to ≥ 1.2 billion and the annual economic growth is predicted at $\geq 5\%$ over the next 30 years (Wilson and Purushothaman 2003). Rapid socio-economic changes have led to increasing pressure on natural areas (Lele et al. 2000). Vast extents of previously undisturbed dry grass-scrub landscapes of western India are vanishing fast (Vanak and Gompper 2010) due to agricultural and infrastructural developments. Such habitat loss can exert detrimental effects on wildlife in species-specific ways. Bustards are obligate grassland birds, highly specialized with k -selected traits and an open nesting system (Lack 1954). These characters render them vulnerable to extinction when faced with environmental changes and direct threats. One of them, the Critically Endangered (IUCN 2011) Great Indian Bustard (*Ardeotis nigriceps*, hereafter GIB), faces serious threat of extinction from hunting, habitat conversion to agriculture and infrastructural development (Dutta et al. 2011, IUCN 2011, Rahmani 1989). Their population, roughly estimated in 1969 at about 1260 individuals (Dharmakumarsinhji 1971) ranging over the western half of India, dwindled down to about 745 individuals by 1978 (Dharmakumarsinhji 1978). Around 600 birds survived at the turn of this millennium (BirdLife International 2001) but currently only ~ 300 (Rahmani 2006) are left, restricted to fragmented pockets in six states of India (fig 1.1, Dutta et al. 2011).

1.1 Current status

In Rajasthan, the Desert National Park in the districts of Jaisalmer and Barmer along with the agro-pastoral landscapes of Bikaner holds the largest global population of the GIB currently numbering between 100–125 birds, along with another 25–50 birds in Ajmer, Pali and Tonk

districts (Rahmani 2006). All other populations number less than 35 birds each (BirdLife International 2001). These populations are located within the states of a) Maharashtra, at the Bustard Sanctuary of Sholapur and Ahmednagar districts having 30–35 birds, Nasik district having 5–8 birds and Chandrapur district having 4–6 birds (Thosar et al. 2007), b) Andhra Pradesh, at Rollapadu Sanctuary of Kurnool district and its adjoining areas of Anantpur district having about 30 birds (Rahmani 2006, Rao and Javed 2005), c) Gujarat, in Abdasa tehsil of Kachchh district having 25–30 birds (Singh 2001), d) Karnataka, where the population status is poorly known, but few birds (2–4) have recently been reported from Sirguppa tehsil of Bellary district (Ahiraj 2008), and e) Madhya Pradesh, where the GIB population has faced a stark decline (Rahmani 2006) and numbers in Gwalior district are less than 10 birds. The Rajasthan and Kachchh populations are probably shared with eastern Pakistan where sporadic seasonal sightings of 15–20 birds have been recorded (Khan et al. 2008). The last two decades have seen a drastic reduction in the range occupancy and population size of the GIB in India (fig 1.1).

Figure 1.1 Current (2008) and historical distribution of Great Indian Bustard within districts of India and occurrence of summer visitors in Pakistan. The numbers are the estimated maximum populations



For instance, within the state of Gujarat, GIB was recorded from Surendranagar, Jamnagar, Bhavnagar, Rajkot, Kheda, Amreli and Kachchh districts (Rahmani 1989, Rahmani and Manakadan 1990) but currently a single population survives in Kachchh with rare transients reported from Bhavnagar, Jamnagar and Surendranagar districts. Similar trends are reported across the GIB range (fig 1.1).

1.2 Species account

The bustard lineage [family *Otididae*, order *Gruiformes*] originated 77 million years ago in Africa, at three focal points: Sub Sahara, East Africa and South Africa (del Hoyo et al. 1996). They lack hind toe, fly rarely, and are terrestrial; deriving their name from the Latin words *avis* (*sensu* bird) *tarda* (*sensu* slow). The current classification recognizes eight genera and 25 species (Sibley and Ahlquist 1990). *Ardeotis* has the largest generic range and is possibly the earliest stock which spread across Eurasia, India and Australia, speciating in discreet ranges of the Old World (del Hoyo et al. 1996, Johnsgard 1991). They have subsequently coevolved with wild ungulates, and depend on grazers to maintain a suitable habitat structure. Since the last thousand years, community of wild grazers has been steadily replaced by domestic livestock in most of the bustards' range outside Africa (Skarpe 1991). Based on white and black contrasting colouration of male plumage, genera *Otis* and *Ardeotis* seem to be the more generalized forms, inhabiting arid grasslands. Whilst *Sypheotides*, *Houbaropsis* and some *Eupodotis* are more specialized, inhabiting savannas (Johnsgard 1991). The GIB *Ardeotis nigriceps* is one of the heaviest flying birds, where the male (11-15 kg weight and 1.2 m height) is twice as large as the female (4-7 kg weight and 0.9 m height) (Elliott 1880, Rahmani 1989, Vyas et al. 1983). Flocks of GIB vagrantly use wide, sparse grass-scrub landscapes with low intensity cultivation in the non-breeding season. They have a broad omnivorous diet chiefly consisting of fruits like *Zizyphus*, insects like grasshopper and beetle, reptiles, and seasonally available food crops like ground nut and millet (Rahmani 1989). They attain sexual maturity at a late age of 2-3 years in females, and 5-6 years in males (del Hoyo et al. 1996, Johnsgard 1991). During mid summer and monsoon, they congregate at traditional areas to breed, and avoid human disturbance (Johnsgard 1991, Rahmani 1989). Organized in a polygynous exploded lek mating system, dominant males show site fidelity to their display stations. This behaviour has been recognized as one of the crucial factors in designing their

conservation strategies (Rahmani and Manakadan 1986). Post copulation, the female typically lays one egg and incubates it for ~25 days without any cooperation from the male. The precocial chick fledges in ~75 days and follows its mother for a year (Rahmani 1989).

1.3 Conservation strategies

Alerted by naturalists about the decline of GIB and the need to conserve grassland resources (Ali and Ripley 1969, Dharmakumarsinhji 1978, Tyabji 1952), State Governments of India declared eight bustard Sanctuaries in post 1980s, with a belief that establishment of 'Protected Areas' might hold the best hope for saving the species (Rahmani and Manakadan 1987). Most of these Protected Areas were either too small, targeting traditional breeding patches following the preservationist approach (Kramer et al. 1997), or very large, covering entire agro-pastoral landscape inclusive even of large townships. Within these reserves, the recommendation was to maintain small, scattered (>100 to <500 ha) refuges with large buffers (Rahmani 1989) that should preferably be traditional breeding spots and protected during the breeding season (Chauhan 2006) to exclude cattle. Refuges were recommended to be managed so as to provide habitat requirements for crucial activities such as lekking, nesting, chick rearing and foraging (Rahmani 1989), and could be rotated over the Protected Area through ≥ 5 years periods (Chauhan 2006).

1.3.1 Limitations

The prevalent legal system in the 1980s–1990s governing PAs was not sufficiently flexible to permit implementation of even these simple recommendations. While declaration, many GIB Sanctuaries were inclusive of, or surrounded by privately owned lands, exemplified by Karera Bustard Sanctuary in Madhya Pradesh and the Bustard Sanctuary of Maharashtra which included the township of Sholapur. Due to enhanced protection and restricted livestock grazing in the Karera Bustard Sanctuary (202 km²), the residing small blackbuck population exploded resulting in crop depredation in adjoining private agricultural lands. Blackbuck *Antilope cervicapra* being a Schedule I species (Wildlife (Protection) Act 1993), could not be hunted. This antagonized local agro-pastoral communities (Rahmani 2003) resulting in a backlash by the communities. At the same time, conservation measures recommended by Rahmani (1989) were not implemented by the State Forest Department. These factors resulted in local extinction of GIB in Karera by 1994, and reduction of blackbuck population through poaching. In another case, the Bustard Sanctuary

of Maharashtra which covers an area of 8,496 km² has faced rapid industrialization and increase in human population during the last 30 years. Much of this Sanctuary is currently non-GIB habitat, while the total aggregate area of scattered suitable patches is <400 km². The large expanse of this Sanctuary has restricted private land owners therein to use their lands freely and profitably, as the stringent Indian legislation is extremely restrictive about land use in legally gazetted Protected Areas (Wildlife (Protection) Act 1993). This again has generated bitterness amongst the local populace. Currently the state government is proposing to rationalize the Sanctuary boundary to accommodate the concerns of private land owners. The cumulative impact of these land-use policies and attitude changes has resulted in decline of GIB in the Bustard Sanctuary of Maharashtra.

On the other end of large Sanctuaries, lie some extremely small conservation areas targeting lekking or nesting patches as in Sonkhaliya (17 km²) in Rajasthan, Gaga-Bhatiya (2 km²) and Lala-Naliya (17 km²) in Gujarat, and Rollapadu (6 km²) in Andhra Pradesh. The vagrant nature of GIB has reduced the benevolent effects of these small sanctuaries outside of the breeding season. Some of these refuges have been subjected to well-intended but ill-informed management interventions such as development of large water bodies, network of roads, delineation of 'reserve grasslands' through trenching-cum-mounding and plantation. Such managerial practices have resulted in severe habitat alteration (Pande and Pathak 2005) and are considered to have caused local extinction of the species from Ranibennur and Gaga-Bhatia Sanctuaries, and decreased usage of Lala Sanctuary.

1.3.2 Threats and knowledge gaps

In the intervening time, most bustard habitats faced new threats, such as 1) widespread agricultural expansion and mechanization of farming; 2) infrastructural development such as irrigation, roads, electric poles, wind turbines and constructions; 3) mining and industrialization; and 4) habitat mismanagement (Anon 2011, Singh et al. 2006). With increased availability of water due to Government irrigation policies, agriculture has spread over vast arid-semiarid grasslands. For example, the Indira Gandhi Nahar Project has caused drastic hydraulic changes and massive agricultural conversion in and around the Desert National Park. Moreover irrigation facilities and changing lifestyles have led to a shift in the crop pattern from bustard-friendly traditional monsoonal crops (*Sorghum*, millet etc.) to cash crops (sugarcane, grapes, cotton,

horticulture etc.) which are not suitable for GIB. Due to fuzzy land distribution policies and the ambiguity arising from segregated ownership between private, community and government bodies, encroachment is a major problem in many bustard areas, especially in bustard sanctuaries of Maharashtra and Kachchh. Activities such as mining, stone quarrying, growth of industries and power projects along with the expansion of roads, electric poles, windmills and other infrastructures have increased the severity of habitat degradation and disturbance (Anon 2011). Traditionally, grasslands and scrub have been considered as *wasteland* and the Forest Department policy, until recently, has been to convert them to *forests* with plantation of fuel/fodder shrub/tree species, even exotics like *Prosopis juliflora*, *Gliricidium* and *Eucalyptus* spp., under social forestry and compensatory afforestation schemes (Forest (Conservation) Act 1988, Indian Forest Act 1927) resulting in further loss of GIB habitat. Overgrazing on *unprotected* lands has also led to degradation of some areas.

Since prevalent conservation strategies have failed to address all ecological requirements of the species, and threats to their survival have increased; their decline in density (20–29%, see BirdLife International 2001) and range (90%, see Rahmani 2001) have continued unabated. In spite of being thoroughly observed by naturalists in the past, there has been little conservation research on GIB.

1.4 Research rationale

Decline of GIB is likely to continue in future under the predicted socioeconomic environment (Dutta et al. 2010, Wilson and Purushothaman 2003) unless well planned conservation initiatives are seriously undertaken. This demands a careful re-evaluation and rectification of current management strategies based on scientific research in prevailing conservation contexts. The present study sought to address this issue by generating crucial information for reformulation of effective bustard conservation strategies. It derives the rationale from unification of *small population* and *declining population* paradigms for management of threatened species (Caughley 1994). The first examines the effect of small population sizes on persistence while the latter examines the causes behind population declines and provides conservation solutions (Norris 2004). The broad research aims are to: 1) assess conservation status, 2) resource requirements and 3) behavioural aspects of GIB, 4) understand local landuse contexts, and 5) provide effective conservation solutions in the light of these information and population

viabilities under simulated scenarios. To achieve these aims, I have used common quantitative ecological tools like population surveys, habitat sampling, behavioural observations and questionnaire surveys, and drawn inferences using statistical analyses, simulations, and auxiliary genetic study. I have focused on a single population in Kachchh to answer most of my research questions. This population along with Rajasthan and (possibly) Pakistan constitutes ~75% of the global GIB population on the largest contiguous habitats, which also faces high mortality risks. Thus, science based conservation of this population is crucial for the long-term persistence of the species.

1.5 Research objectives and organization

This thesis is organized in seven chapters.

Chapter 2 describes the study area, providing information on its location, physical features, climate, wildlife, people, economy and sociological contexts.

Chapter 3 (first research aim) deals with monitoring population parameters of GIB. Due to the lack of standardized protocol, current population status are based on unsystematic surveys. My objective is to fill this gap by developing a monitoring protocol that can be implemented across the species' range for well-timed objective assessment of local status and management efficacy. For this, I estimate population measures at multiple scales and assess statistical powers of various sampling schemes to detect population changes in subsequent years. Little is known about other demographic parameters, such as adult sex ratio and flock size that are also estimated here.

Chapter 4 (second research aim) investigates species-habitat relationships at multiple scales. My objectives are to examine a) how proximity to traditional breeding patch, grassland extent, resources and disturbances influence macro-scale usage of GIB, differing between seasons; and b) how land use and cover, vegetation structure and composition, resources and disturbances influence micro-scale habitat selection, differing between life history activities (foraging, nesting etc.). I assess if current habitat manipulations by Forest Departments and local land uses are concordant with these habitat requirements. These findings will enable more informed conservation management of GIB habitats.

Chapter 5 (third research aim) investigates behavioural aspects of GIB and their conservation implications. My objectives are to determine: a) activity budgets, where I examine differences in time apportionment to behaviours under various conditions; b) benefits of flocking, where I

examine if flocking reduces vigilance, increases feeding rate, and transfers acts; c) patterns of courtship behaviour, where I examine space use dynamics, environmental correlates of courtship frequency, and structure of courtship repertoire; and 4) feeding habits, where I examine seasonal diets and food preference.

Chapter 6 (fourth research aim) deals with pastoralism, the traditional livelihood of this region. Being dependent on grassland resources and threatened by conversion of land into cultivation, pastoralist communities can be a conservation ally if grazing is optimally managed. Hence, my objectives are to a) examine how stocking densities influence vegetation structure and GIB usage within the core breeding area; and b) describe the socioeconomics, resource dependency, herd ecology and institutional arrangements of local pastoralist communities in the context of bustard conservation.

Corresponding to these objectives, I elaborate their research hypotheses, methods used to address them, findings, and conservation implications in respective chapters.

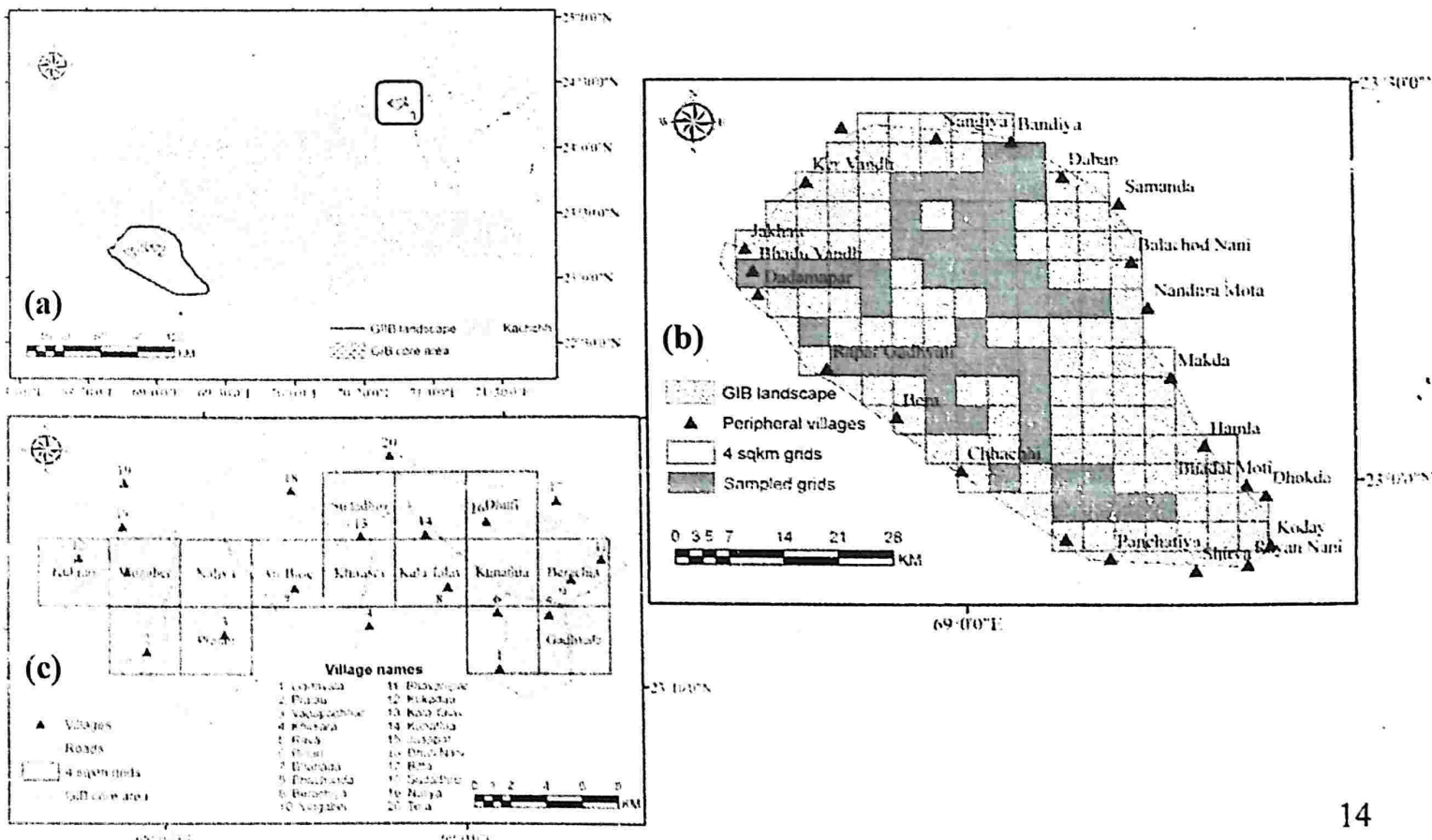
Finally, Chapter 7 estimates population viabilities under simulated scenarios and synthesizes information from this and auxiliary studies (Ishtiaq et al. 2011) to design viable conservation strategies that can mitigate adverse human impacts on the GIB.

Chapter 2. Study area

2.1 Location

The study was conducted in SW Kachchh (Gujarat), located in the extreme west of India (23.13°–24.68°N and 68.10°–71.80°E), encompassing 45,612 km² area (fig 2.1a). It is bounded by the Gulf in south, Pakistan in north, and Gujarat mainland in east. Based on wildlife surveys in last 20 years (Rahmani 1989, Sharma, Bopanna and Jhala unpublished data), communication with local experts and a recent study (Pandey et al. 2008), I identified the potential range of GIB in this region. I conducted reconnaissance of these areas by foot and vehicle searches and discussion with local people during June–November 2007. This helped in delineating the annual and intensive use areas of GIB, respectively termed as the *landscape* and *core* hereafter. The landscape encompassed ca1000 km² area (23.4315°N, 68.6496°E–22.8905°N, 69.2997°E) in Abdasa and partly Mandvi tehsils (fig 2.1b). The core encompassed ca160 km² agro–grass–scrub mosaic (23.21°N, 68.78°E – 23.23°N, 69.05°E) or *Daun* in central Abdasa, comprising of five contiguous patches: *Naliya–Vingaber* (grassland), *KalaTalavo* (agro–grass), *Sudadhro* (agriculture), *Kunauthia–Berachia* (savanna) and *Gadhvala* (grass–scrub) from west to east (fig 2.1c).

Figure 2.1 (a) Study location in Kachchh (India) and (b) delineation of bustard landscape and (c) core usage areas where fieldwork was conducted during 2007–11

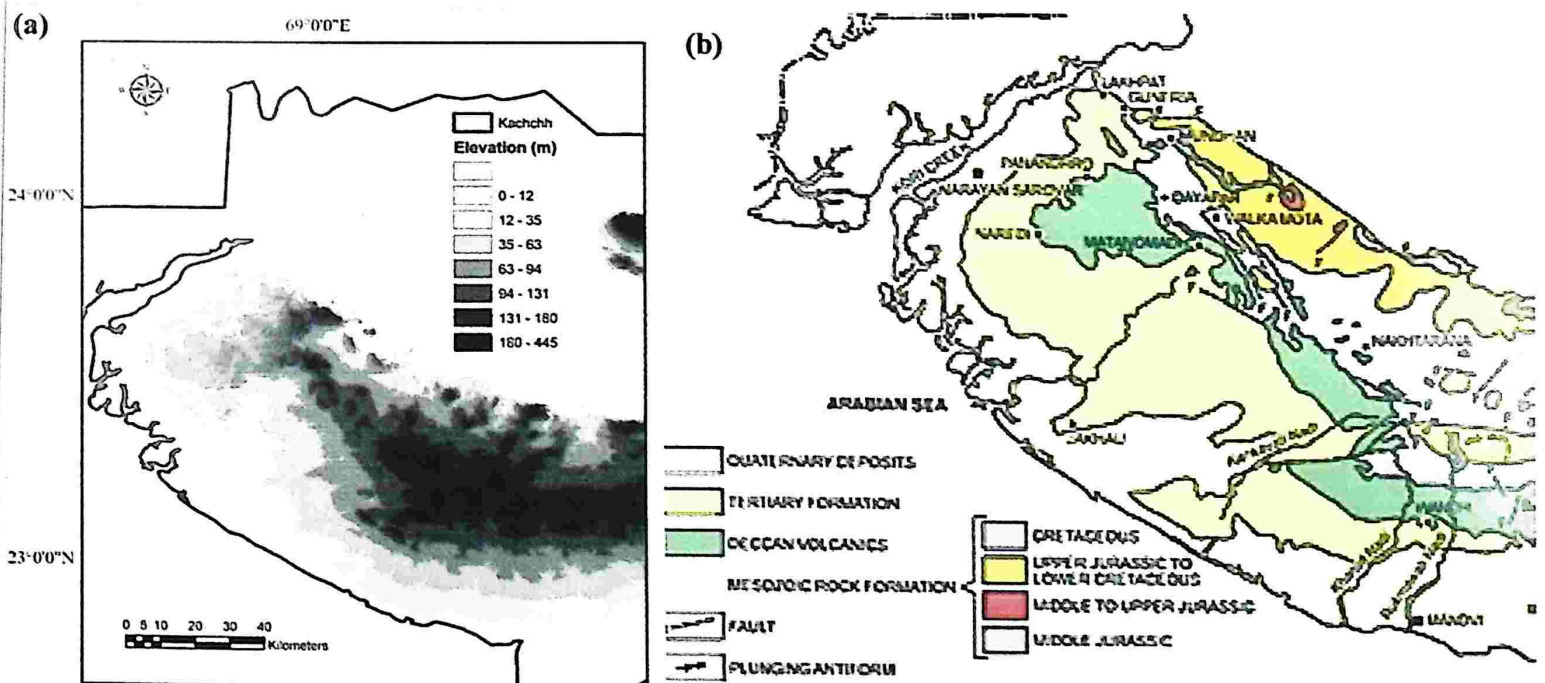


Near Naliya, 17-km² grasslands have been proposed as a Sanctuary for the protection of bustards.

2.2 Physical features

Kachchh can be categorized into four geomorphologic zones bounded by east to west trending faults (Biswas 1980). These are the a) coastal plains (southern portion), b) mainland (central portion comprising of rocky upland and northern hills), c) Banni Plains (raised fluviomarine sediments, mud flats and salt pans), and d) Ranns (the Great Rann and little Rann). Rann, now a saline wasteland in the north east, has played significant role in evolving various aspects of this region. In ancient times, Rann was an arm of the Arabian Sea and Kachchh was an island, forming an Adam's Bridge between Sind and Kathiawad. This condition, island surrounded by gulfs of sea and coastal towns, continued till historical times. The gulf was gradually silted up and led to low elevation of the land (Williams 1958), forming modern Kachchh, *sensu* "tortoise" in Sanskrit language. Tectonics of Kachchh Rift Basin dates back to early Mesozoic era and presents a complete sequence from Triassic to Recent period (Biswas 1992). The region is mostly occupied by sedimentary rocks, such as limestone, shale and sandstone, from Jurassic period to Eocene epoch (Krishnan 1982). Microlithic finds resemble those found on mainland on either side. The terrain is characterized by rolling plains interrupted by ravines and low hillocks (fig 2.2).

Figure 2.2 (a) Elevation and (b) geological maps of Kachchh modified from DRM, GSI, 2002 (http://www.portal.gsi.gov.in/portal/page?_pageid=127,693641&_dad=portal&_schema=PORTAL)



2.3 Climate

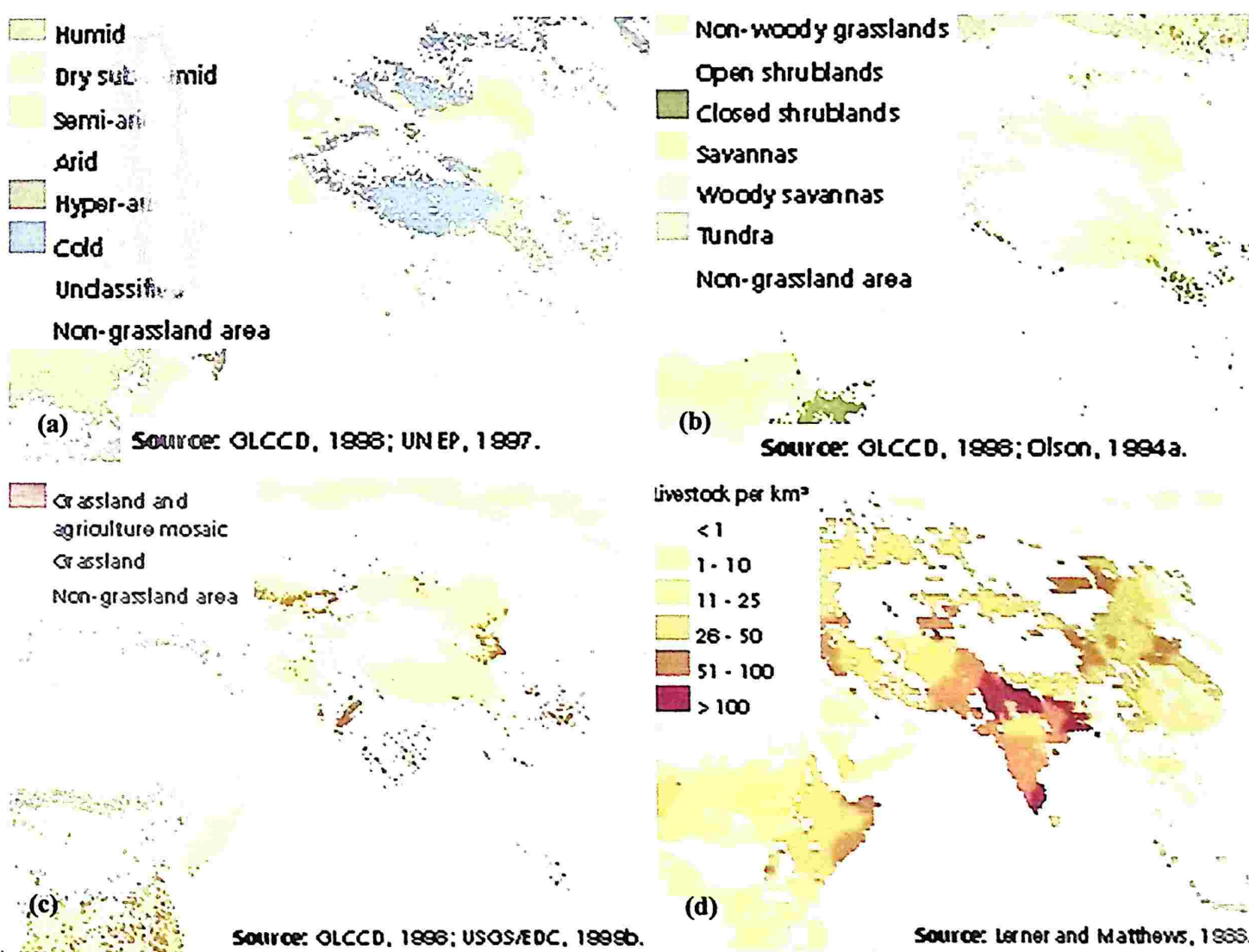
Based on the ratio of mean annual precipitation to mean annual potential evapotranspiration (UNEP 1992), the earth's surface has been divided into six aridity zones (White et al. 2000). The semiarid zone (aridity index 0.2–0.5) covers 17.7% of earth's land surface and is characterized by scanty rainfall with high inter-annual variability. Kachchh falls in the semiarid-arid zone (fig 2.3a). The annual average rainfall is about 384mm, ranging between 78–888 mm during 2000–2010. On an average, there is a drought in every 5–10 years; however rainfall has been relatively more in last 5–10 years. This region also experiences extremes of temperatures with large diurnal and seasonal temperature ranges. The three prominent seasons are winter (November–February), summer (March–June), and monsoon (July–October). The hottest month is May experiencing maximum temperatures of 40–45°C, and the coldest month is January experiencing minimum temperatures of 0–5°C. Rainfall occurs only once in a year, when the south-west monsoons reach the coastal regions (mid-June) thereafter spreading to the other parts (early July). Long term rainfall records indicate that rainfall arrives before July 15 in 65% years whereas late onset occurs in 35% years (Sinha et al. 1972). As a result of high evapo-transpiration rate, natural water sources dry up during lean periods leaving behind a few man-made water sources to exist.

2.4 Habitat and wildlife

This region falls in Biogeographic Zone 3B Kachchh Desert (Rodgers et al. 2002). *Thar*, world's smallest hot desert covering 10% of India's geographical area, extends here. Champion and Seth (1968) has classified the vegetation as Northern Tropical Thorn Forest (6B) Desert Thorn Forest (6B/C1). The broad habitat types are: a) sparse cover to short grasslands dominated by *Cymbopogon*, *Aristida*, *Dicanthium* and *Chrysopogon* grasses; b) savanna to scrubland dominated by *Zizyphus*, *Acacia*, *Capparis*, *Salvadora*, *Euphorbia* and introduced invasive *Prosopis juliflora* shrubs; and c) agricultural matrix including seasonal and annual crops, fallows and ploughed fields (fig 2.4b). Kachchh harbours a plethora of wildlife important from ecological and conservation perspectives. Some of the notable mammals are the rodent Indian desert jird *Meriones hurrianae*, ungulates like chinkara *Gazella bennettii*, nilgai *Boselaphus tragocamelus* and wild pig *Sus scrofa*, and carnivores like the Indian fox *Vulpes bengalensis*, desert cat *Felis silvestris ornata*, jungle cat *Felis chaus*, golden jackal *Canis aureus*, caracal *Caracal caracal*, Indian peninsular wolf *Canis lupus*, and striped hyaena *Hyaena hyaena*. Kachchh falls in the cross-road of bird migratory

routes, and is represented by about 300 Palearctic and Oriental species (Pandey et al. 2008). Important ones are the GIB, lesser florican *Sypheotides indica*, Macqueen's bustard *Chlamydotis macqueenii*, white-backed vulture *Gyps bengalensis*, greater flamingo *Phoenicopterus roseus*, lesser flamingo *Phoeniconaias minor*, and several other raptor, sandgrouse, partridge, quail, courser, wheatear, lark and pipit species (Pandey et al. 2008). A herbivorous reptile, the spiny-tailed lizard *Saara hardwickii*, also occurs at high densities here (Dutta and Jhala 2007).

Figure 2.3 Maps of grasslands, showing (a) aridity zones, (b) extent and ecotypes, (c) pure vs. cultivated systems, and (d) livestock density (# km⁻²) in the Indian neighbourhood modified from White et al. 2000 (<http://pdf.wri.org/pagemaps/grasslandmaps.pdf>)

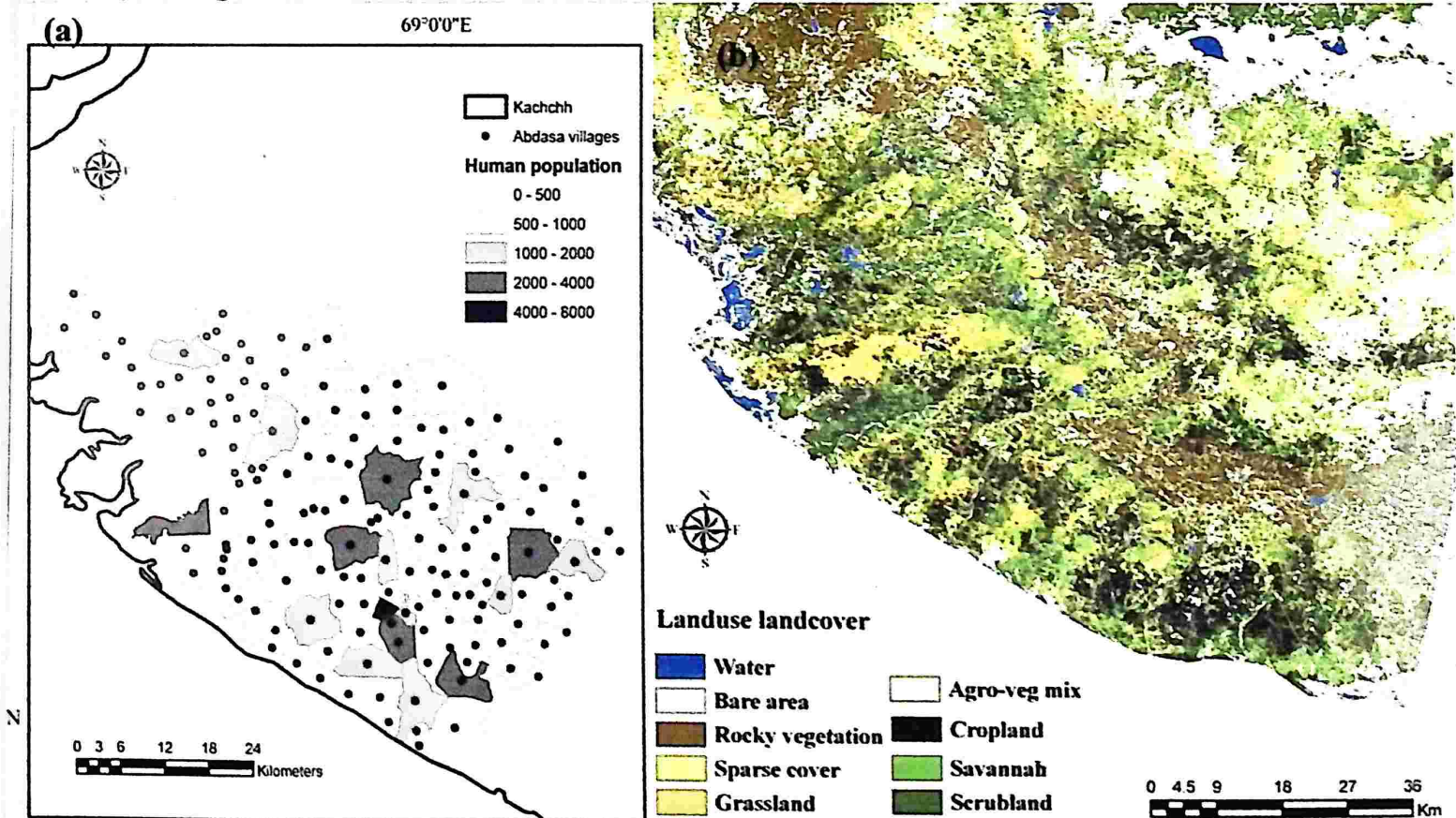


2.5 People

Kachchh has a population of 1,526,321 people inhabiting 949 villages in ten administrative units or *tehsils*, at a density of 33 humans km⁻² (Census of Housing, GoI 2001). The important towns are Gandhidham, Bhuj, Anjar, Mandvi and Mundra. From the traces of Indus Valley

civilization (~3000–1500 BCE) found here, it appears that Harappan people are the first documented inhabitants of this region. Much later, a series of migrations took place from Sindh to Kachchh, during when, Sama Rajputs (now called Jadejas) arrived and ruled this land till the independence (www.portal.gsi.gov.in/portal/page?_pageid=127,693641&_dad=portal&_schema=PORTAL). During the princely time, Kachchh was under feudal or *Zamindari* governance. Based on the beneficiary of the sovereign’s land offerings, the feudal type was either *Girasdari* (offering to relatives), *Inamdari* (for showing valor in battles), and *Barkhalidari* (to Bramhins for their service). Land reforms of 1956 abolished this system but these feudal values had pervaded the populist Kachchhi culture (Joshi 2002). As a step towards decentralizing power and democratizing decision making, Gujarat institutionalized the Panchayati Raj in 1961, a three tier local governance system at the village, tehsil and zilla levels. In modern times, the tribes inhabiting Kachchh belong to Sandhvi, Manni, Rabari, Banjara, Magwar, Samma, Jat, Mutwa and Ahir communities, who are mostly engaged in agriculture, pastoralism, handloom, etc. Currently, Gujarat is one of the most urbanized states of India but Kachchh continues to be predominantly rural (Hirway et al. 2002).

Figure 2.4 (a) Human population at villages and (b) land cover maps of the study area (Kachchh, India) during 2007–11



2.6 Economy

Economically, Gujarat is one of the most developed states of India with the fastest growing state capita. Much of its development is due to the rapid industrial growth marked by 175,000 crores INR investment for industries in 1999–2000. This development has been costly in terms of natural resource depletion and social disparities (Hirway et al. 2002). Agriculture in this region depends on the vagaries of SW monsoons, and 66% of its area (inclusive of Kachchh) receives <750mm annual rainfall. The post-green revolution phase (1967–68 onwards) has seen fast growth and reduced inter-annual variability in crop production. In Kachchh, major crop (jowar *Sorghum bicolor*, bajra *Pennisetum glaucum*, maize *Zea mays*, wheat *Triticum* spp., groundnut *Arachis hypogaea*, sugarcane *Saccharum officinarum* and cotton *Gossypium* spp.) production has increased from 590 (1961–63) to 1088 (1971–73), 1426 (1981–83) and 1641 (1991–93) million INR. This translates into 2.2–3.6% annual rate of increase which is faster than many other districts. Land productivity has grown from 1637 (1961–63) to 6538 (1991–93) INR ha⁻¹ but has stagnated since then. Agricultural development has been achieved mostly through growth in yield and not through increase in arable area, but this is not true for Kachchh. Such agricultural growth has been spearheaded by technological advancements and accompanied by shift to cash crops. For example, number of tractors/1000 ha increased from 0.12 (1961–63) to 3.19 (1991–93) and that of pumpsets/1000 ha increased from 8.03 (1961–63) to 30.50 (1991–93) in Kachchh (Mathur and Kashyap 2002).

2.7 Prevalent socioecological contexts

The bustard landscape is sparsely dotted with villages (0.075 km⁻²) and inhabited by 50 humans km⁻² (fig 2.4a) and 41 livestock km⁻² (fig 2.3d). The land is under mixed ownership: 1) reserved grasslands owned by the Forest Department, 2) Revenue Department lands, 3) community lands owned by village Panchayats and 4) private agricultural lands. Traditionally rural people have engaged in low intensity dry-farming, sedentary and nomadic pastoralism and trade. Cattle (*Bos Taurus indicus*), goat (*Capra aegagrus hircus*), sheep (*Ovis aries*), buffalo (*Bubalus bubalis*) and camel (*Camelus dromedaries*) constitute the major livestock and their grazing action has historically modified the vegetation structure to its current form. However the last 5–10 years have experienced increased anthropogenic pressures in several concurrent ways. Infrastructure has developed in the form of electricity and road network. This has made irrigation and accessibility

available to the remote corners, in turn intensifying and altering cropping patterns. Immigrant farmers are practicing permanent mechanized cultivation of *Bt*-cotton, tomato (*Solanum lycopersicum*) and chili (*Capsicum frutescens*), whilst resident farmers have traditionally grown one-time short duration crops like til (*Sesamun indicum*), groundnut and millets. An emerging boom of industrial development and wind power generation has raised the *hunger for land* ensuing local villagers to illegally encroach and cultivate prime wildlife habitats.

Such socioecological changes necessitate a comprehensive assessment of the conservation status of local fauna and strategies to safeguard their viabilities.

Chapter 3. Monitoring of population parameters

3.1 Introduction

The endangerment of all three resident bustards of India among 25 globally occurring species (IUCN 2001) reflects the prevailing extinction crisis in these grasslands and their (mis)management policies. Indian conservation circles are therefore proposing action plans with bustards as the “flagship” taxa for the grassland fauna (Rahmani 2006). A Bustard Task Force has been recently formalized under the Ministry of Environment and Forest, Government of India to centrally direct the conservation programme. Systematically collected information on resident bustards, essential to formulate management plans and subsequently evaluate their efficacy, are largely missing. The Task Force considers filling up this information gap through robust monitoring programmes as one of the research priorities. This chapter focuses on monitoring population parameters of GIB in the unprotected agro-pastoral landscape of Kachchh, Gujarat. Based on unsystematic surveys in past, GIB numbers in Gujarat seem to have declined from 100 birds in late 1960s (estimated by Dharmakumarsinhji, see Ali 1970) to 50–75 in 1980 (Sinha 1983), when Jamnagar was the prime bustard habitat, to 20–30 birds in 1990 (Rahmani and Manakadan 1990), and about 25–30 birds in 2000 (Singh 2001) restricted only in Kachchh.

Conservation monitoring of endangered species involves intermittent surveillance of population parameters to detect incipient changes (Hellawell 1991). Most commonly this parameter is abundance/density since it affects virtually all aspects of animal biology (Royle et al. 2009). If undesirable population decline is detected under the current regime, conservation practitioners can adopt more informed management to slow the decline (Sutherland 2006). This requires monitoring programs whose sampling methods permit unbiased, statistically powerful results while minimizing costs (Gibbs et al. 1998). Conventional bustard surveys to measure abundance have mostly followed total count techniques (Baral et al. 2003, Davidson 2004, Sankaran 2000). Total counts over large spatial scales (that bustards generally occupy) are effort consumptive and usually do not correct for imperfect detection. If compared over time and space, these count statistics may lead to erroneous inferences if detectability is non-uniform (Mackenzie and Kendall 2002). Consequently, sampling methods that formally incorporate the detection process such as distance sampling (Buckland et al. 2001) and occupancy based approaches (Mackenzie et al. 2002) are being implemented in more recent bustard surveys (Carrascal et al.

2008, Tourenq et al. 2005). These techniques have the dual advantages of low costs and reliable estimation of parameters if assumptions are successfully met (see Buckland et al. 2004, MacKenzie et al. 2006.).

The efficacy of such population measures under a certain monitoring framework lies in their ability to reflect a change in true abundance if it occurs (Cohen 1988, Gerrodette 1987). The power of this statistical procedure ($1-\beta$) is influenced by Type I error (the probability of rejecting a null hypothesis when it is true, ' α '), Type II error (the probability of not rejecting a null hypothesis when it is false, ' β '), coefficient of variation in population measure (the inherent variability due to measurement error and real variation, 'CV'), sample size (n) and effect size (the magnitude of change, ' r '). Given the estimator's CV, how much and how often to sample so that a certain population change is detected at acceptable levels of α and β is a critical management decision at an early stage of monitoring when its structure can still be altered (Gibbs et al. 1998).

Other demographic parameters such as flock size, sex ratio and juvenile to adult ratio are also not reliably known for GIB populations, but are important from ecological and conservation perspectives. For example, most large bustards are gregarious, particularly during their non-breeding season (Johnsgard 1994). Conspecifics form major component of their environment and can potentially influence aspects like predation avoidance, foraging success, information exchange, sexual selection, etc. Consequently, sociality might affect their persistence and evolution to some extent (Krause and Ruxton 2002). Birds commonly exhibit skewed adult sex ratio (hereafter ASR), where males outnumber females by 33% on average, and more frequently in globally threatened than non-threatened species (Donald 2007). On the contrary to this general trend, many large bustards exhibit skewed ASR in favour of females (del Hoyo et al. 1996) and expectedly (or consequently), peculiar life-histories like sexual size dimorphism and polygynous mating behaviour (Mayr 1939, Murray 1991). The ASR results from different mortality rates between males and females due to genetic, physiological or most importantly environmental causes (different vulnerability of sexes to certain dangers) at various life stages. Although these parameters have received little attention in recent years, their accurate reporting is vital for theoretical and conservation research (Donald 2007).

My study objectives were to monitor population status and estimate other parameters of the GIB population in Abdasa tehsil of Kachchh (Gujarat, western India) from data collected during 2007–2011. Birds aggregate in traditional *core areas* for considerable part of the year (especially

during their breeding season) with some annual dispersive use of the larger landscape (Rahmani 1989). While monitoring has to be conducted at the core and landscape scales, implementation of similar methods is logistically unfeasible. I measured GIB occupancy (MacKenzie et al. 2006) and abundance in the larger landscape using extensive transect search; and (2) density in the core area by intensive line transect based distance sampling (LTDS, see Buckland et al. 2001, Burnham et al. 1980). I assessed (3) the statistical power of these population measures in detecting undesirable population changes along increasing levels of sampling efforts and intervals to develop a relatively low cost but effective monitoring design. I investigated (4) the seasonality of space use, and estimated (5) auxiliary demographic parameters such as the flock size, adult sex ratio (ASR) and juvenile to adult ratio.

The study landscape is one of the few remnant habitats in India where GIB still breed, likely harbouring about 9% of their global population (Pandey et al. 2008). In the past, this landscape has been subjected to low-intensity agro-pastoralism but recent years have experienced a socioecological shift to intensive agriculture. This is marked by permanent mechanized cash crop cultivation by immigrant farmers since the last 5–10 years, and illegal land encroachments by local farmers during the last four years. Infrastructure in the form of road networks, electrical structures and wind turbines has also developed rapidly. Because such large-scale activities likely expose the wide ranging GIB to added mortality risks, I predict a decline in its population over the monitored years. The current management regime of reserve grasslands owned by the State Forest Department is limited to exotic shrub/tree species plantation, development of water bodies, nest incentive schemes etc. whose role in bustard conservation is untested, debatable and likely detrimental (Pande and Pathak 2005). I evaluate the overall efficacy of the current management regime based on the population trend of GIB, where declining populations will indicate the need for alternative and effective management.

3.2 Methods

3.2.1. Population monitoring

3.2.1.1 Survey design

I monitored GIB population at the landscape-scale over three years using two population measures; density and occupancy. I converted the landscape into 4X4 km² grids (n=63): a relevant scale to count this extremely low density and highly mobile species. For unbiased population

estimate, probability based selection of sample sites is preferable over selection based upon prior knowledge of their potential population states. But this choice also depends on the study objective (Mackenzie et al. 2005), logistical considerations and analytical requirements (ample observations). I selected potentially occupied (suitable) grids using existing knowledge of habitat use by GIB (Goriup and Vardhan 1983, Rahmani 1989) and reconnaissance habitat data. From a classified land–cover image (see chapter 4), I generated a GIB–habitat mask that included 1) sparse vegetation, 2) grassland, 3) savannah/open scrub, and 4) low–intensity seasonal agriculture land–cover types. I removed non–habitat grids ($n=13$) to reduce monitoring cost and retained 50 sites as the population of prime interest at a risk of subsequent sampling (fig 3.1b).

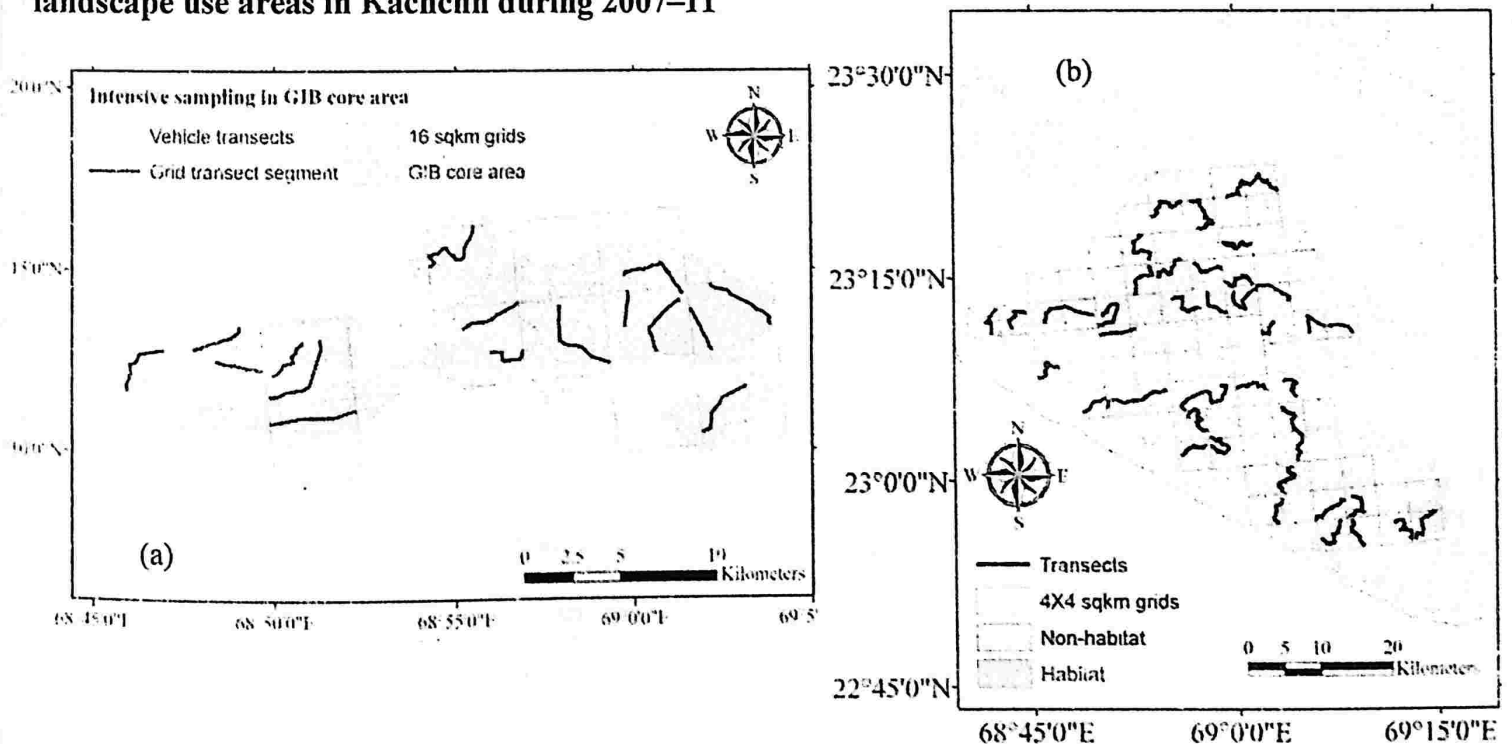
The use of distance and occupancy sampling to obtain precise measures requires ample observations, which is difficult for a rare but widely distributed species like GIB. Hence I opted for relatively long transect surveys (widely used for open-habitat birds, see Sutherland 2006) from vehicles that yield large effort in less time (Ogutu et al. 2006) but are susceptible to violation of assumptions (Buckland et al. 2004). Hence, in laying vehicle transects, I avoided metal roads and used bare ground and dirt trails (used by livestock and human) as distance sampling assumes that transects must be random with respect to the species. Habitat models and behavioural observations (details in chapters 4 and 5) suggested avoidance of metal roads but random use of dirt trails by GIB (also see Rahmani 1989). I realized sampling–grids on ground by a handheld GARMIN 72 GPS unit, and surveyed each grid along one $5.5_{\text{Mean}} \pm 0.7_{\text{SD}}$ km vehicle transect in GIB–habitat over seven primary sampling periods: winter and summer 2007–08; winter and summer 2008–09; and summer, monsoon and winter 2010–11 (fig 3.1b).

Within a primary sampling period, occupancy estimation requires spatial or temporal replication at a site, i.e., secondary surveys (MacKenzie et al. 2006). Temporally separate visits to the same transect is costly and can bias estimates if the occupancy status of a site changes, i.e., species moves between sites within the primary period. Since my chief objective was to obtain snapshot ‘occupancies’ over time (Mackenzie and Royle 2005), I conducted repeated surveys within one visit by considering two $2.5_{\text{Mean}} \pm 0.3_{\text{SD}}$ km segments of one transect separated by a ~ 0.5 km gap as two secondary surveys and quickly surveyed the entire landscape within 10–15 days in each primary period. Such clustered spatial sampling is commonly used in large–scale occupancy studies but can induce spatial dependence between replicates, thus being another source of bias, which needs to be examined (Hines et al. 2010).

Two observers (the author and field assistant) surveyed all transects at a slow speed of 5–10 km hr⁻¹ to count GIB from 07:00 to 11:00 hrs and 17:00 to 19:30 hrs when the birds were most active and easy to detect (Rahmani 1989). Corresponding to GIB detection, I recorded the flock size, composition and perpendicular distance from the transect–line. I estimated distances to observations by ocular assessment aided by a Bushnell laser range finder. Since GIB were frequently detected at large distances >100m and were small targets to hit with a laser range finder, I used the range finder to assess distance of larger objects close to the observation, and then corrected the perpendicular distance by ocular assessment. Along each transect I would also record signage (feather and fecal matter) opportunistically and by time–constrained foot–search in the best possible habitat.

The GIB spatially aggregate in traditional areas for considerable part of the year, especially to accomplish important life–history functions like breeding. Hence, status of the core has much relevance to their conservation. To examine the seasonality and annual trend of core usage, I intensively monitored GIB density across seasons (winter, summer and monsoon, see section 2.3) and years (2007–08, 2008–09 and 2010–11) in the core area. I laid 15 uniformly spaced 4.8_{Mean}±0.6_{SD} km long vehicle transects that were surveyed 2–3 times each season during three sampling years following the same protocol as described above (fig 3.1b).

Figure 3.1 Great Indian Bustard surveys along vehicle transects (black lines) in the (a) core and (b) landscape use areas in Kachchh during 2007–11



3.2.1.2 Estimation of population parameters

3.2.1.2.1 Density and relative abundance

I estimated GIB density by line transect distance sampling (LTDS, Buckland et al. 2001, Burnham et al. 1980) in the Multiple Covariate Distance Sampling (MCDS) Engine of program *DISTANCE* v 5.2 (<http://www.ruwpa.st-and.ac.uk/distance/>). This technique uses key functions and adjustment terms (if necessary) to describe the declining detections as a function of perpendicular distance from the transect line. I fitted half-normal and hazard rate key functions with adjustment terms (cosine and hermite or simple polynomial) to the data. The mathematical form of the half-normal key function is: $k(y) = \exp(-y^2/(2\sigma^2))$ and the hazard-rate key function is: $k(y) = 1 - \exp(-y/(\sigma)^{-b})$; where 'y' is the perpendicular distance and 'σ' is the scale parameter. Recent advancement in distance sampling allows modeling of detection with covariates (in addition to distance), if heterogeneity is suspected among subsets of the data (Thomas et al. 2010). Here the scale parameter is modelled with covariates, as: $\sigma(z) = \exp(\beta_0 + \sum \beta_i z_i)$. I hypothesized that 1) males being more conspicuous would be easily detectable than females; 2) detectability would be higher in the latter two years from experience gain by observers; and 3) detectability would vary between seasons as vegetation growth in monsoon can obstruct visibility. To test these, I constructed possible detection models with alternative combinations of covariates (or factors) such as flock composition (male or female as mixed flocks occur very rarely), season, and year in addition to perpendicular distance.

I considered pooling data across the core and landscape logical since habitat, observers and survey timings were same, in order to increase the number of observations for robust and precise estimation. I truncated observations beyond 800m (2% observations) as there was sign of peaking at greater distance. I sensibly reclassified the distance categories to reduce rounding-bias of field observations and to obtain reliable model fit. From the candidate set of models, I selected the model with minimum AIC_c (Akaike Information Criterion corrected for sample size, see Akaike 1974) and high goodness-of-fit χ^2 -statistic as the best model. It estimated detection probability (\hat{p}) and density (\hat{D}) of GIB in the core for winter, summer, and monsoon of 2007–08, 2008–09 and 2010–11, and the landscape for 2007–08, 2008–09 and 2010–11, by suitable post-stratifications. I computed the annual exponential population change rate by fitting a linear regression on log-transformed GIB density/abundance against three years. I compared this estimate with a similarly estimated long-term global population change rate from crude surveys over last 40 years.

I described the within-core heterogeneity in usage by segregating transects into 16 km² grids and estimating grid-specific GIB densities overall and seasonally. I also described the within-landscape heterogeneity in usage by estimating the ratio of GIB density in core to buffer across seasons. I compared the monthly core-usage in Kachchh with other localities, such as Jaisalmer and Ajmer (Rajasthan), Karera (Madhya Pradesh), Nanaj (Maharashtra) and Rollapadu (Andhra Pradesh) to infer global patterns of seasonal congregations versus non-breeding usage. These localities were/are GIB core areas that were surveyed daily for 1–4 years and total counts of GIB were recorded (see Kapoor and Bhatia 1983, Rahmani 1989, Rathore 1983). I reanalyzed these data sets to estimate a scaled relative abundance of GIB as $\frac{\text{average count in a month } (x_i)}{\text{maximum } x_i \text{ of a year}}$ for each locality, to surrogate its monthly usage-intensity.

3.2.1.2.2 Occupancy

Density of a species and the proportion of sites it occupies in a region tend to be linked (Holt et al. 2002) leading to a recent shift from counting animals to counting occupied sites for cost-effective large-scale monitoring of particularly rare species (following Mackenzie et al. 2002, Mackenzie et al. 2005, Royle et al. 2007). To monitor GIB population status in the landscape, I used multiple season site-occupancy as an alternate measure to density (MacKenzie et al. 2006). I generated the detection/nondetection (1/0) matrix across 7 (primary sampling period) X 2 (secondary surveys) occasions in 49 grids from only sighting information as signs can persist beyond the vacancy of a site violating the closure assumption. Multiple season occupancy technique uses likelihood methods on the detection history to estimate 1) the proportion of sites occupied by the species during a primary sampling period t (ψ_t); after correcting for 2) the probability of detecting it if present (p_t); along with transition parameters such as 3) the probability that a site unoccupied at t is occupied at $t+1$ (colonization, denoted as γ); and 4) the probability that a site occupied at t is unoccupied at $t+1$ (local extinction, denoted as ϵ , see MacKenzie et al. 2003). I maintained the same transects, observers, and timings across surveys to reduce heterogeneity in detection probability. The latter would presumably vary with changes in abundance but the detection history was too sparse in the latter years to robustly estimate period-specific detection probability. Therefore I estimated annual site-occupancies (my primary objective) but constant detection and extinction probabilities in program *PRESENCE v 2.0*

(<http://www.mbr-pwrc.usgs.gov/software/presence/>). I also examined if there was spatial dependence between transect segments following Hines *et al.* (2010). For this, I estimated single season occupancy and detection probability parameters separately for each of the seven primary periods, using 1) a non-spatial model $\psi(.)p(.)$; and 2) a spatial model $\psi(.)\theta(.)\theta'(.)p(.)$, where θ, θ' represent the spatial dependence between transect segments. I compared the AIC values and parameter estimates between paired non-spatial and spatial models to test if occupancy in a transect segment was higher given occupancy in the preceding segment.

To quantify the core vs. buffer usage across seasons, I generated a detection/nondetection matrix from both sighting and signage information. Here the closure assumption could be relaxed without invalidating the analysis (if the occupancy status of sites changed at random), except that 'occupancy' would now be interpreted as 'use' (Mackenzie and Royle 2005). It is important to understand that the proportion of area 'used' by a species is larger than the proportion of area where the species physically occurs at a point of time – its occupancy (Mackenzie and Royle 2005). But my interest for the current question laid only in understanding the seasonal differences in usage or ranging. Hence I split the data into four subsets by winter and summer (2 seasons X 3 primary period per season X 2 secondary surveys per period) in core (11 sites) and buffer (38 sites) areas, and estimated their proportion of sites used using single season occupancy models (Mackenzie et al. 2002).

3.2.2 Flock size and sex ratio

Count data obtained from these systematic surveys also yielded flock-size and sex-ratio estimates of GIB (Kachchh) population. Conventional methods (Rahmani 1989) of estimating flock size strictly followed the *outsider's view* measuring mean group size. But Jarman (1974) recognized that average individuals come from groups larger than the average group size and popularized the *insiders' view* which measures the typical group size or mean crowding (group size in which an individual lives). Following recommendations of Reiczigel et al. (2008), I estimated the mean and 95% accelerated bootstrap confidence intervals of group size and crowding from male, female and mixed GIB flocks across summer, monsoon and winter in program *FLOCKER v 1.1*. Estimation of ASR from count data is generally confounded with sources of errors from the influences of sexual difference in migration time and sexual dimorphism (Mayr 1939). Since in GIB, males are bigger than females and more conspicuous during their

breeding display (mid–summer to late–monsoon), conventional methods (Rahmani 1989) are likely to positively bias the male proportion in a population. I estimated the detection (sex–specific) corrected ASR of this presumably resident population over a large time period (3 years) to reduce errors from temporary (sexually different) local movements. I further segregated ASR into core vs. buffer areas across summer, monsoon and winter, to infer sexual differences in seasonal space use.

3.2.3 Power analysis

The goal of long–term monitoring is to detect actual population trend from the confounding effects of biological processes and sampling errors. According to crude estimates, GIB population likely declined by $\sim 3\% \text{ yr}^{-1}$ during the last 40 years, showing even higher declining rates in recent years (Dutta et al. 2011). Conservation managers should be able to detect such trend in cost–effective ways, and timely intervene to achieve $0\text{--}5\% \text{ yr}^{-1}$ increase to prevent extinction and restore these endangered populations. Thus my objective was to assess how much sampling efforts were required to achieve 70% statistical power of detecting net changes of -20% , -10% , -5% , 0% , 5% and 10% size effects between subsequent surveys (following the aforementioned sampling designs) separated by one or two years, at type I error of $\alpha = 0.1$, 0.2 or 0.3 probability. Choice of a higher than usual type I error was reasonable as rejecting a true null hypothesis of no change was of lesser consequence than falsely rejecting population change from the perspective of conservation management of endangered bustards (see Jhala et al. 2011).

I conducted regression routines through Monte Carlo simulations in program *MONITOR v11.0.2* (<http://www.esf.edu/efb/gibbs/monitor/>) to evaluate the monitoring efficacy of density and occupancy estimates. It performed the following steps: 1) constructed -20% to $+10\%$ exponential trends starting from the initial mean and variance estimates obtained from my surveys and projected it to the next survey occasions; 2) generated sample measures as random values from a log–normal distribution with projected mean and variance at each survey time; 3) determined the significance of the regression slope of sample abundances against survey occasions; and 4) reiterated these simulations 1000 times to estimate power as the proportion of iterations where significant difference was observed between the two survey occasions (Barlow et al. 2008). Since annual population status was derived from seasonal measures and birds exhibited wide seasonal movements, I considered the landscape as a single sample unit and tested the hypothesis that the

difference in overall population measure between successive survey occasions (the regression slope) was different from zero. The other options I opted for in the software were pooled variance, constant coefficient of variance to mean relationship, and two-tailed test as it was necessary to evaluate positive responses of management intervention as well.

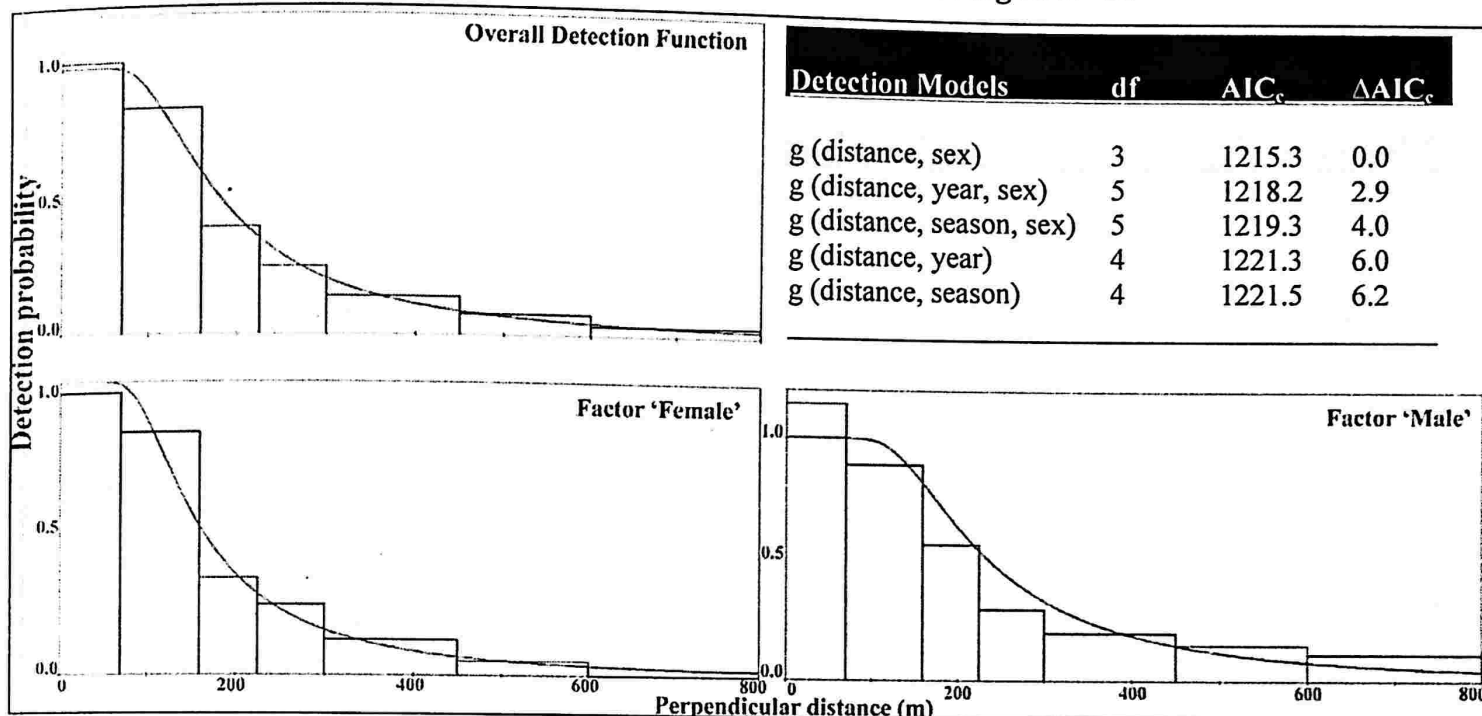
This way, I obtained the statistical powers of different monitoring designs (varying in terms of sampling intensity, scale and measurement) to detect various population trends and their implementation costs. From these variables, I generated surface graphs in program *SLIDEWRITER v6.0* (<http://www.slidewrite.com>) to optimize monitoring decision. The trend-power-cost surface would inform managers about the minimum fund allocations required to detect a certain magnitude of population change with reasonable confidence.

3.3. Results

3.3.1. Density in landscape

I conducted 1428 km search efforts along 234 visits spread over 49 transects and seven sampling sessions in the landscape (fig 3.3) and 1348 km search efforts along 286 visits spread over 15 transects in nine sampling sessions in the core (fig 3.4). This yielded 98 GIB observations which I classified into seven perpendicular distance classes with cut-offs at 0, 70, 160, 225, 300, 450, 600 and 800 m. Hazard rate simple polynomial model with sex as an interaction-factor $g(x*sex)$ best explained the detection data (ΔAIC_c of other models ≥ 3 ; fig 3.2), also obtaining reliable model-fit ($\chi^2=0.55$, $DF=3$, $P=0.91$). Predictably, females tended to have lower detectability than males ($\beta=-0.38_{\text{Mean}\pm 0.25_{\text{SE}}}$; fig 3.2). Detectability barely varied between years ($\beta_{2007-08}=0.12_{\text{Mean}\pm 0.30_{\text{SE}}}$, $\beta_{2008-09}=0.27_{\text{Mean}\pm 0.31_{\text{SE}}}$; reference year 2010-11) and seasons ($\beta_{\text{summer}}=0.21_{\text{Mean}\pm 0.29_{\text{SE}}}$, $\beta_{\text{monsoon}}=0.22_{\text{Mean}\pm 0.34_{\text{SE}}}$; reference season winter). The model $g(x*sex)$ estimated global detection probability at $0.29_{\text{Mean}\pm 0.03_{\text{SE}}}$ and effective-strip width at $233.3_{\text{Mean}\pm 20.8_{\text{SE}}}$ m. Density in landscape declined from $0.092_{\text{Mean}\pm 0.052_{\text{SE}}}$ km^{-2} in 2007-08 to $0.053_{\text{Mean}\pm 0.033_{\text{SE}}}$ km^{-2} in 2008-09 and $0.048_{\text{Mean}\pm 0.025_{\text{SE}}}$ km^{-2} in 2010-11 (fig 3.3). The annual exponential population decline rate in Kachchh was estimated at $-0.33_{\text{Mean}\pm 0.13_{\text{SE}}}$, about tenfold higher than the long-term country-wide population decline rate ($-0.03_{\text{Mean}\pm 0.01_{\text{SE}}}$).

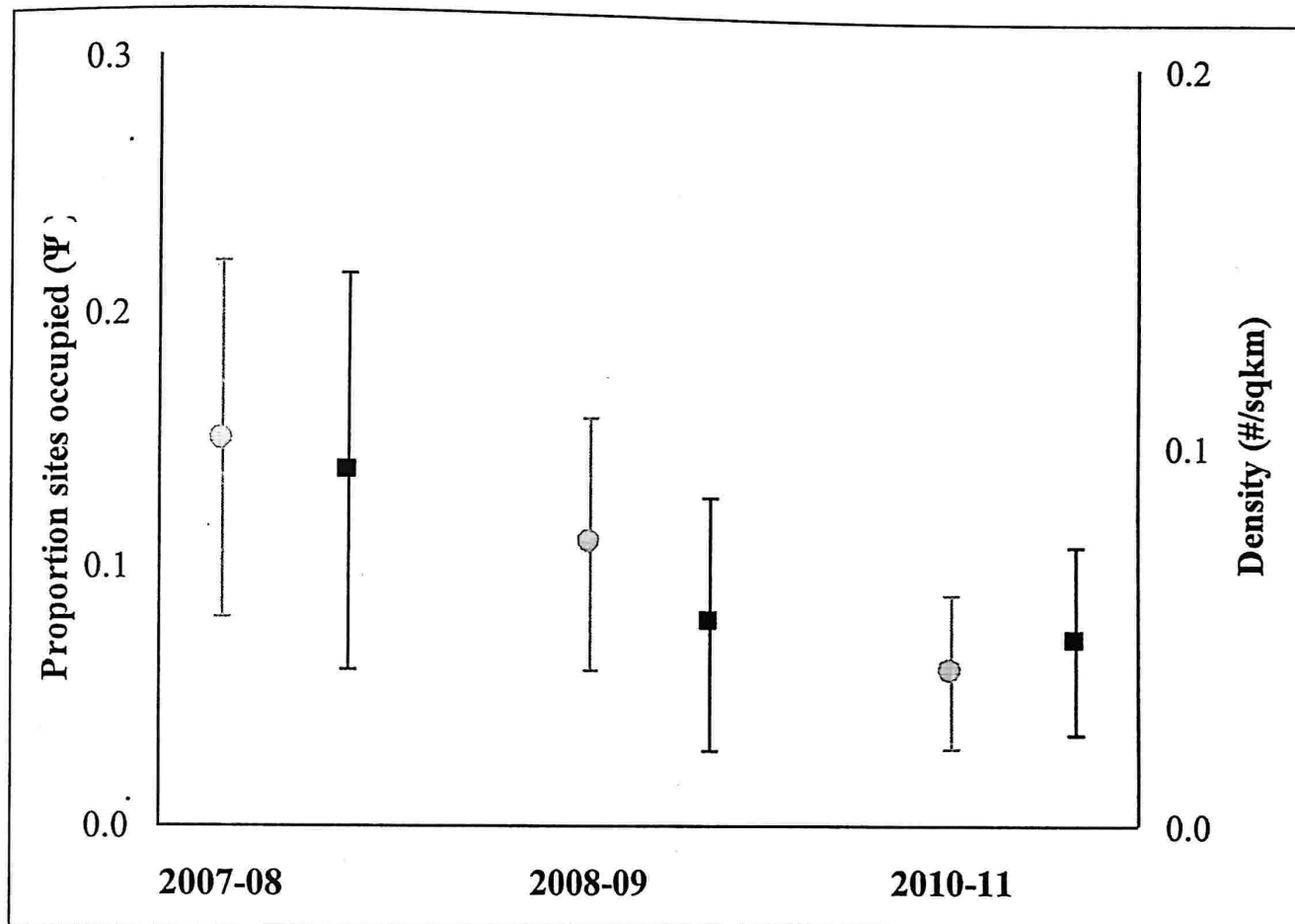
Figure 3.2 Detection functions for the Great Indian Bustard estimated through Multiple Covariate Distance Sampling based on vehicle line transects in Kachchh during 2007–11



3.3.2 Occupancy in landscape

Occupancy surveys in the landscape consisted of 336 visits along $2.5_{\text{Mean}} \pm 0.3_{\text{SD}}$ km transect segments spread over 49 sites and seven sampling periods with 1–14 visits per site in three years. Single season occupancy models estimating parameters for spatial dependence (θ, θ') between transect segments $\psi(\cdot)\theta(\cdot)\theta'(\cdot)p(\cdot)$ obtained less support than the parsimonious models $\psi(\cdot)p(\cdot)$ for all seven primary periods ($\Delta\text{AIC} \geq 4$) and yielded very similar occupancy estimates. Thus the survey design was likely to produce unbiased multiple season occupancy estimates. The probability of detecting GIB at a site given presence of a least one individual was estimated at $0.42_{\text{Mean}} \pm 0.14_{\text{SE}}$, considerably < 1 . About $0.19_{\text{Mean}} \pm 0.16_{\text{SE}}$ proportion of sites faced local extinction between subsequent sampling periods and the probability of colonizing a new site did not offset this rate. Thus, the detection-corrected proportions of sites occupied in the landscape declined from $0.15_{\text{Mean}} \pm 0.07_{\text{SE}}$ in 2007–08 to $0.11_{\text{Mean}} \pm 0.05_{\text{SE}}$ in 2008–09 and $0.06_{\text{Mean}} \pm 0.03_{\text{SE}}$ in 2010–11 (fig 3.3).

Figure 3.3 Great Indian Bustard population trend across sampling years, measured as density \pm SE (closed squares and black whiskers) and occupancy \pm SE (closed circles and grey whiskers) in the landscape of Kachchh during 2007–11



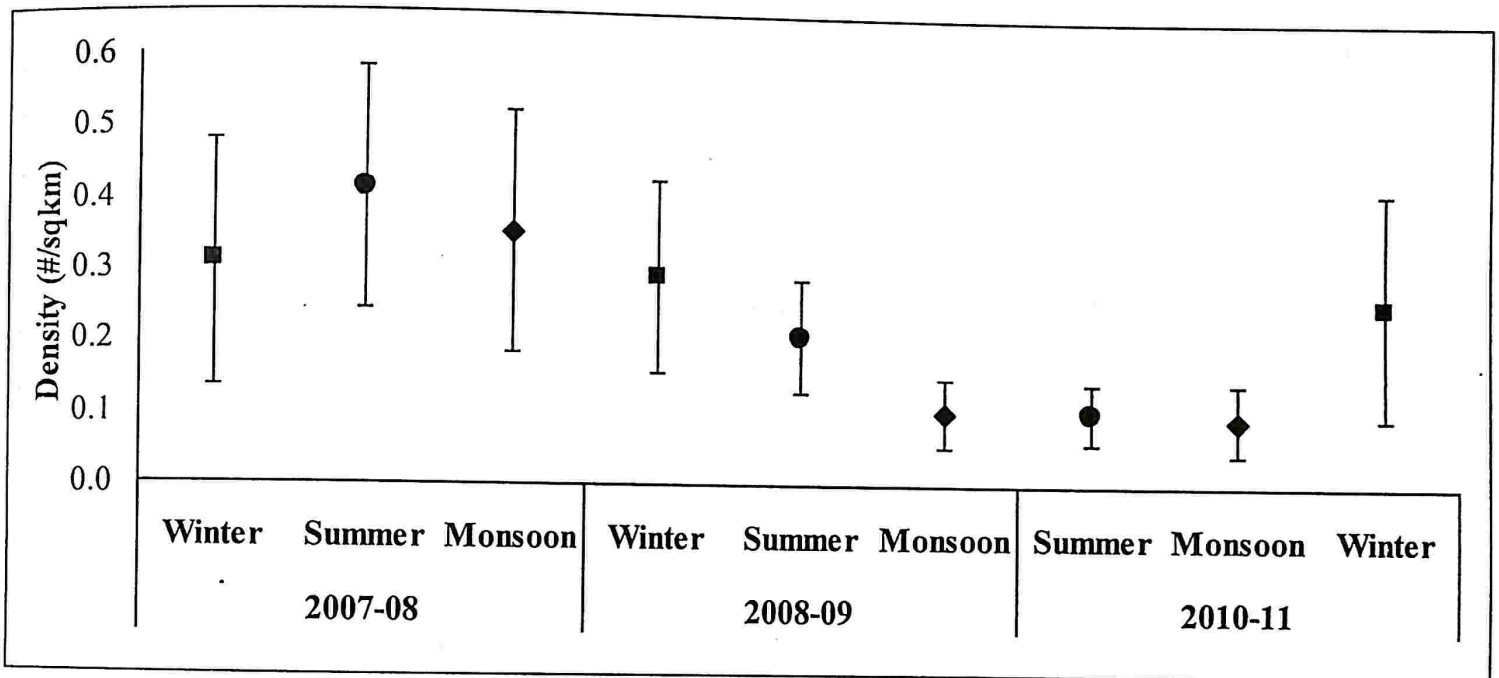
Year	Detections	Trail Efforts			Encounter		D (# km ⁻²)	SE (D)	Ψ	SE (Ψ)
		visits	(km)	100 km ⁻¹						
2007-08	11	29	315	3.49		0.092	0.052	0.15	0.07	
2008-09	8	84	465	1.72		0.053	0.033	0.11	0.05	
2010-11	7	121	648	1.08		0.048	0.025	0.06	0.03	

3.3.3 Temporal usage of core vs. buffer

In the core area, I detected 27, 25 and 21 GIB flocks from 313 km, 548 km and 497 km transect-efforts during 2007–08, 2008–09 and 2010–11 respectively (fig 3.4). Post-stratifying detection probability [estimated by model $g(x*sex)$] and flock size by years, density in the core declined (significant at $\alpha=0.20$) from $0.31_{\text{Mean}} \pm 0.09_{\text{SE}}$ km⁻² to $0.14_{\text{Mean}} \pm 0.04_{\text{SE}}$ km⁻² and $0.12_{\text{Mean}} \pm 0.04_{\text{SE}}$ in successive years (fig 3.4). I detected 36, 19 and 18 GIB flocks from 552 km, 368 km and 442 km transect-efforts in the core during summer, monsoon and winter respectively. Post-stratifying detection probability and flock size by seasons, I found that the declining density in core was primarily due to reduced usage during the breeding season, i.e., summer

($0.33_{\text{Mean} \pm 0.13_{\text{SE}}} > 0.16_{\text{Mean} \pm 0.06_{\text{SE}}} > 0.08_{\text{Mean} \pm 0.03_{\text{SE}}} \text{ km}^{-2}$) and monsoon ($0.27_{\text{Mean} \pm 0.13_{\text{SE}}} > 0.08_{\text{Mean} \pm 0.03_{\text{SE}}} \approx 0.07_{\text{Mean} \pm 0.04_{\text{SE}}} \text{ km}^{-2}$) while usage tended to be constant during winter ($0.28_{\text{Mean} \pm 0.15_{\text{SE}}} \approx 0.27_{\text{Mean} \pm 0.12_{\text{SE}}} \approx 0.24_{\text{Mean} \pm 0.15_{\text{SE}}} \text{ km}^{-2}$) in successive years (fig 3.4).

Figure 3.4 Great Indian Bustard density (mean \pm 1SE) trend across successive summer (March–June, shown as closed circles), monsoon (July–October, shown as closed rhombus), and winter (November–February, shown as closed squares) of 2007–08, 2008–09 and 2010–11 in the core usage of Kachchh



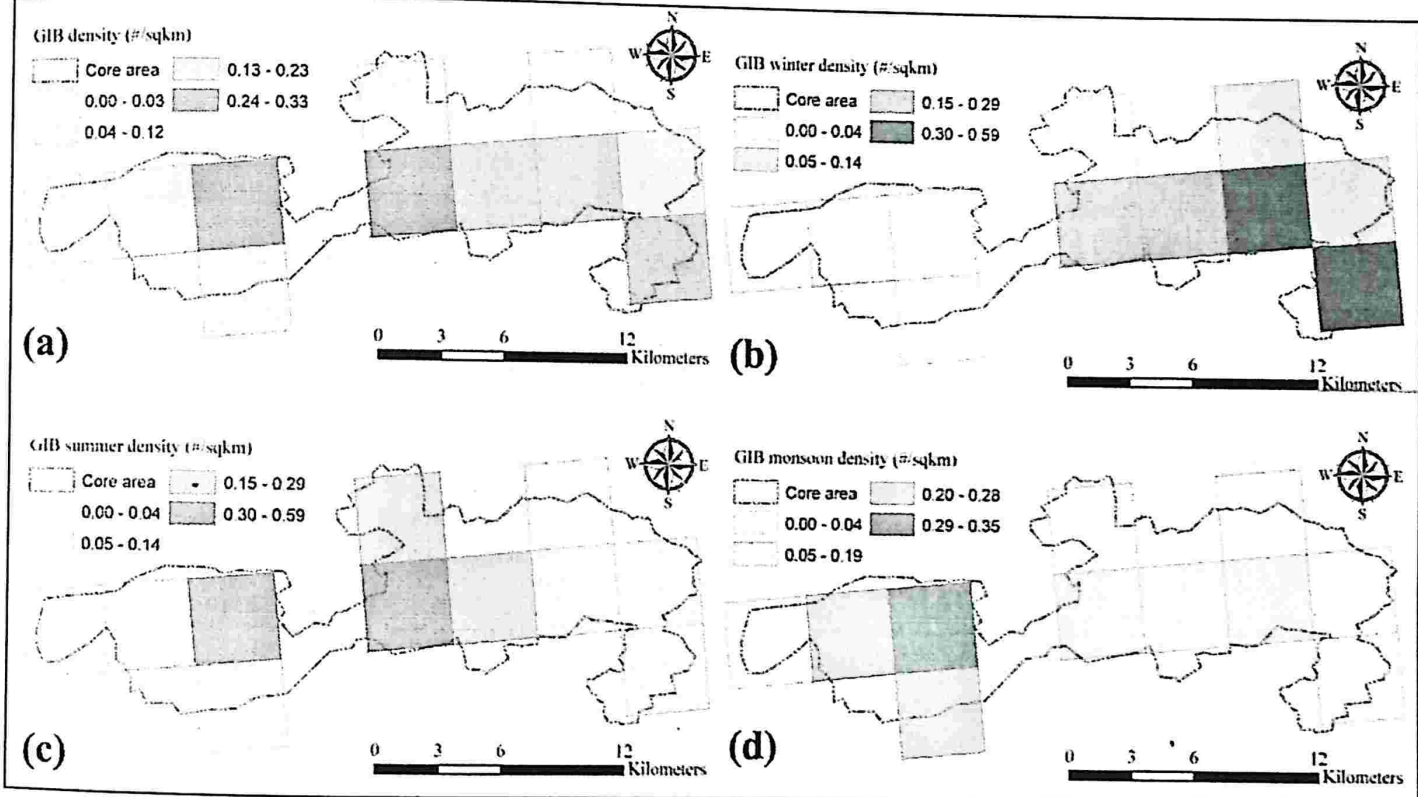
	2007-08			2008-09			2010-11		
	Winter	Summer	Monsoon	Winter	Summer	Monsoon	Summer	Monsoon	Winter
Detections	4	13	9	8	13	5	10	5	6
Transects	21	26	20	42	45	28	46	30	29
Efforts (km)	94	119	95	199	214	131	219	142	140
$\hat{D}_{\text{Flock}} (\#\text{km}^{-2})$	0.095	0.244	0.211	0.090	0.135	0.085	0.096	0.102	0.078
SE (\hat{D}_{Flock})	0.047	0.092	0.097	0.036	0.047	0.037	0.055	0.043	0.039
$\hat{D} (\#\text{km}^{-2})$	0.308	0.412	0.35	0.291	0.208	0.10	0.102	0.09	0.256
SE (\hat{D})	0.172	0.169	0.168	0.136	0.081	0.048	0.043	0.049	0.161

The core was found to hold 11.5_{Mean} (range 5.7–14.8 in 3 years) times higher GIB density than the buffer. Reconnaissance in monsoon 2007–08 and landscape survey in monsoon 2010–11 did not detect any GIB in the buffer but there was some usage of it during summer and winter. Pooling all three years, I detected 0.49 GIB 100 km^{-1} in winter and 1.46 GIB 100 km^{-1} in summer in the buffer as opposed to 12.46 GIB 100 km^{-1} and 6.53 GIB 100 km^{-1} in the core respectively. The species detection probability based upon sighting and signage estimated by the smallest AIC models were $0.29_{\text{Mean} \pm 0.08_{\text{SE}}}$ in summer and $0.23_{\text{Mean} \pm 0.07_{\text{SE}}}$ in winter. Detection-corrected

proportions of sites used by GIB in the core vs. buffer were estimated at $0.94_{\text{Mean}} \pm 0.27_{\text{SE}}$: $0.11_{\text{Mean}} \pm 0.06_{\text{SE}}$ during summer (9 folds difference) and $1.00_{\text{Mean}} \pm 0.00_{\text{SE}}$: $0.17_{\text{Mean}} \pm 0.09_{\text{SE}}$ (6 folds difference) during winter.

A similar pattern of seasonal usage was observed within the core each year, where usage shifted from the eastern savannah-dominated patch in winter to central agro-grass patch in summer and eastern grassland-dominated patch in monsoon (fig 3.5).

Figure 3.5 Spatial pattern of Great Indian Bustard densities (# km⁻²) at 16 km² grids in the core area of Kachchh, (a) pooled over all seasons, and segregated into (b) winter, (c) summer and (d) monsoon 2007–11; darker shades indicating higher densities



3.3.4 Auxiliary demographic parameters

Based upon 98 observations of GIB flocks in three years, I estimated the overall mean group size at 1.8 (1.5–2.1_{95%CI}) and mean crowding at 2.7 (2.2–3.3_{95%CI}) birds. Crowding was low (significant at $\alpha=0.05$) in the breeding season (1.9_{Mean} , 1.5–2.2_{95%CI} in female; 1.6_{Mean} , 1.2–2.1_{95%CI} in male) than the non-breeding (winter) season (3.7_{Mean} , 2.2–5.1_{95%CI} in female; 2.3–4.1_{95%CI} in male). Mixed flocks were rare (4% of all detections) and only observed in the non-breeding season of latter two years. Mixed flocks showed greater (significant at $\alpha=0.05$) crowding (5.3_{Mean} , 3.4–5.8_{95%CI}) than the overall average crowding (table 3.1). I estimated the long-term (3 years) average

population ASR at $0.33_{\text{Mean} \pm 0.20_{\text{SE}}}$ male/female. In contrast, long-term ASR in the core area was $0.62_{\text{Mean} \pm 0.25_{\text{SE}}}$, varying from $0.50_{\text{Mean} \pm 0.24_{\text{SE}}}$ in summer to $0.72_{\text{Mean} \pm 0.43_{\text{SE}}}$ in winter (fig 3.6).

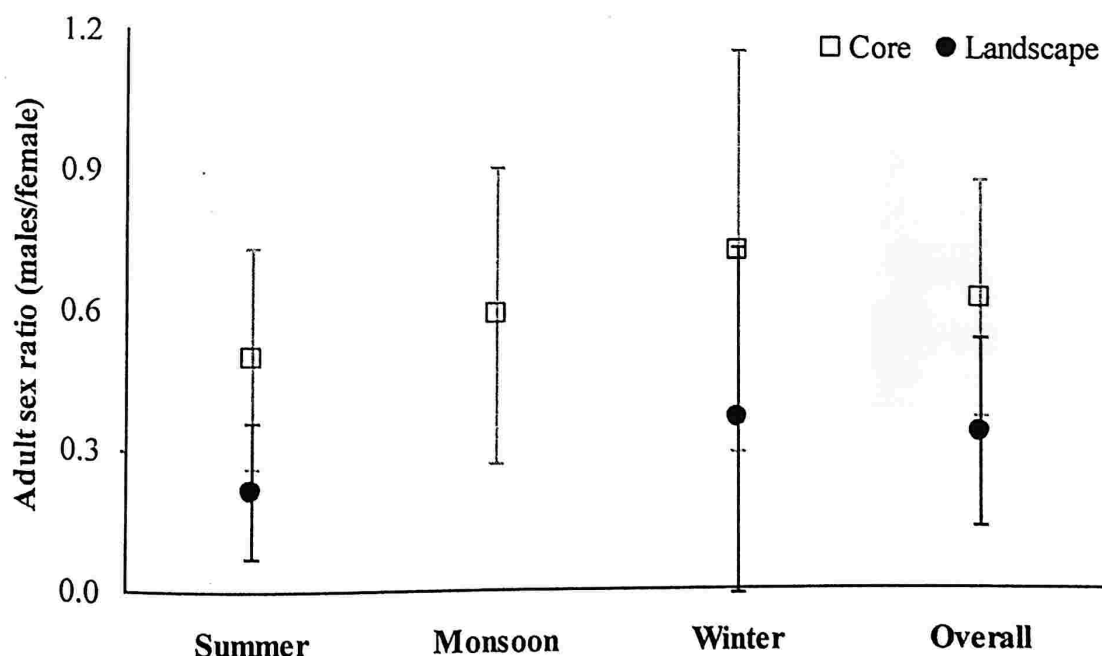
Table 3.1 Mean and 95% CI of flock size and crowding of the Great Indian Bustard (a) across gender and season (summer, monsoon and winter) in Kachchh during 2007–11, (b) across gender and season (breeding and non-breeding) in other landscapes (reanalyzed from Rahmani 1989), and (c) annually in these landscapes

(a) Parameter	Season	Female flock	Male flock	Mixed flock
Mean Flock size (no. of flocks)	Summer	1.40 (35)	1.38 (16)	—
	Monsoon	1.55 (11)	1.20 (10)	—
	Winter	2.31 (13)	2.60 (10)	4.75 (4)
Mean Crowding (95%BCa CI)	Summer	1.86 (1.43–2.39)	1.73 (1.22–2.29)	—
	Monsoon	1.82 (1.43–2.36)	1.33 (1.00–1.57)	—
	Winter	3.73 (2.22–5.08)	3.08 (2.33–4.09)	5.32 (3.36–5.78)

(b) Site	Female flock size		Male flock size	
	Breeding	Non-breeding	Breeding	Non-breeding
Karera	2.21 (1.39–3.03)	4.96 (3.29–6.63)	1.80 (1.41–2.19)	3.08 (2.61–3.55)
Kachchh	1.90 (1.50–2.20)	3.70 (2.20–5.10)	1.60 (1.20–2.10)	3.10 (2.30–4.10)
Nanaj	3.02 (1.77–4.27)	2.13 (1.50–2.76)	1.27 (1.03–1.51)	1.35 (0.92–1.78)
Rollapadu	1.86 (1.51–2.21)	2.92 (1.67–4.17)	2.29 (1.86–2.72)	5.09 (1.99–8.19)

(c) Site	# Flock detections	Mean (95%BCa CI) flock size	Mean (95%BCa CI) crowding	Approx. site abundance
Karera	2012	1.96 (1.89–2.02)	3.17 (3.02–3.35)	28 (1981–87)
Kachchh	98	1.80 (1.50–2.10)	2.73 (2.20–3.30)	23 (2007–11)
Nanaj	1274	1.65 (1.58–1.72)	2.67 (2.48–2.89)	22 (1981–87)
Rollapadu	1105	1.87 (1.77–1.99)	4.03 (3.57–4.57)	45 (1981–87)

Figure 3.6 Mean \pm SE adult sex ratio of the Great Indian Bustard in the landscape (closed circle) and core usage area (open square) of Kachchh during 2007–11



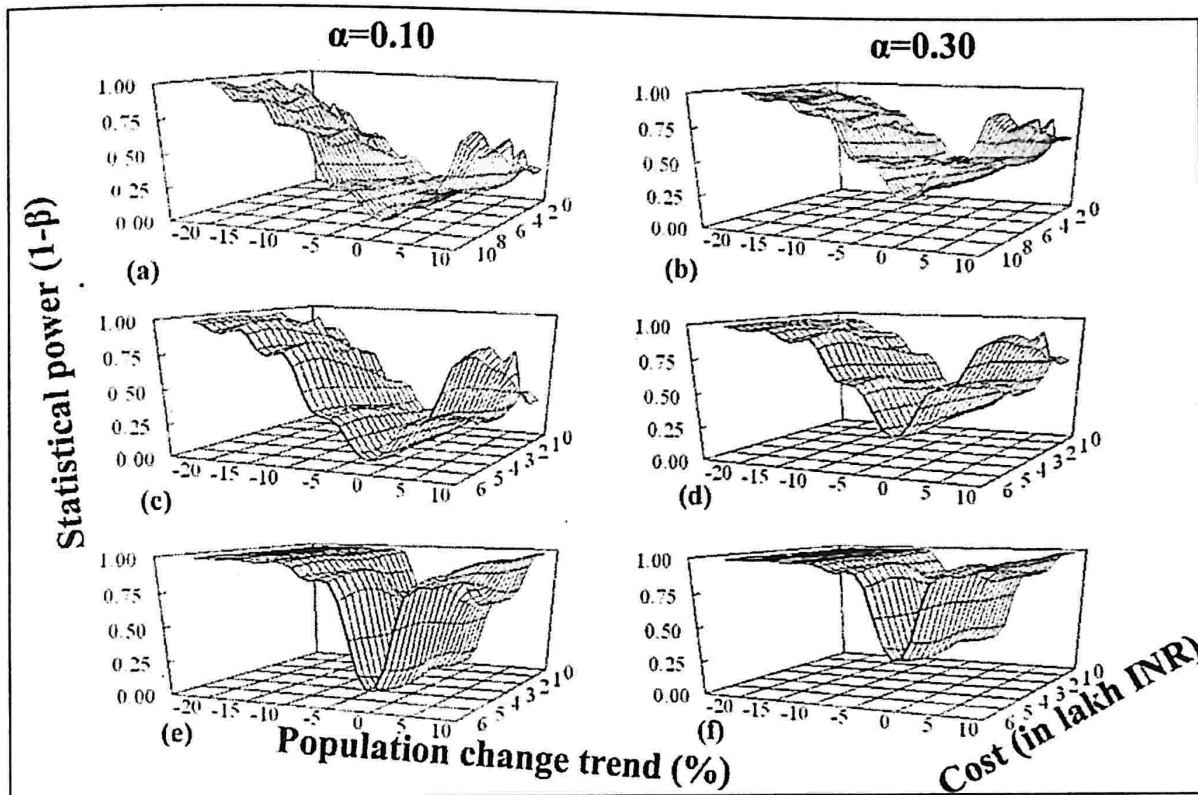
3.3.5 Power analysis

Using LTDS to effectively survey 25% of the landscape twice a year (summer and winter) could detect 21% net change in GIB density between subsequent occasions (2 years) with a statistical power of 0.8 (table 3.2, fig 3.7). The power reduced to 0.5 when I reduced survey efforts to once in a year (summer). However, occupancy sampling once in a year could detect 21% net change in GIB occupancy with a power of 0.75, and this population measure was 2.5 folds less costly than density estimate obtained from the first design (design I in table 3.2, fig 3.7). Using LTDS to effectively survey 40% of the core area thrice each season (summer, monsoon and winter) had a power of 1.0 to detect 21% net change in GIB density between subsequent occasions. When limited to three surveys only in summer, it could still detect this trend with a power of 0.75 (table 3.2, fig 3.7). Effective monitoring of GIB could possibly be carried out in the most economic way by conducting occupancy sampling at the landscape and LTDS in the core (integrating designs 5 & 8 in table 3.2, fig 3.7) during the summer of every alternate year.

Table 3.2 Statistical power and logistic costs of line density and occupancy surveys at landscape and core areas to detect net population changes of -20%, -10% & 10% in 2 years under varying sampling intensities (number & repeats of transects) for monitoring Great Indian Bustard in Kachchh (2007-11)

Design	Measure	Scale	Sampling efforts		% area sampled	Power to detect net trend (2 yrs)			Survey Cost (INR)
			Transects	Repeats		-20%	-10%	10%	
1	Density	Landscape	45 (~5.5km)	2 (S&W)	25	0.99	0.77	0.77	72000
2			45 (~5.5km)	1 (S)	25	0.89	0.50	0.53	36000
3			30 (~5.5km)	1 (S)	17	0.86	0.47	0.48	24000
4	Occupancy	Landscape	45 (2X2.5km)	2 (S&W)	25	1.00	0.91	0.90	58500
5			45 (2X2.5km)	1 (S)	25	1.00	0.92	0.93	29250
6			30 (2X2.5km)	1 (S)	17	0.91	0.55	0.53	19500
7	Density	Core	15 (~5km)	3 (S,M&W)	41	1.00	0.96	0.96	22500
8			15 (~5km)	1 (S)	41	0.99	0.75	0.75	7500
9			10 (~5km)	1 (S)	28	0.98	0.67	0.66	5000

Figure 3.7. Surface graphs of statistical power for detecting population changes (Y-axis) under varying levels of Type I error (0.1 & 0.3), population change rate (X-axis), and logistic costs (Z-axis) involved in estimating density at (a–b) landscape and (e–f) core and (c–d) occupancy at landscape for the Great Indian Bustard in Kachchh (2007–11)



3.4. Discussion

The GIB was historically exploited by uncontrolled hunting and egg collection (documented from 1500 onwards). These direct threats compounded with its extreme k -selected nature possibly endangered its persistence by the first half of the 20th century (Goriup and Vardhan 1983), whilst in the second half new indirect threats confronted the impoverished populations (Rahmani 1989). Although some conservation efforts were installed, they were fraught with shortcomings in the light of species' ecological requirements (Dutta et al. 2011). Due to paucity of reliable ecological knowledge in current conservation contexts, management practices mostly relied on intuitive and anecdotal inputs. Appraisal of management through objective assessment of population status was overlooked. More recently, the Bustard Task Force recognized developing a monitoring protocol as an important prerequisite for effective conservation of the species (Anon 2011, Gibbs et al. 1998). Therefore, this chapter deals with a priority conservation issue: rigorous monitoring of crucial population parameters in cost-effective ways to inform conservation management of extant GIB populations.

3.4.1 Population trend monitoring

Rarity and high mobility of GIB impede their reliable population measurements. In conventional bustard surveys, several teams of observers' conduct coordinated vehicle surveys in known areas to count individuals, assuming perfect detectability of birds. This technique has been successfully implemented to monitor several bustard populations in Europe and Africa (Alonso and Alonso 1992, Gray et al. 2009, Martin et al. 1996). But its implementation has the following disadvantages in the context of GIB: 1) wide landscapes occupied by birds demand huge efforts to be surveyed in this manner; 2) to avoid this, observers restrict themselves to the historically chosen areas (Goriup and Vardhan 1983, Rahmani 1989), sometimes failing to tease apart actual population trends from the artifacts of temporary (seasonal, drought-induced etc.) shifts in distribution; and 3) crude count statistics that are obtained may be unreliable for spatio-temporal comparisons only if detectability varies concurrently. Hence I adopted sampling approaches at two scales: the known range (landscape) and high-usage area (core) of GIB in Kachchh. Ground surveys supported the *a-priori* delineation of GIB landscape (based upon literature, secondary information and reconnaissance) as extensive searches in adjoining areas of Lakhpat, Nakhatrana, Bhuj and Mandvi tehsils did not record any more individuals. I used fixed vehicle-transects in potential habitat to estimate detection-corrected occupancy and density at both scales over years.

Occupancy and density of GIB consistently declined from 2007–08 to 2010–11 (fig 3.3). This decline was sharper between the first two years coinciding with massive agricultural encroachment particularly in the core area by local and immigrant farmers. Extrapolating abundance [\hat{N}] from density [\hat{D}] and the potential habitat area [A] (as $\hat{N} = \hat{D} \cdot A$), I estimated the current (2010–11) population size at about 19 individuals. Pandey et al (2008) estimated 35–48 GIB in this landscape in 2007, also reporting an increasing population trend since 1999 (29 individuals). My assessment indicates that the population has substantially declined since 2007. The current management regime is therefore insufficient in conserving the GIB and needs to be rectified. The Forest Department staff, conservation organizations (GEER and KERK) and I jointly recorded 15 nests during 2006–2010, and 6 chicks and 2 adult bird mortalities during 2008–10. These numbers should be considered as the minimum counts and not estimates of recruitment and mortality measures owing to imperfect detection.

LTDS densities allowed robust intensive population monitoring, but its large-scale (countrywide) use is logistically daunting. Density and proportion of sample units occupied in a

region are often correlated (Holt et al. 2002), and this study observed similar inferences from density and occupancy measures across years (fig 3.3). Hence cost-effective large-scale monitoring is possible by rapid occupancy surveys at several sample units within the species' range (following Mackenzie et al. 2002, Royle et al. 2007). With the aid of power analysis, I propose the following protocol for viable monitoring of all the extant GIB populations in alternate years: (1) occupancy sampling along three ~2 km spatial segments of a ~6 km vehicle-transect covering at least 25% of potential area in the landscape once in summer; and (2) LTDS along ~5 km vehicle-transects effectively covering at least 45% of the core area thrice in summer. Its implementation (inclusive of logistical expenditure and observer salary) in Kachchh will currently cost about 40,000 Indian Rupees. Such a monitoring strategy will enable objective assessment (detecting 20% changes in population with 80% power) of GIB population status, based on which well-informed management interventions have to be regulated (intensified or relaxed). For example, breeding use but not wintering use of the core area in Kachchh is decreasing over years. Therefore, informed habitat manipulations that accommodate breeding preferences (details in chapter 4) should be the immediate conservation objective.

3.4.2 Demography

3.4.2.1 Adult sex ratio

I estimated the ASR of GIB (Kachchh) population at about 3 females per male. Given the polygynous mating system and sexual size dimorphism (males two-times larger than females), such female-biased ASR was expected (Benito and Gonzales 2007, Mayr 1939). Greater number of females in a population increases recruitment rate. On the other hand, despotic polygyny by very few breeding males can be one of the possible reasons behind the extremely low genetic diversity of GIB (Ishtiaq et al. 2011). My extensive field surveys in Kachchh revealed only two territorial males at a time in the traditional breeding patch during April-September (fig 3.1a). There can be more breeding males which are temporally sharing the two display arenas. In the light of the species' genetic crisis, information on lek composition is crucial to obtain through individual-markings, biotelemetry, or genetic analyses. In the core, there was twice the number of males per female than expected from the population ASR, and even more in winter (fig 3.6). This indicated that males were restricted to the core more than the females, or conversely, females

ranged more widely. Hingrat et al. (2004) found that in the related houbara bustard (*Chlamydotis undulata undulata*), females had 4–5 folds larger and multimodal home ranges than males.

There is evidence of a general correlation between ASR and population trend (Nadal et al. 1996, Wilkinson et al. 2002) or habitat quality (Johnson et al. 2006, Zanette 2001) in wild populations. Although ASR is used as an indicator of population status in the management of mammals (Solberg et al. 2005), reptiles (Smith and Iverson 2006) and fish (Han and Tzeng 2006), their use for managing endangered bird populations is yet to be developed (Donald 2007). Recently, ASR has been used to calibrate the effective population size of GIB from effective female population size obtained by genetic analysis (Ishtiaq et al. 2011). For these reasons, reliable estimation and reporting of this parameter are important for other GIB populations as well.

3.4.2.2 Flock sizes

GIB flock sizes ≥ 30 were frequently reported in the past (Goriup and Vardhan 1983) but are popularly believed to have declined to about 2 in recent years. I reanalyzed the flock size and composition data collected by (Rahmani 1989) at three other localities (Karera in Madhya Pradesh, Nanaj in Maharashtra, and Rollapadu in Andhra Pradesh) between 1981 and 1987 for comparison with the current study. I examined 1) if the current flock size in Kachchh differed from the past estimates; 2) if the seasonal flocking pattern was similar between different localities; and 3) if mean crowding corresponded with ecological abundances (Lloyd 1967).

Crowding depends on the number of animals present in an area, their spatial distribution and interactions (Lloyd 1967). Presumably most of the birds in GIB populations aggregate spatially particularly during the non-breeding season (Rahmani 1989). Hence I expected a positive correlation between these two parameters across populations. Past mean flock sizes were 1.96 (1.89–2.02_{95% CI}) in Karera, 1.65 (1.58–1.72_{95% CI}) in Nanaj and 1.87 (1.77–1.99_{95% CI}) in Rollapadu. The present mean flock size in Kachchh (1.80_{Mean}, 1.5–2.1_{95%CI}) fell within this range (table 3.1b). If there had been a historical reduction in GIB flock size, which is a crucial parameter for this gregarious species, such reduction was probably prior to 1980s. Mean crowding estimated at 2.67 (2.48–2.89_{95%CI}) in Nanaj, 2.73 (2.2–3.3_{95%CI}) in Kachchh, 3.17 (3.02–3.35_{95%CI}) in Karera and 4.03 (3.57–4.57_{95%CI}) in Rollapadu (table 3.1c) was correlated ($r=0.99$, $p<0.001$) with the contemporary population sizes of about 22, 23, 28 and 45 birds respectively (mid-values of the estimated range, see Rahmani 1989). Most GIB populations showed similar pattern, where

crowding was more during the non-breeding season than the breeding season. The non-resident population at Nanaj was the only exception, probably because most of the birds left this area in non-breeding season, reducing chances of crowding (table 3.1b).

3.4.3 Spatio-temporal usage patterns

Conservation practitioners frequently identify the highly used areas by a threatened species so that management interventions can be focused on a smaller subset of the landscape to achieve maximum benefit. Despite local movements, GIB remains in its traditionally chosen areas particularly during the breeding season, and sometimes for the entire year (Prakash 1983). For a widely but patchily distributed species like GIB, it is furthermore crucial to understand the spatio-temporal usage of landscape, as it is impossible to protect and control human use over several thousand square-kilometers. But minimum effort has been put in the past to identify the high usage areas outside the traditional breeding patch and compare their intensity of usage with the remaining landscape, to weigh this decision. In Kachchh, GIB is currently restricted to ~1000 km² agro-pastoral landscape mostly in Abdasa tehsil, wherein a ~17 km² traditional breeding (lekking and nesting) patch (*Naliya Daun*) has been proposed as Bustard-PA alongside the existing 2 km² Lala Bustard Sanctuary whose usage has declined due to its isolation. Adjoining ~150 km² agro-grass-scrub mix between 23.21°N, 68.78°E and 23.23°N, 69.05°E (*Vengaber, Kalatalao, Surodhro, Kanauthia, Virachia* and *Gadwara Daun* from west to east) form a contiguous potential but unprotected GIB-habitat, which I identified (and termed) as the probable core area from secondary information and reconnaissance (fig 3.1a). Subsequently, I quantified 1) the intensity of use of the core compared to the buffer, 2) seasonal changes in within-core usage, and compared 3) the monthly core usage pattern with past field observations at other localities.

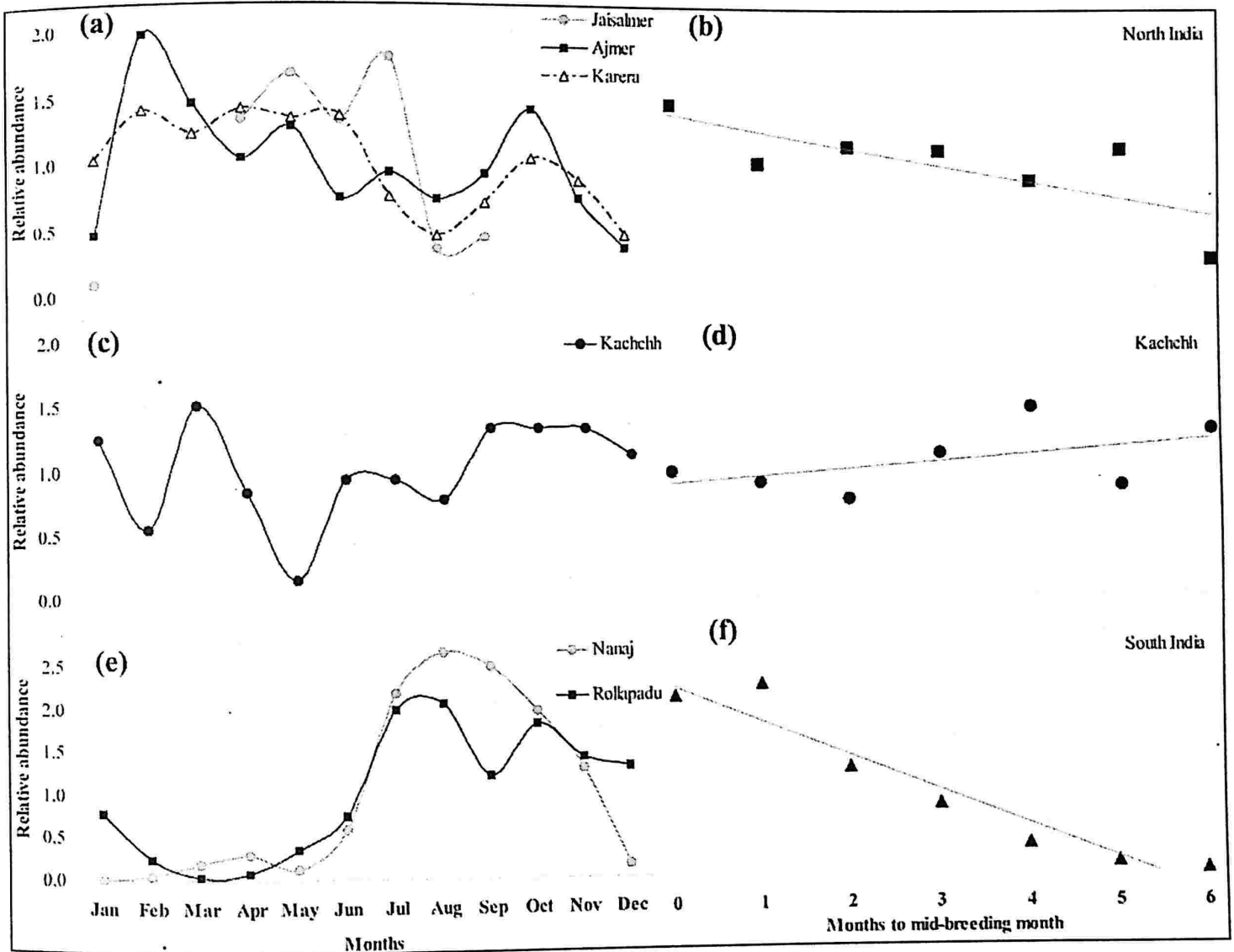
The ratio of core to buffer usage measured as density was $4.5_{\text{Mean}} \pm 0.8_{\text{SE}}$ in summer and $25.4_{\text{Mean}} \pm 6.8_{\text{SE}}$ in winter. When measured as proportion of sites used, the ratio was $8.6_{\text{Mean}} \pm 5.3_{\text{SE}}$ in summer and $5.9_{\text{Mean}} \pm 3.1_{\text{SE}}$ in winter. The discrepancy between the two usage measures can be explained by the more ephemeral nature of sightings than signage, and differences in vagrancy between seasons. It may be possible that GIB, although intensively uses the core area in winter, frequently moves to and back from the buffer areas, thus resulting in clumped sightings in a small area but signage distribution over a larger area. Over the years, I observed a similar seasonal shift in use-intensities within the core (fig 3.5). During winter (November–February), GIB intensively

used the eastern agro-grass-scrub areas (fig 3.5b), probably to benefit from the seasonally available fruit and agricultural food resources. During summer (March–June), intensive use shifted to the center, in the agro-grass and grassland areas (fig 3.5c). During monsoon (July–October), usage shifted westwards to the grassland areas (fig 3.5d). This is the peak breeding season when nesting females prefer undisturbed grasslands, where availability of insects, the primary constituent of GIB diet (see section 5.3.4.1), also increases sharply after rainfall.

Comparing monthly core usage patterns between sites, I found the north Indian populations (Jaisalmer, Ajmer and Karera) differed like a ‘mirror-image’ from the south Indian populations (Nanaj and Rollapadu). This is primarily because of the differences in breeding timing (April–August in north India and August–October in south India) which depends on the vagaries of SW and NE monsoon. In north Indian sites, GIB congregation decreased very gradually from the mid-breeding month (assumed to be the peak), indicating a prolonged breeding period and/or some form of non-breeding usage of these areas (fig 3.8a,b). In south Indian sites, the congregation decreased sharply from the peak breeding month, indicating shorter (sometimes bimodal) breeding period and immediate post-breeding vacancy of the sites (fig 3.8e,f). Experts have speculated long-distance seasonal movements between the desert and Deccan populations (Rahmani 1989). In the absence of biotelemetry, it is impossible to conclude whether monthly differences in core-usage are an artifact of long-distance inter-population movement, or short-distance movement to adjoining areas. However, the described pattern perhaps indicates that populations in south move longer distances or have separate breeding and non-breeding areas than in north. The monthly core usage pattern in Kachchh was intermediate between the north and south populations (fig 3.8c,d). GIB populations in Kachchh breed between mid-March and mid-September. Each year in mid-March, usage sharply increased in the core coinciding with the first lek-formation congregation which continued till late-April. In May, core usage sharply decreased, coinciding with the lean resource period when birds frequently used the buffer. During June–September, core usage increased, coinciding with the second lek-formation congregation (fig 3.8c). Unlike the north and south populations, core usage did not decline from the mid-breeding to the non-breeding months (fig 3.8d). Although female density remained more or less constant in this landscape across seasons, male density increased from the breeding season to winter i.e., November–February (have to put a table here). This may indicate possible seasonal movements of males in and out of the Kachchh population (see section 3.4.3).

average count in a month

Figure 3.8 Scaled relative abundance maximum monthly average of Great Indian Bustard in core areas across months (a, c, e) and months to the mid-breeding month (b, d, f) in three North Indian sites (a,b) – Jaisalmer (Rajasthan), Ajmer (Rajasthan) & Karera (Madhya Pradesh) during 1982–89 (Rahmani 1989, Bhatia and Kapoor 1982, Rathore 1982), two South Indian sites (e,f) – Nanaj (Maharashtra) & Rollapadu (Andhra Pradesh) during 1984–88 (Rahmani 1989), and Kachchh, Gujarat (c,d) during 2007–11 showing different seasonal patterns of congregation



3.4.4 Conservation implications

Habitat heterogeneity in the immediate neighbourhood of the traditional breeding area in Kachchh meets considerable part of GIB's annual ecological requirements leading to its continued year-round usage. Securing this area is necessary, although not sufficient, for the long-term persistence of the population. Apart from the sanctuaries, most of this area belongs to revenue and community lands that have faced severe increase of anthropogenic pressure in last 3 years. This includes ~20% illegal grass-scrub conversion into intensive cultivation and parallel infrastructural development (electricity and road network). An immediate conservation measure would be to

acquire these lands under the State Forest Department's ownership so that direct management becomes possible. Managers should thereafter enforce active protection to the species, minimize infrastructural development, and scientifically manage habitats, herein. Efficacy of management should be regularly assessed following the prescribed population monitoring protocol. Additionally, biotelemetry on some individuals should be conducted for comprehensive understanding of landscape use patterns. This information will go a long way in formulating landscape conservation planning, judiciously investing conservation funding, and refining monitoring methods.

Chapter 4. Habitat relationships: influence of scale, season, and activity

4.1 Introduction

Habitat of an animal is the space where it lives (*sensu lato*, see Morrison et al. 2006) or the distinct set of environment that it uses for life–history needs (*sensu stricto*, see Block and Brennan 1993). The choice of space is a hierarchical process of behavioural and physiological responses to environmental characteristics (Horne et al. 2008, Vanak and Gompper 2010) and is shaped by ecological and evolutionary mechanisms (Cody 1985). This process, semantically *habitat selection* (Jason 2001), results in a pattern of animal distribution termed as *habitat use* (Jason 2001). Due to their obvious significance in autecology (Pianka 2008), describing where animals live and understanding factors influencing that, are critical components of wildlife research. One of the most important of these factors is the distribution of required/selected resources (Bergerud 1974, Horne et al. 2008). Putative factors determining animal's space use are climatic conditions (physiological tolerance), structural characteristics (for shelter, escape etc.) and food; however, conspecifics, competition and predation can also be influential. The hierarchical connotation of habitat selection has laid considerable importance on *scale* in its conceptual development (Morrison et al. 2006). For example, Svardson (1949) has recognized selection as a two–stage process, in which organisms use general features of the landscape to select broadly from different environments and then respond to finer habitat characteristics to choose where to live (Morrison et al. 2006). And Johnson (1980) extends this concept into a formal framework of four selection orders ranging from the macro–scale descriptions of the species' geographical range (first–order) to procurement of resources from micro–sites (fourth–order). Subsequently, resource selection has been assessed at multi–scales for robust inference in empirical studies (Levin 1992).

Habitat choice is explored by functions that either model the population state (presence, index of use or density) with the putative factors, or compare *used* (occupied by the focal species) versus *unused* (unoccupied) or *available* (independent of occupancy status) resource units (Norris 2004). Such statistical functions, which are proportional to the probability of use of a resource unit, are termed as *resource selection function* (or RSF, see Manly et al. 2002 for a complete review of habitat selection designs and analyses). From a conservation perspective, adequate quantities of selected resources are necessary to sustain animal populations, which necessitate rigorous RSF estimation (Manly et al. 2002). This information can be used by wildlife managers to

identify the proximate determinants (and their scales) of habitat choice (Lantz et al. 2007) that can be managed at relevant scales to recover endangered wildlife (Norris 2004, but see Railsback et al. 2003). Application of habitat choice models is particularly valuable to guide conservation management of threatened but sparsely understood species. Several such examples exist in tropical grasslands of the developing world, which are rich in biodiversity, data deficient, and highly endangered (Gray et al. 2009, Rodriguez et al. 2007, Vanak and Gompper 2010).

One such is the GIB, a critically endangered (IUCN 2011) bird (family *Otididae*, order *Gruiformes*) endemic to semiarid grasslands of Indian subcontinent. The global population of about 300 individuals is further fragmented into 8 local populations in the states of Rajasthan (shared with Pakistan), Maharashtra, Andhra Pradesh, Gujarat, Karnataka, and Madhya Pradesh in India (Dutta et al. 2011). Past studies have recognized that GIB, like most other white-plumage bustards (Johnsgard 1991), uses open habitats with 30–70cm tall grassland (but avoids grass >1m tall) interspersed with scrub and arable patches (Ali and Ripley 1969, del Hoyo et al. 1996, Rahmani 1989). It requires five subtly different habitat types: open well drained area with moderate grass for nesting; open elevated ground for display; varied grass–scrub–crop patches for foraging; bare ground for roosting, and shaded site for resting (Rahmani 1989). However, thorough understanding of their habitat selection at local scales is missing.

Habitats selected by wildlife are often altered by human landuses influencing their populations in positive or negative ways depending on the focal taxa (Osborne et al. 2001). For example, the great bustard *Otis tarda* and little bustard *Tetrax tetrax* have benefited from anthropogenic creation of steppe like habitats but both species have suffered from intensification of farming and increased disturbance levels (Silva et al. 2004, Simon et al. 2001, Wolff et al. 2001) much like the Bengal florican *Houbaropsis bengalensis* (Gray et al. 2007). Similarly, human induced habitat loss is a supposed predominant driver of GIB decline (BirdLife International 2001, Dharmakumarsinhji 1978, Dutta et al. 2011, Rahmani 1989). Human population explosion (250 million to >1 billion in last 150 years) and rapid economic growth ($\geq 5\%$ /year predicted over the next 30 years, Wilson and Purushothaman 2003) in India have cascaded unplanned agro–infrastructural developments in previously vast undisturbed GIB habitats, altering, reducing and fragmenting them (Singh et al. 2006, Vanak and Gompper 2010).

The GIB was once widespread in Gujarat, occurring in 8 districts till 1950, but got locally extinct from 5 districts by 1980–2000 (Ali et al. 1985), and currently persists only in Kachchh

(Dutta et al. 2011, Pandey et al. 2008). The current distribution overlaps with multiple dynamic landuse system on mixed ownership lands. They include: 1) Reserved grasslands owned by the State Forest Department, which are mostly subjected to ill-informed habitat management (exotic shrub/tree plantation, development of water bodies, nest incentive schemes etc.) whose effects on bustard conservation are detrimental (Pande and Pathak 2005). 2) Revenue Department lands including village pastures which are traditionally grazed by community-livestock, but have been illegally encroached and developed by local people during last 5 years. 3) Private lands which have faced agricultural desertion in drought years and dry farming in wet years in the past (also see Gray et al. 2007), but are subjected to intensive cropping since the last 5–10 years. Alongside, infrastructure has developed rapidly in terms of road, electricity, wind turbines, and lately industries. Without valid knowledge on selected resources, resource distribution, and response to disturbances; landuse changes disrupting species' needs cannot be confronted. In light of these conservation contexts, habitat models are imperative for effective management of GIB landscapes.

This study investigated birds' habitat selection at two scales: 1) macro-scale, comparable to the birds' transient home range, and equivalent to (but not exactly) a second order selection; and 2) micro-scale, where the decision whether to use or not for life-history needs was possibly taken, and equivalent to a third order selection. I investigated the influence of biological seasons on former; and classified the latter based on daily (foraging, resting and roosting) and breeding (nesting and display) activities to increase the resolution of understanding resource choice. Based on *a-priori* ecological understanding, I hypothesized that second-order-equivalent selection depended on 1) proximity to the traditional breeding patch, 2) grassland area, 3) resources, 4) disturbances, and their combinations and seasonal differences (table 4.1). I tested these hypotheses and quantified habitat relationships by modeling relative abundance of birds with covariates representing the above factors, at 16 km² grids across the landscape using regression technique (Aghainajafi-Zadeh et al. 2010, Mac Nally 2000, Norris 2004). I hypothesized that third-order selection depended on 1) low intensity agro-grass systems, food resources and disturbance for foraging; 2) visibility and disturbances for roosting; 3) concealment and disturbances for resting; 4) concealment vs. visibility, food resources and disturbances for nesting; and 5) visibility and disturbance for display (table 4.1). I tested these hypotheses and estimated RSFs through logistic regression and discrete choice analyses on samples of used and available/unused resource units in the core GIB area (Manly et al. 2002).

Table 4.1 *A-priori* hypotheses and predictions on habitat relationships of the Great Indian Bustard

Scale	Habitat Feature	Hypothesis	Predictions
Macro Scale (16–km ² grids)	Land–cover	Choice of open habitats as an evolutionarily correlated process ¹	Sizeable grassland patches in a site favours summer use, while agro–grass systems in neighbourhood favours winter–use
	Terrain–variability	Avoidance of terrain–variability for surveillance and movement abilities ²	Flat terrain favours site–use for display in summer, but may not influence winter–use
	Isolation from lek	Strong breeding site–fidelity ³	Proximity to lek increases site–use in summer, but not in winter when birds range vagrantly
	Vegetation structure	Trade–off between concealment, resources & visibility: structurally complex vegetation can accommodate various life–history needs ^{3,4*}	Site–use depends on quantity (height & cover) of <1m tall vegetation (+) and their correlated effect on food resources (+), i.e., herbaceous productivity in both seasons
	Food resources		
	Vegetation assemblage		
	Anthropogenic disturbances	Birds avoid disturbances more during breeding as an adaptive response to historical hunting and mortality risks in human–modified environment ⁵	Human pressure, modern infrastructure & human presence reduce site–use in summer, but influence winter–use to lesser extent
Micro Scale (3.14–ha plots)	Land–use	Evolutionary choice of open natural habitats but opportunistic benefits from extensive habitat alterations *	Birds select grassland over scrub & agriculture for all activities, particularly nesting, but selects extensive agro–grass systems for foraging
	Food resources	Site–selection depends on the prevalence of the more patchier of the required food resources ⁶	Fruits (more patchy resources) rather than insects (more uniform resource) favour site–use for foraging, but not for other activities
	Vegetation structure	Differential preferences of concealment, and visibility for different life–history needs and activities ⁴	Sparse vegetation, by enhancing surveillance ability and reducing ambush predation, favours roosting–use. Moderate shady vegetation, by reducing thermal stress, favours resting–use. Short vegetation cover, by enhancing display signaling, favours display–use. Relatively tall herbaceous but no scrubby vegetation, by enhancing concealment but allowing surveillance ability, favours nesting–use. Short–moderate herbaceous vegetation, by enhancing small–prey detectability, favours foraging–use
	Vegetation assemblage		
	Grazing pressure	Grazing optimization concept ⁷ & differential responses of life–history activities to grazing *	Intermediary grazing pressure, by maintaining suitable vegetation structure & making dung–beetles transiently available, favours foraging. Grazing & related disturbances are totally detrimental to nesting–use. Effects on other activities are less obvious
	Human artifacts	Differential responses to disturbance depend on the prolonged, stationary nature of lifehistory activities and coincidence with human activity *	Based on the hypothesized criteria, human artifacts negatively influence nesting > display > resting > roosting > foraging uses.

¹Johnsgard 1991, ²Osborne et al. 2001, ³Rahmani 1989, ⁴Magna et al. 2010, ⁵Dutta et al. 2011, ⁶Stephens and Krebs 1986, ⁷Hilbert et al. 1981, and *personal observations / logical deductions

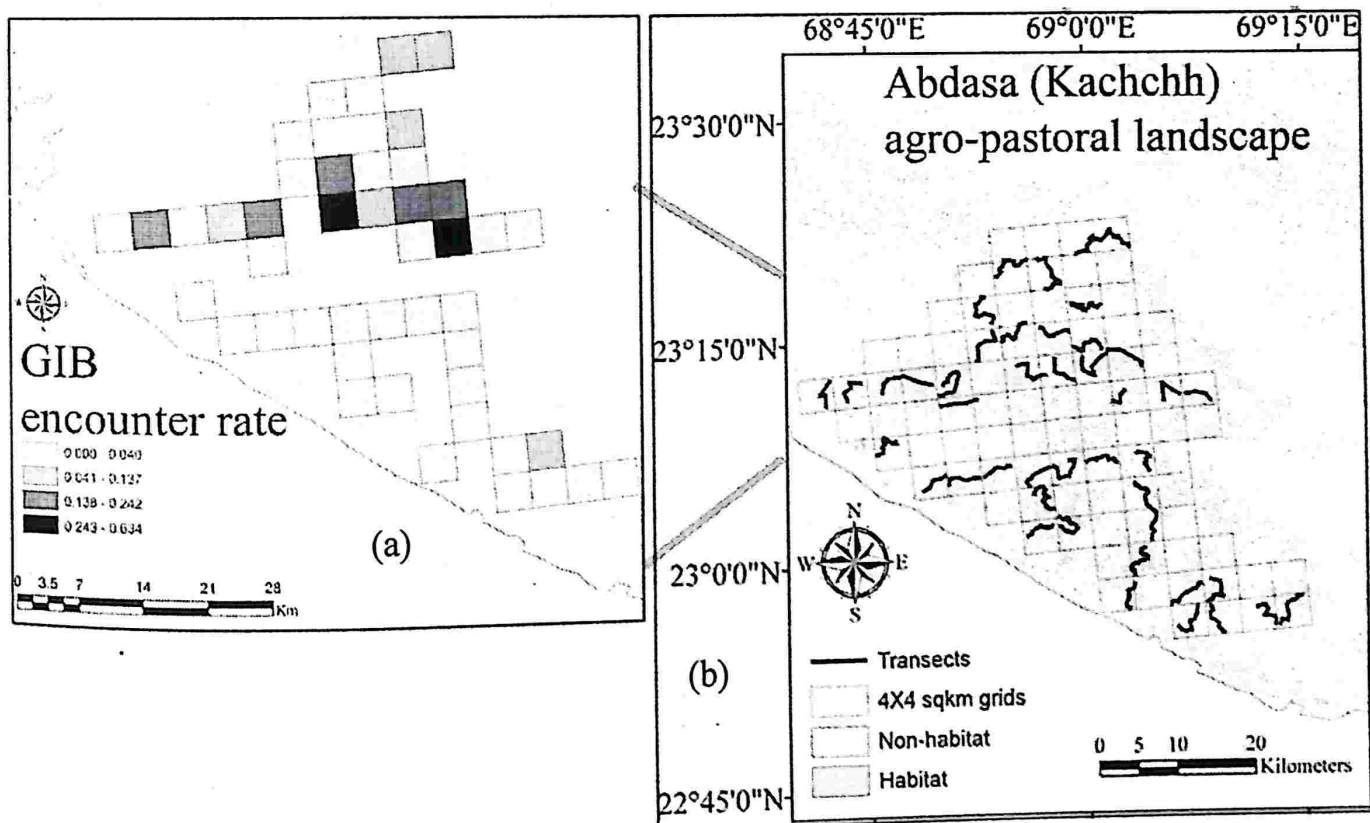
4.2 Methods

4.2.1 Macro-scale use

4.2.1.1 Field surveys

I converted the GIB landscape into $4 \times 4 \text{ km}^2$ grids ($n=63$) realized on ground by a handheld GARMIN 72 GPS unit. I considered this scale as equivalent to the transient homerange area of GIB and relevant for counting this extremely low density and highly mobile bird. A recent study on the Australian bustard *Ardeotis australis*, the closest relative of GIB inhabiting similar habitats, estimated their short-term 95% Kernel homerange at $12.4 \pm 1.2 \text{ km}^2$ from 18 radio-tagged birds monitored during 17–32 days (Ziembicki 2009), further justifying the choice of grid-size. I selected 49 grids for sampling, and in each grid I measured GIB population state along one $5.5_{\text{Mean}} \pm 0.7_{\text{SD}} \text{ km}$ vehicle transects over six surveys: winter and summer of 2007–08, 2008–09 and 2010–11 (fig 4.1): Two observers (the author and field assistant) surveyed all transects at a slow speed of $5\text{--}10 \text{ km hr}^{-1}$ to count GIB from 07:00 to 11:00 hrs and 17:00 to 19:30 hrs when birds were most active and easy to detect (Rahmani 1989).

Figure 4.1 (a) Great Indian Bustard surveys based on vehicle transects and (b) their encounter rates at 16 km^2 grids in the landscape of Kachchh (2007–11)



During each transect survey, I also recorded signage (feather and fecal matter) opportunistically from vehicle and by additional $21_{\text{Mean}} \pm 11_{\text{SD}}$ man-minutes foot search (equivalent to $1.8_{\text{Mean}} \pm 0.9_{\text{SD}}$ man-km) in the best possible habitat. Sparse agro-grass-scrub habitats in Kachchh allowed high detectability of signage. Since GIB flocks varied in sizes and used sites over variable time periods, the same quanta of signage could reflect a single bird residing over long time or several birds residing over short time. To avoid these confounding issues, I considered all sightings and signs in a grid during a survey as occurrence. I derived a relative abundance measure from frequency of occurrences across all surveys ($1_{\text{min}} - 6_{\text{max}}$) scaled by the total effort (lengths of vehicle transect + foot search) in each grid. Indices could reliably represent site-usage intensity provided they were linearly related to actual numbers. I verified this assumption by comparing the large-scale survey based index with intensive line-transect distance sampling based bird density (see chapter 3) in a subset of 11 grids within the core area.

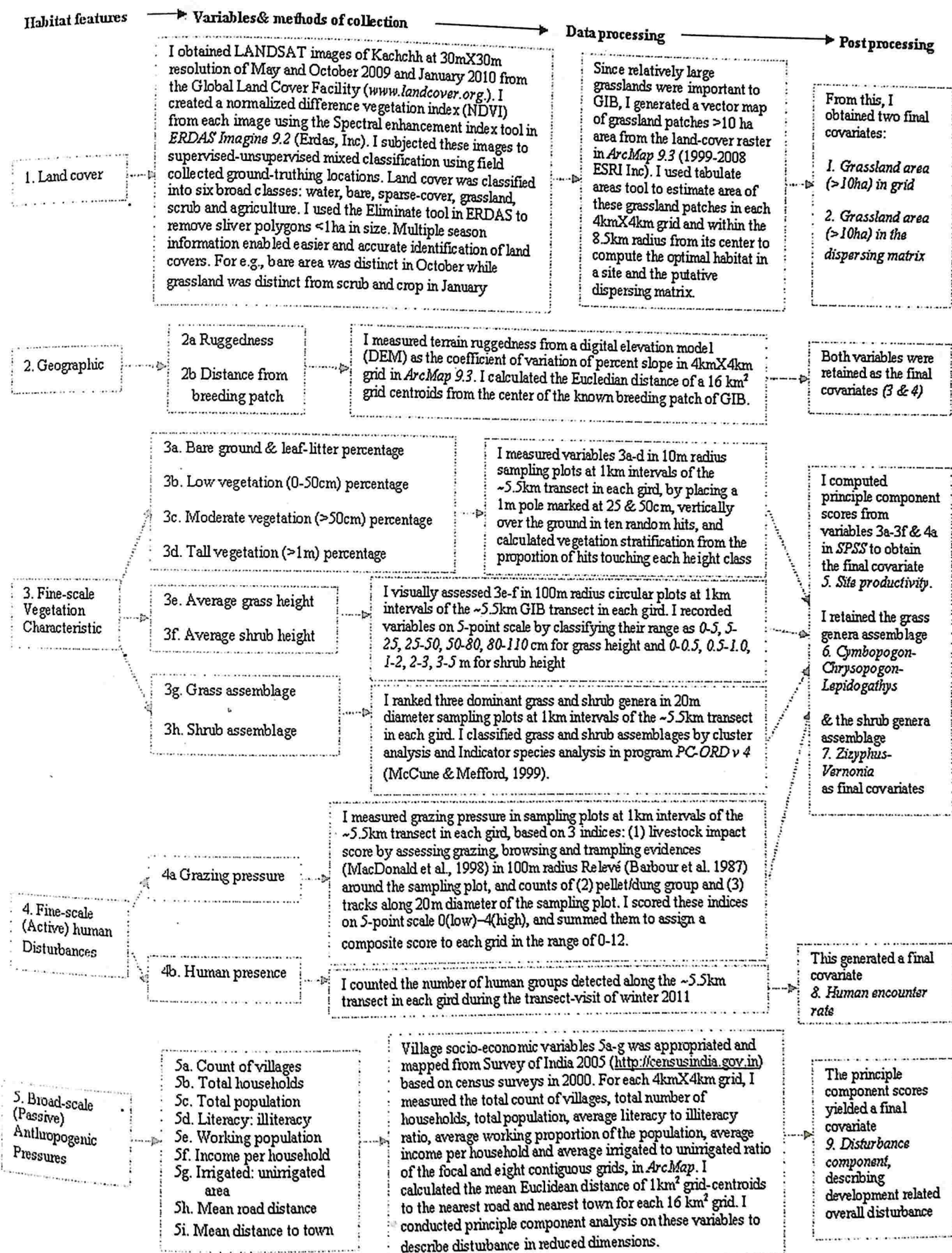
Bustards generally use open landscapes with low disturbance and less visual hindrance (Le Cuziat et al. 2005, Osborne et al. 2001, Silva et al. 2004), while site usage by GIB probably depends on grassland, moderately short vegetation, and type and intensity of anthropogenic disturbances (del Hoyo et al. 1996, Rahmani 1989). Habitat use may vary seasonally: birds vagrantly use wide, sparse grass-scrub landscapes with low intensity agriculture in the non-breeding season (Rahmani 1989) but congregate at traditional areas and avoid human disturbance in the breeding season (Rahmani 1989, Johnsgard 1991). Based on these a-priori knowledge and field observations, I collected and processed ecologically meaningful habitat variables within 16 km^2 grids (table 4.2), where bird usage had also been determined.

4.2.1.2 Modeling habitat use

I formulated alternative hypotheses regarding birds' macro-scale habitat use (table 4.1) and tested these predictions using multiple regression technique (generalized linear gaussian models). The response variable was number of GIB detections in grids from 44 km search-effort, i.e., the average search-effort from six surveys per grid.

Regression techniques assume independence of observations (Legendre 1993) but population states of lekking species at geographic proximity may be more similar to each other than expected by random chance (Osborne et al. 2001).

Table 4.2 Collection and processing of variables in 16-km² grids for macro-scale analysis of Great Indian Bustard habitat use in Abdasa, Kachchh during 2007–2011



Subsequently regression residuals may no longer remain independent and identically distributed, which can bias coefficient estimates. A common way of circumventing this issue is by explicitly modeling the spatial structure along with ecological relationships (see Dormann et al. 2007 for review on these methods). In case of GIB, proximity of grids to lek, calculated as reciprocal of distance (declines sharply and asymptotically as distance increases), was an ideal covariate to surrogate the spatial dependence process during breeding season. I used Moran's I statistic on Euclidian distance and inverse distance spatial relationship in program *ARCMAP v 9.2* to examine for spatial autocorrelation in the response and residual variables. While species distribution is a complex ecological process requiring elaborate collection of inherently correlated habitat variables (predictors), such multicollinearity can complicate interpretation of regression results (Graham 2003). Multicollinearity can be ignored if analysis is solely predictive but not if emphasis is on examining functional relationships or contribution of individual predictors (Graham 2003). Therefore, I estimated Pearson's correlation coefficients among habitat variables (r , see Zar 1999) and subjected correlated variables ($|r| > 0.4$, $p < 0.05$) to the following treatments. When correlation was restricted to an exclusive pair of variables (for e.g., grassland and scrubland), 1) I discarded the less ecologically meaningful one (here scrubland) from further analysis; or 2) conducted residual/sequential regression if exclusion of variable was unwanted. This technique (Graham 2003) teased apart unique versus shared effects of variables by considering one more important than other, thereby attributing the shared effect to the former. For this, I regressed the less important variable on the more important one, and computed its residuals. For e.g., *Zizypus-Vernonia* assemblage was expected to be less important than grassland area (correlated variable); hence prior importance (or shared effect) was attributed to grassland area and residuals of *Zizypus-Vernonia* contained the unexplained information (or unique effect). 3) When a group of variables were cross-correlated, I extracted their principle components separately to represent similar ecological gradients. For e.g., percentage bare ground, short, and tall vegetation, average grass and shrub height, grazing and insect abundance were synthesized into one principle component whose average score in a grid represented site-productivity. All passive disturbance variables were synthesized into another principle component. As an alternative to such piece wise analyses, I also extracted Principle Components jointly from all variables, but the components were difficult to interpret ecologically and hence not preferred for regression modeling.

I subjected these derived covariates to exploratory analyses such as graphs (scatter and box plots) and univariate regressions to settle on the appropriate function (linear or quadratic) prior to formal modeling. Thereafter I built candidate models with additive and interactive combinations of final covariates defined by alternate hypotheses on macro-scale habitat use (table 4.1). I used residual diagnosis to validate model assumptions and coefficient of determination to assess proportion of variance in response explained by model. I used information-theoretic approach to test which hypothesis obtained maximum support from data (Kullback and Leibler 1951). When several non-nested candidate models have similar Akaike Information Criteria (corrected for sample size, $AICc < 2$ units), thus being equally close to the full truth, inference from any single model can be less reliable (Burnham and Anderson 2002). In such case, uncertainty associated with parameter estimates can be formally incorporated through multi-model averaging. Following Burnham and Anderson (2002), I computed Akaike-weight (W_i) of select candidate models to produce model-averaged regression coefficients, unconditional standard errors, and importance (summed Akaike-weights) of each predictor using package *MuMIn* in program *R v 2.13.0*. Inferences on macro-scale species-habitat responses were based on standardized regression coefficients and their significance levels. I mapped the predicted seasonal usage of GIB by fitting habitat covariates to final model coefficients in sampled 4 km² grids. Since few significant predictors were obtained from ground surveys and their remotely sensed information was not available, I could not predict GIB usage beyond sampled areas.

4.2.2 Micro-scale selection

4.2.2.1 Field surveys

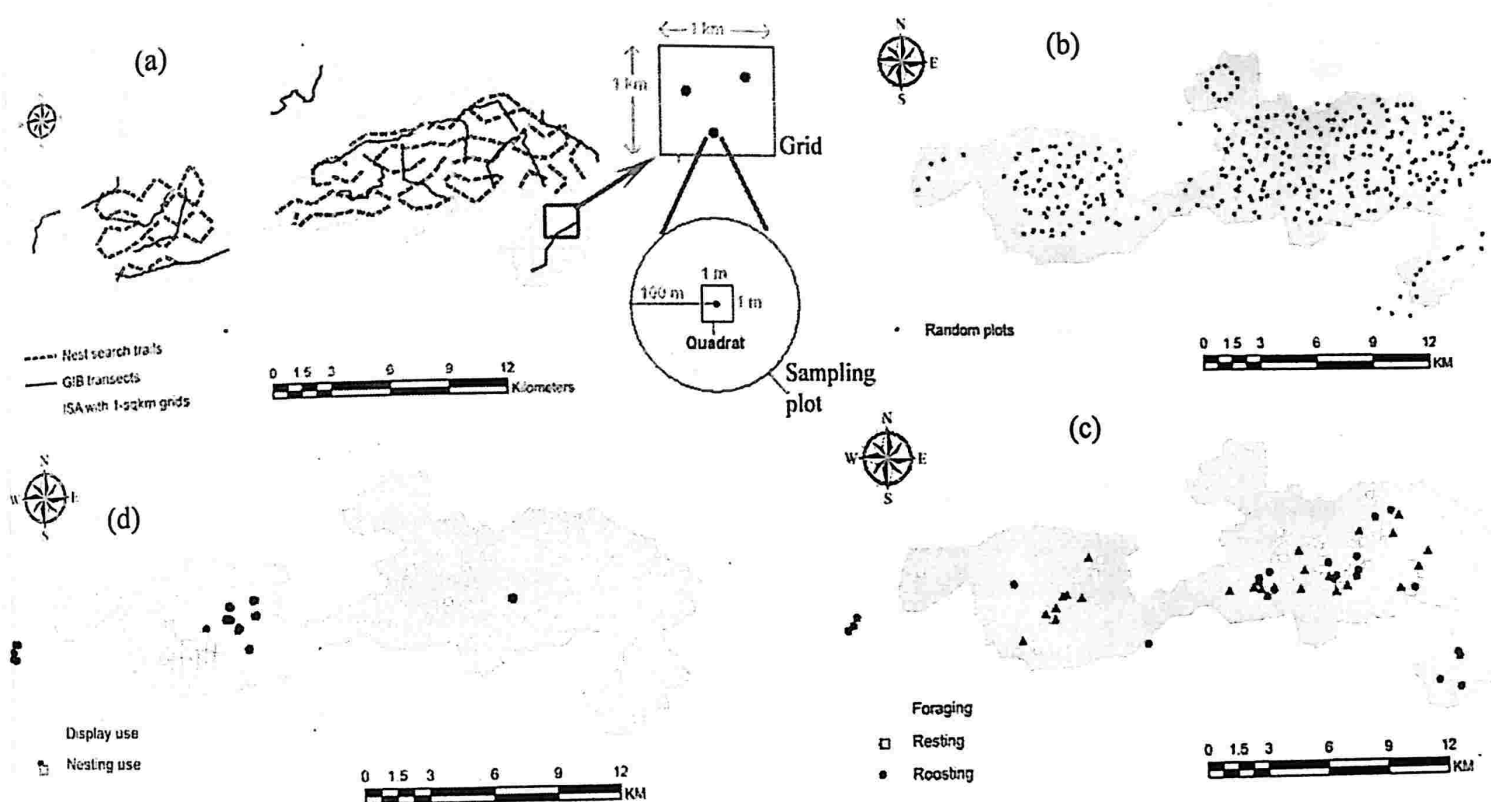
The rare GIB shows strong association with particular patches in a landscape. For efficient accrual of information and conservation interests, fine scale habitat selection should be studied in these patches. I conducted fieldwork in the core bustard usage, collecting data during two peak months of winter, summer, and monsoon of 2008–2011. Of my particular interest were daily activities, viz., foraging, resting and roosting, and breeding activities, viz., display and nesting. I estimated resource selection functions (RSF) of birds' daily and breeding season usage from "used vs. available" and "used vs. unused" resource units respectively (fig 4.2). Resource units were sampled under Manly et al.'s (2002) design I, by characterizing habitat of a set of locations used by unidentified individuals and another set of what was available or unused in the environment

(Boyce et al. 2002). I obtained “use” locations by recording bird activity states whenever they were detected in the core area during 1) complete search along trails from a slowly moving vehicle in short sessions of 2 days once or twice a season, 2) systematic search along 15 uniformly spaced $4.8_{\text{Mean}} \pm 0.6_{\text{SD}}$ km vehicle transects repeated twice or thrice a season, and 3) bird behaviour observations from opportunistic scan points. Since nesting females were highly elusive, I searched them along systematically distributed foot transects during peak nesting season (July to August) by 737 km walk efforts (fig 4.2). I also obtained GPS locations of nests during 2006–2011 from a recent study (Pandey et al. 2008) and Gujarat Forest Department’s nest incentive scheme where agro–pastoralists were rewarded on reporting nests. Use–availability sampling was appropriate to estimate RSF for daily activities since high mobility and rarity of birds along with sampling constraints could ensue several false absences (see Johnson et al. 2006). However, for breeding activities, use–unuse sampling was better as strong site fidelity of birds and intensive long-term efforts did not detect breeding use in areas designated as unused.

Simple topography of the area alongside high mobility and weak intraspecific competition of GIB (due to rarity) for daily use resources ensured that the latter’s availability was constant for all birds and spread throughout the study extent. But breeding resource selection was likely confounded with strong intraspecific competition and site fidelity due to ecological and historical decisions (Rahmani 1989). For instance, males might strategically display at female “hotspots” (section 5.3.3.1) due to which suitable areas outside hotspots would be unavailable, or the alpha male might force beta male to display in low ranking arena. And females might return to existing nesting site if their past efforts in that site were successful. Consequently, alternative choices available to birds for selection might vary among individuals and scales. Some of these issues could be handled through wise choice of sampling design. So I characterized resource availability for daily activities from two to three random plots ($n = 344$) in every 1-km^2 grid of the core area (fig 4.2). But for breeding activities, I characterized resource availability as a unique set of choices within putative area for each display and nesting event. The choice set for a display event was the average habitat of two plots within 500m buffer (used) paired with that of four random plots within 501–4000m ring (not used) excluding adjoining areas of display use. Similarly, the choice set for a nesting event was the average habitat of three plots within 250m buffer (used) paired with that of four random plots within 251–3000m ring (not used) excluding adjoining areas of nesting use. Choice of buffer distances was based on relative mobility of displaying males and nesting

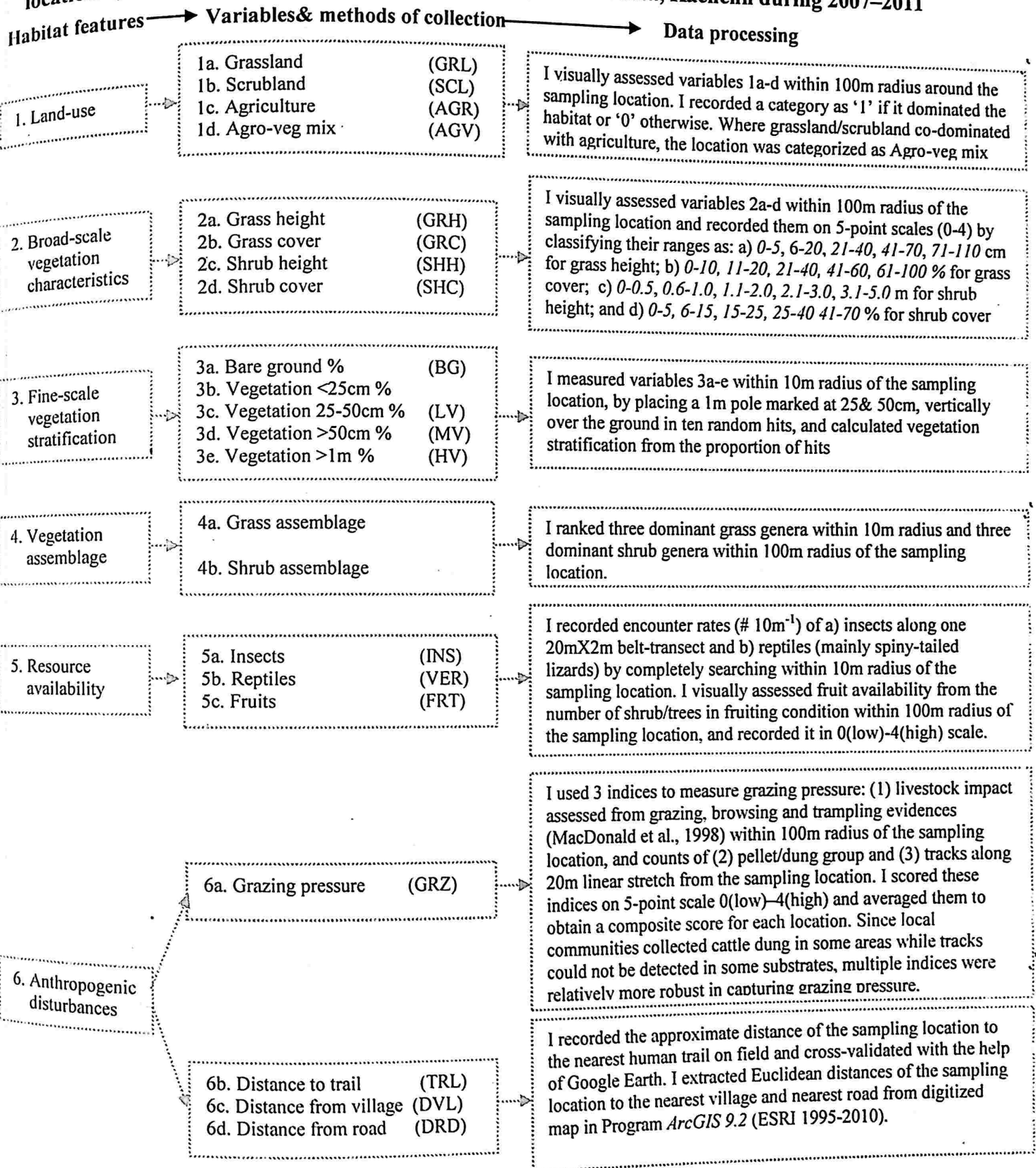
females from behavioural observations and literature on similar bustards (Alonso et al. 2009, Rahmani 1989, Ziembicki 2009).

Figure 4.2 (a) Great Indian Bustard surveys in the core area of Kachchh (2007–11) to record *usage*; habitat sampling in (b) *available* areas from random plots in 1-km² grids along with (c) daily (foraging, resting & roosting) and (d) breeding (display & nesting) use areas



I collected 28 ecologically meaningful habitat variables (table 4.3) from 10m and 100m radius concentric circular plots (n=573 plots) at used locations (n= 76 foraging, 24 roosting, 24 resting, 29*2 display, and 12*3 nesting sites) after birds had left the spot, and at available/unused locations. This sampling scheme was preferred over alternatives after field trials, as it was relevant in contexts of a) bird mobility (Gray et al., 2007 used 50 m radius plots for the smaller bengal florican); b) scale disparity among variables (variables such as habitat type and fruit availability are produced by larger scale processes than variables like vegetation stratification and insect availability); and c) practicality of sampling (e.g., shrub characteristics can be visually assessed in a wider area than grass characteristics).

Table 4.3 Collection and processing of variables from Great Indian Bustard use and random locations (n=573 plots) for micro-scale habitat analysis in Abdasa, Kachchh during 2007–2011



4.2.2.2 Modeling resource selection functions

I explored habitat differences between various GIB activity areas and the background represented by 120 randomly subsampled “available” plots, using univariate statistical tests (Zar

1999). I examined data normality by Kolmogorov–Smirnov test and compared normally distributed variables by t-test, non-normal variables by Mann Whitney U-test, and categorical variables by Fisher's exact test (Zar 1999). Based on *a-priori* knowledge (Rahmani 1989) and field observations, I formulated alternate hypotheses regarding birds' micro-scale habitat selection (table 4.1). I tested these predictions by modeling RSF through logistic regression for daily activities (Manly et al. 2002) and discrete choice analysis for breeding activities (Cooper and Millsbaugh 1999).

4.2.2.2.1 Daily activity use

Logistic regression is a widely used powerful tool in wildlife habitat studies. It is applied on data of *successes* (resource units used) in *trials* (resource units sampled) with corresponding attribute values (resource characteristics), and models the probability of success as a function of these attributes. My sampling scheme involved independent draws of used and available resource units without replacement (unit in available set did not appear in used set), characterized by variables $x_p = 1 \dots k$. In such cases, the probability of use of a resource unit is proportional to the exponential function: $\exp(\beta_0 + \beta_1 x_1 + \dots + \beta_k x_k)$, where $\beta_p = 1 \dots k$ are coefficients that need to be estimated. Here logistic regression estimates the probability of a resource unit being used given that it has been sampled, as:

$$\tau(x) = \frac{\exp(\beta'_0 + \beta_1 x_1 + \dots + \beta_k x_k)}{1 + \exp(\beta'_0 + \beta_1 x_1 + \dots + \beta_k x_k)},$$

where the original intercept β_0 (in exponent form) is

modified into β'_0 to include sampling probabilities of available and used units (see Manly *et al.*, 2002). I constructed models on data from foraging (76 plots), resting (24 plots) and roosting (24 plots) use vs. availability (344 plots) using *glm* function in *program R v 2.13.0* (see details on modeling in section 4.2.2.3).

4.2.2.2.2 Breeding activity use

Discrete choice analysis stems from economic *utility* theory and assumes that resource units are selected from available choices to maximize satisfaction (an unknown quantity which is a function of known resource characteristics). Given this assumption, many alternative modeling techniques can estimate the probability of selecting a resource unit from available alternatives as a function of the resource characteristics (Manly et al. 2002). My sampling scheme defined a choice

set of five alternative resource units (one used vs. four unused, following McFadden 1978) per breeding event i , characterized by variables $x_p=1 \dots k$. In discrete choice framework, the probability of selecting unit j is proportional to the exponential function: $\exp(\beta_1 x_{ij1} + \dots + \beta_k x_{ijk})$, where $\beta_p=1 \dots k$ are coefficients that need to be estimated. The actual probability of selecting unit j from alternatives ($m=1..j..5$) equals to
$$\frac{\exp(\beta_1 x_{ij1} + \dots + \beta_k x_{ijk})}{\sum_1^5 \exp(\beta_{im1} + \dots + \beta_{imk})}$$
 (see Manly et al. 2002). I constructed

Cox regression or proportional hazard models (which can be tricked to perform discrete choice analysis) on data from 12 nest choice sets (60 plots) and 29 display choice sets (104 plots since some sets had only three unused plots) in *program SPSS v 14* (SPSS 2007).

4.2.2.2.3 Model building, selection and inference

I performed the following analyses on use-availability/unuse data for each life history activity. Since plant productivity increased with rainfall in this semiarid landscape, there was a proportional difference between dry (summer and winter) and wet (monsoon) season measurements of certain variables (viz., grass height, grass cover, bare ground, vegetation <25cm, vegetation 25–50cm, vegetation >50cm, vegetation >1m and fruit availability). So I grouped observations into dry and wet seasons, and z-standardized seasonal variables as $z(x_{ij}) = \frac{x_{ij} - \bar{x}_j}{\sigma(x_j)}$, where x_{ij} is the i^{th} observation of variable x taken in season j , and \bar{x}_j and $\sigma(x_j)$ are the mean and standard deviation of variable x in season j . By centering data on the seasonal average, I approximately corrected for the constant difference described above. For example, the lower (mean-1SD), higher (mean+1SD) and typical (mean) values of a variable in both seasons were now comparable at -1, +1 and 0 respectively. Data on foraging, resting and roosting use-availability, and display choice set (since it spanned summer and monsoon) but not nesting choice set (since it was restricted to monsoon) were subjected to such scaling. I computed Spearman's rank correlation coefficients to identify substantially correlated variable pairs ($|\rho|>0.4$, $P<0.05$). To avoid multicollinearity issues in regression analysis, I either a) conducted Principle Component Analysis on cross-correlated variables using correlation matrix and varimax rotation that extracted orthogonal components representing similar ecological gradients; or b) discarded the less ecologically meaningful variable from the analytical model (based on AICc values of univariate

logistic regression models, see Gray et al. 2007); or c) used residuals of one of the correlated variables by regressing it on the other (Graham 2003) for further analysis. I used exploratory analyses such as graphs (scatter and box plots) and univariate regressions to choose the best among several indices corresponding to a single a-priori hypothesis and settle on the appropriate function (linear or quadratic) prior to formal modeling. Thereafter, I built candidate regression models with combinations of final covariates defined by alternate hypotheses on habitat correlates of life history activities (table 4.1). I used information-theoretic approach to select between candidate models (Kullback and Leibler 1951), either selecting the one with smallest AIC_c value or conducting multi-model averaging if non-nested candidate models had similar AIC_c values (<2 units). I estimated multi-model averaged parameters, unconditional standard errors, and summed Akaike weights of covariates following Burnham and Anderson (2002) using package *MuMIN* in program *R v 2.13.0*. I examined species-habitat responses based on standardized coefficients and precision estimates in final models. Since resting and roosting information was obtained from low sample sizes, I replicated 10 model runs on randomly resampled (without replacement) data subsets of 20 used vs. 40 available plots for each activity. Model replicates allowed a sensitivity analysis on standardized regression coefficients for important predictors to assess the bias and variability related with low sample sizes. I assessed the accuracy of model prediction on breeding RSF (Fielding and Bell 1997) using Receiver Operating Characteristic curve (Beck and Shultz 1986) on fitted probabilities of use vs. observed state.

If resource needs differ between activities, then presumably birds have to accommodate characteristically diverse spaces within their daily use through movements. Also, area suitable for one activity but cut off from areas suitable for other activities may not be used altogether. Hence I tested the hypothesis that bird densities would be higher in patches with high intersection of resource envelopes for various daily activities. For this I mapped the estimated relative probabilities of selecting 1km^2 pixels for foraging, resting and roosting use across the core bustard area. This was done by fitting habitat covariate values at sampled random plots within 1km radius of pixel centroids into the final models, and returning their average exponential values. I estimated the (joint) probability of selecting pixels for daily use as the product of relative probabilities of selection for the three activities. I pooled the latter estimates at 16km^2 grids (transient homerange scale) that were simultaneously surveyed for seasonal bird densities by vehicle transect based distance sampling for three years (details in section 3.3.1.3). Thereafter, I computed

Spearman's rank correlation to examine any correspondence between relative daily use probabilities and breeding and non-breeding densities at grids.

4.3 Results

4.3.1 Macro-scale use

4.3.1.1 General habitat

General habitat characteristics of this landscape within 16 km² grids were as follows: 1) Land-cover was typically dominated by scrub (36.6_{Mean}±1.9_{SE} % area) > agriculture (29.9_{Mean}±1.9_{SE} %) > grassland (17.1_{Mean}±2_{SE} %) > bare areas (16.4_{Mean}±1.5_{SE} %). 2) Terrain ruggedness was 12.5_{Mean}±1.0_{SE} % CV of pixel elevation values. 3) Fine-scale vegetation structure was typically dominated by bare-ground (49.8_{Mean}±2.5_{SE} % area) > low (<50cm) vegetation (37.0_{Mean}±1.9_{SE} %) > high (50–100cm) vegetation (13.3_{Mean}±1.1_{SE} %), with 31_{Mean}±2_{SE} cm grass height, 41.4_{Mean}±2.6_{SE} % grass cover and 1.7_{Mean}±0.1_{SE} m shrub height. 4) The GIB exhibits an omnivorous diet chiefly comprising of arthropods, lizards, fruit and crops (see section 5.3.4.1). The availability of arthropods and lizards were estimated at 1550_{Mean}±75_{SE} ha⁻¹ and 150_{Mean}±25_{SE} ha⁻¹ respectively. 5) Vegetation assemblage was typically dominated by indicator grass genera *Aristida–Dicanthium* (41_{Mean}±4_{SE} % relative frequency of occurrence) > *Cymbopogon–Lepidagathis* (23_{Mean}±3_{SE}%) > *Dactyloctenium–Cenchrus* (20_{Mean}±3_{SE}%), and indicator shrub genera *Acacia–Prosopis juliflora* (41_{Mean}±4_{SE}%) > *Zizyphus–Vernonia* (33_{Mean}±3_{SE}%) > *Capparis–Prosopis stephaniana* (12_{Mean}±2_{SE}%). 6) Anthropogenic pressures were estimated at 7.5_{Mean}±0.3_{SE} villages 100–km⁻², 977_{Mean}±74_{SE} households 100–km⁻², 4968_{Mean}±400_{SE} humans 100–km⁻², 47_{Mean}±1_{SE} % working population, 0.10_{Mean}±0.01_{SE} irrigated: unirrigated area, 1.1_{Mean}±0.1_{SE} km distance to nearest road and 16.0_{Mean}±1.5_{SE} km distance to nearest town (see table 4.2 for computations).

4.3.1.2 Univariate comparison between occupied and unoccupied grids

We detected GIB use in 33% of 50 grids from six surveys during 2007–08 to 2010–11. This sampling design had ~0.3 probability of detecting GIB in a site during a visit (details in chapter 3). Therefore the probability of detecting GIB presence in a site at least once out of six visits $[1-(1-p)^n]$ equals to 0.9, ensuring that nearly all occupied sites in this landscape had been detected. Compared to unoccupied grids, occupied grids had 1) twofold more grassland patch area but similar percentage of other land-cover types; 2) higher grassland patch (>10ha) area in

adjoining 227 km² matrix, equivalent to the seasonal home range size of similar species like the Great Bustard (see Alonso et al. 2009); 3) threefold proximity to the traditional breeding patch; 4) less terrain ruggedness; 5) different fine-scale vegetation characteristics, relatively tall grass height and more grass cover; 6) higher availability of food resources; 7) lower disturbance regimes in terms of grazing index, human population 100-km⁻² and modernity index; and 8) different vegetation composition in terms of higher proportion of *Cymbopogon-Lepidagathis-Chrysopogon* grass genera assemblage and *Zizyphus-Vernonia* shrub genera assemblage but lower proportion of *Acacia-P. juliflora* shrub genera assemblage (table 4.4).

Table 4.4 Mean±SE habitat variables and their univariate comparison between Great Indian Bustard occupied vs. unoccupied 16-km² grids in Abdasa, Kachchh during 2007–11

Habitat variables	Absence grid (n=29)	Presence grid (n=16)	t-stat	Df	P
Land cover					
Bare/sparse-cover area (km ²)	2.74 ± 2.02	2.00 ± 0.90	1.38	43	0.17
Grassland (>10ha) area (km ²)	2.06 ± 1.47	4.02 ± 3.00	-2.47	19	0.02
Agricultural area (km ²)	4.80 ± 2.22	4.38 ± 1.78	0.65	43	0.52
Grassland (>10ha) area in matrix(km ²)	19.50 ± 8.24	31.81 ± 13.03	-3.42	22	0.00
Savannah area (km ²)	2.53 ± 1.34	2.57 ± 1.56	-0.09	43	0.93
Scrubland area (km ²)	3.03 ± 1.85	2.26 ± 2.09	1.28	43	0.21
Geographical					
Ruggedness (% variation in slope)	14.20 ± 7.95	9.91 ± 3.15	2.06	43	0.05
Proximity to lek (1/km)	0.07 ± 0.04	0.24 ± 0.31	-2.25	15	0.04
Fine-scale vegetation characteristics					
Bare ground area (%)	57.25 ± 13.12	37.69 ± 15.62	4.47	43	0.00
Low (<50cm) vegetation (%)	33.00 ± 11.53	43.87 ± 11.46	-3.03	43	0.00
Tall (>50cm) vegetation (%)	9.80 ± 4.94	18.67 ± 8.72	-3.75	20	0.00
Grass height (m)	0.25 ± 0.1	0.41 ± 0.12	-4.54	43	0.00
Grass cover (%)	34.52 ± 14.57	53.42 ± 17.11	-3.91	43	0.00
Shrub height (m)	1.66 ± 0.47	1.51 ± 0.43	1.02	43	0.31
Vegetation assemblage					
<i>Aristida Dicanthium</i>	0.37 ± 0.28	0.44 ± 0.23	-0.86	43	0.40
<i>Cymbopogon-Lepidagathis</i>	0.18 ± 0.16	0.33 ± 0.20	-2.68	43	0.01
<i>Dactyloctenium-Cenchrus</i>	0.25 ± 0.23	0.13 ± 0.13	2.27	43	0.03
<i>Acacia-P. juliflora</i>	0.46 ± 0.25	0.30 ± 0.28	1.97	43	0.06
<i>Capparis-P. stephaniana</i>	0.11 ± 0.11	0.12 ± 0.09	-0.31	43	0.76
<i>Zizyphus-Vernonia</i>	0.26 ± 0.2	0.48 ± 0.22	-3.41	43	0.00
Resource availability					
Insect availability/ha	1310.0 ± 45.5	2015.0 ± 580.0	-4.51	43	0.00
Vertebrate (lizard) availability/ha	110.0 ± 92.5	212.5 ± 142.5			
Anthropogenic disturbances					
Distance to road (km)	1039.36 ± 761.42	1168.78 ± 642.06	-0.58	43	0.57
Distance to trail (m)	95.27 ± 41.98	160.65 ± 69.5			
Grazing index (0–12)	7.11 ± 1.12	5.89 ± 0.96	3.66	43	0.00
Village count/100km ²	7.34 ± 1.93	7.81 ± 1.94	-0.78	43	0.44
Human population/100km ²	5706.72 ± 2946.87	4246.88 ± 2321.62	1.71	43	0.09
Income/household	5.92 ± 6.93	5.55 ± 10.16	0.15	43	0.89
Irrigated/unirrigated area	0.12 ± 0.09	0.10 ± 0.06	0.58	43	0.56
Literacy/illiteracy rate	1.08 ± 0.19	1.01 ± 0.41	0.59	19	0.56
Modernity index (0–5)	2.20 ± 0.88	1.72 ± 0.66	1.90	43	0.06

4.3.1.3 Multivariate modeling of GIB habitat usage

Population indices of GIB varied from 0.00 to 0.05 detections km⁻² among grids (fig 4.1e). Scaled to 44 km total efforts in a grid, intensity of grid use ranged within 0.0–3.7 (0.52_{Mean}) and 0.0–3.6 (0.52_{Mean}) detections in summer and winter respectively. Population indices were spatially autocorrelated (summer: I=0.09, Z=5.25 SD; winter: I=0.08, Z=4.65 SD) and the observed clustered pattern was unlikely to be caused by random chance (p<0.01). Out of 578 possible pairs of 34 habitat variables, 79 pairs were correlated ($|r|>0.4$, P<0.05, see table 4.5). Fine-scale habitat characteristics and passive anthropogenic pressures exhibited high group-collinearity. Therefore I extracted two principle components from fine-scale habitat characteristics: the first principle component (PC1) explained 52% variance in data and was positively correlated with vegetation attributes but negatively correlated with grazing and bare area, thus surrogating productivity. The second component (PC2) explained 20% variance in data and was positively correlated with arthropod and lizard availability but negatively correlated with shrub height, thus surrogating resource vs. visibility. Similarly, I extracted one principle component from passive anthropogenic pressures (PC3) that explained 46% variance in data and was positively correlated with most of the disturbance measures; thus representing an overall development related disturbance index (table 4.5). Most of the remaining collinearity among variables was restricted to exclusive pairs and not groups. Among these, I discarded the ecologically unimportant variables: bare/sparse, savanna, and scrub land-cover types, and *Aristida-Dicanthium*, *Dactyloctenium-Cenchrus*, *Capparis-P.stephaniana* and *Acacia-P.juliflora* vegetation assemblages. Thereafter I computed residuals of a) grid grassland area and b) proximity to lek by regressing them with matrix grassland area; b) PC1 and c) PC2 by regressing them with grid grassland area; e) ruggedness by regressing it with PC2; f) *Cymbopogon-Lepidagathis* by regressing it with PC1, PC2 and grid grassland area; and g) *Zizyphus-Vernonia* by regressing it with grid and matrix grassland areas. Thus, I was left with nine final uncorrelated covariates, hereafter termed as matrix grassland, grid grassland, productivity, resource vs. visibility, disturbance, human presence, ruggedness, *Cymbopogon-Lepidagathis*, *Zizyphus-Vernonia*, and lek proximity; the latter to model spatial structure of the response variable.

Table 4.5 (a) Pearson's correlation matrix between habitat variables showing significant correlations ($|r| > 0.4$, $P < 0.05$); principle components extracted from correlated variables representing (b) fine-scale habitat characteristics (vegetation, resources and grazing) and (c) passive anthropogenic disturbances in the bustard landscape of Kachchh during 2007–11

(a)	Land-cover types						Geographical		Fine scale vegetation structure						Resource		Vegetation assemblage						Active disturbances		Passive human disturbance										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
Matrix grassland 1																																			
Grassland 2	0.8																																		
Bare/Sparse 3																																			
Agriculture 4																																			
Scrubland 5	-0.5	-0.6																																	
Savannah 6																																			
Proximity to lek 7	0.7	0.7																																	
Ruggedness 8			0.5																																
Bare ground 9																																			
Low (5-50cm) veg 10									-0.9																										
Tall (50-100cm) veg 11									-0.7	0.4																									
Grass height 12		0.5							-0.8	0.6	0.8																								
Grass cover 13									-1.0	0.9	0.7	0.7																							
Shrub height 14																																			
Insect 15	0.6	0.6					0.5		-0.6	0.6	0.6	0.5																							
Reptiles 16	0.4	0.5																																	
<i>Aristida-Dicotyllum</i> 17																																			
<i>Dactyloctenium-Cenchrus</i> 18			0.5								-0.4	-0.5																							
<i>Cymbopogon-Leptogathys</i> 19	0.4	0.6					0.5		-0.5	0.4	0.6	0.5			0.5	0.4																			
<i>Acacia-P.juliflora</i> 20	-0.5	-0.5	0.4			0.6																													
<i>Capparis-P.stephaniana</i> 21																																			
<i>Zizyphus-Terminalia</i> 22	0.6	0.5	-0.4		-0.6	0.4	0.4																												
Distance to trail 23	0.4																																		
Grazing index 24									0.6	-0.5	-0.5	-0.7	-0.5																						
Village count 25																																			
Households 26																																			
Human population 27																																			
Working population 28																																			
Income/ household 29																																			
Irrigated: unirrigated 30																																			
Modernity index 31																																			
Literacy: Illiteracy 32																																			
Distance to road 33								0.4																											
Distance to town 34	-0.6						-0.5								-0.5																				

(b) Fine-scale habitat characteristics			(c) Passive anthropogenic disturbances	
Variables	Component 1	Component 2	Variables	Component 1
Bare ground	-0.95		Agriculture	0.59
Low (5–50cm) veg	0.81		Village count	0.75
Tall (50–100cm) veg	0.81		Households	0.92
Grass height	0.88		Total population	0.91
Grass cover	0.90		Literate:Illiterate	0.64
Shrub height		-0.82	Irrigated:Unirrigated	0.58
Grazing	-0.76		Modernity index	0.73
Insect	0.57	0.53	Distance to road	
Reptiles		0.73	Distance to town	
Variance explained	52 %	20%		46 %
Interpretation	Productivity (+)	Resource vs visibility (+)		Disturbance (+)

Key factors influencing second order usage by GIB differed between seasons (table 4.6). I fitted a global model with nine covariates and 19 subset models indicating various plausible ecological hypotheses about summer use (early breeding season) based on a-priori expectations. Three candidate models incorporating proximity to lek, matrix grassland, anthropogenic disturbances with/without grid grassland and ruggedness obtained greater support ($\Delta AICc < 2$) and were subjected to multi model averaging. These models explained reasonably high proportion of variance in the response ($R^2 = 0.50-0.56$; table 4.6a). Important predictors, indentified by simultaneously inspecting the summed Akaike weights, model-averaged standardized regression coefficients and their precision, were grassland area in adjoining matrix (positive effect) and passive disturbances (negative effect), apart from squared proximity to lek which was included in all models (positive effect) and indicated a sharp decline of use away from the lek. Influences of grassland area in grid (positive tendency), terrain ruggedness and human presence (negative tendencies) had relatively low importance and precision (table 4.7). I found very little support for patch productivity ($W = 0.08$) and *Cymbopogon-Lepidagathis* assemblage ($W = 0.01$). Results confirmed the view that during early breeding season bustards converged towards traditional breeding grounds, showing preference for grassland neighbourhood with fewer disturbances, while discounting on patch productivity.

I fitted a global model with six covariates and 15 subset models indicating plausible hypotheses about winter use (non-breeding season). Two candidate models incorporating matrix grassland, productivity and *Zizyphus-Vernonia* with/without ruggedness obtained greater support ($\Delta AICc < 2$) and were subjected to multi model averaging. They explained relatively low proportion of variance in the response ($R^2 = 0.29-0.33$, see table 4.6b) than did models on summer use. Important predictors, indentified from summed Akaike weights, model-averaged standardized regression coefficients and their precision estimates, were grassland area in adjoining matrix, patch productivity and *Zizyphus-Vernonia* assemblage (all positive effects). Influence of terrain ruggedness (negative tendency) had relatively low importance and preciesion (table 4.7). I found very little support for passive disturbances ($W = 0.18$) and grassland area in grid ($W = 0.11$). Results confirmed the view that winter space use was mostly influenced by food resource dispersion. As birds ranged from traditional breeding grasslands to foraging areas, proximity to lek lost importance, while productive patches and grassland dominated matrix allowing accessibility

became stronger correlates of space use. *Zizyphus*, a short abundant bush fruiting in winter and constituting 23–31% of birds' seasonal diet (section 5.3.4), was highly selected.

Table 4.6 Summary statistics [loglikelihood (LogL), degrees of freedom (df), Akaike Information Criteria (AICc), relative support for hypothesis ($\Delta AICc$), Akaike weights (W_i) and coefficient of determination (R^2)] of candidate regression models explaining Great Indian Bustard usage of 16 km² grids in Kachhh during (a) summer and (b) winter of 2007–11

Model	W_i	$\Delta AICc$	AICc	df	LogL	R^2
(a) Summer second order usage explained by alternate hypotheses						
(prox ² + mat + distb + hum)	0.24	0.00	113.80	6	-49.80	0.50
(prox ² + mat + grl + distb + hum + rug)	0.21	0.26	114.06	8	-47.03	0.56
(prox ² + mat + grl + distb + hum)	0.16	0.88	114.68	7	-48.83	0.52
(prox ² + mat)	0.09	2.05	115.85	4	-53.43	
(prox ² + mat + grl)	0.08	2.34	116.14	5	-52.30	
(prox ² + mat + grl + rug)	0.05	3.11	116.92	6	-51.35	
(prox ² + mat + rug)	0.05	3.30	117.10	5	-52.78	
(prox ² + mat + prod + res.shr)	0.04	3.55	117.36	6	-51.57	
(prox ² + mat + grl + prod + res.shr)	0.03	4.15	117.96	7	-50.47	
(prox ² + distb + hum + rug)	0.01	6.30	120.10	6	-52.95	
(prox ² + rug)	0.01	7.03	120.83	4	-55.91	
(prox ² + mat + grl + distb + hum + rug + prod + res.shr + cym)	0.01	7.10	120.90	11	-45.45	
(prox ² + grl + rug)	0.01	7.50	121.30	5	-54.88	
(prox ²)	0.01	7.74	121.54	3	-57.48	
(prox ² + distb + hum)	0.00	8.17	121.98	5	-55.22	
(prox ² + grl)	0.00	8.93	122.73	4	-56.86	
(prox ² + prod + res.shr)	0.00	9.22	123.03	5	-55.74	
(prox ² + distb + hum + rug + prod + res.shr)	0.00	9.49	123.29	8	-51.64	
(prox ² + grl + distb + hum)	0.00	10.13	123.94	6	-54.86	
(prox ² + grl + prod + res.shr)	0.00	10.67	124.47	6	-55.13	
(.)	0.00	20.98	134.79	2	-65.25	
(b) Winter second order usage explained by alternate hypotheses						
(mat + prod + ziz)	0.25	0.00	132.11	5	-60.34	0.29
(mat + prod + ziz + rug)	0.23	0.16	132.27	6	-59.11	0.33
(mat + prod + grl + ziz)	0.09	2.01	134.12	6	-60.03	
(prod + ziz + rug)	0.08	2.16	134.27	5	-61.42	
(mat + prod)	0.08	2.35	134.46	4	-62.77	
(mat + prod + ziz + distb + rug)	0.07	2.42	134.53	7	-58.87	
(mat + prod + ziz + distb)	0.07	2.46	134.57	6	-60.26	
(prod + ziz)	0.03	4.35	136.46	4	-63.76	
(mat + prod + grl + ziz + distb + rug)	0.02	5.04	137.15	8	-58.73	
(ziz)	0.02	5.52	137.63	3	-65.54	
(mat)	0.01	6.24	138.35	3	-65.90	
(mat + rug)	0.01	6.38	138.49	4	-64.78	
(prod + ziz + distb)	0.01	6.85	138.96	5	-63.76	
(prod)	0.01	6.97	139.08	3	-66.27	
(rug)	0.01	7.48	139.59	3	-66.52	
(mat + distb)	0.01	7.65	139.76	4	-65.41	
(.)	0.00	9.30	141.41	2	-68.57	
(distb)	0.00	11.31	143.42	3	-68.44	

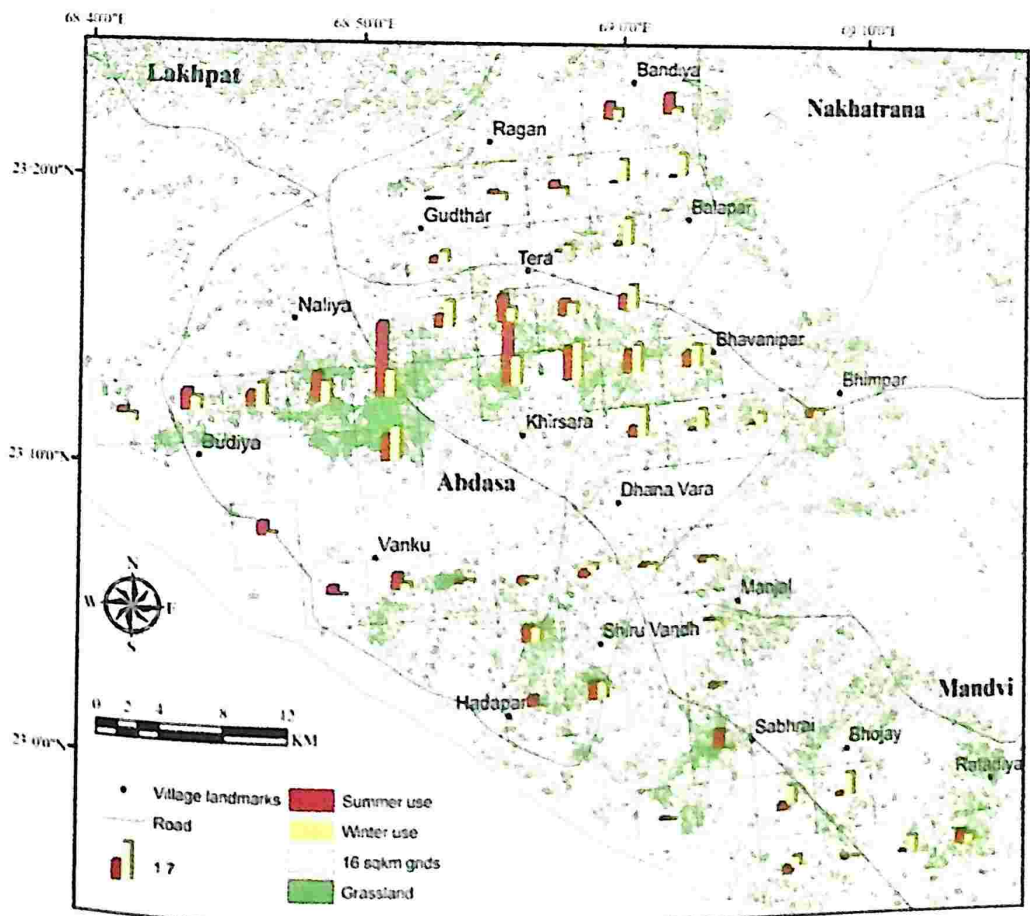
Covariates are proximity to lek (prox), matrix grassland (mat), grid-grassland (grl), patch productivity (prod), food-resource vs. visibility (res.shr), ruggedness (rug), *Zizyphus-Vernonia* (ziz), *Cymbopogon-Lepidagathis* (cym), passive anthropogenic pressures (distb), and human presence (hum).
Top candidate models ($\Delta AICc < 2$) are marked in grey shade; global model in italics; and null model as (.)

Table 4.7 Model-averaged parameter estimates [coefficients (β), unconditional standard errors (SE_{Unc}), significance statistics and summed Akaike weights ($W+$)] of influential habitat correlates of Great Indian Bustard usage of 16 km² grids in Kachchh during summer and winter (2007–11)

Habitat covariates	Summer use			Winter use		
	β	SE_{Unc}	$W+$	β	SE_{Unc}	$W+$
Lek proximity ²	0.33	0.13	1.00			
Matrix grassland	0.39	0.13	0.96	0.30	0.14	0.85
Grid grassland	0.18	0.13	0.55			
Productivity				0.28	0.13	0.95
Ruggedness	-0.21	0.12	0.35	-0.20	0.13	0.43
<i>Zizyphus-Vernonia</i>				0.28	0.13	0.88
Passive disturbance	-0.25	0.12	0.64			
Human presence	-0.13	0.13	0.64			

Predicted summer usage was negatively correlated with Universal Transverse Mercator easting ($r=-0.34$, $p=0.02$), indicating higher breeding use to the west of the study landscape. Predicted winter usage was not correlated with Universal Transverse Mercator easting ($r=0.009$, $p=0.95$) or northing ($r=0.20$, $p=0.18$), indicating more dispersed non-breeding use (fig 4.3).

Figure 4.3 Model predicted seasonal landscape use by Great Indian Bustard in Kachchh (2007–11)



Residuals of average models did not show any spatial structure during summer ($I=-0.03$, $Z=-0.21$ SD, $p \gg 0.10$) or winter ($I=0$, $Z=1.15$ SD, $p > 0.10$). Those from the top seasonal model followed standard normal distribution except for some deviation towards the higher end of their range (appendix 4.1 i&ii b). Residuals should be independent and homoskedastic in relation with fitted values of response, but those from the top seasonal models deviated from the ideal “random scatter” towards the lower end of fitted range (appendix 4.1 i&ii a). Further, error rates in predicting usage was relatively higher in unoccupied grids than occupied grids (appendix 4.1 i&ii d). Hence second order models should be interpreted with less reliability under low predicted/observed usage but with certainty under high predicted/observed usage.

4.3.2 Micro-site selection

4.3.2.1 Habitat description

General habitat characteristics of the core bustard area were as follows: 1) Land-cover was typically dominated by grassland (35% relative frequency of occurrence) > agro-vegetation (25 %) > open scrub (18%) > cropland (12 %) > dense scrub (11%). 2) Terrain was mostly flat (85% relative frequency of occurrence) and occasionally sloping, undulating or broken (15%). 3) Plant community was dominated by *Cymbopogon* (64.5 % relative frequency of occurrence) > *Aristida* (53.8%) > *Dicanthium* (39.2%) > *Lepidagathis* (22.7%) > *Dactyloctenium* (21.2%) > *Chrysopogon* (16.0%) grass genera; and *Zizyphus* (72.1%) > *Acacia* (31.4%) > *P. juliflora* (29.7%) > *P. stephaniana* (26.7%) > *Capparis* (18.3%) > *Vernonia* (14.5%) shrub genera. 4) Vegetation structure was dominated by bare-ground ($43.2_{\text{Mean} \pm 1.4_{\text{SE}}}$ % relative frequency of occurrence) > vegetation <25cm ($31.2_{\text{Mean} \pm 1.0_{\text{SE}}}$ %) > vegetation 25–50cm ($13.3_{\text{Mean} \pm 0.6_{\text{SE}}}$), > vegetation 51–100cm ($11.4_{\text{Mean} \pm 0.6_{\text{SE}}}$) > vegetation >100cm ($2.5_{\text{Mean} \pm 0.3_{\text{SE}}}$). Other vegetation characteristics included $35.9_{\text{Mean} \pm 1.3_{\text{SE}}}$ cm grass height, $59.4_{\text{Mean} \pm 1.5_{\text{SE}}}$ % grass cover, $1.77_{\text{Mean} \pm 0.06_{\text{SE}}}$ m shrub height, and $17.6_{\text{Mean} \pm 0.7_{\text{SE}}}$ % shrub cover. 5) The availability of arthropods and lizards were estimated at $2619_{\text{Mean} \pm 108_{\text{SE}}}$ ha⁻¹ and $68.8_{\text{Mean} \pm 5.3_{\text{SE}}}$ ha⁻¹ respectively. 6) Anthropogenic pressures were estimated at $185_{\text{Mean} \pm 9.8_{\text{SE}}}$ km distance to nearest human trail, $1.21_{\text{Mean} \pm 0.04_{\text{SE}}}$ km distance to nearest road and $1.54_{\text{Mean} \pm 0.04_{\text{SE}}}$ km distance to nearest village (table 4.8).

Table 4.8 Descriptive statistics and univariate comparison (F: Fisher's exact test, T: t-test & U: Mann-Whitney U test) of habitat variables at random vs. activity sites in core bustard area of Kachchh (2007-11); sample size denoted as n₁ (random sites) and n₂ (activity sites).

Habitat covariates	Random (n ₁ =120)			Foraging (n ₂ =76)			Roosting (n ₂ =24)			Nesting (n ₂ =12)			Display (n ₂ =29)		Test	
	Freq %	Freq	P-value	Freq %	Freq	P-value	Freq %	Freq	P-value	Freq %	Freq	P-value	Mean ±SE	test-stat		P-value
Land cover type																
Agriculture	11.63	1.32	0.004	4.17	4.17	0.497	4.17	4.17	0.497	0.00	0.014	0.00	43.43 ± 2.3	-0.01	0.035	F
Agro-veg mix	25.00	44.74	0.001	20.83	20.83	0.810	33.33	33.33	0.340	9.09	0.020	6.06	41.3 ± 2.28	-4.54**	0.016	F
Grassland	34.59	43.42	0.150	54.17	54.17	0.080	50.00	50.00	0.180	90.91	0.000	93.94	12.54 ± 1.48	6.47**	0.000	F
Scrubland	28.78	10.53	0.007	20.83	20.83	0.490	12.50	12.50	0.101	0.00	0.000	0.00	6.31 ± 1.04	8.77**	0.000	F
Vegetation stratification (% area)																
Bare ground	43.18 ± 1.38	39.88 ± 2.31	-1.04	34.91 ± 3.92	34.91 ± 3.92	-1.89'	41.34 ± 4.6	41.34 ± 4.6	-0.37	26.9 ± 2.17	test-stat	0.00	43.43 ± 2.3	-4.35**	test-stat	T
Very low (<25cm)	31.21 ± 1.01	34.6 ± 1.84	0.52	34.04 ± 3.42	34.04 ± 3.42	0.19	40.74 ± 3.28	40.74 ± 3.28	1.85'	18.79 ± 1.72	test-stat	0.00	41.3 ± 2.28	-4.54**	test-stat	T
Low (26-50 cm)	13.27 ± 0.62	14.67 ± 1.07	1.47	17.72 ± 2.05	17.72 ± 2.05	2.13*	11.92 ± 2.12	11.92 ± 2.12	-0.19	24.67 ± 1.54	test-stat	0.00	12.54 ± 1.48	6.47**	test-stat	T
Medium height (51-100 cm)	11.41 ± 0.64	10.25 ± 1.11	-0.18	13.01 ± 1.79	13.01 ± 1.79	1.08	5.36 ± 1.37	5.36 ± 1.37	-3.12**	27.78 ± 1.85	test-stat	0.00	6.31 ± 1.04	8.77**	test-stat	T
High (>101 cm)	2.54 ± 0.26	1.04 ± 0.19	5039	1.87 ± 0.41	1.87 ± 0.41	1417	0.55 ± 0.14	0.55 ± 0.14	1456	0.99 ± 0.37	test-stat	0.00	1.02 ± 0.25	856	test-stat	U
Coarse scale vegetation characteristics																
Grass height (cm)	35.92 ± 1.27	34.53 ± 1.9	4591	48.21 ± 3.48	48.21 ± 3.48	929**	28 ± 3.63	28 ± 3.63	1401	57.32 ± 1.48	test-stat	0.00	25.26 ± 2.51	261**	test-stat	U
Grass cover (%)	59.36 ± 1.47	63.57 ± 3.07	1.23	73.43 ± 4.32	73.43 ± 4.32	2.46*	65.76 ± 5.29	65.76 ± 5.29	1.15	83.4 ± 3.02	test-stat	0.00	64.47 ± 2.71	6.21**	test-stat	T
Shrub height (m)	1.77 ± 0.06	1.29 ± 0.09	3970**	1.59 ± 0.24	1.59 ± 0.24	1429	1.11 ± 0.14	1.11 ± 0.14	1096**	0.42 ± 0.06	test-stat	0.00	0.92 ± 0.13	275**	test-stat	U
Shrub cover (%)	17.63 ± 0.72	16.68 ± 1.19	4982	14.56 ± 1.72	14.56 ± 1.72	1516	14.56 ± 1.72	14.56 ± 1.72	1516	3.41 ± 0.39	test-stat	0.00	12.23 ± 1.71	275**	test-stat	U
Plant genera (0-3 dominance index)																
<i>Aristida</i>	1.31 ± 0.07	1.41 ± 0.15	5029	1.17 ± 0.28	1.17 ± 0.28	1438	2.08 ± 0.25	2.08 ± 0.25	1180*	0.45 ± 0.14	test-stat	0.00	0.79 ± 0.2	676**	test-stat	U
<i>Chrysopogon</i>	0.27 ± 0.04	0.51 ± 0.11	4479*	0.5 ± 0.19	0.5 ± 0.19	1448	0.42 ± 0.2	0.42 ± 0.2	1575	0.43 ± 0.13	test-stat	0.00	0.3 ± 0.13	922	test-stat	U
<i>Cymbopogon</i>	1.57 ± 0.07	1.8 ± 0.13	4435'	2.17 ± 0.21	2.17 ± 0.21	1132*	1.38 ± 0.23	1.38 ± 0.23	1491	2.66 ± 0.11	test-stat	0.00	2.18 ± 0.17	512**	test-stat	U
<i>Dicanthium</i>	0.74 ± 0.06	0.64 ± 0.12	4958	0.46 ± 0.16	0.46 ± 0.16	1449	0.63 ± 0.22	0.63 ± 0.22	1517	0.7 ± 0.16	test-stat	0.00	0.21 ± 0.1	898	test-stat	U
<i>Lepidagathis</i>	0.35 ± 0.04	0.38 ± 0.08	4961	0.83 ± 0.21	0.83 ± 0.21	1217*	0.29 ± 0.11	0.29 ± 0.11	1591	0.73 ± 0.13	test-stat	0.00	1.12 ± 0.18	828	test-stat	U
<i>Acacia</i>	0.61 ± 0.05	0.58 ± 0.12	4975	0.33 ± 0.13	0.33 ± 0.13	1453	0.92 ± 0.22	0.92 ± 0.22	1317'	0 ± 0	test-stat	0.00	0.27 ± 0.11	770***	test-stat	U
<i>P. juliflora</i>	0.62 ± 0.06	0.21 ± 0.07	4572'	0.42 ± 0.19	0.42 ± 0.19	1595	0.04 ± 0.04	0.04 ± 0.04	1317*	0.14 ± 0.08	test-stat	0.00	1.3 ± 0.18	835*	test-stat	U
<i>Zizyphus</i>	1.89 ± 0.07	2.54 ± 0.11	3396**	2.38 ± 0.22	2.38 ± 0.22	1191*	2.04 ± 0.25	2.04 ± 0.25	1409	1.98 ± 0.21	test-stat	0.00	2.76 ± 0.13	919	test-stat	U
Food resources																
Insect count (#/ha)	2619 ± 108	2485 ± 275	5061	1915 ± 214	1915 ± 214	1287	2193 ± 298	2193 ± 298	1457	4387 ± 585	test-stat	0.00	2107 ± 271	641**	test-stat	U
Vertebrate (#/ha)	68.83 ± 5.35	91.66 ± 10.18	3917**	63.89 ± 18.11	63.89 ± 18.11	1581	72.82 ± 13.1	72.82 ± 13.1	1324	103.11 ± 19.26	test-stat	0.00	100.48 ± 15.17	820	test-stat	U
Fruit index (0-3)	1.26 ± 0.06	1.76 ± 0.17	4254*	1.25 ± 0.25	1.25 ± 0.25	1516	1.09 ± 0.2	1.09 ± 0.2	1487	0.76 ± 0.2	test-stat	0.00	1.44 ± 0.14	600**	test-stat	U
Anthropogenic disturbances																
Grazing index	1.91 ± 0.05	1.98 ± 0.08	0.84	1.94 ± 0.17	1.94 ± 0.17	0.30	1.81 ± 0.19	1.81 ± 0.19	-0.32	1.04 ± 0.08	test-stat	0.00	2.1 ± 0.09	-6.44**	test-stat	T
Distance to road (km)	1.21 ± 0.04	1.22 ± 0.07	-0.01	1.36 ± 0.15	1.36 ± 0.15	0.85	1.01 ± 0.11	1.01 ± 0.11	-1.35	1.33 ± 0.09	test-stat	0.00	0.92 ± 0.1	1.28	test-stat	T
Distance to village (km)	1.54 ± 0.04	1.35 ± 0.07	-1.63'	1.68 ± 0.17	1.68 ± 0.17	1.15	1.39 ± 0.15	1.39 ± 0.15	-0.79	1.01 ± 0.08	test-stat	0.00	2.07 ± 0.08	-4.64**	test-stat	T

Variables at activity site significantly different from the expected at (') 0.10, (*) 0.05 & (***) 0.01 levels

4.3.2.2 Resource selection for daily life–history activities

In contrast to the general habitat, bustard foraging areas were characterized by shorter shrub height, higher prevalence of *Chrysopogon* (palatable grass) and *Zizyphus* (short fruiting shrub), greater availability of fruit resources, and relative proximity to villages. Resting areas were characterized by more 26–50 cm tall vegetation, less bare ground, relatively tall and dense grass cover, and higher prevalence of *Cymbopogon* (relatively tall unpalatable grass) and *Zizyphus* than random sites. Whilst roosting areas were characterized by more <25 cm tall vegetation, less 51–100 cm tall vegetation, shorter shrub height, higher prevalence of *Aristida* (very short unpalatable grass) and very low prevalence of *P. juliflora* (tall invasive shrub) than random sites (table 4.8).

In daily use vs. availability analysis, 24 out of 378 paired combinations of habitat variables were strongly correlated ($|\rho| > 0.4$, $P < 0.05$, see table 4.9a). Broad–scale vegetation characteristics and fine–scale vegetation stratification showed high group–collinearity. I extracted three principle components from them: 1) the first component (MV/S) explained 29% variance in data, reflecting a gradient of sparse (low scores) to moderately tall herbaceous vegetation (high scores); 2) the second component (LV/B) explained 23% variance, reflecting a gradient of bareness (low scores) to short herbaceous vegetation (high scores); and 3) the third component (SV) explained 21% variance, surrogating scrub attributes (high scores, see table 4.9b).

To explain foraging microhabitat choice, I specified a global model with additive effects of 12 potential predictors that reliably fitted the data (residual-deviance/df=0.8). Out of the 19 subset models indicating various plausible ecological hypotheses, three models obtained complete support ($W=1.00$) and were subjected to multimodel inferences (table 4.10a). Important predictors, based on summed Akaike weights, standardized coefficients and their precision, were distance to road, grazing pressure, shrub assemblage, land-cover, moderately tall vs sparse vegetation and fruit resource (table 4.10b). Foraging use increased in presence of agro–grass and less certainly grassland cover (compared to scrub), *Zizyphus* shrub and fruit resources; decreased in presence of *P. juliflora*; while peaked at intermediate levels of grazing pressure, distance from road, and moderately tall vs sparse vegetation (table 4.10b, fig 4.5 & 4.6). Results provided less support for variables like grass assemblage, short vegetation vs bareness and insect resource. I examined if habitat characteristics of foraging sites differed between genders based on 24 observations (12 per gender) in dry season (summer=8, winter=16). Only the first vegetation component differed

($t=3.84$, $df=16$, $p<0.001$) between female ($0.25_{\text{Mean}} \pm 0.19_{\text{SE}}$) and male (-0.56 ± 0.09) birds, indicating that males foraged in relatively sparse areas while females in moderately tall cover.

Table 4.9 (a) Rank correlations between habitat variables at Great Indian Bustard daily use and random sites (n=573 plots) showing substantial correlations ($|R|>0.4$, $P<0.05$); (b) principle components extracted from correlated variable-pairs in core bustard area of Kachchh (2007–11)

(a)

	BG	VI	LV	MV	HV	INS	VER	FRT	GRH	GRC	SHH	SIC	ARI	CHR	CYM	DAC	DIC	LEP	ACA	CAP	PSE	PRO	VERN	ZIZ	GRZ	TRL	DRD	DVL
BG										-0.8																		
VI														0.4														
LV	-0.5				0.5				0.5	0.5																		
MV	-0.5				0.5				0.7	0.5																		
HV											0.5																	
INS																												
VER																												
FRT																												
GRH				0.5	0.7						0.1																	
GRC	-0.8			0.5	0.5				0.4																			
SHH						0.5																						
SIC												0.6																
ARI		0.4																										
CHR																												
CYM																												
DAC																												
DIC																												
LEP																												
ACA																												
CAP																												
PSE																												
PRO																												
VERN																												
ZIZ																												
GRZ																												
TRL																												
DRD																												
DVL																												

(b)

Variables	PC1	PC2	PC3
Bare ground	-0.53	-0.81	-0.11
Vegetation <25cm	-0.42	0.87	0.02
Vegetation 25–50cm	0.69	0.21	-0.16
Vegetation 50–100cm	0.83	-0.04	0.03
Vegetation >100cm	0.12	-0.04	0.76
Grass height	0.80	0.05	-0.08
Grass cover	0.54	0.77	0.01
Shrub height	-0.21	0.00	0.80
Shrub cover	-0.09	0.12	0.76
Variance explained	29 %	23 %	21 %
Ecological Interpretation	Sparseness (low scores) vs. moderately tall herbaceous vegetation (high scores)	Bareness (low scores) vs. short herbaceous vegetation (high scores)	High scores surrogate scrub attributes, i.e., reduce visibility

To explain microhabitat choice for resting, I specified a global model with additive effects of 8 potential predictors (residual-deviance/df=0.5) and 15 subset models indicating various plausible ecological hypotheses. Out of these, six hypotheses obtained greater support from data ($W=0.89$) and were selected for multi model inferences (table 4.11a). Important predictors, based

on summed Akaike weights, model-averaged standardized coefficients and precision estimates, were moderately tall vs sparse vegetation followed by shrub assemblage and distance from village (table 4.11b). Resting use peaked at moderately tall vegetation and tended to increase in presence of the short shrub *P. stephaniana* (table 4.11b, & fig 4.6). I found relatively less importance of *Zizyphus*, *Cymbopogon*, scrub attributes, land-cover and short vegetation vs bareness in influencing resting use.

Table 4.10 (a) Summary statistics of candidate logistic regression models on foraging use of Great Indian Bustard; (b) model averaged parameter estimates (standardized coefficients, unconditional SE) and summed Akaike weight (W+) of predictors in the core bustard area of Kachchh (2007–11)

(a) A-priori hypotheses					
	Wi	ΔAICc	AICc	df	logL
HAB+MV/S ² +SV ² +DRD+DRD ² +GRZ+GRZ ² +FRT+PRO+ZIZ	0.47	0.00	336.66	13	-154.88
HAB+MV/S ² +SV ² +DRD+DRD ² +GRZ+GRZ ² +FRT+PRO+ZIZ+CHR+DAC	0.35	0.57	337.24	15	-153.02
HAB+MV/S ² +SV ² +VL/B+DRD+DRD ² +GRZ+GRZ ² +FRT+INS+PRO+ZIZ+CHR+DAC	0.18	1.96	338.62	17	-151.55
HAB+MV/S ² +SV ² +DRD+DRD ² +GRZ+GRZ ² +FRT	0.00	10.98	347.64	11	-162.50
HAB+MV/S ² +SV ² +VL/B+DRD+DRD ² +GRZ+GRZ ² +FRT+INS	0.00	13.01	349.67	13	-161.39
HAB+SV ² +DRD+DRD ² +GRZ+GRZ ² +FRT	0.00	13.36	350.02	10	-164.74
HAB+MV/S ² +PRO+ZIZ	0.00	17.68	354.34	7	-170.03
HAB+MV/S ² +SV ² +GRZ+GRZ ² +FRT	0.00	20.18	356.84	9	-169.20
MV/S ² +SV ² +DRD+DRD ² +GRZ+GRZ ² +FRT	0.00	23.95	360.61	8	-172.13
HAB+MV/S ² +GRZ+GRZ ² +FRT	0.00	26.22	362.88	8	-173.27
HAB+FRT	0.00	29.31	365.98	5	-177.92
HAB+MV/S ²	0.00	34.61	371.28	5	-180.57
HAB+GRZ+GRZ ²	0.00	38.16	374.82	6	-181.31
HAB	0.00	39.83	376.50	4	-184.20
MV/S ² +GRZ+GRZ ² +FRT	0.00	47.06	383.73	5	-186.79
MV/S ² +FRT	0.00	47.86	384.53	3	-189.23
FRT	0.00	53.44	390.10	2	-193.03
MV/S ² +GRZ+GRZ ²	0.00	53.75	390.41	4	-191.16
MV/S ²	0.00	54.84	391.51	2	-193.74
GRZ+GRZ ²	0.00	59.68	396.34	3	-195.14
(.)	0.00	62.53	399.19	1	-198.59

(b)				
Habitat features	Predictors	βStd	SEUnc	W+
Land cover (HAB)	Agriculture	-0.97	0.90	
	Grassland	1.00	0.59	1.00
contrast scrub	Agro-veg mix	1.25	0.57	
	Moderately tall vs sparseness ² (MV/S) ²	-0.99	0.52	1.00
Vegetation structure	Low vegetation vs bareness (LV/B)	0.80	0.48	0.18
	Scrub attributes ² (SV) ²	-2.25	1.39	1.00
	Grazing (GRZ)	3.93	1.99	1.00
Anthropogenic pressures	Grazing ² (GRZ) ²	-3.82	1.88	
	Distance to road (DRD)	5.23	1.64	1.00
Resources	Distance to road ² (DRD) ²	-5.79	1.81	
	Fruit availability (FRT)	0.96	0.38	1.00
	Insect availability (INS)	-0.25	0.44	0.18
Vegetation composition	<i>Zizyphus</i> (ZIZ)	1.48	0.48	1.00
	<i>P. juliflora</i> (PRO)	-1.13	0.60	1.00
	<i>Chrysopogon</i> (CHR)	0.44	0.34	0.53
	<i>Dactyloctenium</i> (DAC)	-0.57	0.48	0.53

Mean regression coefficients of 10 bootstrapped model iterations returned similar predictor-effects as the average model on global dataset. However, predictor importance (based on terms in top models and mean summed Akaike weight) and precision derived by bootstrapping were higher for moderately tall vs sparse vegetation followed by *Zizyphus* than other variables (table 4.11c).

Table 4.11 (a) Summary statistics of candidate logistic regression models explaining resting use of Great Indian Bustard; (b) model-averaged ($\Delta AIC_c < 2$) parameter estimates (standardized coefficient & unconditional SE) of predictors; and (c) generality of predictions through model bootstrapping returning predictor importance (mean Akaike weight [W_{+Mean}] & incidence in top models [M]) and mean and precision of effects (β_{Mean} , SD_{β} & CV_{β}) in core bustard area of Kachchh (2007–11)

(a) <i>A-priori hypotheses</i>	W_i	ΔAIC_c	AICc	Df	logL
MV/S+MV/S ² +PSE+CYM+ZIZ	0.19	0.00	169.69	6	-78.73
MV/S+MV/S ²	0.15	0.39	170.08	3	-82.01
MV/S+MV/S ² +PSE+CYM+ZIZ+DVL+DVL ²	0.14	0.55	170.24	8	-76.92
MV/S+MV/S ² +DVL+DVL ²	0.14	0.55	170.24	5	-80.04
MV/S+MV/S ² +SV	0.13	0.69	170.38	4	-81.14
MV/S+MV/S ² +SV+DVL+DVL ²	0.12	0.83	170.52	6	-79.14
MV/S+MV/S ² +LV/B+SV+PSE+CYM+ZIZ+DVL+DVL ²	0.05	2.85	172.54	10	-75.96
HAB+MV/S+MV/S ²	0.02	4.93	174.62	6	-81.20
HAB+MV/S+MV/S ² +PSE+CYM+ZIZ	0.01	5.35	175.04	9	-78.27
PSE+CYM+ZIZ	0.01	5.52	175.21	4	-83.55
HAB+MV/S+MV/S ² +PSE+CYM+ZIZ+DVL+DVL ²	0.01	5.58	175.27	11	-76.26
HAB+MV/S+MV/S ² +SV	0.01	6.48	176.17	7	-80.93
HAB+MV/S+MV/S ² +LV/B+SV	0.00	7.55	177.24	8	-80.42
HAB+MV/S+MV/S ² +LV/B+SV+PSE+CYM+ZIZ+DVL+DVL ²	0.00	9.05	178.74	13	-75.86
DVL+DVL ²	0.00	9.75	179.44	3	-86.69
(.)	0.00	9.76	179.45	1	-88.72
HAB	0.00	11.60	11.30	4	-86.6

Habitat features	Predictors	(b) Global data			(c) Bootstrapped data subsets				
		β_{std}	SE_{unc}	W_{+}	β_{Mean}	SD_{β}	CV_{β}	M	W_{+Mean}
Land cover (AB)	Agriculture			0.1	-8.30			1	0.0
	Grassland			0.1	-0.47			1	0.0
	Contrast scrub			0.1	0.55			1	0.0
Vegetation structure	Moderate vs sparse veg. (MV/S)	3.82	1.57	1.0	2.13	0.54	25.45	10	0.8
	Moderate vs sparse veg. ² (MV/S) ²	-3.76	1.54	1.0	-2.10	1.61	76.44	10	0.8
	Low vegetation vs bareness (LV/B)			0.1	2.96			1	0.0
	Scrub attributes (SV)	-1.18	0.94	0.3	-0.88	0.25	28.88	6	0.2
Disturbance	Distance to village (DVL)	-5.02	3.33	0.5	-4.76	3.84	80.78	5	0.3
	Distance to village ² (DVL) ²	5.74	3.21	0.5	5.43	3.30	60.90	5	0.3
Vegetation composition	<i>Cymbopogon</i> (CYM)	0.94	1.09	0.4	0.24	0.79	335.57	6	0.4
	<i>P. stephaniana</i> (PSE)	1.46	0.78	0.4	0.99	1.33	133.98	6	0.4
	<i>Zizyphus</i> (ZIZ)	1.60	1.18	0.4	1.10	0.45	40.66	6	0.4

To explain microhabitat choice for roosting, I specified a global model with additive effects of 6 potential predictors (residual-deviance/df=0.5) and 11 subset models indicating various plausible ecological hypotheses. Out of these, two hypotheses obtained greater support from data ($W=0.91$) and were selected for multimodel inferences (table 4.12a). Important predictors, based on summed Akaike weights and model-averaged standardized coefficient and precision estimates, were plant

assemblage (*P. juliflora*, *Aristida*) and vegetation structure (scrub, moderately tall vs sparse vegetation). Roosting use increased in presence of *Aristida* (uniformly short grass) and sparse vegetation, while decreased in presence of *P. juliflora* (dense, thorny shrub) and scrub attributes (table 4.12b, & fig 4.6). Results indicated relatively less importance of distance to road and land cover. Model bootstrapping returned similar nature of predictor-effects as the average model on global dataset. It also demonstrated greater prediction importance (M, W^+_{mean}) and precision (CV_{β}) for *Aristida* than scrub, sparse vegetation and *P. juliflora* (table 4.12c).

Table 4.12 (a) Summary statistics of candidate logistic regression models explaining roosting use of Great Indian Bustard; (b) model-averaged ($\Delta AIC_c < 2$) parameter estimates (standardized coefficient & unconditional SE) of predictors; and (c) generality of predictions through model bootstrapping returning predictor importance (mean Akaike weight [W^+_{Mean}] & incidence in top models [M]) and mean and precision of effects (β_{Mean} , SD_{β} & CV_{β}) in core bustard area of Kachchh (2007–11)

A-priori hypotheses	W_i	ΔAIC_c	AICc	df	logL
MV/S + SV + ARI + PRO	0.50	0.00	150.16	5	-70.00
MV/S + SV + ARI + PRO + DRD + DRD ²	0.41	0.40	150.56	7	-68.12
HAB + MV/S + SV + ARI + PRO + DRD + DRD ²	0.06	4.22	154.38	10	-66.88
ARI + PRO + DRD + DRD ²	0.01	7.87	158.03	5	-73.93
HAB + ARI + PRO + DRD + DRD ²	0.01	8.65	158.81	8	-71.21
HAB + ARI + PRO	0.00	9.97	160.13	6	-73.95
ARI + PRO	0.00	10.30	160.46	3	-77.20
MV/S + SV + DRD + DRD ²	0.00	19.43	169.59	5	-79.71
MV/S + SV	0.00	20.50	170.66	3	-82.30
DRD + DRD ²	0.00	25.99	176.15	3	-85.04
HAB + DRD + DRD ²	0.00	26.66	176.82	6	-82.29
(.)	0.00	29.29	179.45	1	-88.72
HAB	0.00	29.37	179.53	4	-85.71

Habitat features	Predictors	(b) Global data			(c) Bootstrapped data subsets				
		β_{std}	SE _{unc}	W+	β_{Mean}	SD _{β}	CV _{β}	M	W ⁺ _{Mean}
Land cover (HAB) contrast scrub	Agriculture				-2.11	12.66	600.39	2	
	Grassland			0.1	2.68	0.96	35.69	2	0.1
	Agro-veg mix				2.50	1.41	56.56	2	
Vegetation structure	Moderate vs sparse veg. (MV/S)	-2.35	1.12	1.0	-1.33	0.94	70.33	8	0.6
	Scrub attributes (SV)	-3.63	1.44	1.0	-2.01	0.51	25.59	8	0.6
Disturbances	Distance to road (DRD)	4.66	4.39		3.69	3.90	105.81	9	
	Distance to road (DRD) ²	-7.29	5.39	0.5	-5.79	4.18	72.27	9	0.5
Vegetation composition	<i>Aristida</i> (ARI)	3.80	1.05	1.0	1.84	0.52	28.49	10	1.0
	<i>P. juliflora</i> (PRO)	-6.78	3.50	1.0	-9.24	13.31	144.15	10	1.0

4.3.2.3 Resource selection for breeding life-history activities

Unpaired comparison of GIB display areas with the general habitat revealed higher use of grassland and lower use of other land cover types, more <25 cm tall vegetation and less 51–100 cm tall vegetation, very low shrub height, higher prevalence of *Cymbopogon-Lepidagathis* and

lower prevalence of other grass genera, lower insect count, greater distance from settlement and proximity to roads, and higher grazing pressure (table 4.8). Within display choice sets, 40 out of 300 paired combinations of 25 habitat variables were strongly correlated ($|\rho| > 0.4$, $P < 0.05$, table 4.13a). Broad-scale vegetation characteristics, fine-scale vegetation stratification and distance to village showed high group collinearity. I extracted four principle components from them: 1) the first component (PC1) explained 30% variance in data, reflecting a gradient of bareness (low scores) to herbaceous cover (high scores); 2) the second component (PC2) explained 22% variance, reflecting a gradient of short (low scores) to moderately tall (25–100 cm) vegetation (high scores); 3) the third component (PC3) explained 15% variance, surrogating relatively tall vegetation (> 100 cm); and 4) the fourth component (PC4) explained 14% variance, representing shrub height and cover (table 4.13b). Plant assemblages were expectedly correlated among each other, and the statistically less meaningful ones were screened out. I computed residuals of distance to village by regressing it on PC2.

I examined the influence of vegetation structure, human disturbance (indexed as distance to village) and food (insect density) on display site selection by paired comparison of used vs. unused areas within choice sets. Since displaying bustards would prefer vegetation openness (visibility), I considered short vs moderately tall cover (PC2), grazing effects on ground vegetation, and thorny *Acacia-P. juliflora* shrubs as potential predictors. Distance to road, surrogating human traffic but also the rare water sources due to pipe-line leakages in hot dry season, was also included. I fitted a global model with seven potential predictors and 22 subset models to indicate various plausible ecological hypotheses on arena requirements. Four of these hypotheses obtained greater support from data and were selected for multimodel inferences ($\Delta AIC < 2$, table 4.14a). Important predictors, based on summed Akaike weights and model-averaged coefficient and precision estimates, were grazing intensity, distance to road/water and insect density. Probability of site use for display peaked at intermediate levels of grazing impact on ground vegetation, and increased along proximity to road/water and insect density (table 4.14b). Predictive accuracy of model was reasonably high (table 4.14d). Effect size and precision of important predictors in the average model showed little difference from those returned by univariate models (table 4.14c). Terrain variability, an important *a-priori* predictor of display use, was negligible within the core area and hence discarded from analyses.

Table 4.13 (a) Rank correlations between habitat variables at Great Indian Bustard display and random locations (n=160 plots) showing substantial correlations ($|r|>0.4$, $P<0.05$); (b) principle components extracted from correlated variable-pairs in core bustard area of Kachchh (2007-11)

(a)

	BG	VI	LV	MV	HV	INS	VER	GRII	GRC	SHI	ARI	CHR	CYM	DAC	DIC	LEP	ACA	CAP	PSE	PRO	VERN	ZIZ	GRZ	DRD	DVI	
BG			-0.6	-0.5					-0.8																	
VI								-0.5																		
LV	-0.6			0.6				0.4	0.6																	
MV	-0.5		0.6					0.5	0.6																	0.6
HV															0.4											
INS																										
VER																										
GRII		-0.5	0.4	0.5																						
GRC	-0.8		0.6	0.6																						0.4
SHI															0.4											-0.6
ARI																										
CHR													-0.5			-0.4										
CYM																										
DAC																										
DIC				0.4					0.4																	
LEP																										
ACA												-0.4	0.5	-0.4												
CAP																										
PSE																										
PRO																										
VERN																										
ZIZ																										
GRZ																										
DRD																										0.4
DVI	0.6						0.4	-0.6																		

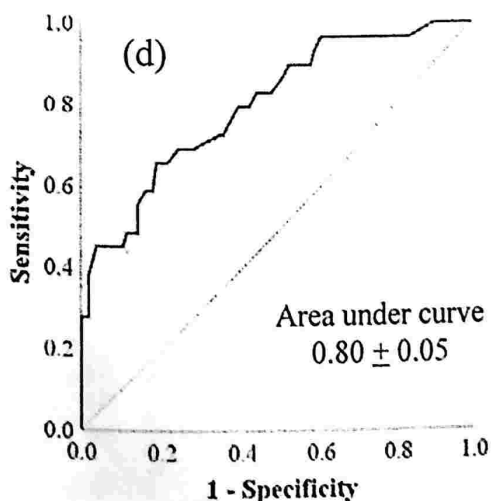
(b)

Variables	PC 1	PC 2	PC 3	PC 4
Bare ground	-0.97			
Vegetation <25cm	0.43	-0.77		
Vegetation 25-50cm	0.63	0.41		
Vegetation 50-100cm	0.49	0.67		
Vegetation >100cm				
Grass height			0.92	
Grass cover		0.85		
Shrub height	0.92			
Shrub cover			0.58	0.55
Variance explained %	30	22	15	0.86
Ecological interpretation	Bareness (-) to herbaceous cover (+)	Short (-) to moderately tall vegetation (+)	Relatively tall vegetation (+)	Shrub height and cover (+)

Table 4.14 (a) Summary statistics of candidate discrete choice models on Great Indian Bustard display use; (b) model-averaged parameter estimates; (c) univariate coefficient estimates of potential predictors; and (d) Receiver Operating Characteristic Curve to assess predictive accuracy of the average model in core bustard area of Kachchh (2007–11)

(a) <i>A-priori hypotheses</i>					
	Wi	ΔAICc	AICc	df	-2logL
GRZ + GRZ2 + ACA-PRO + DRW + INS	0.19	0.00	78.11	5	67.64
PC2 + GRZ + GRZ2 + DRW + INS	0.16	0.32	78.43	5	67.96
PC2 + GRZ + GRZ2 + ACA-PRO + DRW + INS	0.13	0.75	78.86	6	66.20
GRZ + GRZ2 + ACA-PRO + DVL + DRW + INS	0.09	1.40	79.52	6	66.85
PC2 + ACA-PRO + DRW + INS	0.06	2.21	80.32	4	72.01
GRZ + GRZ2 + ACA-PRO + DRW	0.06	2.23	80.34	4	72.03
PC2 + GRZ + GRZ2 + DVL + DRW + INS	0.06	2.33	80.45	6	67.78
PC2 + ACA-PRO + GRZ + GRZ2 + DVL + DRW + INS	0.05	2.54	80.66	7	65.76
PC2 + ACA-PRO + DVL + DRW + INS	0.05	2.79	80.90	5	70.43
PC2 + GRZ + GRZ2 + ACA-PRO + DRW	0.03	3.97	82.09	5	71.62
GRL + PC2 + GRZ + GRZ2 + ACA-PRO + DVL + DRW + INS	0.02	4.56	82.67	8	65.51
DRW + INS (Resources)	0.02	4.58	82.69	2	78.60
PC2 + GRZ + GRZ2 + DRW + DVL	0.01	5.32	83.43	5	72.96
PC2 + ACA-PRO + DVL + DRW	0.01	5.73	83.84	4	75.53
PC2 + ACA-PRO + GRZ + GRZ2 + DVL + DRW	0.01	5.75	83.86	6	71.20
GRZ + GRZ2 + ACA-PRO	0.01	5.79	83.91	3	77.72
GRL + DRW + INS + DVL	0.01	6.02	84.13	4	75.82
PC2 + ACA-PRO + GRZ + GRZ2 (Vegetation structure)	0.01	6.39	84.50	4	76.19
PC2 + GRZ + GRZ2	0.00	7.45	85.56	4	77.25
PC2 + GRZ + GRZ2 + ACA-PRO + DVL	0.00	8.28	86.39	5	75.92
PC2 + ACA-PRO	0.00	9.16	87.27	2	83.18
DVL (Disturbance)	0.00	10.04	88.15	1	86.12
GRL (Land-cover)	0.00	11.46	89.57	1	87.54

(b)		(c)				
Habitat features	Predictors	β	SE	Odd's ratio	W+	βuni±SE
Optimal vegetation structure	Short vs moderately tall veg cover (PC2)	-0.18	0.25	0.84	0.6	-0.43±0.23
	<i>Acacia-P. juliflora</i> (ACA-PRO)	-0.23	0.24	0.79	0.7	-0.22±0.18
	Grazing intensity (GRZ)	3.80	1.96	44.48	0.8	4.05±1.85
	Grazing intensity ² (GRZ ²)	-1.01	0.49	0.36		-1.06±0.46
Disturbance	Distance to village residuals (DVLr)	0.08	0.19	1.09	0.3	0.64±0.49
Resources	Distance to water/road (DRW)	-0.91	0.41	0.40	1.0	-0.79±0.35
	Insect density (INS)	0.65	0.30	1.92	0.8	0.33±0.24



Unpaired comparison of GIB nesting areas with the general habitat in monsoon revealed greater use of grassland than other land cover types, more moderately tall vegetation and less sparse vegetation, relatively dense grass cover but very little scrubbyness, higher insect count, lower grazing pressure, higher prevalence of *Cymbopogon* and lower prevalence of *P. juliflora* (table 4.8).

Within nest choice sets, 52 out of 136 paired combinations of 17 habitat variables were strongly correlated ($|\rho| > 0.4$, $P < 0.05$, see table 4.15a). Based on *a-priori* understanding of nesting requirements, I merged variables into sparse vegetation (bare ground + <25 cm vegetation), 26–100cm tall vegetation, and shrub volume (shrub height x cover). Thereafter, I extracted four principle components from vegetation, food resources and disturbances. Larger values of the first component (PC1) indicated remote, insect-rich areas with relatively tall herbaceous cover. Larger values of the second component (PC2) indicated impediment to visibility in disturbed areas. Larger values of the third component (PC3) indicated remote but intensely grazed areas, and the fourth component (PC4) represented distance from village (table 4.15b).

I examined the influence of habitat gradients PC1, PC2 and PC3 on nest site selection by paired comparison between used and unused areas within choice sets. I fitted a global model with additive effects of these three potential predictors and five candidate models from their alternate combinations. Models incorporating PC1 with/without PC2 and PC3 obtained maximum support from data ($W=1.0$, table 4.16a) and were subjected to multimodel inference. Summed Akaike weights and standardized coefficients ranked PC1 as the most important predictor followed by PC3. Probability of nesting use tended to be higher in remote areas with relatively tall herbaceous cover and more insects. Grazing intensity (PC3) and road-side scrub impeding detectability of disturbances tended to reduce usage but lacked precision (table 4.16b). Predictive accuracy of the average model was very high (table 4.16d). When compared with univariate models, predictor effects in the average model were similar but with highly inflated variances (table 4.16c).

Table 4.15 (a) Rank correlations between habitat variables at Great Indian Bustard nesting and random sites (n=160 plots) showing substantial correlations ($|r|>0.4$, $P<0.05$); (b) principle component extracted from correlated variables in core bustard area of Kachchh (2007-11)

(a)	BG	VL	LV	MV	HV	INS	VER	GRH	GRC	SHH	SHC	CYM	DIC	PRO	GRZ	DRD	DVL
BG																	
VL			-0.6	-0.6													
LV	-0.6					0.4	0.5										
MV	-0.6							0.7	0.6	-0.6	-0.4				0.6		0.4
HV									0.8	-0.6	-0.4	0.5				0.4	
INS			0.4											0.6			
VER			0.5														
GRH				0.7						-0.4							
GRC				0.8				0.5									
SHH	-0.8		0.6						0.5								
SHC	0.4		-0.6	-0.6						-0.5	-0.4	0.4					
CYM			-0.4	-0.4			-0.4			-0.5	0.8				0.4		
DIC				0.5				0.4	0.4	0.8							
PRO					0.6												
GRZ		0.6															
DRD			0.4							0.4							
DVL		0.4															

(b) Variables	PC 1	PC 2	PC 3	PC 4
Short (0-25 cm) vegetation	-0.93			
Medium-tall (26-100 cm) vegetation	0.91			
Grass height	0.75			
Grazing intensity				
Distance to road	0.45		0.88	
Distance to village		-0.57	0.45	
Insect density ($\sqrt{\quad}$)	0.60			0.94
Shrub volume ($\sqrt{\quad}$)				
Variance explained %	36	0.87	18	15
Ecological interpretation	Sparse (-) to tall, insect-rich vegetation in remote areas (+)	Dense scrub close to roads (+)	Grazing intensity in remote areas (+)	Remoteness from settlement (+)

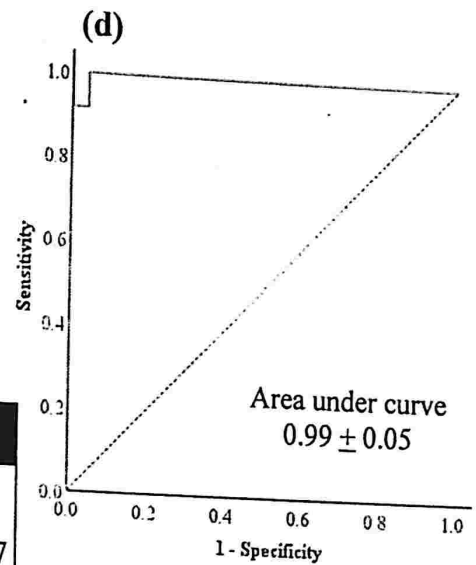
Table 4.16 (a) Summary statistics of candidate discrete choice models on Great Indian Bustard nesting use; (b) model-averaged parameter estimates; (c) univariate coefficient estimates of potential predictors; and (d) Receiver Operating Characteristic Curve to assess predictive accuracy of the average model in core bustard area of Kachchh (2007–11)

(a) <i>A-priori hypotheses</i>	W_i	ΔAIC_c	AIC_c	Df	$-2\log L$
PC1 + PC3	0.43	0.00	7.80	2	3.53
PC1+PC2+PC3	0.20	1.49	9.29	3	2.74
PC1	0.20	1.55	9.35	1	7.26
PC1 + PC2	0.17	1.89	9.69	2	5.42
PC3	0.00	24.03	31.83	1	29.74
PC2	0.00	30.01	37.81	1	35.72

(b)

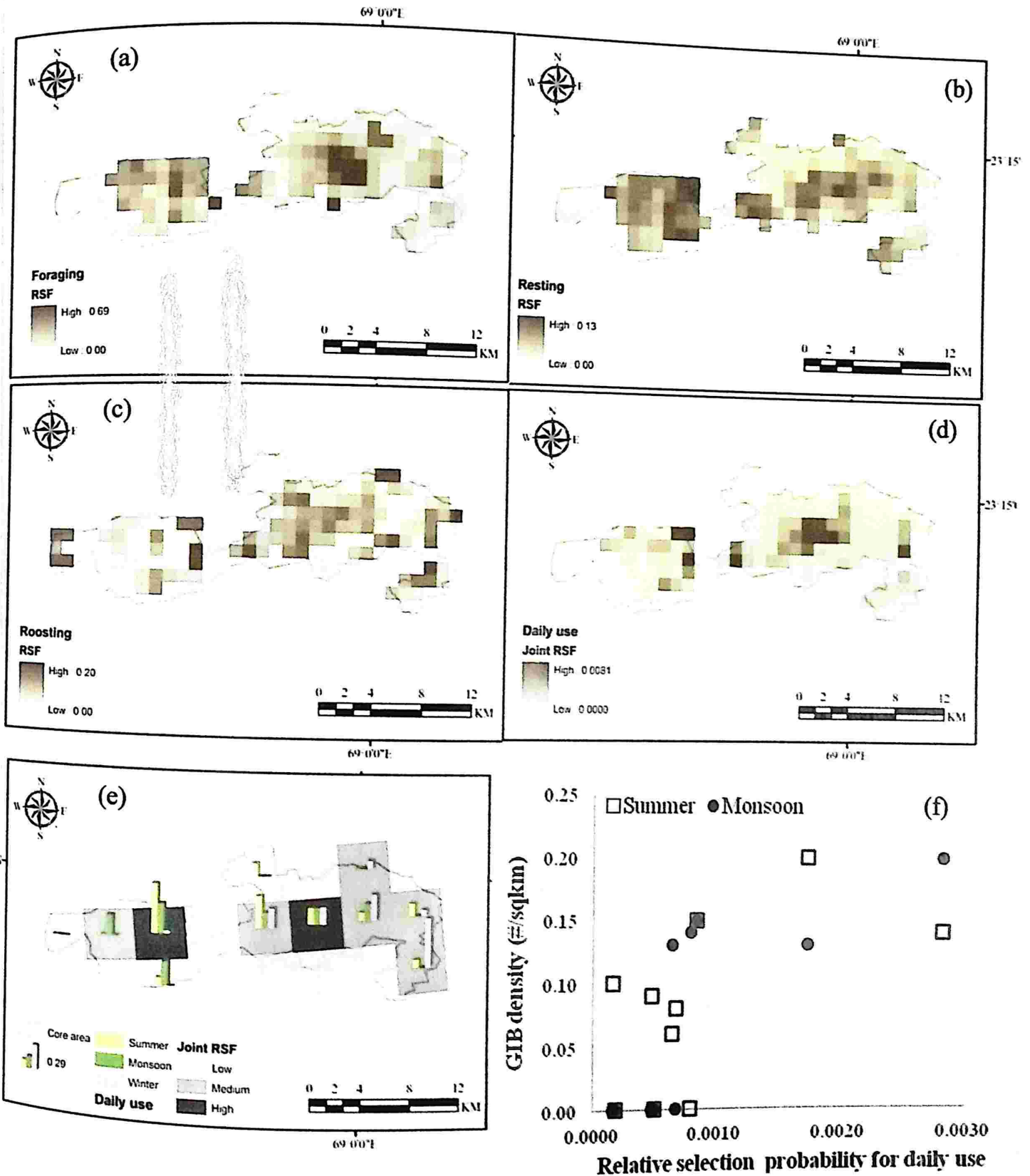
(c)

Predictors	β	SE_{Unc}	W+	Odd's ratio	$\beta_{Uni} \pm SE$
Productivity, remoteness (PC1)	4.87	3.48	1.0	131	4.91 ± 2.61
Road-side scrub (PC2)	-0.42	0.85	0.4	0.67	-0.59 ± 0.37
Grazing intensity (PC3)	-1.61	2.34	0.6	0.28	-1.19 ± 0.48



Model predicted relative probabilities of selecting areas were clustered for foraging ($I=0.14$, $z=17.2$, $p<0.01$), resting ($I=0.15$, $z=18.2$, $p<0.01$) and roosting ($I=0.04$, $z=5.9$, $p<0.01$) uses (fig 4.4a–c). Their intersection returned the relative probabilities of selecting areas for daily use, which ranged from 0 to 0.0081, also exhibiting clustered pattern ($I=0.09$, $z=11.3$, $p<0.01$; fig 4.4d). When pooled at 16 km² scale ($n=10$), relative selection probabilities of grids for daily use varied by 92% CV (0.00016_{Min}–0.0028_{Max}). Survey efforts of 1358 km yielded 73 detections, based on which, annual grid densities showed 64% CV (0–0.13 birds km⁻², fig 4.4e). Data suggested positive correlation between predicted daily use and actual densities at grids during breeding season ($\rho=0.78$, $p=0.007$, fig 4.4f), thereby providing support to my hypothesis. No such correlation was observed in the wintering season ($\rho=0.30$, $p=0.40$), wherein bird space use could be determined by other (unknown) life cycle needs.

Figure 4.4 Estimated relative probabilities of selecting 1km² pixels by Great Indian Bustard for (a) foraging, (b) resting, (c) roosting, and (d) consolidated daily use, (e) which were pooled at 16km² grids where seasonal bird density was also estimated, to assess (f) the correspondence between breeding season density and selection probabilities in core bustard area of Kachchh (2007–11)



4.4 Discussion

This is the first comprehensive study of habitat selection by the Critically Endangered Great Indian Bustard that quantified its resource choices at multiple scales, seasons and life-history needs. The study tested ecological hypotheses and explored little known aspects of their habitat relationships. Models were built on high-resolution ground data and authentic secondary information collected over four years. Spatial coverage of 1000 km² and 160 km² had strong ecological basis as they represented the overall and core distribution areas of this population (fig 4.1, 4.2); and were inclusive of realistic resource gradients for generality of predictions at the second and third order equivalent scales respectively. Additional surveys of ~500 km in adjoining parts of the landscape did not detect any more bird (although sporadic sightings have been reported from Bhachhau, Banni and Little Rann of Kachchh in the last 5–10 years) and 88% of detections in landscape surveys were within the supposed core area. Considering the rarity of these birds, sample-sizes used for various analyses were mostly adequate. Wherever necessary, I conducted bootstrapped sensitivity analyses to examine for bias related to low sample size. Birds in Kachchh, perhaps in connection with Rajasthan and Pakistan, form the most important population crucial for the species' continued existence. Scientifically formulated inferences on habitat relationships from this study can crucially inform effective conservation management of this important population (Sutherland et al. 2004). General inferences from these analyses such as preference of birds for undisturbed grasslands on flat terrains with ample insect and fruit resources, or activity based differences in vegetation structure are likely transferable across GIB landscapes. However, variables like plant community, disturbance regimes etc. may be site specific, so untested transferability of inferences on these aspects to other GIB landscapes is not recommended. These birds exhibit behavioural plasticity in adapting to local conditions (Rahmani 1989) and studies at local scales should be urgently conducted to fill those voids.

4.4.1 Methodological issues

The exploded lek polygynous mating system (Johnsgard 1994) imparts two kinds of problem in investigating habitat relationships of bustards (Gray et al. 2007). The first results from birds congregating in traditional breeding patch during mid-summer and/or monsoon and ranging outwards during winter (Rahmani 1989). This may result into heaped detections concentric to a point in the landscape, which ensues spatial dependence in response, and violates regression assumption (McCullagh and Nelder 1989). Hence I considered the proximity to traditional lek as

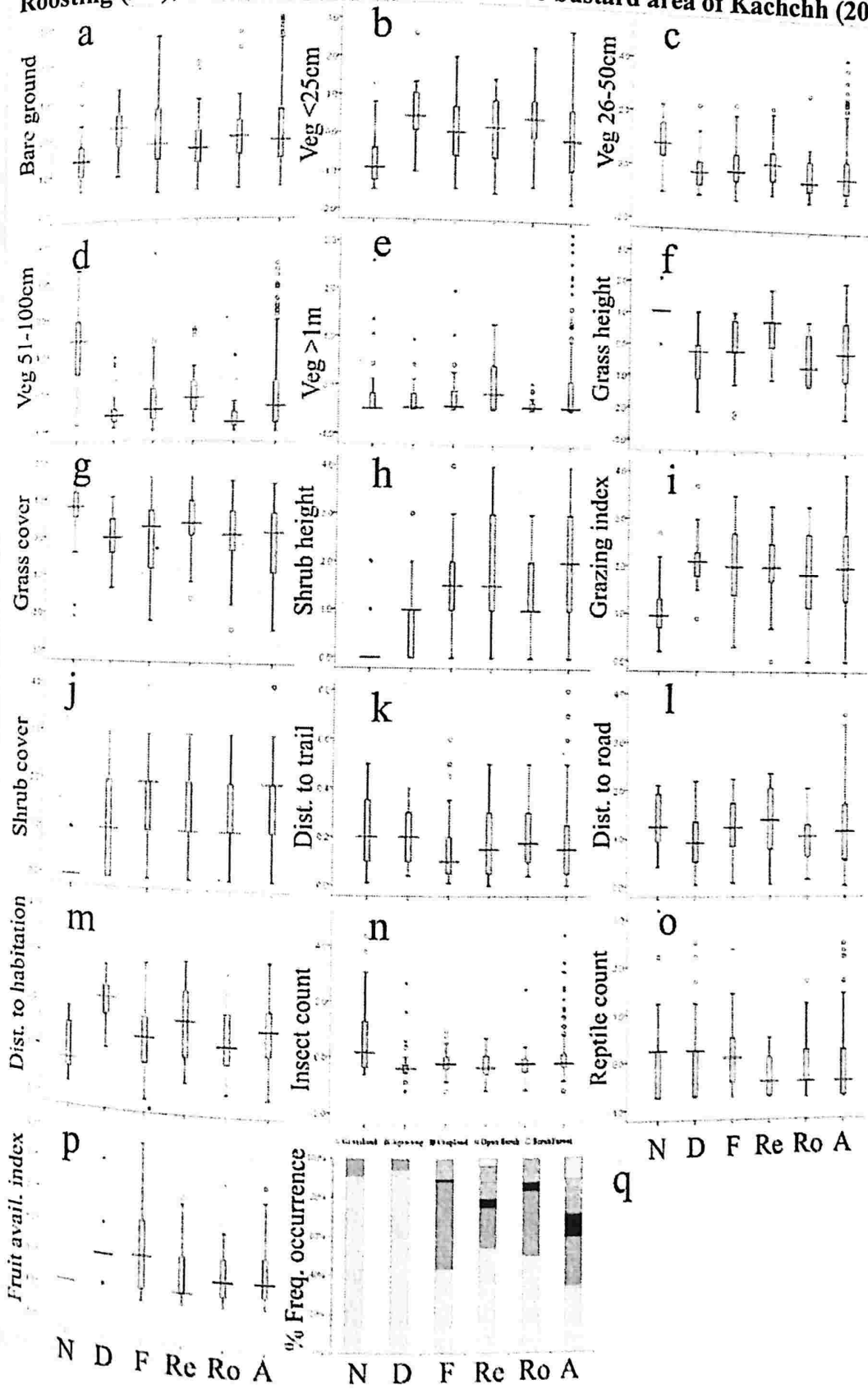
an additional covariate in habitat models to explicitly account for such spatial autocorrelation. Second-order site usage increased as the squared proximity to the traditional lek during breeding season but not in non-breeding season. Model residuals were spatially uncorrelated, justifying the above presumption, also indicating high use of areas adjoining the lek. Suitable habitats in the immediate vicinity of traditional breeding patch thus bears high conservation value for GIB. The traditional breeding patch (four 16km² grids) had more grassland (51_{Mean}±7_{SE} % area), <50cm tall vegetation (50.49±2.21% area), grass height (0.47±0.05 m), cover (57.21±3.03 % area) and insects (2762±187 ha⁻¹) but shorter shrub height (0.98±0.08 m) than non-breeding patches (21±1 % grasslands %, 35.77±1.95 % <50cm tall vegetation, 0.30±0.02 m grass height, 39.97±2.78 % grass cover, 1450±72 ha⁻¹ insects, and 1.72±0.07 m shrub height in fortyfive 16km² grids). I used a relative abundance index to surrogate second-order site usage. This measure did not incorporate detection-correction and could lead to a biased assessment of grid use **only if** detectability varied over time and space. However, the index was convincingly correlated with actual detection corrected densities in a subset of 11 grids ($r=0.64$, $P<0.05$), where both measures were obtained through separate surveys. Alternatively, a double sampling approach could have been used to convert the index into corrected densities prior to habitat modeling (Eberhardt and Simmons 1987, Jhala et al. 2011, Pollock et al. 2002). But I avoided this approach since the doubly sampled units came from a single area and were not spatially representative of the entire landscape (fig 4.1 & 4.2). The second problem results from site fidelity of males towards display leks, and females towards nesting sites. Breeding philopatry can make individuals non-responsive to habitat changes (Lane et al. 2001) raising doubts on model inferences. I attempted to address this issue by restricting the analysis of display and nesting site selection to spatially paired resource units or choice sets. I used discrete choice analysis that stems from economic *utility* theory and estimates the probability of use of a resource unit among n available alternatives. Here I assumed that even though birds showed fidelity to traditional areas (defined as 3–4 km radius buffer around usage), they could possibly choose between available micro-sites within that. This was perhaps realistic since one nesting and display site were shifted after agricultural conversion, but birds continued using their vicinity for breeding purpose. To examine third-order habitat choice for daily activities, I used use-availability sampling tied with logistic regression, a widely used powerful statistical tool in wildlife studies (Manly et al. 2002). Although debated for issues of

contamination and overlap between used and available sets (Keating and Cherry 2004), recent evaluation has restored the validity of this technique under such designs (Johnson et al. 2006).

4.4.2 Differential selection of habitat structure based on season, sex and behavior

Bustard species are distributed across arid-semiarid Old World grasslands, and differ in their choices of habitat structure (del Hoyo et al. 1996, Johnsgard 1991). Even within a species, differential selection of habitat structure can arise from differences in gender, life cycle requirement, and season. For examples, in Bengal florican, males choose open grasslands while females choose more cover (Gray et al. 2009). In houbara bustard, habitat preferences change seasonally that appear to be influenced primarily by vegetation phenology, abundance and cover (Heezik and Seddon 1999). In case of GIB, subtle differences between gender, season and behaviour exist (Rahmani 1989) that have not been rigorously quantified so far. Such understanding is crucial for effective conservation, particularly when birds' response to landuse changes depend on these aspects. At a macro-scale, GIB occupied sites were characterized by dominance of grasslands, less ruggedness, more herbaceous vegetation (mostly <50cm) than bare ground, *Cymbopogon-Lepidagathis* grass and *Zizyphus-Vernonia* shrub assemblages, and more food resources. Birds were more selective of sites in summer, when usage was positively and strongly influenced by grasslands, flat terrain and minimal disturbances. In winter, birds opportunistically used productive sites with grassland dominated adjoining matrix, exhibiting more tolerance to disturbances. At a micro-scale, habitat requirements differed between life-history needs. Females nested in more 26–100cm tall vegetation (55_{Mean}% area) and less <25cm tall (44%) or >1m tall (1%) and scrub vegetation. Males displayed and birds roosted in more sparse cover (75_{Mean}% area) but less >26 cm tall (19%) and scrub vegetation. Resting sites were intermediate, characterized by 59_{Mean}% sparse cover, 33_{Mean}% moderately tall and 2_{Mean}% tall vegetation; while foraging sites were closely similar to the general habitat but with more food resources (fig 4.5).

Figure 4.5 Quartile distribution of seasonally z-standardized variables: percentages of a) bare ground, b) <25cm tall vegetation, c) 26–50 cm tall vegetation, d) 51–100cm tall vegetation & e) >1m pressure index; ranks of f) grass height, g) grass cover, h) shrub height, j) shrub cover, i) grazing insect $10m^{-1}$ and o) reptile $20m^{-1}$; p) fruit availability index, and q) %frequency occurrence of scrub-forest (oblique shade) cover types at Nesting (N), Display (D), Foraging (Fo), Resting (Re), and Available (A) sites in core bustard area of Kachchh (2007–11)



Some gender differences were also observed in vegetation structure of preferred foraging sites. As hypothesized, patches accommodating such diverse habitat envelopes for daily activities also harboured higher breeding bird densities. Securing large contiguous patches that naturally include structural heterogeneity or managing small patches to provide such heterogeneity is thus crucial to accommodate life cycle needs of birds.

4.4.3 Management implications

4.4.3.1 Grazing

Bustards have coevolved with wild ungulates and depend on grazers to maintain a suitable habitat structure. Since the last thousand years, community of wild grazers has been steadily replaced by domestic livestock in most of the bustards' range outside Africa (Skarpe 1991). The role of livestock grazing in GIB conservation has been a contentious management topic. Earlier studies have speculated detrimental effects of livestock grazing on these birds based on non-quantitative data (Rahmani 1989, Rahmani 2006). Broadly speaking, the effect of herbivory on stimulation of primary productivity follows a hump-shaped pattern leading to the "grazing optimization conceptual model" (Hilbert et al. 1981, McNaughton 1979). A high net primary production implies increased insect abundance (Whitford and Creusere 1977) – a chief constituent of bustard diet (Bhushan and Rahmani 1992). Theoretically, intermediary levels of livestock grazing will be beneficial to these birds. I have tested this prediction by modeling birds' site usage with grazing pressure index at two scales.

Livestock grazing was less in occupied macro-sites than unoccupied ones. Grazing was negatively correlated with vegetation and insect count, or productivity, at this scale. Productivity was an important predictor of macro-site usage in winter. Choice of micro-sites depended on livestock grazing only for foraging and nesting uses (table 4.10, 4.16). Birds, expectedly, selected moderate grazing pressure for foraging since less grazing would lead to high vegetation growth and less visibility, while over-grazing would lead to food scarcity. Nesting choice was negatively related to livestock grazing pressure. Past studies occasionally reported livestock trampling of GIB nests (Rahmani 1989). However, the association of herders and domestic dogs with livestock caused more disturbances to nesting birds that were known to abandon nests due to human interference (Rao and Javed 2005). Conservation management should therefore maintain

therefore maintain intermediary levels of grazing pressure in GIB habitats, and exclude livestock from prime nesting areas during peak breeding season. The latter is not difficult since GIB is a site-specific restricted area breeder, and nesting areas are generally known.

4.4.3.2 Agriculture and landuse changes

Much of the arid-semiarid GIB landscapes have been traditionally subjected to low-intensity agriculture, characterized by monsoon crops, long rotation period and organic farming. But recent developments in irrigation policies and technologies have favoured water availability and agricultural expansion in these regions. Subsequent changes in cropping pattern from traditional monsoon crops (like groundnut and millet) that provide ideal GIB habitat to year-round pesticide-intensive cash crops (like sugarcane, grapes, cotton and horticulture) are widespread. Some instances are the Indira Gandhi Canal Project (Rajasthan), Narmada canal project (Gujarat) and ground water extraction through electric pumps. Earlier studies on GIB have reported the occurrence of birds in low-intensity agro-grass systems but have speculated adverse effects of intensive farming on them (Dharmakumarsinhji 1978). I have tested this prediction in Kachchh, where grasslands are being extensively converted to agriculture since the last 5–10 years. Here in the core GIB area, conversion rate has increased in last 3–5 years, characterized by ~20% natural area conversion, mostly illegal, into cultivation of *Bt*-cotton crop. Such changes also include reduction of crop-rotation period and unpredictable substrate changes. Global bustard initiatives have identified the comprehensive understanding of birds' responses to landuse types as a vital research input for effective conservation of their habitats (Lane et al. 2001, Silva et al. 2004, Wolff et al. 2001).

I observed that grassland area in 16 km² grids and their adjoining dispersing matrix were strong positive predictors of bird usage, and were twofold more in occupied macro-sites than unoccupied ones. Conversion of grassland area to any other purpose would likely be detrimental to GIB. Birds responded variedly to agriculture for micro-site choice: grassland and low-intensity agriculture were selected but intensive agriculture was avoided compared to scrubland, for foraging and roosting use; while nesting was exclusive to grasslands (fig 4.3, table 4.10–4.16). Because of the unpredictable landuse changes, I could not estimate substrate availability from the proportion of surface area, and resorted to a non-mapping technique of assessing the proportion of sample plots (systematically laid 100-m radius circular plots) in different substrate types. Jacob's

selectivity index $D = \frac{r - p}{r + p - 2rp}$ (where r and p were proportional use and availability of a substrate, see Jacobs, 1974) ranked grass cover as the most and cropped field as the least preferred substrate types. Birds preferred grass cover ($D=0.36$) > fallow fields (-0.20) > shrubby cover (-0.25) > bare or ploughed field (-0.48) > cropped fields (-0.58) for overall use ($G=17.02$, $df=4$, $P=0.002$). They preferred fallow fields ($D=0.36$) > grass cover (-0.01) > shrubby cover (-0.07) > cropped field (-0.46) > bare or ploughed field (-0.61) for foraging use ($G=7.72$, $df=4$, $P=0.10$).

A similar study on great bustard (Lane et al. 2001) observed birds to prefer stubble fields and avoid ploughed and uncultivated areas. Another study on little bustard (Bretagnolle et al. 2011) observed remarkable recovery of the population after providing favourable crops through Agri-Environmental Incentive Schemes (AIS). Conservation management should reduce agricultural expanse and intensification in GIB habitats. To avoid antagonizing local populace in the process, implementation of well-informed AIS might be considered, such as 1) shifting to organic farming of seasonal GIB-friendly crops (see Bretagnolle et al. 2011), 2) subsidizing farmers for voluntary reduction in cropping frequency, 3) compensating pastoralists by fodder supplementation to prevent livestock grazing in nesting areas during the wet season, and 4) securing critical breeding habitats by purchasing private or community lands through Government channels. It would be possible to loop such schemes and internalize their costs-benefits by innovative ways, such as buying back residual production from organic farming to supplement livestock fodder. The AIS would benefit birds as food supply would increase and possible nest trampling would minimize. Local communities would be benefited as pasture productivity and lean-period fodder supply would increase (Donald and Evans 2006).

4.4.3.3 Infrastructure and disturbance

Infrastructural development in terms of mining, industries, roads, electricity, and wind power generation have been widespread in many GIB landscapes including Kachchh over the recent past (Anon, 2011). Apart from being a new source of disturbance, unfriendly infrastructure increases mortality risks of adult birds from fatal collisions with human superstructures. Such instances have been reported from Kachchh and Sholapur (Anon 2011).

I observed that modernity index, measured as a) working proportion of population, b) income per household, c) hospital, d) telephone, e) bank and f) power facilities in the 4-km radial

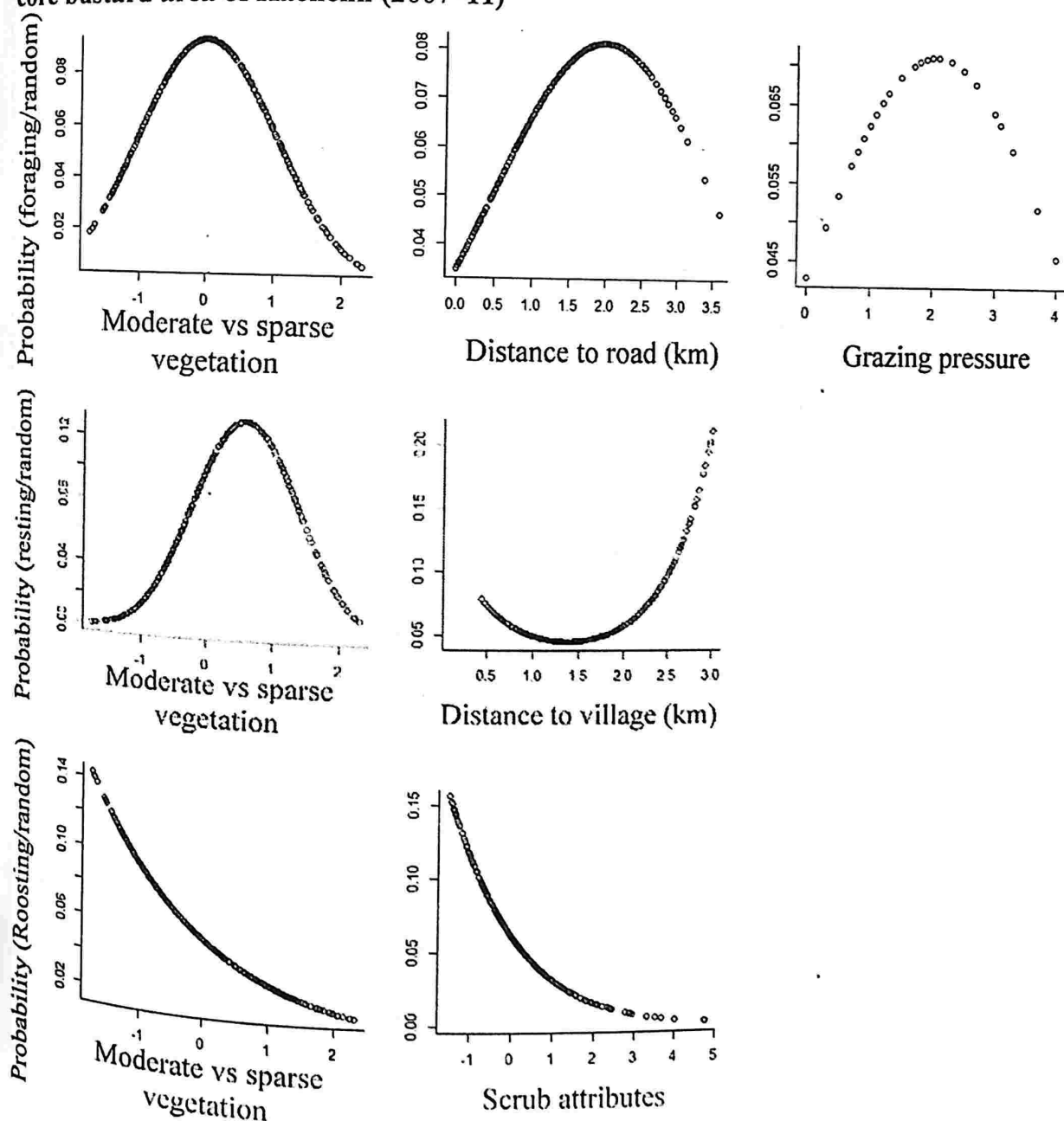
zone of influence, was lower in occupied 16-km² grids than unoccupied ones (table 4.4). At this macro-scale, disturbance was indexed by a principle component that was positively correlated to agricultural area, village count, household count, human population, literacy to illiteracy ratio, irrigated to unirrigated area, and modernity index. Disturbance was a strong negative predictor of summer/breeding usage by birds but not of wintering usage (table 4.6, 4.7). Micro-scale disturbance was measured as distances from use and available points to nearest trail, road and village. Background disturbance was characterized within the core bustard area, where available plots within or very close to villages were not sampled. Hence results should be interpreted as preference within the tolerable limits of disturbance. Birds variedly responded to the above disturbance measures. For e.g., nesting use increased with distance from road with central 50% (25–75% percentiles) observations (2nd & 3rd quartiles, hereafter Q2–3) within 0.9–1.9 km. Birds tended to maintain greater distance from habitation for display (Q2–3 1.9–2.5 km) as also nesting use (Q2–3 0.9–2.3 km). Interestingly, foraging use peaked at intermediate distance from road (Q2–3 0.8–1.7 km) probably to trade-off the disturbance costs but food benefits of human-modified areas. Compared to random locations, birds used slightly greater distance to trail for nesting and display (Q2–3 0.09–0.35 km) but not for other activities (fig 4.5). Although passive disturbances did not exert strong negative effects on site selection contrary to expectation, suggesting some tolerance of GIB, they were always cautious of active human presence (details in chapter 5). Prolonged human presence reduced the foraging efficiency of birds and often caused them to escape (pers. obs.) that could be thermally stressful and fatal for a low-flyer in human-modified landscapes. Avoidance was more towards new forms of disturbance (e.g., vehicles and mechanized farming) compared to traditional human artifacts (e.g., bullock carts, see Rahmani 1989 and solitary farmers, pers. obs.). Conservation management should minimize active human presence in GIB habitats, and sensitize local populace, photographers, and tourists to avoid approaching these birds closer than 100–200m particularly during their breeding season.

4.4.3.4 Plantation

Traditionally, grasslands and scrub have been considered as “wasteland” and the Forest Department policy, until recently, has been to convert them to “forests” with plantation of fuel/fodder shrub/tree species, even exotics like *Prosopis juliflora*, *Gliricidium*, and *Eucalyptus* spp., under social forestry and compensatory afforestation schemes (Forest (Conservation) Act 1988, Indian Forest Act 1927). Since bustards are generally known to prefer open habitats with

high visibility, I have tested the prediction that birds' usage will be negatively related to such shrub/tree plantation. Scrubland area and shrub height was low, but not significantly, in occupied macro-sites than the unoccupied ones, probably because the surveyed area had generally low levels of scrub attributes tolerable to the birds (table 4.4). Birds preferred short *Zizyphus-Vernonia* scrub-assemblage particularly in winter to benefit from *Zizyphus* fruits (see chapter 5). Scrub characteristics influenced birds' choice of microhabitat: roosting use declined most strongly followed by declining tendency of display, nesting and resting uses, whereas foraging use peaked at relatively low levels along increasing scrubbiness. Indian State Forest Departments should therefore abandon and reverse shrub/tree species plantation programmes in GIB habitats.

Figure 4.6 Estimated relative probabilities of selecting resource units by Great Indian bustard for foraging (top panel), resting (middle), and roosting (bottom) along few important habitat gradients in core bustard area of Kachchh (2007–11)



4.4.4 Comparative review of bustard–habitat relationships

Similar patterns of habitat responses had been observed in other bustard species. Broadly speaking, they inhabit a range of short–grassland to open–woodland habitats on flat terrain subjected to fewer disturbances (Gray et al. 2007, Heezik and Seddon 1999, Lane et al. 2001, Osborne et al. 2001, Silva et al. 2004, Wolff et al. 2001, Ziembicki 2009). Great bustard and little bustard had benefited from extensive agriculture in steppe habitats but intensification of farming (reduced crop–rotation–period, pesticide use, mechanization etc.) led to their population declines (Lane et al. 2001, Wolff et al. 2001). Similarly, GIB preferred grasslands, followed by extensive agriculture (fallow–fields and agro–vegetation edges) but agricultural intensification had been the most likely cause behind its population decline from 2008 to 2011 in Kachchh (details in chapter 3). While great bustard avoided human structures (e.g., roads, tracks and power–lines, see Lane et al. 2001) and houbara bustard was sensitive to human disturbances (e.g., livestock, human presence etc., Heezik and Seddon 1999), the Bengal florican males were more tolerant to such disturbances (Gray et al. 2007). Distribution of GIB was negatively influenced by human disturbances at larger scales mostly during the breeding season.

Nest selection by bustards could be driven by a trade–off between concealment and visibility that minimized predation pressure. Nesting female great bustard preferred fallow and cereal fields with good horizontal visibility (Magana et al. 2010) while houbara bustard preferred sparse vegetation and avoided dense or tall cover (Yang et al. 2003). The GIB in Kachchh preferred dense cover of 26–100cm vegetation and avoided bare–ground and >1m tall scrubby vegetation. Such site selection supported the above hypothesis that nesting birds simultaneously required concealment and surveillance facility while incubating (also see Magana et al. 2010). The marginal replacement rate of concealment (more cover) by visibility (less cover) might vary with landscapes, depending on local adaptation to reduce predation. For e.g., in Madhya Pradesh, a savanna habitat with sparse ground cover, female GIB are known to nest in bare areas (Rahmani pers. comm.).

4.4.5 Recommendations

It was observed in great bustards that strong site fidelity and conspecifics probably determined distribution, leaving suitable habitat elsewhere unoccupied (Lane et al. 2001). The same seemed valid for GIB, where grassland patches farther from the lek and known to be occupied in the past, were currently unoccupied. However, it should be considered that suitable

habitat (modelled from species occurrence data) might not accommodate the varied resource envelopes required by different activities, sex and season, within or in vicinity, preventing their continued usage. Paucity of information on ranging patterns between fragmented resource envelopes was a pitfall in this context, and should be immediately addressed through biotelemetry research. However, conservation management should immediately secure all traditional breeding areas, which were mostly known from the past but getting highly endangered. Large, contiguous and structurally heterogeneous habitats should be maintained or created around them (Wolff et al. 2002) by enforcing the above-recommended scientific habitat manipulations and landuse planning through legislative provisions. But considering the wide ranging nature of this bird at least for some important aspects of its life-history, other priority areas in the landscape should be gradually identified by understanding their movements within and between landscapes. These areas should be brought under flexible conservation regimes, such as (a) Conservation Reserve, (b) Community Reserve, and (c) Ecologically Sensitive/Fragile Area (Section 5 of Environment (Protection) Act 1986, Section 31 of Wildlife (Protection) Amendment Act 2003) by addressing local livelihoods (Dutta et al. 2011) through a sustainable use approach (IUCN 1991).

Chapter 5. Behavioural Ecology

5.1. Introduction

Conservation biology is a multidisciplinary *crisis* science that studies anthropogenic effects on wildlife populations and applies that learning to solve real world problems (Soulé 1985). Despite significant progress in the discipline of animal behaviour, its applicability in conservation biology has been recognized only recently. A shift of interest from pure understanding of how behavioural patterns influence survival and reproduction of animals (Anthony and Blumstein 2000, Krebs and Davies 1993) to using that knowledge for fixing conservation problems has been advocated since 1990s (Gosling and Sutherland 2000). Given that individuals make decisions to maximize fitness; knowledge on their resources, behavioural strategies, mechanisms of competition, and fitness consequences can be integrated into behaviour-based models to estimate population parameters under predicted scenarios for species management (Norris 2004). This calls for behavioural case studies of endangered and flagship species at the interface of local conservation issues as policy makers often target them to conserve whole ecosystem processes (Caro 2007). One important conservation threat faced by grassland ecosystems of the Indian subcontinent is from expanding modernization into remote areas, facilitated by more accessibility, technovations, and policy changes. This has led to fragmentation of habitats, increased hunting, and disturbance from human presence and structures (Anon 2011). These developments can interrupt movements, foraging and other activities depending on the species' characteristics. In such cases, human use should be minimized in key habitats, which is often challenging and runs the risk of antagonizing and detaching local communities from the path of nature conservation. For all these reasons, accurate quantification of disturbances, species-specific responses, and tolerance mechanisms are crucial (Gill et al. 2001). Behavioural studies can be an effective tool in such situations.

The GIB is a Critically Endangered bird (IUCN 2011) endemic to the Indian subcontinent and a conservation flagship for semiarid grassland fauna. Extreme *k*-selected life history compounded with anthropogenic pressures threaten their persistence in the immediate future (Dutta et al. 2011). Although rural population density, the strongest correlate of habitat alterations, has been predicted to decline in future responding to urbanization (United Nations 2004), at least currently, the GIB habitats are facing manifold higher and modernized human demands along

with related disturbances than the recent past (Dutta et al. 2011). While earlier works have broadly described some behavioural aspects of the species (see Rahmani 1989 for review), quantitative information and clear conservation links are missing. All these direct towards augmenting behavioural understanding of GIB in the light of above perspectives. I have focused on four such aspects in this chapter: 1) activity budgets; 2) benefits of flocking; 3) courtship behaviour; and 4) feeding habits. I illustrate the scientific and conservation values of each of these aspects, and their specific research questions in the following section.

5.1.1. Behavioural pattern

Behavioural acts are motor patterns triggered by changes in the internal and external environments to carry out proximate functions that have ultimate fitness consequences (Huntingford 1984, Krebs and Davies 1993). Since time and energy spent on one act reduces that on others, individuals face trade-off decisions in apportioning time between acts (Sibly and McFarland 1976). Such trade-offs will be adaptive in nature, i.e., depend on environmental and individual conditions (Paulus 1988) in order to maximize fitness. Conditions that may influence these decisions are individuals' age (Sullivan 1988) and gender (Enoksson 1990), presence of conspecifics (details in section 5.1.2., see Caraco 1979), time of day (Frederick and Klaas 1982), season (Weathers and Sullivan 1993), habitat (Martinez 2000) or abiotic factors like temperature (Combreau and Launay 1996). Time-activity budgets describing proportion of time spent on acts under different environmental conditions (Paulus 1988) provide the foundation for detailed understanding of behavioural processes.

The GIB is a large terrestrial bird, in which adult males reach up to 1.2m height and 11–15 kg weight while females reach up to 0.9m height and 4–7 kg weight (Elliott 1880, Rahmani 1989, Vyas et al. 1983). They range widely, and fly less often mostly close to the ground (BirdLife International 2001) rendering them prone to collisions with modern infrastructures (Janss and Ferrer 2000). Their habitats are typically semiarid sparse grasslands with scattered short scrub and low-intensity cultivation (Rahmani and Manakadan 1986). Within these habitats, they prefer <1 m grass height that allows vigilance (Rahmani 2001). They are mostly diurnal, broadly active during 0630–1200 and 1630–2000 hours IST although with some seasonal variations (Rahmani 1989); such patterns resembling that of the closely related Australian bustard *Ardeotis australis* (Ziembicki 2009). Complying with patchy food distribution, individuals do not guard resource

territories, but exploit a wide array of foraging grounds through local movements in temporary flocks. Consequently, they do not retain the same resting and roosting spots over a long run (Rahmani 1985). Ali and Ripley (1969) have described them as resident and seasonally nomadic. They congregate in select patches during mid-summer and monsoon (April–September) to breed (Goriup 1983) when males display elaborately from traditional arenas (Rahmani 1991). Although the species has evolved amidst several predators that may have determined its present behavioural patterns, the only extant predators on the adult birds are the wolf *Canis lupus pallipes* (Rahmani and Manakadan 1987) and perhaps jackal *Canis aureus*. However, species like the Indian fox *Vulpes bengalensis*, crow *Corvus* spp., mongoose *Herpestes* spp. and monitor lizard *Varanus bengalensis* pose threat to their eggs, while domestic dogs are known to predate on chicks (BirdLife International 2001, Saxena and Sen 1983). Probably due to historical hunting pressures, these birds show prominent human avoidance nature (Rahmani 1989). In spite of being a well-studied species, published information on their time-activity budgets are lacking.

My study objectives were to estimate 1) activity budgets and 2) environment in terms of flock size and disturbances, segregated by seasons, daily hours, and gender. I addressed these objectives by scan sampling of birds, recording behaviours as functional states (Altmann 1973).

5.1.2. Functions of flocking

Conspecifics form an important component of individuals' environment influencing their behaviour in several ways (Caraco 1979). The selective function of flocking is possibly an outcome of multiple benefits over costs. The benefits most likely include reduced vigilance (Pulliam 1973) due to many eyes (Elgar 1989b, Lima 1994) and efficient detection of threats (Beauchamp 2003, Jones et al. 2009), enhanced foraging efficiency in the long and short terms (Cody 1971, Krebs et al. 1972, Thompson et al. 1974), and/or social learning (Murton 1971). The latter has attracted a large body of recent literature, and may include transfer of acts from conspecifics (Fritz and Kotrschal 1999) or their altered performance in presence of conspecifics (called social and response facilitation, see Broom 1999, Hoppitt et al. 2007). How flocking may benefit individuals in terms of feeding have been explained by game-theoretic models. These models highlight benefits of acquiring information about resources from conspecifics and predict that flocking will be particularly preferred under scarce and patchy resources (Clark and Mangel 1984). On the other hand, the costs involved are aggressive interactions from increased crowding

intrusive competition, see Bednekoff and Lima 2004) and food depletion (exploitative competition, see Hart 1987). Birds may choose to flock if proximate benefits outweigh costs, and this ratio will depend on ecological factors such as resource vs. threat levels (Amano et al. 2006). Thus, under variable environment, flock size will also be adaptive in nature to maximize fitness.

The GIB is a gregarious species found in spatial aggregations. Males and females generally occur in separate flocks and flock sizes vary across seasons and sites (Rahmani 1991, Rahmani and Manakadan 1986). Conspecifics are likely to play important functions influencing survival value of individuals, but those mechanisms are not known for this species. Since flock size is most possibly a function of patch size and quality, which are being affected by ongoing human alteration of habitats, understanding environment specific benefits of flocking is important.

My study objectives were to test whether flocking 1) reduce vigilance rate thus allowing more time for other behaviours; 2) increase feeding rates (Rahmani 1989); and/or 3) transfer certain acts such as preening (Hoppitt et al. 2007, Nicol 1989) through social facilitation (Broom 1999). These functions seemed likely from field observations and theoretical perspectives. I compared scan samples of behavioural states between solitary and flocking birds to answer these questions. Frequency of acts differed widely among males during the breeding season depending on their social dominance and courtship status. Whereas during the non-breeding season males mostly occurred in flocks and solitary males were rare that precluded such comparisons. Hence, I included only adult females in analyses, which showed variation in flock sizes within each season.

1.3 Courtship behaviour

When conspecifics vary in traits that can influence the outcome of their competition over mates, differences in reproductive success ensue in the population (Andersson 1994). This process, sexual selection, has evolved many conspicuous traits or secondary sexual characters which do not carry any apparent survival value (Darwin 1859, Darwin 1897). Among these are, mate-competition via contests (intrasexual selection, see Huxley 1938) promoting sexual size dimorphisms and weaponry (Selander 1972), and that via mate choice (intersexual selection, see Huxley 1938) promoting wasteful ornaments and behavioural traits (or sexual diethism, see Johnsgard 1994). The latter involves acoustic (Searcy and Andersson 1986) and visual signaling (Goransson et al. 1990) such as courtship displays, often characterized by complex repertoires (del Hoyo et al. 1996, Johnsgard 1994). Such displays are common in bustards that also exhibit sexual

chromatism and species-specific sexual size dimorphism (mean male/female body mass of selected species ≈ 2 , see Bennett and Owens 2002) The larger species perform ground displays that may have favoured larger male body size, while smaller species perform aerial rocket displays favouring similar to smaller male body size (Sankaran 1997). *Ardeotis* bustards perform "balloon" display, where the male inflates its oesophagus, raises its tail, and vocalizes. This long-distance signaling is highly effective in their open habitats (Johnsgard 1991) and can be seen even from a kilometer away (Rahmani 1989). Although these general features are maintained across species, the shape and size of balloons and repertoires vary (Johnsgard 1994). Courtship behaviour of GIB has been described by many authors (Dharmakumarsinhji 1962, Hume and Marshall 1879, Rahmani 1989). In Rahmani's words (1989) "adult cock selects a prominent place...struts with a semi-pendulous gular pouch...stands and looks all around, holding his head as high as possible. Slowly he puffs and the chin feathers are erected...gular pouch starts inflating...hangs like a balloon...tail is cocked...every 14 seconds it gulps air and utters a deep moaning resonant call... (made of) three sounds...a low *chuck*, a deep booming call, and a slow and long *burr* (by inhaling air, resonating it inside the gular pouch and expelling it)". Display peaks at early monsoon, intensifies during early morning and evening hours with occasional displays at moonlit nights, and continues from 5 minutes to 2–3 hours (Rahmani 1989). While these descriptions provide the blueprint of GIB courtship hinting on a wide collection of component acts, my aim is to augment and substantiate on their release, structural composition and proximate causation through systematic quantitative information. One potential correlate of courtship is female density in arena (Rahmani 1989) which has direct conservation implications through the onset of *Allee* effect (Stephens et al. 1999) for such traditional breeders. Other correlates can be weather conditions, time of day and anthropogenic disturbances (Rahmani 1989).

Sexually selected characters are associated with mating systems (Bennett and Owens 2002) and may have greater selective value in polygynous species (Selander 1965). Males of some polygynous species do not participate in parental care at all (Bradbury 1981), and display in aggregated spots, hereafter *arenas* (sensu Armstrong 1947) which females visit solely for mating (Höglund and Alatalo 1995). This mating system, lekking, is very rare and found in <0.5% birds (Davies 1991). Arenas may be separated by large distances in some species, a condition known as exploded lek (Höglund and Alatalo 1995, Morales et al. 2001). Twenty out of 25 bustard species exhibit exploded lek mating system (Morales et al. 2001) but it is becoming clear that mating

aggregations depend on ecological factors and can vary between populations (Isvaran 2005). For e.g., the great bustard mating system ranges from resource based territories to typical leks (Carranza et al. 1989). The general mating system of the GIB is probably exploded lek (Ali and Rahman 1984) where male arenas are separated by large distances and are highly traditional (BirdLife International 2001). Lek formation has been explained as: 1) female preference for mating in large aggregations of males for benefits (Bradbury 1981) such as predation avoidance (Gosling 1986), reducing search of mates (Alexander 1974), comparing mates (Emlen and Oring 1977) etc.; 2) highly skewed mating generates opportunities for subordinate males to increase their mating chances through proximity to attractive or 'hotshot' males (Beehler and Foster 1988); and 3) female space use generating locally high encounter rates or 'hotspots' that induces clustering of male arenas (Bradbury and Gibson 1983). Field studies have shown that clustering of arenas can be driven by both the first and second hypothesis but they fail to explain why arenas are clustered where they are (Gibson 1996). The third hypothesis holds much promise in this regard (Bennett and Owens 2002) although lacking wide acceptance due to mixed results of empirical studies (Gibson 1996). Arena species have very specific habitat requirements during the breeding season that renders destructions of leks as one of the most serious conservation problems (Anthony and Blumstein 2000). My aim is to study mating aggregations of GIB. I have defined arenas as 1km consolidated buffer around all locations of a male since displaying bustards confine their daily movements mostly within this area and are generally visible to human eye, and presumably to females across this distance (Rahmani 1989).

The study objectives were to 1) describe space use of male and female birds during the breeding season; 2) examine the proximate environmental correlates of courtship release; and 3) describe the structural composition of courtship acts. I addressed the first objective by mapping female encounter rates at 4-km² grids which matched their daily movement scale; and male occupancy at arenas on a spatio-temporal basis, thereafter examining their correspondence patterns. I addressed the second objective by instantaneous sampling of males in arenas and modeling courtship frequency with arena environmental factors, such as female density, disturbance and weather conditions. For the third objective, I categorized courtship acts into a catalogue and developed a novel method for quantifying courtship structure from deviations from a benchmark "normal" posture, thereafter examining how courtship structure depends on arena environment.

1.4. Feeding habits

Foraging is the sole mechanism by which birds acquire energy for all life-history actions. Searching and handling food items involve the expenditure of metabolic energy (Maurer 1996), hence individuals will try maximizing the balance-sheet between energy intake and loss. Morphological and behavioural adaptations to facilitate this outcome in the face of competitive interactions have presumably evolved under selective pressures the specific foraging apparatus and diet choices of species (Stephens and Krebs 1986). Thus trophic resources determine several ecological aspects, and are required in adequate quantities to sustain populations (Manly et al. 2002). Accurate knowledge of species' diet, food abundance, and preference are therefore crucial. Such information can address many conservation questions, such as carrying capacity of patches, possibility of seasonal food depletion, consequences of habitat changes (Sutherland 2004) and in case of agro-grassland birds, the implications of modern agricultural food (Anon 2011).

The GIB has been described as a generalized forager (Ali and Ripley 1969); consuming insects, plant matter, *Zizyphus* fruits, crops, lizards, and rodents (Bhushan and Rahmani 1992). Among insects, *Orthoptera* and *Coleoptera* were mostly consumed along with small quantities of *Hymenoptera* and *Dictyoptera*. Among crops, soya *Eruca sativa*, Bengal gram *Cicer arietinum*, groundnut *Arachis hypogea* and millet *Hordeum vulgare* were consumed (Rahmani 1989). Since availability of water is less in their dry habitats, birds presumably obtain moisture from fruits, roots and invertebrates (Vyas and Jacob 1983). These studies reported fecal dry weight composition of food items on a monthly basis in three study sites: Karera (Madhya Pradesh), Mananjari (Maharashtra) and Rollapadu (Karnataka). However information on the abundance and preference of food items, important to assess foraging choice decisions (Manly et al. 2002), are scanty. Moreover, in the intervening period of 20–30 years, most GIB landscapes have undergone land use changes that can potentially interfere with the species' dietary requirements. Variability in food can force a forager to new diet although such transformation takes time (Morse 1980). My study aims at determining seasonal feeding habits of birds in Kachchh that represent a different region and more modified environment than previous studies.

This landscape has originally been a mix of short grasslands interspersed with short scrub. Traditional agricultural practices include seasonal dry farming of GIB-palatable crops, such as sesame, pulses, millets and groundnut. However, in response to electricity powered deep bore tube wells and relatively more rainfall in recent years, local people have intensified their farming

practices and immigrant farmers have introduced year-round *Bt*-cotton cultivation. Such changes can affect birds, in terms of reduced availability of natural food, more contribution of crops to the diet, and possible detrimental effects of pesticides to birds' physiological processes. Semiarid ecosystems are characterized by strong seasonality and annual fluctuations of food items. Energetic requirements for life-history activities, and hence diet choice, are also likely to vary seasonally. The unknown movements of GIB (Rahmani 1989) may be partly influenced by such seasonal food and feeding regimes. A clear understanding of these aspects can aid in the formulation of land use conservation policies. The study objectives were to: 1) determine seasonal diet composition, for which I analyzed fecal pellets (Korschgen 1969) and corrected for digestibility differences using published literature; 2) estimate seasonal densities of natural food items, for which I sampled the core GIB habitat along belt transects; and 3) assess the order of preference of natural food items, for which I compared their dry weight composition in diet and proportion biomass in the environment following Johnson (1980).

5.2. Methods

The GIB occur at very low densities of 0.05 km^{-2} in fragmented habitats across $\sim 1000\text{-km}^2$ landscape in Kachchh. Their rarity, human avoidance nature, and vagrant movements constrain sampling techniques and systematic collection of adequate data for robust description and inferences on behaviour. To yield observations with relative efficiency, I focused field efforts in $\sim 150 \text{ km}^2$ core bustard usage ($23.21^{\circ}\text{N } 68.78^{\circ}\text{E} - 23.23^{\circ}\text{N } 69.05^{\circ}\text{E}$). This area harbours $\sim 75\%$ birds of the population round the year in five contiguous patches (section 2.1). I conducted fieldwork from November 2008 to February 2011, covering winter, summer and monsoon seasons (section 2.3).

5.2.1. Behavioural pattern

5.2.1.1. Field sampling

Time-activity budgets of diurnal species are conventionally estimated from 12 hours daylight data. However, a reconnaissance survey in July-December 2007 confirmed that birds ceased most of their activity during mid-day, i.e., 1230-1630 hours IST (also see Rahmani 1989). I was interested in estimating time apportionment to major behaviours during the active phase of birds, which I referred to as active-time-budget hereafter. It should not be confused with diurnal

time-activity budget in the conventional sense of the term since it underestimated the proportion of resting behaviour. However, it would be possible to reconstruct diurnal time-activity budget from active-time-budgets by assuming $\approx 80\%$ resting during mid-day. I confined most of the field work (89% days) to two peak months in each season, viz. April-May, July-August, and January-February. On these months I searched birds from sunrise to sunset with daybreak during 1230-1430 hours along fixed routes that exposed the study extent to uniform search efforts. On encountering birds, I selected them for sampling if there was a suitable vantage location (a slightly elevated point with natural hide that provided unobstructed view of the subject within 100-500m). I observed bird behaviour following instantaneous and scan sampling techniques (Altmann, 1973) at 5 minutes interval till they moved out of sight or had rested for $\sim 20-30$ minutes. Since this mostly happened during late morning sessions that represented only 4% of sampling coverage (table 5.1), it could lead to some incosequential underbias in resting allocation. I terminated this activity after 3-5 successful sampling days per month. I classified bird behaviour into the following mutually exclusive and exhaustive states (Lehner 1979) based on the reconnaissance:

- 1) Resting – sitting with head drawn against the body;
- 2) Vigilance – standing with head erect and scanning around;
- 3) Moving – walking with head and neck erect or bobbing;
- 4) Foraging – standing or walking with neck down while feeding or searching for food;
- 5) Preening – also included occasional acts like dust bathing (Rahmani 1989), scratching, flapping wings and puffing up feathers (Lichtenberg and Hallager 2008);
- 6) Courtship – included display behaviour (standing, encircling or walking with head straight or up, neck straight, tilted or curved, air sac enlarged into gular pouch and balloon, tail cocked, and occasional 'booming' calls) and territorial agonistic rituals; and
- 7) Other acts – included rare acts like flight, drinking and mating.

I used direct observation aided by 8 x 50 binoculars and stopwatch to record these behavioural acts for $2.9_{\text{Mean}} \pm 1.9_{\text{SD}}$ (range 1-9) hours per sampling day (table 5.1). When I encountered two simultaneous acts, for e.g., when an individual was feeding with enlarged air sac and cocked tail (foraging + courtship), I assigned a "0.5" occurrence to each act. I kept a tally of undetected individuals during each scan. I quantified the environment of scanned bird(s) in terms of 1) flock size (counts and age-gender composition of conspecifics showing coordinated movements); 2) disturbance (occurrence of humans, vehicles, and potential predators such as dogs,

jackals and raptors within 500m); and 3) weather (cloudy, rainy, bright, sunny or dusk). Between successive scans, whenever feasible, I recorded pecking rates of a focal bird for 3–4 minutes as the frequency of feeding strikes and their vertical strata, categorized as ground (<5cm), low (5–50cm) and high (51–100cm) strata.

5.2.1.2. Data analysis

All through the chapter, I had referred to 1) a scan as the parallel observations on a group of individuals; 2) a bird-scan as an observation on any one of those individuals (implies for solitary birds scan \equiv bird-scan); and 3) a scan-hour as observations lumped into hourly intervals (7AM: 0700–0759, 8AM: 0800–0859, 9AM: 0900–0959, 10AM: 1000–1059, 11AM: 1100–1159, 5PM: 1700–1759, 6PM: 1800–1859, 7PM: 1900–1959 hours IST) on each sampling day (table 5.1). Within a scan-hour sample, I generated the 1) proportion of time spent on each behaviour as bird-scans exhibiting that behaviour divided by total bird-scans; 2) mean flock size; 3) peck rate as total pecks divided by total observation time; and 3) frequency occurrence of disturbance as the proportion of scans where disturbance occurred. I used hourly measures as replicates provided they had ≥ 4 scans to avoid less reliable replicates from influencing results. Such data lumping was a preferable trade-off between treating each scan as replicate (that would potentially generate several pseudo-replicates) versus daily set of scans as replicate (that would erase time tags and pool non-uniform sample sizes). I quantified daily and seasonal patterns of time allocation to various behaviours by birds and their environment. For this, I stratified replicates into 18 subsets according to day periods (early morning: 0700–0859, late morning: 0900–1159 and evening: 1700–1959 hours IST), gender (male and female), and season (summer, monsoon and winter). I constructed daily activity patterns by averaging hourly proportional time spent on behaviours across sampling days for each data subset. I constructed seasonal activity budgets by averaging across hourly mean proportional time spent on behaviours for each gender. I preferred this over global averaging since sampling was non-uniform across activity hours (generally more during 8–10 AM and 6 PM). I estimated daily and seasonal patterns of flock size, pecking rates and disturbance in similar ways. I attempted normalizing data on proportional time spent in behaviours by arcsine transformation and pecking rates by square root transformation. After checking for data normality by Kolmogorov–Smirnov tests, I tested if transformed distributions differed between seasons and day periods by two-way ANOVA. I tested if frequency occurrence of disturbance

differed between seasons by Kruskal–Wallis test. Analyses was done following Zar (1999) in program SPSS v 16 (SPSS 2007).

Table 5.1. Sampling efforts for behavioural study of the Great Indian Bustard, as 5–minutes interval scans and days (in parentheses) grouped by gender, seasons and activity hours in Kachchh (2007–11)

Gender	Season	Early morning		Late morning		Evening			Day	Subtotal	Total
		7 AM	8 AM	9 AM	10 AM	11 AM	5 PM	6 PM			
Female	Summer	44 (6)	110 (13)	103 (12)	34 (5)	6 (1)		43 (5)	32 (6)	372 (21)	824 (45)
	Monsoon	9 (1)	34 (5)	38 (4)	36 (4)	8 (1)	4 (1)	30 (3)	25 (3)	184 (11)	
	Winter		18 (3)	77 (8)	61 (6)	7 (1)	44 (6)	61 (7)		268 (13)	
Male	Summer	73 (9)	120 (13)	113 (12)	58 (7)	6 (1)	4 (1)	99 (11)	78 (12)	551 (22)	1222 (45)
	Monsoon	6 (1)	86 (10)	116 (11)	113 (10)	59 (7)	4 (1)	78 (10)	98 (10)	560 (17)	
	Winter		13 (2)	34 (3)	17 (2)		11 (1)	31 (4)	5 (1)	111 (6)	

5.2.2. Functions flocking

5.2.2.1. Vigilance

First, I asked whether individual vigilance decreased with flocking, thus providing more time for feeding. For this, I modelled count of vigilance versus other acts in a scan (response) with additive and interactive effects of explanatory variables using binomial regression (generalized linear model with logit link and binomial errors, see Crawley 2007). The explanatory variables were a) if birds were part of a flock (variable *flock*: values 1/0), b) if there was disturbance (variable *disturbance*: 1/0), and c) season (as dummy variable with monsoon as the standard). Although treating flock as a continuous rather than binary variable would have been more appropriate, inadequate sampling of various flock sizes across disturbances and seasons did not offer sufficient power for this treatment in regression analysis. Probability of vigilance was likely to be influenced by preceding behavioural states; hence, I included vigilance in the preceding scan (1/0) as an autoregressive term (hereafter, lag–vigilance). I built candidate models following plausible hypotheses using *glm* function and assessed model validation through residual diagnosis using *plot* function in program *R* v 2.13 (R Development Core Team 2010). I compared hypotheses by Information Theoretic approach (Akaike Information Criteria corrected for sample size) between models. I assessed predictor effects by examining the regression coefficient and standard error estimates from top models.

Second, I asked if group vigilance was higher in bigger flocks thereby promoting early threat detection. I used data from breeding season since seasonality could complicate inferences

and winter flocks were mostly large and nonrepresentative of the flock size range. I defined group vigilance as at least one individual in vigilance state during scans (hereafter, flock vigilance). Proportion of scans in a scan-hour where the flock was vigilant (response) was modelled with flock size (predictor) in program R (R Development Core Team 2010). I tested the effect of flock size on flock vigilance from its parameter and precision estimates. Additionally, I tested whether individuals in a flock coordinated their vigilance behaviour by taking turns while others could feed. For this, I split the data into small (2–3 individuals) and large (4–7 individuals) flocks. For each flock-size class, I adopted a similar approach as described in the next section (5.2.2.3) to examine if vigilance was cooperative (coordinated between associates), random (independent of associates), or synchronous (induced by associates).

5.2.2.2. Foraging

I compared pecking rates of focal samples between solitary birds, small flocks (2–3 individuals) and large flocks (4–8 individuals) by one-way ANOVA for summer and winter, and t-test for monsoon (since there was no large flock) following Rahmani (1989). Relying on short-term feeding rates was insufficient to assess foraging efficiency since it ignored encounter rates of food patches, an event of large temporal scale. Rather, long-term feeding rates of particular individuals (by tracking marked birds) were required (Krebs 1980), which was beyond the scope of study. To partly circumvent this problem, I tested a prediction of theories that considered flocking to enhance patch encounter rate through an increase in detectors and information about resources (Clark and Mangel 1984). This being the case, flocking would be most beneficial in patchy resource conditions. In this semiarid landscape, the chief food types during winter (fruits and crops) were more patchily distributed than the chief food of summer-monsoon (insects). Hence, I tested if flock size was higher in winter than other seasons using Kruskal-Wallis test (Zar 1999) to indirectly examine if flocking might benefit foraging.

5.2.2.3. Preening

I compared seasonal preening rates between solitary and flocking birds using Mann-Whitney U-test (Zar 1999) to examine if birds preened more in flocks. I examined if preening was synchronous in flocks. In this case, preening act in a bird-scan could be considered as the *success* of a Bernoulli trial. If birds were preening independently of each other, then the count of preening

birds in a scan would be a binomial outcome of variable (flock sizes differed) uncorrelated Bernoulli trials. Under this assumption, I generated expected number of preening birds during a scan from the observed binomial mean and variance. If birds preened synchronously, then Bernoulli trials would be correlated and the actual number of preening birds during a scan would deviate from the expected. Also, the variance of proportional birds preening during a scan would be higher (see table 5.2 for illustration). I used Chi-square test to examine if actual proportion of birds preening during a scan differed from expected. I also checked if variances differed between actual and expected distributions using Levene's test for homogeneity of variance (Zar 1999), in which case, was actual variance greater than expected.

Table 5.2 (a) Illustration of hypothetical scenario of synchronous (A) vs. asynchronous (B) behaviours, indicating higher variance/mean ratio of the synchronous behavior

(a) Scan	Behavioural state					
	A	≠A	Total	B	≠B	Total
1	0	5	5	2	3	5
2	0	5	5	0	5	5
3	5	0	5	2	3	5
4	0	5	5	1	4	5
5	0	5	5	0	5	5
Mean	0.20			0.20		
Variance	0.19			0.04		

5.2.3. Courtship behaviour

5.2.3.1. Space use dynamics

To study breeding space use dynamics of birds, I made weekly field visits during April–September and searched birds throughout the study extent, recording their gender and location. I overlaid visited routes buffered by 250-m (simulating the effective detection width) on a 4-km² grid map. This scale matched with the daily movements of GIB (pers. obs.) and the closely related Australian bustard (Ziembicki 2009). I considered grids whose >25% area was exposed to detection during a visit as sampled. Through six consecutive breeding seasons (summer & monsoon 2008–2010), I sampled 27 grids by $12_{\text{Mean}} \pm 7_{\text{SD}}$ (range 2–39) seasonal visits. I generated a detection/non-detection history of grids from bird locations on multiple visits. Based on this, I mapped the seasonal and overall patterns of female space use (FSU) and arena occupancy by male (MAO) in program ArcGIS v 9.2 (ESRI 1995-2010). I delineated seasonal arenas as 1-km consolidated buffers around courtship locations during that season, and stacked buffers to delineate the long-term arenas. I estimated MAO seasonally for each arena as the proportion of seasonal

and plumage characteristics) but not over the years. I assessed the proximate correlates of courtship behaviour by examining how courtship rates were influenced by biotic (female density and rival male) and abiotic (disturbance and weather) environment of the arena. I quantified environment within bird's arena (1-km buffer around daily courtship locations) by recording weather, number and location of female(s), disturbance, and rival males during bird-scans. Courtship rate might not just respond to presence of females but also their distribution from the center to periphery of the arena. Hence I converted arena into concentric donuts of geometrically progressing radii (0.625, 0.125, 0.25, 0.5 & 1 km) and estimated female density in arena as the mean density of five donuts. This estimator (hereafter, female radial density) gave more weightage to females at the center than towards the periphery. For e.g., 1 female at 0.5–1 km from male

translated into: $\left(\frac{0/0.012 + 0/0.037 + 0/0.147 + 0/0.589 + 1/2.355}{5} \right) = 0.08 \text{ female km}^{-2}$; while 1

female within 50–75 m radius of male would mean:

$\left(\frac{1/0.012 + 0/0.037 + 0/0.147 + 0/0.589 + 0/2.355}{5} \right) = 16.31 \text{ female km}^{-2}$. Similarly, I scored

disturbance as 1.0, 0.75 and 0.50 when it occurred within 0–0.25, 0.26–0.50 and 0.51–1.0 km donuts, or 0 otherwise.

I modeled courtship (binary response) with logical alternate combinations of female radial density, disturbance, weather, rival male, and arena identities (two) using logistic regression (logit link and binomial errors, see McCullagh and Nelder 1989) with scans as observations. Since scans were nested within repertoires, observations were not independent, although separated by 5 minutes, which would violate regression assumption (Mac Nally 2000). Exploratory logistic regression with repertoire identity as an interaction factor suggested that probability of courtship significantly differed between 50 repertoires. However, this cost 49 degrees of freedom when the primary interest rested on environmental variables and not inter-repertoire variations. To circumvent the problem, I used generalized linear mixed effect logistic regression with behavioural repertoire as random intercept (Bolker et al. 2009). This technique recognized the natural grouping of observations, and explicitly accounted for random inter-group variations in the response that might arise from intra-group correlations (Zuur et al. 2009). Following Bolker et al. (2009) and Zuur et al. (2009), I built candidate models by Laplace approximation and Maximum Likelihood parameter estimation using *glmer* function of *lme4* package in program R v 2.13 (R

Development Core Team 2010). I compared models by their Akaike Information Criteria, thereafter obtaining final parameter estimates for the smallest AICc model using Restricted Maximum Likelihood method. I assessed the influence of environmental factors on courtship rate from regression coefficients and precision estimates, and generated ROC curve (Beck and Shultz 1986) from fitted courtship probabilities versus observed courtship state (0/1) to assess model accuracy (Fielding and Bell 1997) in program SPSS (SPSS 2007).

5.2.3.3 Courtship catalogue

Apart from recording behavioural state (as described in 5.2.1.1), I studied the structure of courtship by objective decomposition of six components: position of body, orientation of head, curvature of neck, sizes of gular pouch and balloon, and orientation of tail. I observed a bird for 1 minute ($n=290$ observations from 31 repertoires; $11.4_{\text{Mean}} \pm 5.8_{\text{SD}}$ (range 3–29) observations per repertoire) and scored these components according to their maximum deviations from the ‘normal’ posture within this time (see fig 5.10b–d for illustrations). This was analogous to capturing multiple snapshots within a short duration and superimposing them to highlight the most distinct features of the photo–sequence. Since deviations from normal posture like enlarging air sac, cocking tail, or encircling are energy–costly, they should directly correspond with the quality of courtship. The component scoring technique exploited this link: scores were given as 0 for normal posture, 0.5 for partial deviation and 1 for complete deviation (fig 5.10). I developed a courtship catalogue by defining an act as unique observed combinations of 19 postures from six components. I ranked acts by their frequencies of occurrence, and against those ranks plotted the relative and cumulative frequencies of observations. This helped in classifying widespread, fairly common and rare acts. I identified widespread acts from the point of inflexion on frequency curves, rare acts as the ones with $<1\%$ relative frequency (i.e., ≤ 3 observations), and fairly common acts as the intermediate ones. I described these acts, screening the rare ones, in section 5.3.3.3.

5.2.3.4 Courtship anatomy

Courtship behaviour was a large set of acts, possibly with many (unknown) rules regarding their release and function. Certain acts were typically preceded by others; for example, curving neck and vocalizing was frequently preceded by raising head and waving balloon, position remaining static and tail cocked throughout. I was interested in understanding the structure and

relationships of various acts, hereafter courtship anatomy, and whether their release was related to arena environment. Since discreet data on the occurrence of multiple acts constrained such pattern diagnoses, I used Non-metric Dimensional Scaling (NMS, McCune and Grace 2002) on 19 component postures across 290 bird-scans. In the input matrix, a cell value "1" indicated occurrence of the target component posture in that bird-scan and "0" indicated non-occurrence. Since component postures were generally correlated (thus forming common acts), I applied Beals smoothing on this matrix (McCune 1994). It replaced each cell with a probability of the target component posture occurring in that bird-scan, based on the joint occurrences of the target component posture with component postures that are actually in the bird-scan (McCune and Grace 2002). The purpose of NMS ordination was to reduce this complex multivariate data into fewer synthetic axes, enabling pattern identification. The ordination began by constructing Sørensen dissimilarity matrix from original data, then generating random axes to recalculate the dissimilarity matrix, and reiteratively modifying those axes so as to minimize the difference between actual and modified dissimilarity matrices (also called stress). I conducted this analysis in program PCORD v 4 (McCune and Mefford 1999) by selecting the "slow and thorough" autopilot mode. It ran up to 400 iterations on 40 real runs starting from 6 to 1 axis, saving the best solution (least stress) for each run, selecting a suitable dimensionality by comparing the final stress among best solutions, and checking if the final stress from real runs was <95% of that from 50 randomized runs using Monte Carlo test (Mather 1976). Outputs of this exercise were synthetic scores of component postures on NMS axes, and based on that, unique bivariate scores of acts. I used these act-scores of bird-scans to describe courtship anatomy at the interface of environmental factors. Factors of interest were period of day (levels: early morning, late morning and evening hours), female radial density (levels: nil, low 1-4k m⁻² and high >5 km⁻²), and arena type (levels: permanent and transient). I plotted bivariate distributions of act-scores grouped into the above factor levels in program ArcGIS v 9.2 (ESRI 1995-2010). I generated 75% minimum convex polygons (MCP) to bound >1 SD on these distributions using HRTTools extension for visually examining effects of these factors on courtship anatomy. I used Multi-response Permutation Procedure (MRPP, McCune and Grace 2002) to test whether distribution parameters (mean and dispersion) of act-scores differed between factor levels using *vegan* package in program R (R Development Core Team 2010). This procedure compared the overall mean of mean Euclidean distances within factor-levels (observed delta) with distances within 999 permuted datasets expected under no

factor effect (expected delta), thereafter testing what fraction of expected deltas \leq observed delta (McCune and Grace 2002). If this fraction is very small (typically $<5\%$), then it signifies that distributions differ between factor levels.

5.2.4. Feeding habits

5.2.4.1. Field collection of fecal pellets

I studied GIB diet by non-invasive analysis of food remains in fecal pellets (Korschgen 1969). This technique is less accurate than stomach analysis and direct observations in determining biomass consumption of food items because of digestibility differences (Lane et al. 1999). However, this was the only viable option since the species' conservation precedence (Critically Endangered and legally protected under the Wildlife Protection Act 1972) and human avoidance nature (preventing direct observations from short-enough distances to identify small food items) precluded other techniques. To correctly identify GIB fecal pellets, I followed birds to their resting and roosting spots and searched signage once the birds had moved away, during November–December 2007. Having gained experience, I performed monthly searches during January 2008–August 2010 across the study extent to collect fecal pellets, optimizing search in high bird usage areas. I collected 379 fecal pellets (summer=151, monsoon= 44, winter=189), sun dried them in field, and stored them in polythene zip-lock bags. A subsequent genetic analysis of Cytochrome-b, conducted on a subset of these pellets ($n=20$ amplified samples), confirmed that all pellets belonged to GIB. I selected 178 pellets for analysis (summer=68, monsoon=40, winter=70) by stratified random sampling so that sample distribution across patches and seasons imitated bird densities (see chapter 1).

5.2.4.2. Fecal analysis

I weighed each pellet, ground it by hand, passed it through a 0.5-mm sieve, and evenly spread the fecal residue over a $3 \times 3 \text{ cm}^2$ metal grid. I identified indigestible components in each grid under a magnifying lens (following Korschgen 1969, Tigar and Osborne 2000) and visually estimated their volumetric contribution from proportion of completely occupied grids. I classified indigestible components into fruit seeds, crops, plant matter, arthropods, and vertebrates. I identified fruit seeds and crops to genus based on known samples of common ones in field. I identified arthropods to their order by comparing exoskeletal fragments (head, mouth part, elytra

and leg) with a voucher collection. I identified vertebrates to class based on characteristic fragments (claw, scale, feather, egg-shell, hair and bone).

To assess the adequacy of sampling for accurate description of diet, I examined if the cumulative proportional contribution (by number) of major food items plotted against the number of pellets analyzed, in increments of five pellets, reached asymptotes (Jethva and Jhala 2004). I represented seasonal and annual diets of GIB based on frequency and volumetric measurements. For each food item, I computed its 1) frequency as proportion of pellets where it occurred (Leopold 1986, Reynold 1991); 2) numerical frequency as the proportion of total food items where it occurred (Corbett 1989); and 3) whole pellet equivalent as its proportional dry volume in pellet (Angerbjörn et al. 1999). I also assumed that volume of food items would fairly represent their dry weight. From these measurements, it is possible to estimate the true diet composition (DC) through feeding trials; which was however not possible due to the lack of captive birds. To circumvent this problem, I reconstructed the diet profile using two approaches, and compared their results: 1) correcting the percentage of food items by dry weight in feces (DWC_p) for their apparent assimilated mass coefficients (AMC) obtained from literature review (see table 5.7 footer); and 2) combining frequency and volumetric measurements, since they were individually biased but collectively comprehensive (Zabala and Zuberogitia 2003), into the Index of Relative Importance ($IRI = \text{frequency} \times (\text{numerical frequency} + \text{whole pellet equivalent}) / 100$, see Home and Jhala 2009; Pinkas et al. 1971). I generated 95% bootstrapped confidence intervals on the IRI from 1000 replications in program R v 2.13 (R Development Core Team 2010) for seasonal comparison of food habits.

5.2.4.3. Food availability

I estimated abundance of bustard's important natural foods (Bhushan 1985) from 24 randomly distributed $1000 \times 2 \text{ m}^2$ belt transects across the study extent. I sampled each transect once every season from winter 2007–08 to monsoon 2009 during 0700–1100 and 1700–1900 hours IST (bird activity period). Two observers walked these transects parallel to each other at a very slow speed (1 km hr^{-1}); regularly beating the ground vegetation for arthropods, stopping at shrubs/trees for total counts of fruits, and counting active spiny-tailed lizard *Saara hardwickii* burrows (following Dutta and Jhala 2007) and other reptiles. Although such large sampling dimension is not recommended for arthropod studies (due to observers' fatigue and non-

detectability issues), I preferred it for capturing spatial heterogeneity (typical of semiarid ecosystems resulting in patchy food resources) and gaining precision. To avoid observer's fatigue, search was paused for 5-mins after every 200m walk. The ground vegetation being typically short and sparse permitted ~100% detection of food items within 0.5-m on either side of the search path. I categorized arthropods as: *Orthoptera* (grasshoppers and crickets), *Coleoptera* (beetles), *Hymenoptera* (ants and bees) and others; and recorded fruits and reptiles to their species level. I did not quantify crops because recent landuse practices in this region were highly dynamic with short rotational cycles precluding accurate quantification of crop abundances; and unlike natural food, crop abundance would depart from their availability to birds due to the associated human interventions in agricultural areas. I converted densities of food items into unit area biomass by multiplying with their body weights which were obtained by weighing specimens in field.

5.2.4.4. Order of food preference

I ordered seasonal preference of naturally occurring food items by comparing their usage (% dry weight in diet) and availability (biomass/100m² in habitats) following Johnson (1980). This ranking method was relatively robust to the arbitrary choice of available food items (in this case, exclusion of crops) that would invalidate inferences from other use-availability analyses (Jacobs 1974, Neu et al. 1974) as pointed out by Johnson (1980) and Aebisher et al. (1993). However, due to the lack of true replicates, as fecal pellets could not be identified to individual birds, I could not support these use-availability comparisons with tests of statistical significance.

5.3. Results

5.3.1. Behavioural pattern and environment of birds

Females (n=824 scans, 101 scan-hours, 45 days) apportioned more time of their annual activity phase to foraging (41.2_{Mean}±2.1_{SE}% time) than moving (17.1±4.8%), vigilance (15.9±2.0%), preening (6.7±2.1%) and other acts (0.7±0.1%). Males (n=1222 scans, 139 scan-hours, 45 days) also allocated more time in foraging (34.4_{Mean}±15.3_{SE}%) than courtship (22.4±11.3%), moving (17.9±3.9%), vigilance (11.4±2.8%), preening (5.6±1.6%) and other acts (0.8±0.5%). Most of the data subsets on arcsine transformed proportional time spent in behaviours split into gender, season and day period combinations were normally distributed (90% subsets showed KS test p>0.05), but for preening behaviour (45% data subsets showed KS test p<0.05).

subsets showed KS test $p < 0.05$). There were seasonal and day-period differences in active-time-budgets (fig 5.1). Females allocated more time in moving during monsoon than summer ($F_{df\ 2,92} = 6.68$, $p = 0.01$, Tamhane's $T_2 = 0.16$, $p = 0.05$) and more time in preening during summer than winter ($F_{df\ 2,92} = 3.16$, $p = 0.05$, Tamhane's $T_2 = 0.07$, $p = 0.01$, fig 5.1). They spent equal percentage of time in preening across day periods in summer ($10.4_{\text{Mean}} \pm 3.9_{\text{SE}}\%$ in early morning $\approx 10.8 \pm 3.2\%$ in late morning $\approx 8.6 \pm 3.3\%$ in evening) but not in monsoon (0% in early morning $< 10.8_{\text{Mean}} \pm 3.0_{\text{SE}}\%$ in late morning $\approx 6.5 \pm 4.4\%$ in evening) and winter (0% in early morning $< 5.6_{\text{Mean}} \pm 1.7_{\text{SE}}\%$ in late morning $\approx 1.9 \pm 0.9\%$ in evening). Their time allocation in preening was tenfold higher in presence of male (12.2_{Mean} , $9.4\text{--}15.1_{95\% \text{CI}}\%$) than in its absence (1.7_{Mean} , $0\text{--}3.8_{95\% \text{CI}}\%$) during breeding season but equal during non-breeding season ($\sim 4\%$).

Consistent male presence in arena, indicative of courtship activity, was first observed on an average 159th day (124th, 213th and 144th in 2008–10 respectively) from the start of year. It continued till an average 252nd day (268th, 249th and 238th in 2008–10) although fieldwork was aborted for the season after the 270th day (fig 5.7). Mean day of male presence in arena was $196.6_{\text{Mean}} \pm 40.2_{\text{SD}}^{\text{th}}$. Thus, courtship activity extended through summer and monsoon, comprising of 31% and 36% activity times respectively (fig 5.1). Daily time allocation to courtship was higher ($F_{df\ 2,130} = 3.46$, $p = 0.03$) in early morning (Tamhane's $T_2 = 0.24$, $p = 0.07$) and evening (Tamhane's $T_2 = 0.39$, $p = 0.001$) compared with late morning (fig 5.2), and this pattern remained similar between two seasons ($F_{df\ 4,130} = 0.63$, $p = 0.60$). Males spent more time foraging in winter than summer and monsoon ($F_{df\ 2,130} = 16.18$, $p = 0.001$, Tamhane's $T_2 = 0.46$ & 0.39 , $p = 0.001$). Male pecking rates were also higher ($F_{df\ 2,74} = 4.77$, $p = 0.01$) in winter ($1.48_{\text{Mean}} \pm 0.22_{\text{SE}}$, $n = 7$ scan-hours) than summer ($0.49_{\text{Mean}} \pm 0.16_{\text{SE}}$, $n = 44$, Tamhane's $T_2 = 0.73$, $p = 0.001$) and monsoon ($0.64_{\text{Mean}} \pm 0.13_{\text{SE}}$, $n = 32$, Tamhane's $T_2 = 0.52$, $p = 0.01$, fig 5.3c). Female pecking rates were marginally higher ($F_{df\ 2,48} = 4.00$, $p = 0.05$ Tamhane's $T_2 = 0.42$, $p = 0.15$) in winter ($1.86_{\text{Mean}} \pm 0.39_{\text{SE}}$ pecks min^{-1} , $n = 13$ scan-hours) than summer ($0.71_{\text{Mean}} \pm 0.096_{\text{SE}}$, $n = 30$). Pecking rates of both sexes were similar between day periods controlling for seasons (female: $F_{df\ 4,48} = 0.70$, $p = 0.50$; male: $F_{df\ 4,74} = 0.24$, $p = 0.90$, fig 5.3c). Segregating by seasons, disturbance was lower (K-W $\chi^2_{df\ 2} = 14.4$, $p = 0.001$) in winter ($3.39_{\text{Mean}} \pm 0.96_{\text{SE}}\%$ scans, $n = 44$ scan-hours) than summer ($11.69_{\text{Mean}} \pm 2.36_{\text{SE}}\%$, $n = 114$) and monsoon ($18.64_{\text{Mean}} \pm 2.80_{\text{SE}}\%$, $n = 82$, fig 5.3b). Segregating by gender, activity areas of males faced more disturbance during breeding season ($15.7.7_{\text{Mean}} \pm 2.5_{\text{SE}}\%$) than that of females ($8.9_{\text{Mean}} \pm 2.3_{\text{SE}}\%$) but not in the wintering season.

Figure 5.1. Seasonal (summer in dark grey, monsoon in light grey & winter in open bars) and gender-specific time allocation to behaviours by the Great Indian Bustard in Kachchh (2007–2011)

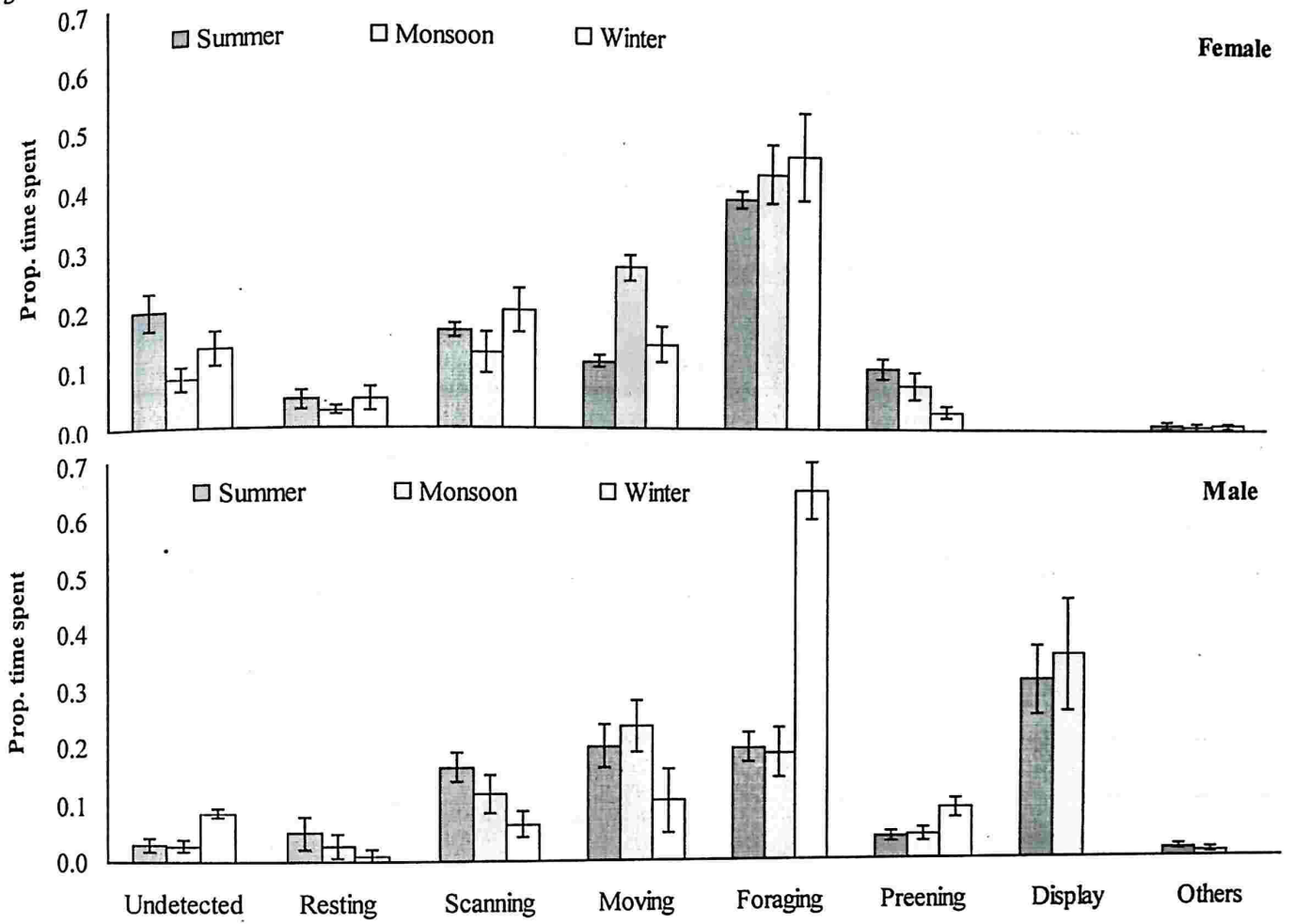


Figure 5.2. Time allocation to behaviours during daily activity periods: early morning or 0700–0859 hours (EM), late morning or 0900–1159 hours (LM) and evening or 1700–2000 hours (EV) across season (rows) and gender (columns) of the Great Indian Bustard in Kachchh (2007–2011). Stacked bars with error lines represent mean \pm 1SE proportion time spent in resting, vigilance, moving, foraging, preening and courtship

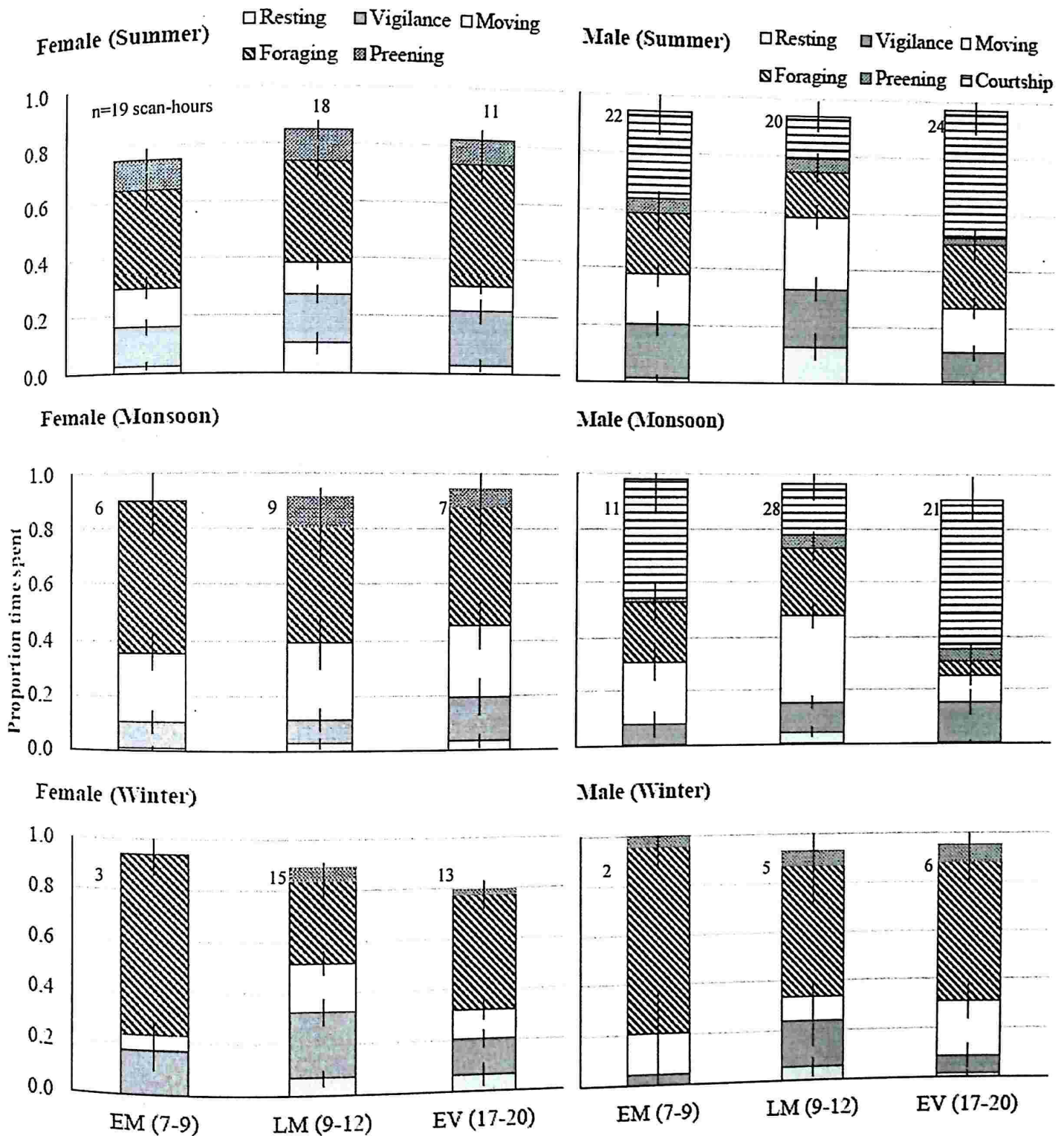
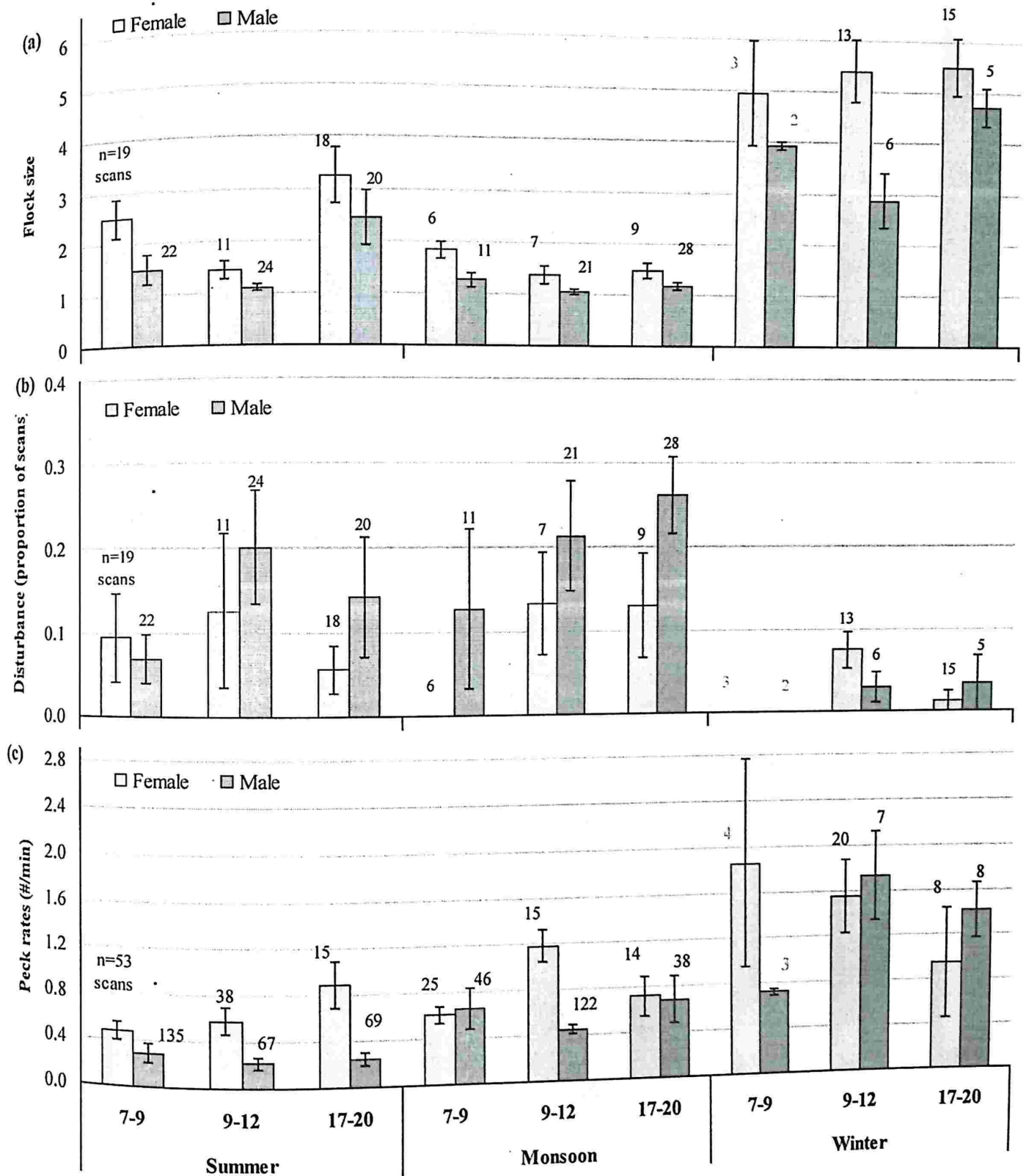


Figure 5.3. Mean±SE (a) flock size, (b) anthropogenic disturbance (as proportional frequency in hourly scans), and (c) feeding rates (as pecks min⁻¹) during daily activity periods: early morning or 0700–0859 hrs (EM), late morning or 0900–1159 hrs (LM) and evening or 1700–2000 hrs (EV), across season and gender of the Great Indian Bustard in Kachchh (2007–2011)



5.3.2. Functions of flocking

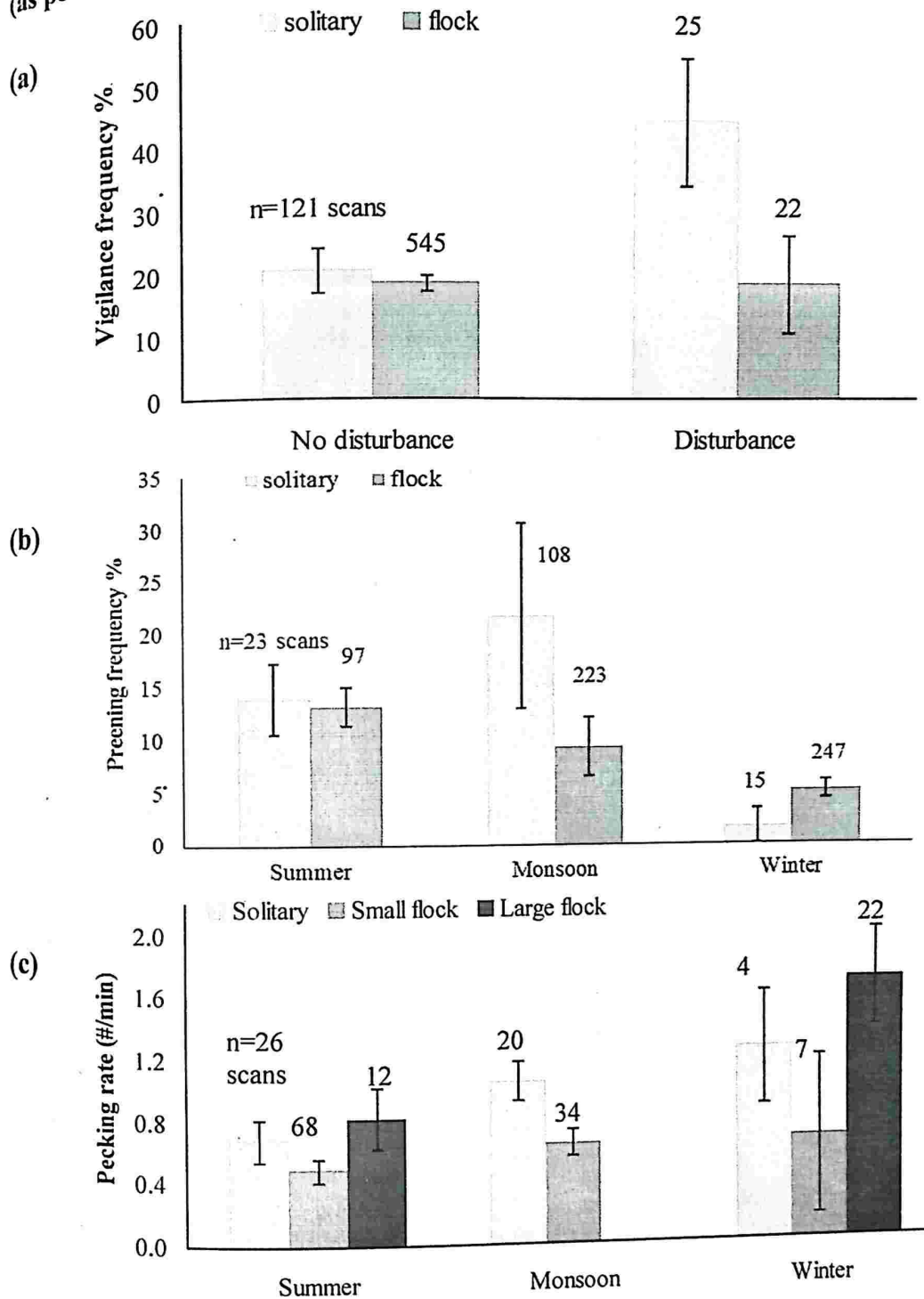
5.3.2.1. Vigilance

Number of female birds in a scan ($n=713$ scans excluding missing observations) varied from one to eight, three on average. Out of these, zero to five birds was found vigilant, on average 20% of the scanned samples. I fitted a global model with four variables and eight subset models indicating plausible ecological hypotheses about vigilance behaviour. Compared to the model assuming constant vigilance (see (.) in table 5.3a), incorporation of the temporally autocorrelated term (see Lag in table 5.3a) reduced AICc by 39 units, and was retained in all subsequent models. Models incorporating flock and season with/without disturbances obtained greater support from data ($W=0.73$, table 5.3a). Although there were three models within 2 AICc units, I based inferences on the more complex (global) model since the additional parameter was ecologically and statistically important (table 5.3b). This model showed tolerable level of over-dispersion (residual-deviance/df = 1.5) and satisfactory validation based on residual plot diagnosis (appendix 5.1). Vigilance during an observation was positively correlated with that in the preceding observation. Accounting for this, vigilance depended on flocking ($W=0.98$) with greater allocation in solitary birds (table 5.3b); seasonality ($W=0.81$) with greater allocation in winter than monsoon; and disturbance ($W=0.72$). Although vigilance increased in presence of disturbance (table 5.3b), the increase tended to be less if birds were flocking (fig 5.4a). However, model predictive power was low indicated by weak correlation ($r=0.23$, $p<0.001$) between fitted and observed proportion of vigilant birds. The flock vigilance model indicated that increasing flock size led to increasing incidence of at least one vigilant bird ($\beta_{Unstd}=0.29_{Mean}\pm 0.04_{SE}$), thereby aiding in threat detection.

Table 5.3. Proximate correlates of individual vigilance frequency in Great Indian Bustard in Kachchh (2007–2011). (a) Candidate models ranked by Akaike weights (W_i); and (b) parameter estimates [mean \pm SE unstandardized regression coefficients] of predictors from the top model

(a) A-priori hypotheses	W_i	$\Delta AICc$	AICc	df	logL	(b) Parameter	β_{unstd}	SE
Lag + Season + Flock x Disturbance	0.29	0.00	1442.80	7	-714.32	Intercept	-1.69	0.30
Lag + Season + Flock + Disturbance	0.26	0.24	1443.04	6	-715.46	Lag vigilance	0.23	0.04
Lag + Season + Flock	0.18	0.94	1443.73	5	-716.82	Flock vs solitary	-0.50	0.22
Lag + Flock x Disturbance	0.10	2.16	1444.95	5	-717.43	Summer	0.41	0.25
Lag + Flock	0.09	2.30	1445.10	4	-718.52	Winter	0.57	0.25
Lag + Season + Disturbance	0.07	2.83	1445.63	3	-719.80	Disturbance	1.00	0.45
Lag + Disturbance	0.01	7.88	1450.68	3	-722.32	Disturbance * Flock	-0.82	0.54
Lag + Season	0.00	9.70	1452.50	4	-722.22			
Lag	0.00	10.04	1452.83	2	-724.41			
(.)	0.00	48.78	1491.57	1	-744.78			

Figure 5.4. Mean±SE (a) vigilance frequency (% occurrence in scans) in presence vs. absence of disturbances, (b) seasonal preening frequency (% occurrence in scans), and (c) seasonal feeding rates (as pecks min⁻¹) between solitary and flocking Great Indian Bustards in Kachchh (2007–2011)



However, proportion of vigilant birds in large flocks during a scan ($0.24_{\text{Mean} \pm 0.05_{\text{SE}}}$) did not deviate ($G=6.14$, $df=5$, $p=0.29$) from what was expected ($0.25_{\text{Mean} \pm 0.03}$) under the assumption of random (conspecific independent) vigilance. Similarly, proportion of vigilant birds in small flocks ($0.17_{\text{Mean} \pm 0.02_{\text{SE}}}$) was also the same ($G=7.08$, $df=4$, $p=0.13$) as expected ($0.16_{\text{Mean} \pm 0.02_{\text{SE}}}$). Thus, although flock size reduced individual vigilance and enhanced flock vigilance, it was not because of cooperative action but solely due to many eyes working at random.

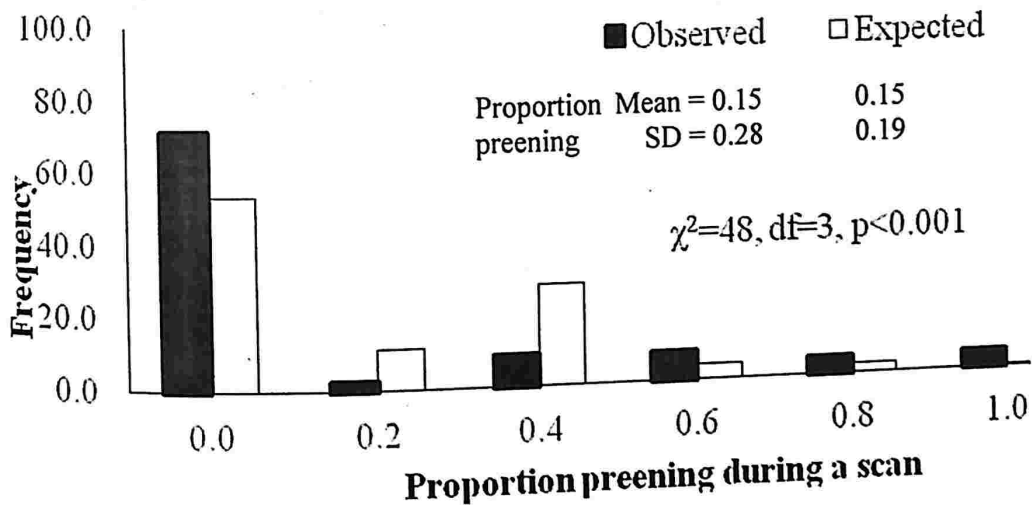
5.3.2.2. Foraging

Female pecking rates ($n=194$ focal samples) were similar between solitary birds, small and large flocks (summer: $F_{df\ 2,103}=1.72$, $p=0.18$ & winter: $t_{df\ 2,30}=1.45$, $p=0.25$), except for monsoon (fig 5.4c), when contrary to prediction, pecking rates were lower in small flock than solitary birds ($t_{df\ 52}=2.75$, $p=0.01$). As predicted, flock sizes were larger (K-W $\chi^2_{df\ 2}=45.66$, $p=0.001$) in winter ($5.42_{Mean} \pm 0.38_{SE}$, $n=31$ scan-hours) than other seasons ($2.22_{Mean} \pm 0.19_{SE}$, $n=70$, fig 5.3a).

5.3.2.3. Preening

Proportion of female birds preening during a scan deviated from what was expected (fig 5.5) under the assumption of conspecific-independent preening ($\chi^2_{df\ 3}=48$, $p=0.001$). Variance to mean ratio of proportional birds preening during a scan (0.53) was also higher (Levene's test: $F=13.44$, $p=0.001$) than expected under conspecific-independent preening (0.24). Controlling for seasons, preening rates were similar between solitary and flocking birds (summer: $U=240$, $p=0.59$, $n=48$ scan-hours & monsoon: $U=40$, $p=0.15$, $n=22$; see fig 5.4b). Results supported the hypothesis that preening was socially facilitated but not enhanced in GIB.

Figure 5.5 Frequency (%) of observed vs. theoretically (binomial distribution) expected preening birds during a scan, to test if preening was conspecific-dependent in Great Indian Bustard in Kachchh (2007-11)

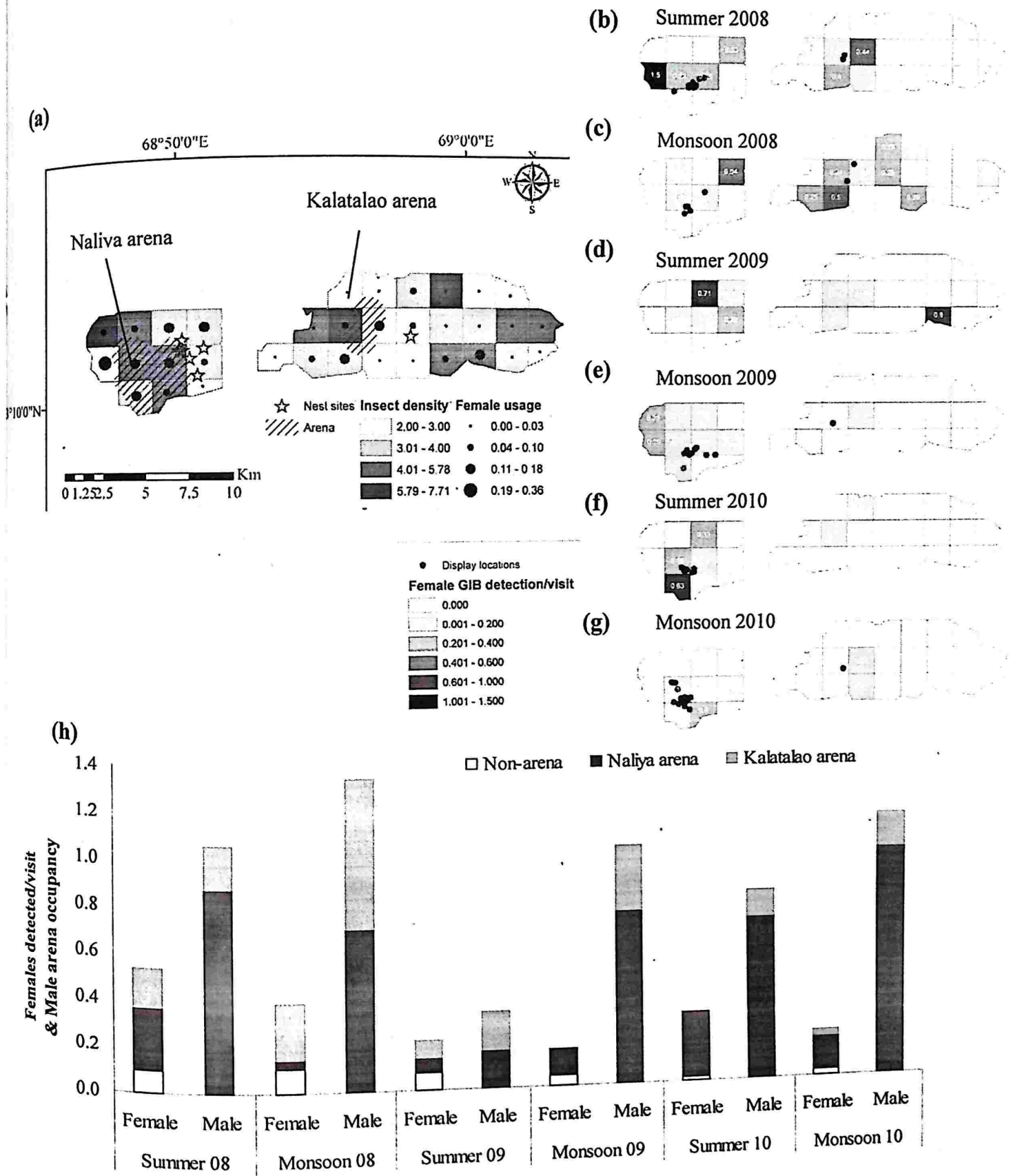


5.3.3. Courtship behaviour

5.3.3.1. Space-use dynamics

Courtship activity in this population occurred at two arenas, Naliya and Kalatalao which are separated by 12 km aerial distance (fig 5.6). Total 841 visits to 27 grids yielded 66 female detections in 19 grids across six breeding seasons.

Figure 5.6 Space use dynamics of Great Indian Bustard in the breeding area of Kachchh: (b–g) male courtship locations (closed circles) and female detections/visit (grey shades) for six breeding seasons (summer and monsoon 2008–2010); (a) the long-term arena (parallel shading) and average female usage (variable sized bubbles); and (h) stacked bars representing male occupancy (presence/visit) and female use within Naliya (black) and Kalatalao (grey) arenas vs. outside of arenas (white)

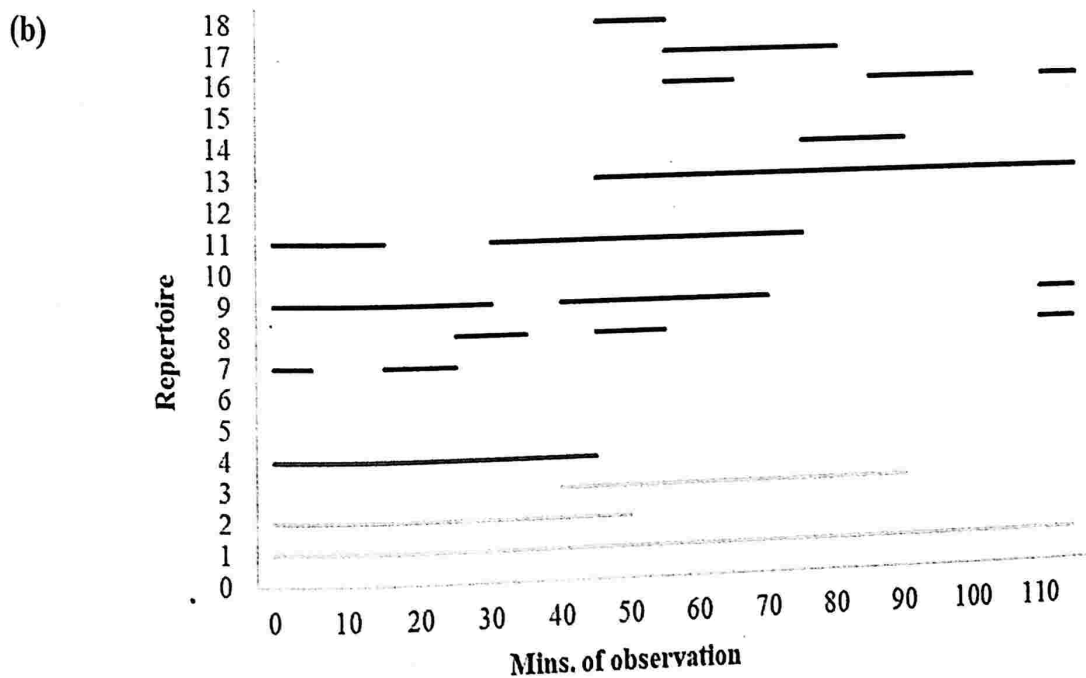
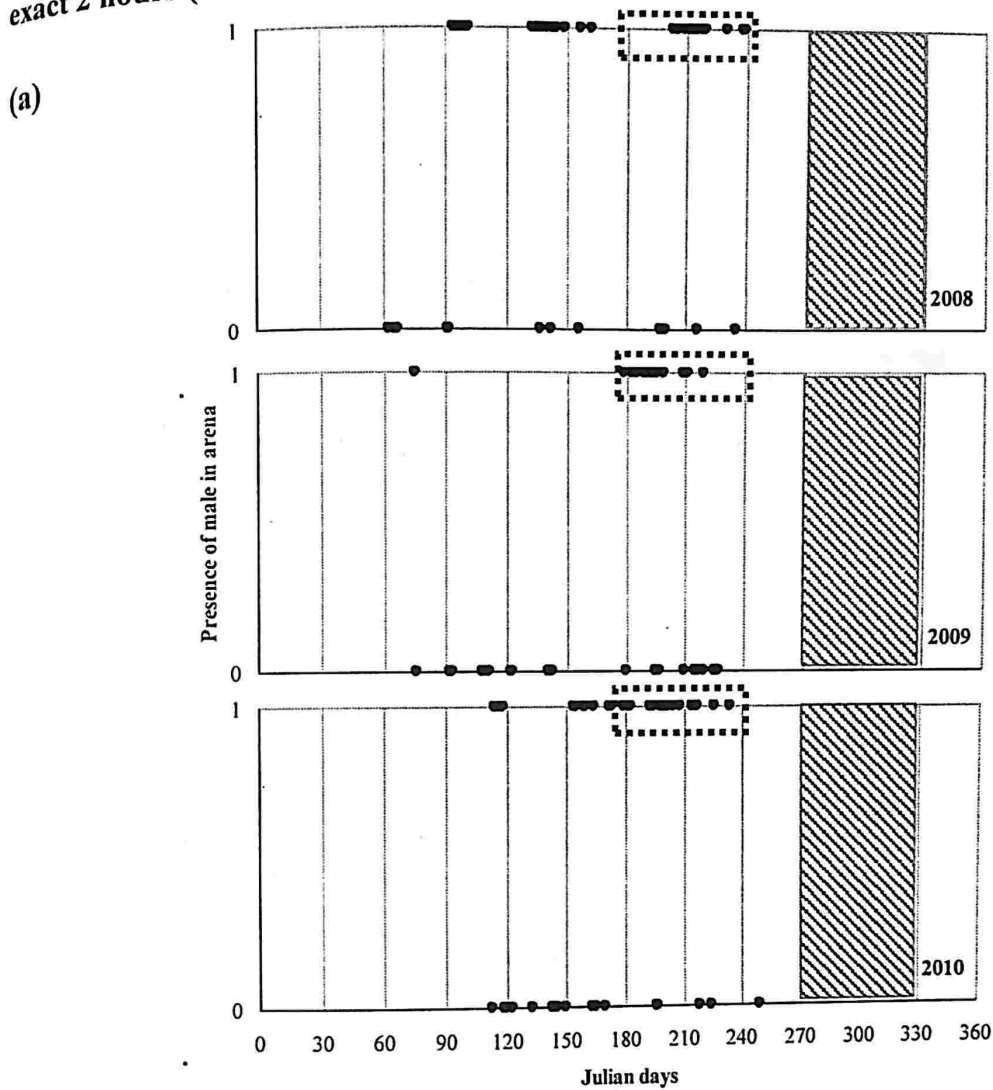


Overall FSU varied between grids at 0–0.18 female visit⁻¹ (fig 5.6a), which was threefold higher ($t_{df\ 26} = 3.7$, $p=0.001$) within arenas ($0.112_{Mean} \pm 0.018_{SE}$) than that outside ($0.036_{Mean} \pm 0.011_{SE}$). Inter-seasonal variations in FSU was high (fig 5.6b–g), estimated at 175_{Mean} (65–245_{range}) % CV among used grids. The three grids with relatively steady FSU (<100% CV) fell within Naliya (65 & 82%) and Kalatalao (96% CV) arenas. Thus, the two arenas spatially overlapped with relatively high and steady long-term female usage (fig 5.6a). There were inter-seasonal variations in MAO (0.2–1.0 at Naliya & 0.1–0.7 at Kalatalao), which was less at Naliya (41% CV) than that at Kalatalao (78% CV), although not significantly different (Levene's test: $F=0.18$, $p=0.70$, see fig 5.6h). Pooling across arenas, seasonal MAO was correlated with arena FSU ($r=0.61$, $p=0.03$, $n=12$). However at the level of individual arena, this correlation broke down for Naliya ($r=0.44$, $p=0.38$) but not for Kalatalao ($r=0.74$, $p=0.09$), indicating arena (or possibly individual) specific responses of courtship investment to female usage (fig 5.6h). Seasonal MAO was consistently higher (paired $t_{df\ 5} = 3.17$, $p=0.02$) at Naliya ($0.70_{Mean} \pm 0.12_{SE}$) than Kalatalao ($0.25_{Mean} \pm 0.08_{SE}$), although seasonal FSU did not consistently differ between the two arenas (paired $t_{df\ 5} = 1.03$, $p=0.35$); indicating the role of different factors behind male versus female breeding space use (fig 5.6h). Additionally, behavioural observations on 39 days recorded 1 copulation (monsoon 2010) and 12 territory rituals (90% in July and 10% in August), all at Naliya.

5.3.3.2. Courtship frequency

Among 50 repertoires of males in breeding season, time spent in courtship varied from 0 to 100% ($47_{Mean} \pm 34_{SD}$ %). Female radial density in arena was $2.5_{Mean} \pm 4.5_{SD}$ km⁻², rival male was present on 38% occasions, and weather condition was mostly cloudy/dark ($55_{Mean} \pm 31_{SD}$ % times), followed by bright ($23_{Mean} \pm 23_{SD}$ %), sunny ($15_{Mean} \pm 25_{SD}$ %) and rainy ($7_{Mean} \pm 17_{SD}$ %). Since, typically 47% of activity time (5 morning hours and 3 evening hours) was composed of courtship, I selected continuous observations of ≥ 2 hours (long enough to potentially include an entire courtship bout), available for 18 repertoires, to estimate the approximate duration and sequence of courtship versus non-breeding bouts through exact 120 minutes (fig 5.7). Excluding cases where courtship was not observed (28%), repertoires comprised of one to three courtship bouts, each continuing for $28_{Mean} \pm 29_{SD}$ (range 5–115) minutes, with relapse time of 5 to >55 minutes. Thus, courtship rate varied considerably among repertoires, and I examined if that was related to environmental characteristics, which also showed wide variations.

Figure 5.7 (a) Annual sequence of arena occupancy (1) versus non-occupancy (0) by males along dates from start of the year. (b) Courtship sequences of Great Indian Bustard in Kachchh (2007–2011). Lines (light grey for 2008, dark grey for 2009 and black for 2010) and gaps represent courtship bouts vs. other acts in 18 repertoires (identity marked on the y-axis) observed through exact 2 hours (x-axis)



Courtship state in bird-scans (n=1120 observations) when modeled with random variations among repertoires and fixed additive effects of disturbance, female radial density, weather and rival male, received maximum support from data (table 5.4a). According to this model, odds of courtship varied largely among repertoires, by 7.1 SE around the intercept ($1.2_{\text{Mean}} \pm 1.5_{\text{SE}}$). A reduced model, excluding rival male, was within 1 AICc unit. Since the additional parameter was important ($W=0.65$) and nearly significant, I based inferences on the complex model. The estimated odds of courtship increased by 14(6–21_{95%CI})% with unit increase in female radial density, decreased by 67(35–83)% in presence of disturbance, and decreased by 82(53–94)% and 68(44–82)% in rainy and sunny conditions respectively when compared with bright weather (table 5.4b). Results indicated similar courtship rate between arenas. The model had satisfactory predictive accuracy (area under ROC curve $0.90_{\text{Mean}} \pm 0.01_{\text{SE}}$, fig 5.8).

Table 5.4. Proximate environmental correlates of Great Indian Bustard courtship behaviour in Kachchh (2007–2011). (a) Summary statistics of candidate Generalized Linear Mixed Effect binomial models explaining frequency of courtship in scan samples; (b) parameter estimates of top model. Figure 5.8 Receiver Operating Characteristic curve to assess the predictive accuracy of the model

(a) A-priori hypotheses	Wi	ΔAICc	AICc	df	logL
Female-density + Weather + Disturbance + Male-rival	0.45	0.00	1066.81	9	-524.32
Female-density + Weather + Disturbance	0.37	0.40	1067.21	8	-525.54
Female-density + Weather + Arena + Disturbance + Male-rival	0.16	2.03	1068.84	10	-524.32
Female-density + Weather + Male-rival	0.01	9.01	1075.82	8	-529.85
Female-density + Weather	0.00	9.32	1076.13	7	-531.02
Weather + Disturbance	0.00	18.29	1085.10	7	-535.50
Weather + Arena + Disturbance + Male-rival	0.00	19.02	1085.83	9	-533.83
Weather + Male-rival	0.00	25.11	1091.92	7	-538.91
Female-density + Disturbance	0.00	25.79	1092.60	4	-542.28
Female-density + Disturbance + Male-rival	0.00	25.81	1092.61	5	-541.28
Weather	0.00	26.25	1093.06	6	-540.49
Female-density	0.00	33.97	1100.78	3	-547.38
Female-density + Male-rival	0.00	34.03	1100.83	4	-546.40
Disturbance + Male-rival	0.00	47.63	1114.44	4	-553.20
Disturbance	0.00	48.51	1115.32	3	-554.65
Arena + Disturbance + Male-rival	0.00	49.45	1116.26	5	-553.10
Male-rival	0.00	54.80	1121.60	3	-557.79
(.)	0.00	55.66	1122.47	2	-559.23

(b) Parameter	β_{unstd}	SE	Summed Akaike wt
Intercept	0.14	0.41	
Female density	0.13	0.03	1.00
Weather Cloudy	-0.11	0.24	
Dark	0.55	0.43	1.00
Rainy	-1.74	0.5	
Sunny	-1.14	0.29	
Disturbance	-1.11	0.34	0.99
Male rival	0.9	0.56	0.65

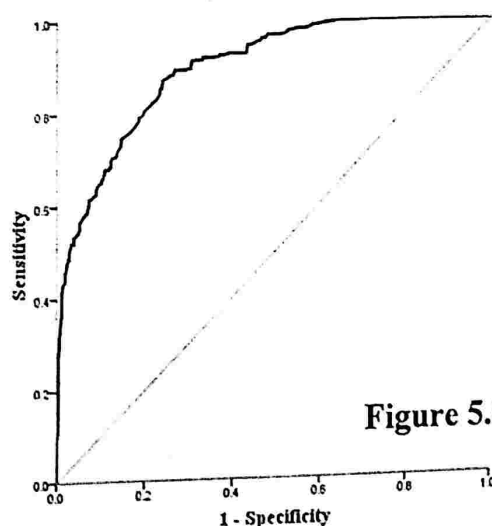
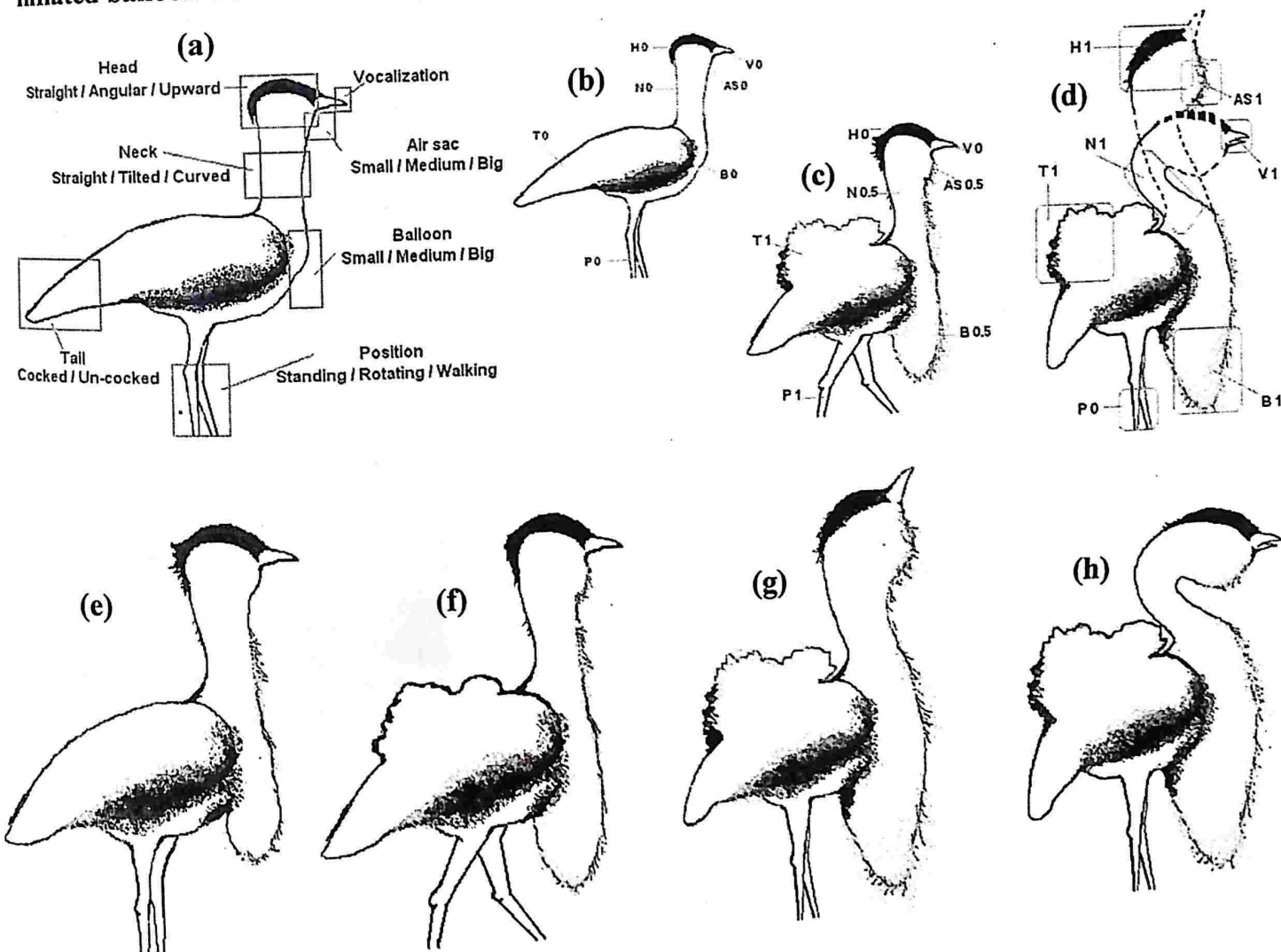


Figure 5.8

5.3.3.3. Courtship catalogue

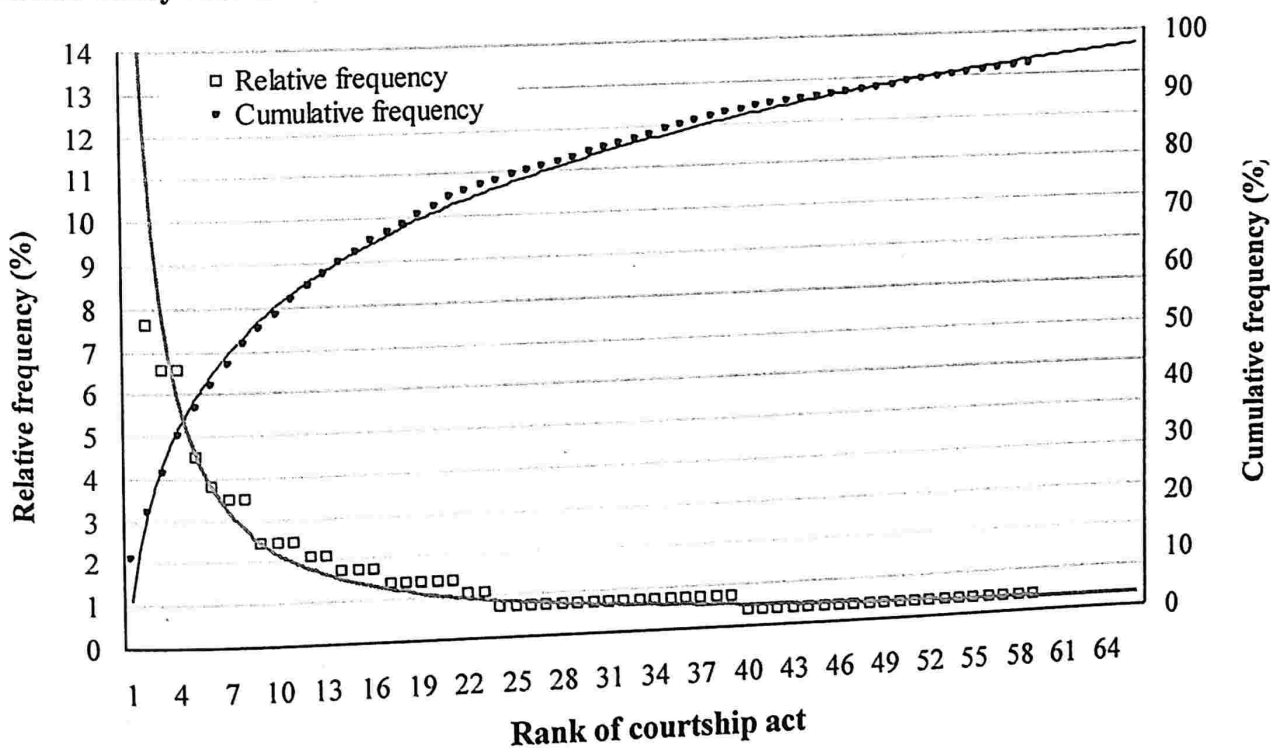
Components used for display and agonistic territorial rituals, such as, gular pouch, balloon, tail, vocalization, and various body orientations differed in their elaborations within and between courtship sequences (fig 5.9e-h). Thus, not only the quantity of courtship demonstrated in a male's repertoire varied, but also its quality, which could possibly influence mate choice. The courtship catalogue was described as a set of 58 acts, defined by unique combinations of component postures in 290 observations.

Figure 5.9 Description of courtship behaviour of Great Indian Bustard in Kachchh (2007–2011). (a) The structural components of courtship are head (H), neck (N), tail (T), body position (P), air sac inflated into gular pouch (AS) and balloon (B), and vocalization (V). (b) The normal posture, (e-h) various courtship postures of low to high intensities, and (c) the common agonistic posture during territorial rituals where rival males pace parallel to each other in zigzag motion, have been provided. For objective description of courtship quality (a subjective trait), displaying males were observed for 1-min at 5-min intervals, and their components were scored on the basis of maximum deviations from the 'normal' posture (b). For e.g., straight head and neck, flat tail, and deflated balloon were scored '0' (coded as H0, N0, T0, B0... in fig b), while raised head, curved neck, cocked tail and inflated balloon were scored '1' (H1, N1, T1, B1, P0... in fig d)



Seven of these acts were widespread, each having >3% relative frequency of occurrence that summed up to 50% observations. Fifteen acts were fairly common, having 1–3% relative frequency of occurrence that summed up to 30% observations. The remaining 20% observations were comprised of 36 rare acts (fig 5.10). The commonest act, 'A' (19% observations) involved standing, cocking up tail, fully inflating gular pouch and balloon, raising head, intermittently curving neck, and vocalizing (fig 5.9d). Vocalization was in the form of a low-pitch, resonant 'booming' call that could be heard from at least 0.5 km (also see Rahmani 1989). The second common act, 'C' (12% observations), was similar to this but for curving of neck and vocalization (fig 5.9g). Another similar act, with no vocalization but curving of neck (D) was next in commonness; along with the act, 'B', of walking with cocked tail, straight head, tilted neck, partly inflated gular pouch, fully inflated balloon and no vocalization (9% observations each, see fig 5.9f). The act, 'G', where the bird waved its balloon and encircled (moving in small circles), other components similar to C, was observed in 6% observations. Acts A, C, D and G were solely for displaying, whilst the act B occurred during agonistic rituals as well.

Figure 5.10 Relative (open squares and grey trend line on primary Y-axis) and cumulative frequencies (closed circles and smoothed black trend line on secondary Y-axis) of acts in the courtship catalogue of Great Indian Bustard in Kachchh (2007–2011). Acts were defined as unique combinations of component (head, neck, gular pouch, balloon, tail, position & vocalization) postures. Seven widespread acts were identified from the point of inflexion on these curves, while their long tails indicated many rare acts



I described all common acts in terms of their component postures and frequencies of occurrence in table 5.5, providing diagrams of the widespread ones and illustrations on the component posture scoring technique in figure 5.9.

Table 5.5. Mean±SE % frequency of common acts A–T (see table footer for detailed scoring on each component posture) in the courtship repertoire of the Great Indian Bustard in Kachchh (2007–11)

Act	Head	Neck	Gular	Balloon	Tail	Position	Vocal	Freq%	SE
A	1	1	1	1	1	0	1	18.6	5.4
B	0	0.5	0.5	1	1	1	0	9.5	4.7
C	1	0	1	1	1	0	0	12.3	3.7
D	1	1	1	1	1	0	0	9.1	3.9
E	1	1	1	1	1	1	1	4.3	2.5
F	0	0	0.5	1	1	1	0	3.7	2.2
G	1	0	1	1	1	0.5	0	5.7	2.4
H	1	0	1	1	1	0.5	1	1.1	0.6
I	1	0.5	1	1	1	0	0	4.9	2.8
J	1	1	1	1	1	0.5	1	4.4	2.3
K	0	0	1	1	1	1	0	2.9	1.2
L	1	0	0.5	1	1	0	1	4.3	4.3
M	0	0.5	1	1	1	1	0	4.1	2.7
N	1	0.5	1	1	1	0.5	0	2.8	1.7
O	1	1	1	1	1	1	0	2.9	1.6
P	0	0	0.5	0.5	0	1	0	1.8	1.4
Q	0	0.5	0.5	1	1	0	0	2.4	1.3
R	1	0	0	0	0	0	0	1.9	1.9
S	1	0	1	1	1	0	1	1.3	0.7
T	1	1	1	1	1	0.5	0	1.8	1.1

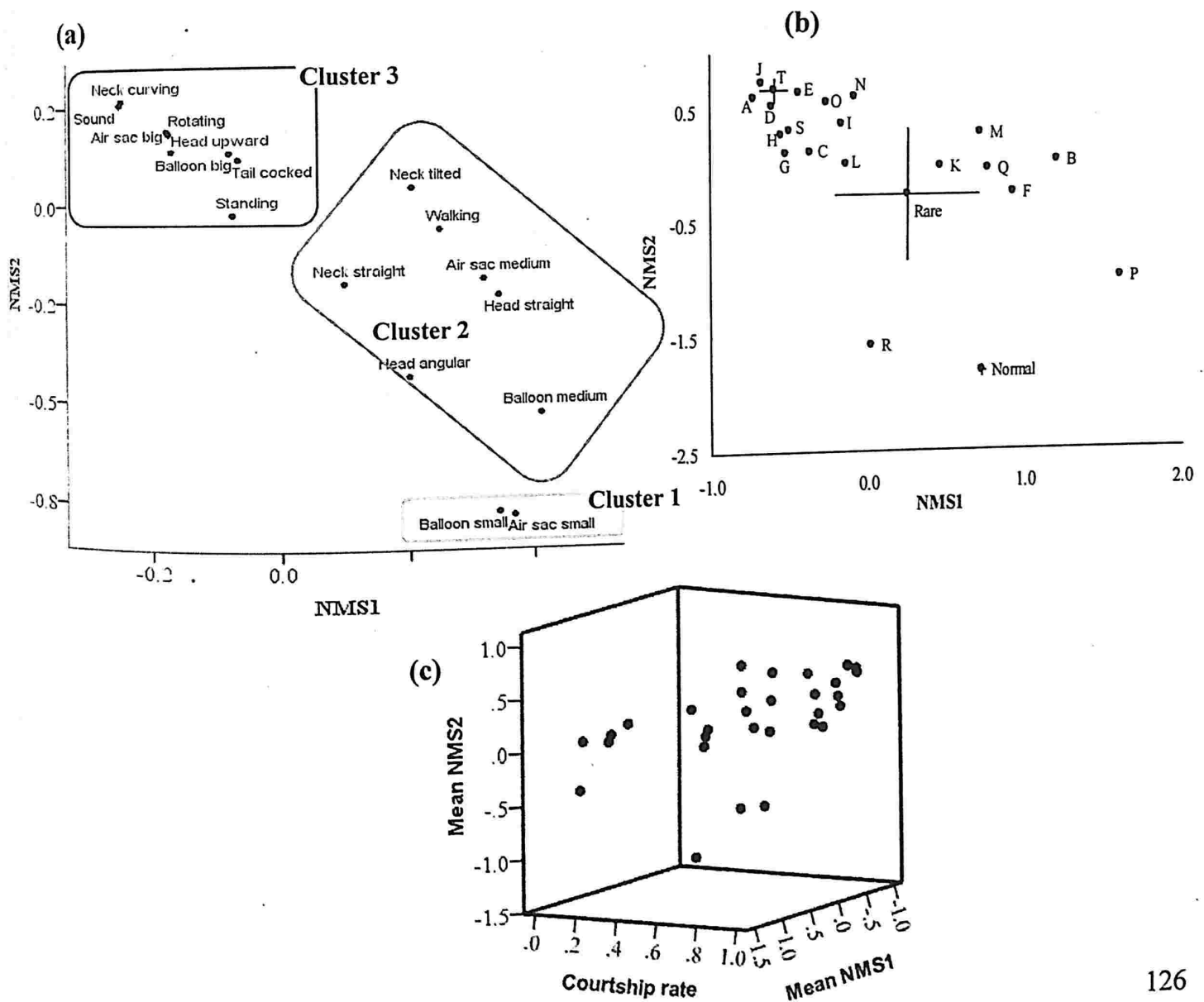
Straight=0 Straight=0 Small=0 Small=0 Un-cocked=0 Standing=0 No-sound=0
 Angular=0.5 Tilted=0.5 Medium=0.5 Medium=0.5 Cocked=1 Rotating=0.5 Sound=1
 Up=1 Curving=1 Big=1 Big=1 Walking=1

5.3.3.4. Courtship anatomy

Non-Metric Dimensional Scaling of component posture scores found a two-axes solution to be the best, having a satisfactory stress of 6.5 (stress <10 allows safe interpretations, see McCune and Grace 2002) that only 2% randomized runs could have produced, and final instability of 0.009. Hence, I considered that structural patterns of courtship were reliably represented by NMS axes. The NMS coefficients of component postures in an X–Y plot segregated into three clusters (fig 5.11a): cluster 1) deflated gular pouch and balloon (NMS1 > 0 & NMS2 << 0); cluster 2) partly inflated gular pouch and balloon, straight and angular head, straight and tilted neck, and linear walk (NMS1>0 & NMS2≤0); and cluster 3) fully inflated gular pouch and balloon, raised head, cocked tail, curved neck, static and small circular walk, and vocalization (NMS1<0 & NMS2>0). Clustering indicated higher probability of co-occurrence of intra-cluster postures than inter-cluster postures. Thus, component deviations from normal posture and their co-occurrences in repertoire (table 5.5) were synthesized into a quality measure that was higher for component postures in cluster 3 than cluster 2 followed by cluster 1. Correspondingly, acts A, C–E, G–J, L, N,

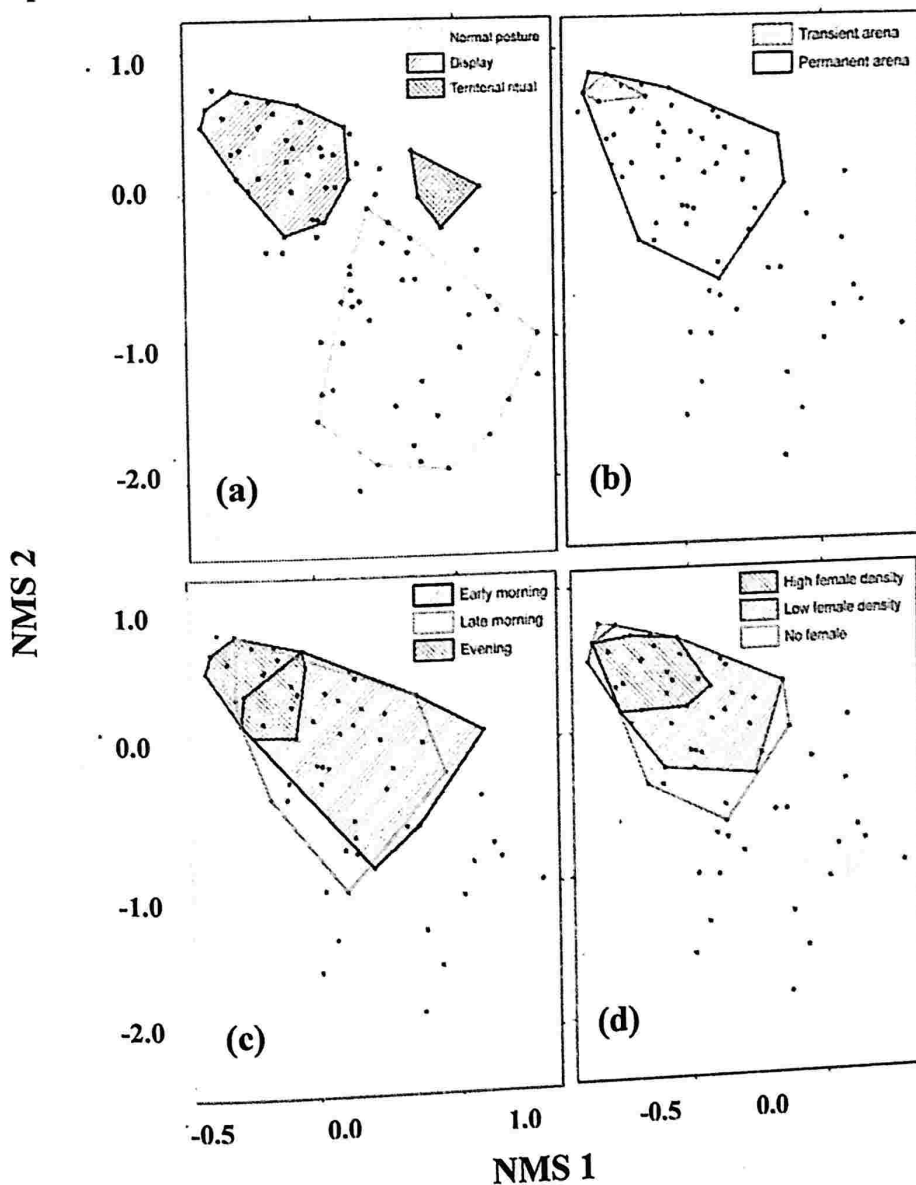
O, S and T qualified as high quality courtship; acts B, F, K, M, Q and the rare ones as moderate quality; and acts R and P as low quality (table 5.5 & fig 5.11b). The NMS coordinates of bird-scans (act-scores) represented a gradient of courtship quality, from low (NMS 1, 2 = 1.5, -2.5) to high (-1, 1), along the diagonal of figure 5.11 panels. The MCPs bounded 75% central distribution of act-scores, grouped into, behavioural states (fig 5.12a), arena type (fig 5.12b), daily activity periods (fig 5.12c) and female radial density classes (fig 5.12d).

Figure 5.11 Structural composition of Great Indian Bustard courtship repertoire in Kachchh (2007-11) based on Non Metric dimensional Scaling (NMS) of component postures in 290 observations. (a) Distribution of these component postures in bivariate NMS space revealed three clusters (enclosed in open polygons), with maximally deviating postures in cluster 3 and least deviating ones in cluster 1. (b) Based on bivariate NMS scores of component postures, acts (unique combinations of component postures) were also scored, which were (roughly speaking) of high quality if their NMS 2 scores > 0 and of low quality if NMS 1 score > 0. Common, rare and normal acts have been marked in the ordinal space. (c) Three dimensional scatter showing correlation between proportional frequency of courtship in a repertoire (X-axis) against mean scores of NMS 1 & 2 (Y-Z axes)



The mean and spread of act-scores differed (MRPP: $\Delta_{Obs}=0.79$, $p=0.001$) between display ($n=250$ bird-scans) and territorial rituals ($n=49$); the former comprising of more diverse and higher quality acts than the latter (fig 5.12a). Mean and spread of act-scores also differed between transient ($n=40$) and permanent ($n=259$) arenas (MRPP: $\Delta_{Obs}=0.87$, $p=0.001$, see fig 5.12b), early morning ($n=71$) and evening ($n=159$) hours (MRPP: $\Delta_{Obs}=0.79$, $p=0.001$, see fig 5.12c), and high ($n=71$) versus low ($n=53$) or nil ($n=175$) female radial density (MRPP: $\Delta_{Obs}=0.89$, $p=0.003$, see fig 5.12d). Courtship sequences observed in transient arenas, during evening hours, and in high female radial density were exclusively composed of high quality acts (fig 5.12).

Figure 5.12 Distribution and 75% Minimum Convex Polygons of bivariate NMS scores of bird observations grouped into (a) behavioural states: normal (open polygon), display (oblique shaded) and territory ritual (cross shaded); (b) arena type: permanent (open polygon) and transient (oblique shaded); (c) daily activity hours: (oblique shaded), late morning (open polygon) and evening (cross-shaded); and (d) female radial density: nil (open polygon), low or $<5\text{km}^{-2}$ (oblique shaded) and high or $>5\text{km}^{-2}$ (cross shaded) of the Great Indian Bustard in Kachchh (2007–2011). Diagonals of figure panels represent a gradient of low (NMS 1, 2=1.5, -2.5) to high (NMS 1, 2=-1, 1) courtship quality

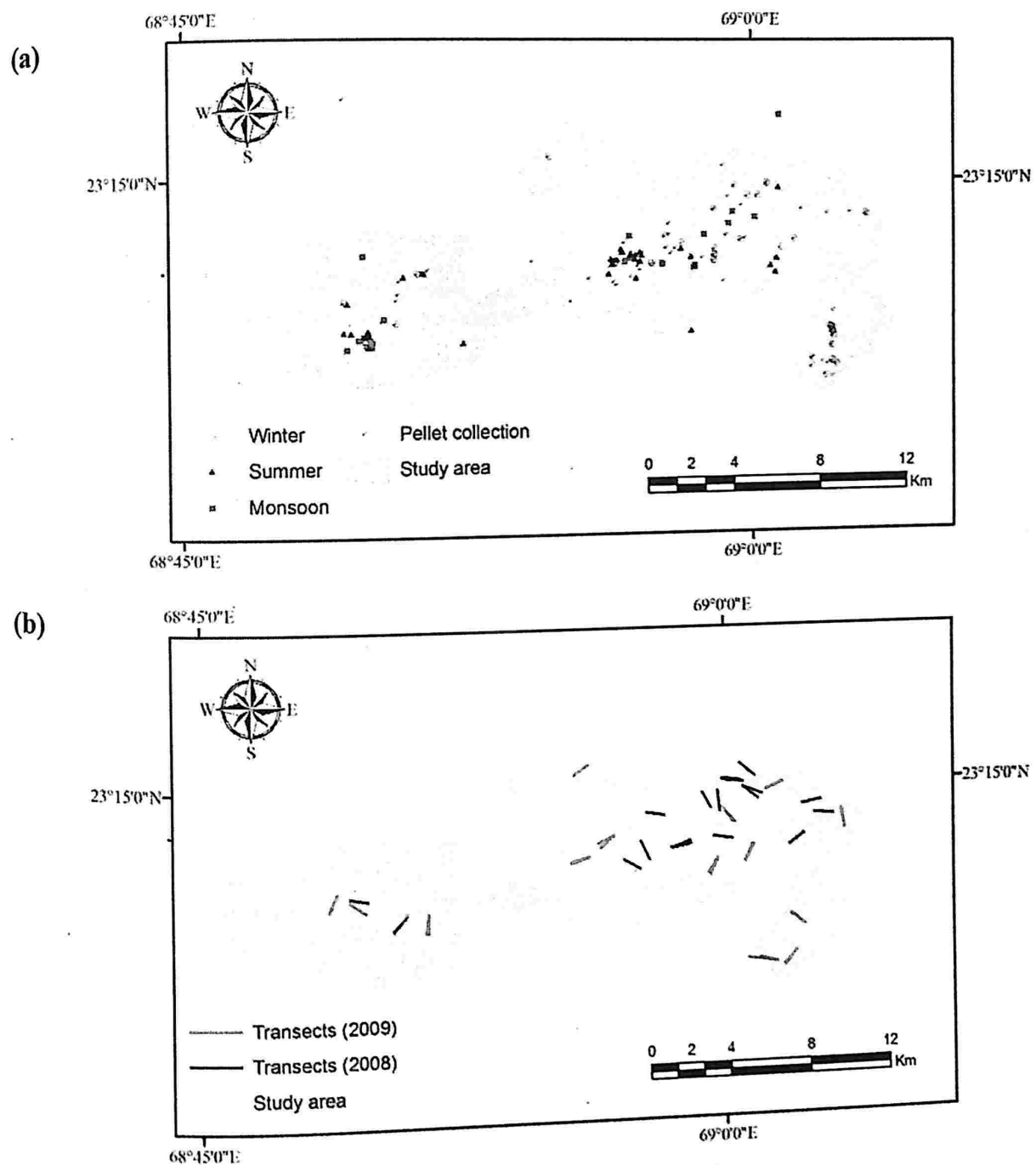


5.3.4. Feeding

5.3.4.1. Diet

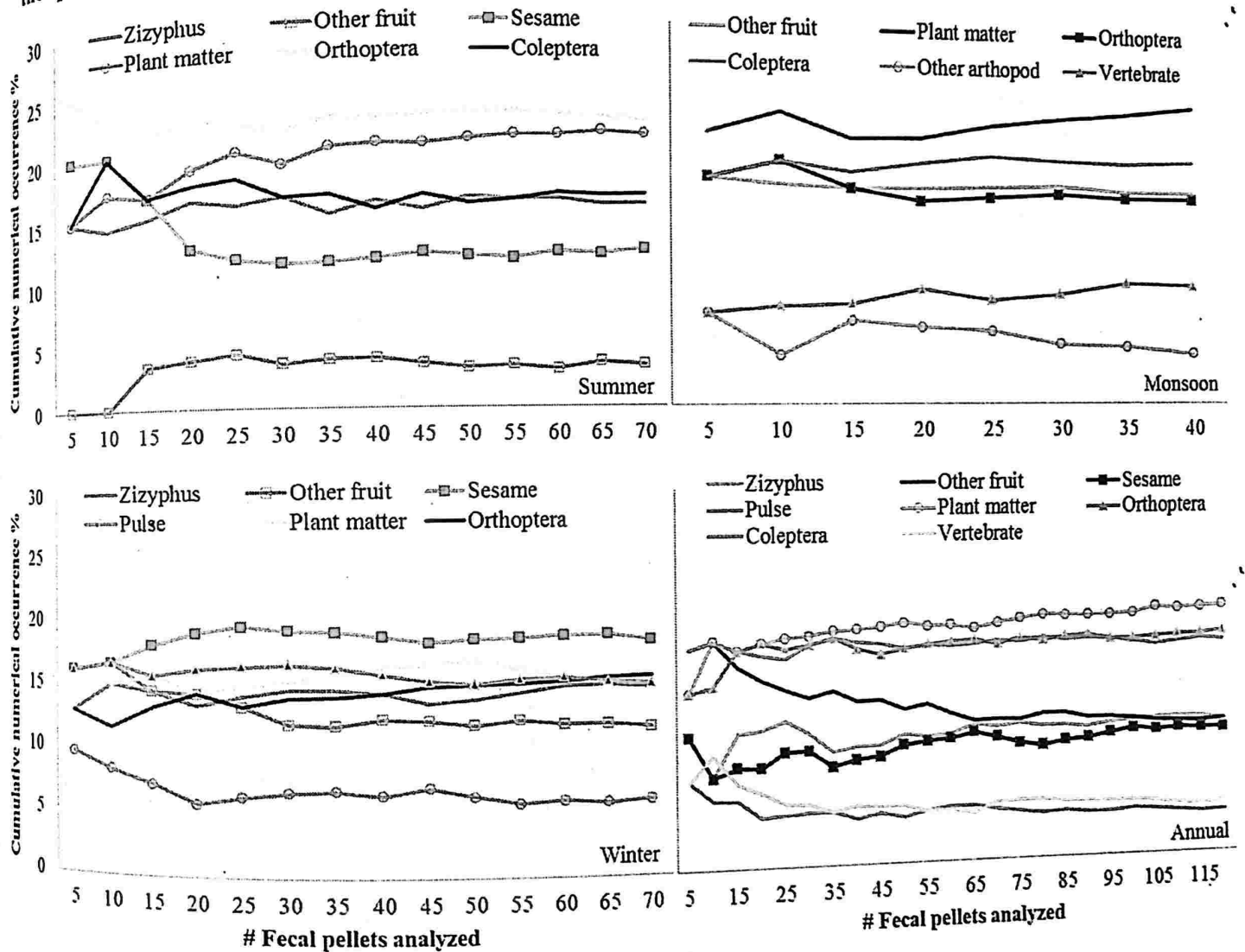
The annual diet of GIB was determined from 120 fecal pellets (40 randomly selected per season, see fig 5.13a) weighing 759 gm dry matter. Diet profile revealed 17 distinguishable food items (table 5.6), whose mean (standard deviation) and median biomass were 29.02 (71.92) and 2.96 gm respectively.

Figure 5.13 Sampling coverage to determine feeding habits of the Great Indian Bustard in Kachchh (2007–2011): (a) locations of fecal pellets that were collected (tic-marked) and analyzed (circle for winter, triangle for summer and square for monsoon); and (b) belt-transects (black line for 2008 and grey line for 2009) for estimating abundance of naturally occurring food items



Number of items per pellet was $4.7_{\text{Mean}} \pm 1.5_{\text{SD}}$, ranging from 1 (2.5% samples) to 9 (1% samples). The numerical proportion of major items in the annual diet (>5% numerical frequency) stabilized between 100–110 pellets (fig 5.14).

Figure 5.14 Seasonal and annual diet stabilization curves of the Great Indian Bustard in Kachchh (2007–2011). Cumulative proportional contribution by number, of major food items are plotted against the number of pellets analyzed, to assess the adequacy of sampling for accurately determining the species' food habits



Orthoptera, *Coleoptera* and herbage were most frequent, also constituting bulk of the fecal matter (each >80% frequency, 21% numeric frequency & 16–20% whole pellet equivalent). The IRI estimates ranked food usage as *Coleoptera* \approx *Orthoptera* \approx herbage > *Zizyphus* \approx *Sesame* \approx other fruits \gg other items (table 5.6). Correcting for differential digestibility, diet was broadly composed of 44% plant material, 55% arthropod and 1% vertebrate matter. The estimated dry weight contribution to diet was highest for *Coleoptera* and *Orthoptera*, followed by *Sesame* and *Zizyphus*, followed by herbage and other fruits (fig 5.15b). All other items cumulatively

constituted only 4.5% of diet. The two approaches yielded similar inferences but for the contribution of herbage (table 5.6 & fig 5.15b).

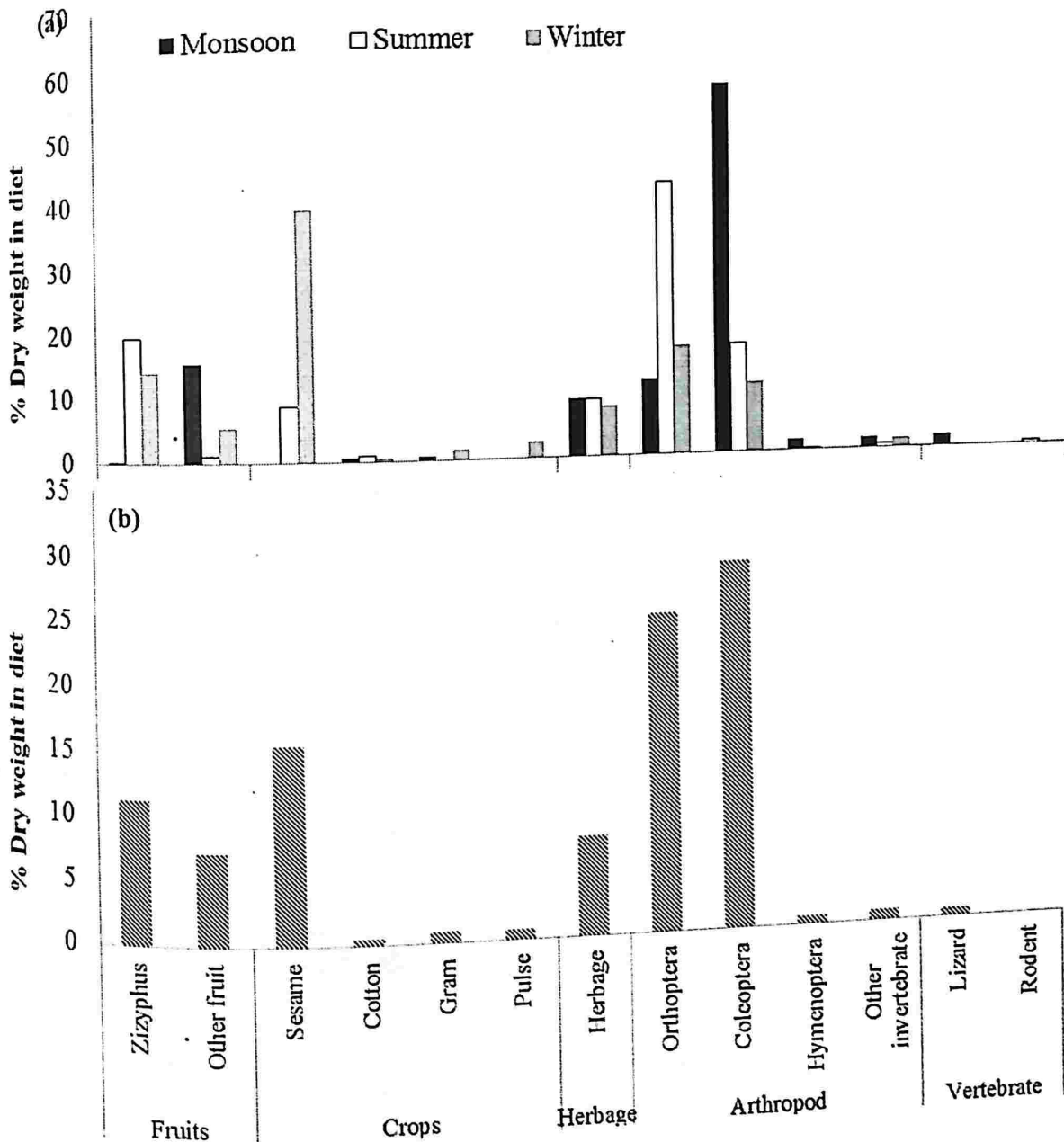
Table 5.6 Seasonal and annual diets of the Great Indian Bustard in Kachchh (2007–2011); represented as frequency (FO%), numerical frequency (NF%), whole pellet equivalent (WPE), and Index of Relative Importance (IRI) with 95% bootstrapped confidence intervals (in parentheses) of 15 food-item groups

Food_item	Season	Seasonal diet				Annual diet			
		FO%	NF%	WPE	IRI (95% CI)	FO%	NF%	WPE	IRI (95% CI)
<i>Zizyphus</i>	Winter	74.5	16.1	22.7	28.9 (23.5–34.4)	50.7	12.8	18.6	15.9 (12.3–19.6)
	Summer	64.8	19.9	31.3	33.2 (25.8–40.7)				
	Monsoon	10.1	2.2	0.4	0.3 (0.1–0.6)				
Other fruits (<i>Cucurbitaceae</i> , <i>Acacia</i> ?)	Winter	54.1	11.8	8.8	11.1 (8.5–14.7)	47.4	12.0	11.9	11.3 (8.8–14)
	Summer	13.2	4.1	1.7	0.8 (0.3–1.4)				
	Monsoon	80.5	18.0	25.8	35.3 (27.5–42.9)				
Sesame	Winter	92.8	20.1	30.4	46.8 (41.3–51.9)	47.3	12.0	12.2	11.5 (8.9–14.5)
	Summer	50.0	15.5	6.7	11.1 (8–14.6)				
Gram	Winter	14.2	3.1	1.3	0.6 (0.3–1)	11.0	2.7	0.7	0.4 (0.2–0.6)
	Monsoon	12.6	2.8	0.5	0.4 (0.1–0.8)				
Pulse	Winter	15.9	3.4	1.9	0.8 (0.4–1.4)	5.0	1.3	0.7	0.1 (0–0.2)
	Summer	4.2	0.9	0.4	0.1 (0–0.1)				
	Monsoon	10.1	2.3	0.5	0.3 (0.1–0.6)				
Cotton	Winter	4.2	0.9	0.4	0.1 (0–0.1)	5.8	1.5	0.5	0.1 (0–0.2)
	Summer	5.9	1.8	0.7	0.1 (0–0.3)				
	Monsoon	10.1	2.3	0.5	0.3 (0.1–0.6)				
Herbage	Winter	78.5	17.0	15.5	25.6 (20.9–30.5)	84.9	21.5	16.2	32 (28.3–36.1)
	Summer	82.4	25.4	17.8	35.6 (29.3–42.5)				
	Monsoon	97.4	21.9	19.2	40.1 (35.8–44.7)				
<i>Coleoptera</i>	Winter	75.7	16.4	7.4	18 (15.2–21.4)	81.7	20.6	20.0	33.2 (28.4–38.1)
	Summer	67.4	20.9	11.4	21.8 (16.6–27.2)				
	Monsoon	97.6	22.0	40.9	61.4 (54.4–68.9)				
<i>Orthoptera</i>	Winter	78.6	17.0	11.5	22.4 (18.7–26.4)	84.9	21.5	17.3	32.9 (28.8–37.4)
	Summer	91.1	28.1	28.7	51.8 (44.4–59.4)				
	Monsoon	82.6	18.6	8.3	22.2 (18.2–26.4)				
<i>Hymenoptera</i>	Summer	4.4	1.4	0.1	0.1 (0–0.2)	6.7	1.7	0.5	0.1 (0.1–0.3)
	Monsoon	12.3	2.8	1.1	0.5 (0.1–1)				
Other arthropod (Scorpion, Silverfish etc.)	Winter	8.6	1.9	0.9	0.2 (0.1–0.5)	12.4	3.2	0.6	0.5 (0.2–0.7)
	Summer	9.1	2.7	0.3	0.3 (0.1–0.6)				
	Monsoon	20.0	4.5	1.1	1.1 (0.5–2)				
Lizard	Monsoon	44.6	10.1	2.5	5.6 (3.6–7.8)	15.0	3.8	0.8	0.7 (0.4–1.1)
Bird	Summer	4.4	1.4	0.5	0.1 (0–0.2)	1.7	0.4	0.0	0 (0–0)
	Monsoon	2.4	0.6	0.0	0 (0–0.1)				
Rodent	Summer	5.9	1.8	0.6	0.1 (0–0.3)	2.5	0.6	0.2	0 (0–0.1)
Unidentified	Summer	5.9	1.8	0.2	0.1 (0–0.3)	1.7	0.4	0.0	0 (0–0)

I examined seasonal food utilization patterns. Summer and winter diets stabilized well within the number of pellets analyzed (fig 5.14). However, there were some indications of inadequate depictions of herbage and other arthropods in monsoon diet (probable errors up to

$\pm 5\%$, see fig 5.14). Dry fecal matter per pellet was higher in summer ($8.5_{\text{Mean}} \pm 7.2_{\text{SD}}$ gm) and winter ($7.7_{\text{Mean}} \pm 6.0_{\text{SD}}$ gm) compared to monsoon ($3.7_{\text{Mean}} \pm 2.3_{\text{SD}}$ gm). Seasonal diet breadths were similar but composed of slightly different arrays of 10–11 items (table 5.6). Digestibility corrections showed seasonal shifts (fig 5.15a) from a predominantly herbivorous diet in winter (71% plant material & 29% arthropod) to insectivorous in monsoon (26% plant material & 72% arthropod) and mixed in summer (39% plant material & 61% arthropod).

Figure 5.15 (a) Seasonal (open bars for summer, black for monsoon and grey for winter) and (b) annual diet compositions of the Great Indian Bustard in Kachchh (2007–11), represented as % dry weight of food items after digestibility corrections (dividing the dry volume of an item in feces by its 1-assimilated mass coefficient). (c) Assimilated mass coefficients of food items were obtained from published information on other bird species



(c) Following Lane et al. (1999), I converted plant matter using Withers' (1983) estimate (0.3 for ostrich *Struthio camelus* feeding on alfalfa); crops using Halse's (1984) estimate (0.7 for spur-winged goose *Plectropterus gambensis* feeding on corn); fruits using Karasov's (1990) estimate (0.5), arthropods using Bell's (1990) estimate (0.8); and vertebrates using Karasov's (1990) estimate (0.6 averaged across several raptors).

The IRI estimates ranked winter food utilization as *Sesame* > *Zizyphus* \approx herbage \approx *Orthoptera* \approx *Coleoptera* > other frutis >> other items; summer food usage as *Orthoptera* > herbage \approx *Zizyphus* > *Coleoptera* > *Sesame* >> other items; and monsoon food usage as *Coleoptera* > herbage \approx other fruits > *Orthoptera* > lizard >> other items (table 5.6). Estimated dry weight composition of food items returned comparable results to IRI estimates (fig 5.15a) but for reducing the contribution of herbage (to \sim 10% of diet in each season) that was consistently overestimated by the former approach (table 5.6).

5.3.4.2. Food abundance

I sampled important naturally occurring food items in GIB habitat from 62 transect visits (winter=21, summer=23 & monsoon=18, see fig 5.13b). Annual densities (numbers/100m²) were estimated at 0.95_{Mean} \pm 0.11_{SE} lizards, 9.81_{Mean} \pm 3.00_{SE} *Zizyphus* fruits, 2.01_{Mean} \pm 1.33_{SE} other fruits, 0.39_{Mean} \pm 0.08_{SE} *Coleoptera*, 4.22_{Mean} \pm 0.57_{SE} *Orthoptera*, 3.90_{Mean} \pm 0.65_{SE} *Hymenoptera* and 0.15_{Mean} \pm 0.02_{SE} other arthropods. Food items, ranked by individual body weights, were: *Saara hardwickii* (200gm) and other lizards (8.18gm) > other fruits (4.82gm) > *Orthoptera* (2.93gm) > *Coleoptera* (2.13gm) > other arthropods (1.33gm) > *Zizyphus* (0.48gm) > *Hymenoptera* (0.006gm). Densities of food items multiplied by their individual body weights provided seasonal and annual estimates of unit area biomass (hereafter referred to as biomass, in #gm/100m², table 5.7). Bulk of annual food biomass in environment (121_{Mean} \pm 12_{SE}) was constituted of lizards (77%) followed by *Orthoptera* (10%) and fruits (11%). Across seasons, biomass of arthropods did not differ (14.1_{Mean} \pm 2.6_{SE} in summer, 12.5_{Mean} \pm 3.0_{SE} in monsoon and 13.4_{Mean} \pm 3.2_{SE} in winter) but that of fruits showed fluctuations (9.5_{Mean} \pm 4.9_{SE} in summer, 0.9_{Mean} \pm 0.8_{SE} in monsoon and 31.5_{Mean} \pm 19.3_{SE} in winter). Accordingly, total seasonal biomasses were 142_{Mean} \pm 20_{SE} in summer, 106_{Mean} \pm 21_{SE} in monsoon and 112_{Mean} \pm 22_{SE} in winter (table 5.8). The actual consumable biomass in winter was higher than estimated here, since available crops were not quantified. During the study period, fruit and arthropod biomass underwent considerable temporal variations (fig 5.16), where the latter dipped from the beginning to monsoon 2008 and slowly increased thereafter. During monsoon 2008, rainfall was much less (350mm) than the half-decadal average (550mm), and arthropod biomass (2.5_{Mean} \pm 0.4_{SE} gm/100m², n=5 transects) was sevenfold less than the following monsoon (16.3_{Mean} \pm 3.7_{SE} gm/100m², n=13), and least among all seasons (fig 5.16).

Differences in use-availability ranks ordered the preference of major natural food items as: *Coleoptera* \geq *Zizyphus* \approx *Orthopetra* > other food items (figure 5.17) across seasons.

Figure 5.16 Temporal fluctuations of arthropod (closed squares on primary Y-axis) and fruit biomass (open circles on secondary Y-axis) from winter 2007–08 to monsoon 2009 in Kachchh

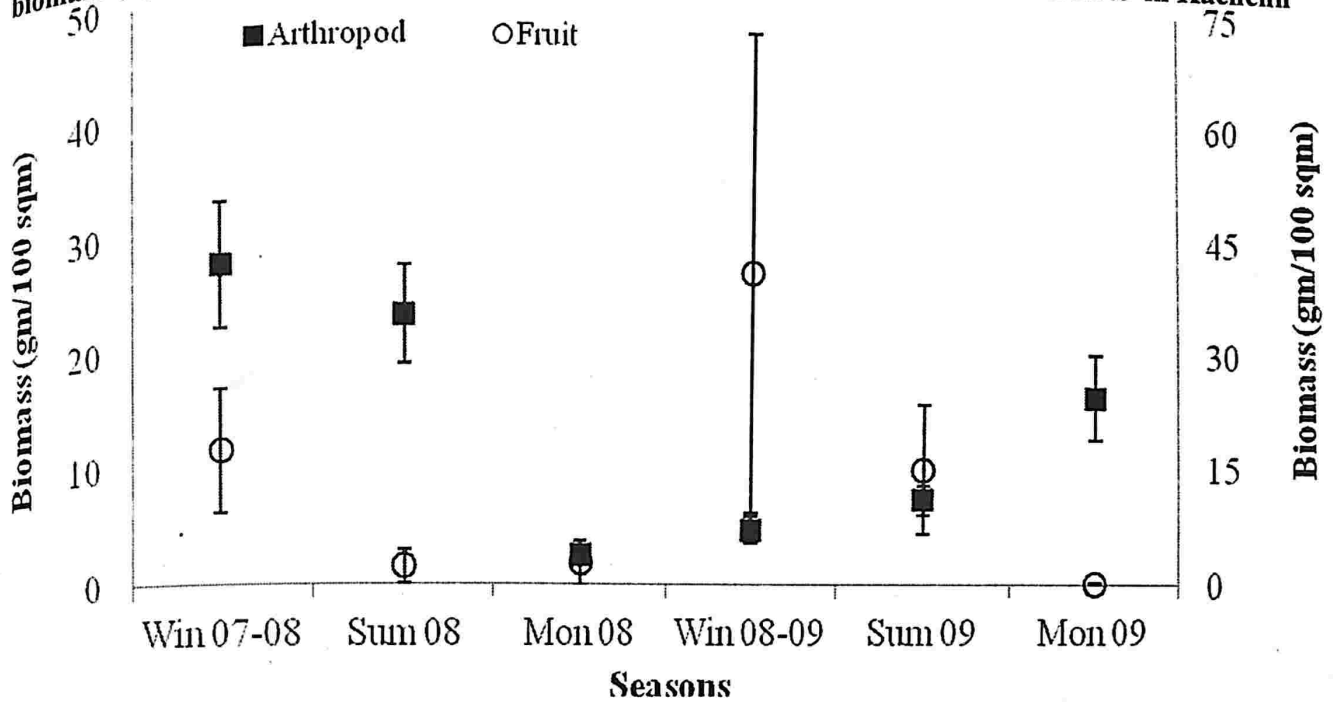
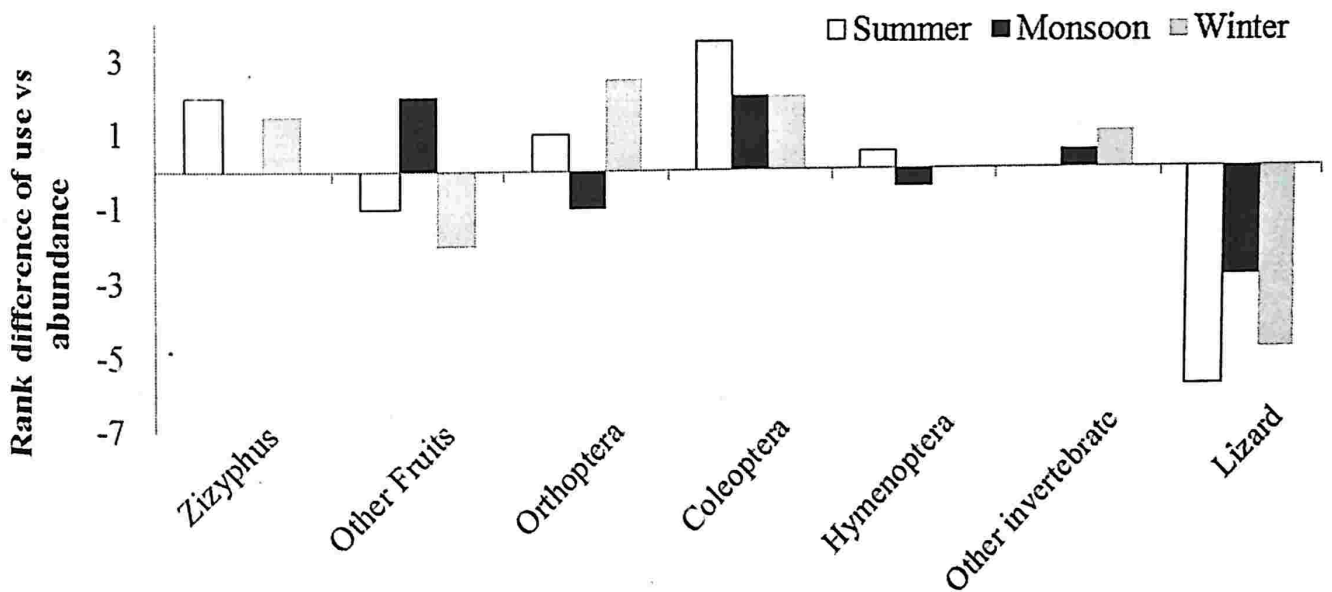


Figure 5.17 Order of preference of major natural foods in the seasonal diets of the Great Indian Bustard in Kachchh (2007–11)



5.4. Discussion

5.4.1. Behavioural pattern

This study provides the first published information on activity budget of GIB, describing seasonal and daily time allocation between six primary behavioural states during the active phase of birds. Rahmani (1989) and my reconnaissance surveys indicated a bimodal activity pattern, which is common among other large bustards (Martinez 2000, Trucios and Carranza 1991, Ziembicki 2009). Morning activity ceased on >50% occasions at 1045_{female}–1100_{male} hours in

summer, 1115_{female}–1215_{male} hours in monsoon, and 1100_{female}, male hours in winter. Activity patterns result from interactions between endogenous physiological cycles (circadian rhythm) and environmental conditions (Aschoff 1966). Minimizing activity during hottest part of the day to avoid thermal stress and water loss (Trucios and Carranza 1991, Ziemicki 2009) possibly carried survival value in arid environments, allowing physiological cycles to converge (Pittendrigh 1958) and give rise to morning–evening activity peaks. Time budgets calculated from 8–9 hours activity phases (under similar sampling schemes) of three large bustards, the Great Bustard (5-11 & 17-20 h, see Martinez 2000), GIB (7–12 & 17–20 h, current study) and Australian bustard (6-11 & 16-19 h, see Ziemicki 2009) were compared. Percentage time spent foraging was higher in Australian Bustard (~49%) than GIB (~38%) or Great Bustard (~37%).

On an annual basis, male GIB apportioned less activity time to foraging (34%) than females (41%) although being 2.5 times heavier. While females foraged for equal proportion of time across seasons, males traded–off their foraging time with courtship for ~100 days/year and partly compensated for it by spending 65% winter activity time in foraging. Similar phenomenon was reported in Australian Bustard (Ziemicki 2009) and Great Bustard (Martinez 2000). Following Bennett and Harvey (1987), I calculated approximate field metabolic rate (FMR; kcal/g) from body weight (BM; g) of male (13000g) and female (5500g) birds as: $\ln(\text{FMR}) = 1.18 + 0.61 * \ln(\text{BM})$, and converted that to kJ/day (considering 1kcal=4.186kJ). Male FMR (4403 kJ/d) was 69% higher than that of female (2605 kJ/d), raising questions on what mechanisms allowed males to meet their metabolic demands in spite of 17% reduced foraging time. Plausible hypotheses are: 1) males might partly compensate for less time apportionment to foraging by remaining active (and foraging) longer. Data indicated that male activity duration was significantly higher (by 1hr) than that of female only in monsoon, which was not sufficiently compensatory. On the other hand, Ziemicki (2009) observed longer resting duration in male than female Australian Bustard, falsifying this argument. Alternately, 2) genders might differ in their feeding efficiency, food utilization, and/or digestive efficiency (also see Martinez 2000). Results did not support any gender difference in feeding rates (male: $1.04_{\text{Mean}} \pm 0.10_{\text{SE}}$ & female: $0.92_{\text{Mean}} \pm 0.08_{\text{SE}}$ peck min^{-1}) when birds were actively foraging (Rahmani 1989). Even though I conducted fecal analysis, I could not assign pellets to the respective gender and examine diet differences. This possibility should be probed in future with the help of genetic tools (Ishtiaq et al. 2011). Mean prey size of male Australian bustard (34.1) was larger than that of female (15.7),

reanalyzed from Ziembicki (2009) who analyzed 15 male and 5 female gizzards. Gender differences in digestion had also been observed in birds (Markman et al. 2006) where one study suggested strong positive correlation between digestive efficiency and body weight (in white stork *Ciconia ciconia*, Kwiecinski and Tryjanowski 2009). Bailey et al. (1997) reported sexual dimorphism of alimentary tract lengths in four bustard species: the kori (*Ardeotis kori*), houbara (*Chlamydotis undulata*), white-bellied (*Eupodotis senegalensis*), and rufous-crested (*Eupodotis ruficrista*) bustards. Lengths of stomach, small intestine and large intestine of five female versus five male kori bustards (a close relative of GIB) were 131_f:160_m, 791_f:1151_m and 150_f:259_m mm respectively. This should also hold true for other large bustards like GIB, where 1.5 times longer alimentary tract in males than females should translate into better digestive and assimilatory efficiencies. On the contrary, it is also possible that greater reproductive costs in females (egg production and food provisioning to chicks) than males (display) demand more energy and may render similar absolute metabolic requirements between genders. Feeding rates were higher in winter than other seasons for both genders (fig 5.3c). Likewise, available biomass of major natural food items (fruits and insects; see section 5.4.4) was higher in winter (4488 gm ha⁻¹) than summer (2426 gm ha⁻¹) and monsoon (1256 gm ha⁻¹). Winter, being the harvesting season, also offered food crops that substantially contributed to the diet. Furthermore, Rahmani (1989) observed threefold higher pecking rates in croplands followed by grasslands and *Zizyphus* scrublands. Thus, the seasonal trend of feeding rates corresponded with that of trophic resource quantities, and was fine tuned by landuse specific returns.

I determined annual courtship schedule from consistent presence of male in arena through repeated visits during breeding season. This method was effective since males rarely used arena for other purposes and not detecting courtship did not guarantee that it was not performed. Courtship activity continued from April to September, similar to many other north Indian bustard landscapes (Goriup and Vardhan 1983). Its schedule was more variable in summer than monsoon across years (fig 5.7), and its time allocation was higher during early morning and evening (also see Rahmani 1989). These behavioural adaptations were possibly to minimize thermal stress of this metabolically costly activity under high temperatures (Moller 2000). However, proportion of time allocated to courtship did not significantly differ between seasons (fig 5.1). While high temperatures during summer added physiological costs, higher female radial density (3.66_{Mean}±0.49_{SE} km⁻²) than monsoon (1.99_{Mean}±0.15_{SE} km⁻²) was more rewarding. Thus, although

males chose to display less frequently in summer, when they did they tended to apportion more time to this act ($59_{\text{Mean} \pm 7_{\text{SE}}\%}$) than in monsoon ($49 \pm 6\%$), which might have nearly equalized courtship investment between seasons. Non-feeding directional movements of females were twofold more frequent during monsoon (28%) than other seasons (11–14%). This could result from regular exploratory movements of females, interested in displaying males, between arenas and foraging grounds during this time. Alternatively, food depletion due to drought in monsoon 2008 might have required more movements.

Preening behaviour plays important role in maintaining flight feathers, thermoregulation, removal of ectoparasites, and ornamentation (Henson et al. 2011, Zampigaa et al. 2004). Proportional time spent by females in preening was more in summer than monsoon and winter. This could be because dry weather and dusty winds in summer soiled birds' plumage requiring more maintenance; or high summer temperatures posed higher thermoregulatory needs. Alternatively, more maintenance might be associated with greater need of *cleanliness* on the onset of breeding activity. Preening was observed even in early morning (0700–0900) hours of summer but was restricted to late morning and evening hours in monsoon and winter. Scheduling preening on the daily budget would logically depend on the ratio of food demands versus thermoregulatory needs across day hours. Food satiation and thermoregulatory needs were likely to increase from early to late morning and decrease to evening in monsoon and winter. However in summer, thermoregulatory needs remained high throughout the day (mean air temperatures of 31° , 37° and 31° Celsius in early morning, late morning and evening respectively). It was also observed that when a female approached a displaying male, the latter performed more vigorously (details in section 5.4.3) while the former engaged in preening. A test of the hypothesis that genders mutually elicited these behaviours obtained good support from data. Particularly, solitary females visiting displaying males preened several times more regularly than on average; a condition that had probably increased the mean and spread of preening rate of solitary birds in monsoon (fig 5.4b). Explanations to why females preened more often in front of males during breeding season could be to advertise her *attractiveness*. This might imply that some levels of reverse mate choice (Bennett and Owens 2002) might operate in GIB, but would require confirmatory support before its acceptance, due to the serious theoretical implications (Johnsgard 1994). Females evaded detection (9–20% observations across seasons) more often than males (2–9%) due to their smaller body size and less conspicuous acts. Evasion could be either through resting or moving out of vision. The

former condition would slightly bias the estimated time allocation for resting, but the latter was unlikely to introduce any systematic error in active-time-budgets.

Birds typically faced anthropogenic interventions for ~9% (or 45-mins) of their activity duration. Such human incidence was relatively high for this shy species. Kachchh is an unprotected landscape, where varying levels of anthropogenic interventions occur almost everywhere under current scenarios. These include livestock grazing during 0900–1800 hours, traffic, farming activity from late summer to early winter, and domestic dogs (of villages and farm households) attempting to hunt small wild prey (pers. obs.). Although birds are known to prefer undisturbed sites for breeding (Chapter 4, also see Rahmani 1989), disturbance was 4.5 times higher in breeding than wintering areas (fig 5.3b). Human activity in the latter was particularly low in early mornings and evenings due to cold conditions. Palacin et al. (2012) also reported less disturbance in wintering than breeding areas of migrant female Great Bustard. However, seasonal differences in disturbances were not indicative of birds' preferences, but were artifacts of their strong inertia to breeding sites. Females being more mobile than males during breeding season showed greater human avoidance. I examined behavioural responses of birds to disturbance. Probability of vigilance versus that of other acts (odds) was 2.7 times in presence of disturbance than in its absence (details in section 5.4.2). The odds of courtship in presence of disturbance were one-third than in its absence (table 5.4). Thus, anthropogenic interventions significantly reduced time apportionment to the vital activities of GIB. Based on these results, it is recommended that key breeding habitats be made inviolate of human disturbances during breeding months. Consumptive human use such as grazing and farming should be curtailed, while vehicle movements and tourism should be regulated.

5.4.2. Functions of flocking

I tested if flocking mediated three potential behavioural functions in female bustards: 1) group-size effect on vigilance; 2) enhancement of feeding rates; and 3) transfer of social acts.

Vigilance was predicted to play an important anti-predatory function for GIB because they evolved among several grassland carnivores and faced human poaching from historical to current times. Since birds obtained food mostly by lowering their heads (71% pecks from ground) thereby occluding their vision to approaching threats (Bertram 1980), conflict and trade-offs between feeding and vigilance were likely (Pulliam 1973). In such case, living in a flock might be

beneficial although functional explanation of such benefits would not be straightforward (Roberts 1996). Individual vigilance in a flock could decrease in response to easier detection of threats, also called the *many-eyes* (Powell 1974), *collective detection* (Lima 1994) or *detection* (Dehn 1990) effects. Alternatively, it could decrease in response to reduced perceived risk of living in a group from *dilution* or *confusion* effects (dilution hypothesis, see Roberts 1996). Results suggested a statistically significant, albeit practically weak, declining effect of flocking on vigilance. Odds of vigilance in flocking bird were two-third of that in solitary bird. Reduction of individual vigilance in groups is a common phenomenon (Elgar 1989a, Lima 1994, Pulliam 1973) and has been reported from >50 birds and mammals (Treves 2000). I would briefly elaborate the mechanisms associated with this pattern based on breeding season data (to control for effects of seasonality). Firstly, assuming one vigilant individual in a flock was sufficient to detect threats, I found that proportion of times a flock remained vigilant increased by 30% with addition of one member. Therefore, larger flocks were more efficient in detecting threats. But this efficiency was not due to cooperative vigilance among associates. Birds in small and large flocks did not take turns to feed and scan, but increased their group vigilance ability by the sheer number of eyes operating randomly at any point of time. A cooperative mechanism is more likely in species where the vigilant individual can alarm its associates on detecting threats by signaling. But GIB did not exhibit any prominent alarm call, except for a barking "groo-groo" sound after a close encounter with jackal once. Anecdotal observations suggested that birds not only scanned for threats, but also for associates, and wary associates elicited response of caution in them (Treves 2000). Secondly, increase of vigilance in presence of disturbance tended to be less in flocks than solitary birds (table 5.3b). Vigilance rate differed between solitary and flocking birds by 5.6% of activity time when there was no disturbance but by 24% under disturbances. This indicated a relief from disturbance related stress to birds, perhaps safety from risk in presence of associates (table 5.3b). While these findings hinted at some group-detection and/or dilution effects of flocking (also suggested by Dehn 1990) it should be borne in mind that the decrease in individual vigilance with flocking was not very strong. There was also one contradiction: while solitary bird's vigilance rate was $22.4_{\text{Mean}} \pm 4.7_{\text{SE}}\%$ ($n=18$ scan-hours); flock vigilance increased from small ($25.97_{\text{Mean}} \pm 3.46_{\text{SE}}\%$, $n=33$) to large ($49.10_{\text{Mean}} \pm 4.76_{\text{SE}}\%$, $n=33$) flocks but individual vigilance did not decrease from small ($15.59_{\text{Mean}} \pm 2.44_{\text{SE}}\%$) to large ($20.49_{\text{Mean}} \pm 3.09_{\text{SE}}\%$) flocks. This could be because crowding beyond a point intensified competition for food and possibly elicited behavioural monitoring of

associates. Typical flock size in this landscape (2.7_{Mean} , $2.2\text{--}3.3_{95\%CI}$) fell within the range where individual vigilance was least.

In comparison to solitary birds, females in small flocks could reduce up to ~30 mins of vigilance from their ~8 hours daily activity phase. This difference should translate into higher food intake in flocking birds, but analysis of peck rates did not support this prediction. Only a small fraction of studies reporting decrease of vigilance with group size, had reported no increase in feeding rates (Beauchamp 1998). There could be two possible reasons behind this inconsistency. One being that crowding could lead to food depletion, increase competition, and reduce feeding rates (Caraco 1979). An extreme case was observed in monsoon, when solitary birds showed higher peck rates than small flocks, and large flocks were absent. Most of these observations (95% of 54 focal samples) came from the drought period (monsoon 2008) when chief seasonal food biomass (insects) was at its lowest (fig 5.16). Such low resource levels might have severed food depletion and intensified exploitative competition, rendering flocking counterproductive in terms of feeding. Alternatively, pecking rates measured food intake in patches when birds could be tracked on foot, but ignored time taken by birds to detect successive patches. The latter, patch detection rate, is often considered to increase with many eyes and many information sources in a flock (Ekman and Rosander 1987). If individuals want to benefit from the collective ability of patch detection, they are likely to show more tendency of flocking when good amount of resources are trapped within patches in an otherwise resource-scarce environment. This is to ensure that returns are sufficiently high to offset the competitive costs of crowding. In this landscape, food (natural and agricultural) biomass peaked during winter and the chief seasonal food types (fruits and crops) were also very patchy. I observed largest flock sizes in winter which could therefore be an adaptation to increase patch detectability and information sharing under such patchy and abundant resource conditions. Conversely, smaller flock size during summer and winter (breeding season) could result from intrasexual breeding competition for mating and nesting territories. Release of such competition in winter could have facilitated crowding to exploit the anti-predatory benefits of larger flocks without any direct foraging benefit.

Individuals of many species copy acts from conspecifics (Henson et al. 2011, Zajonc 1965). Preening was more synchronized in female flocks than would be expected at random, sometimes producing a wave of this act across flock members, also called *co-action* effect (Zajonc 1965). However, preening rate did not differ between solitary and flocking birds indicating that

preening was socially facilitated but not enhanced in GIB. Similar examples are found in literature, such as synchronized feeding bouts in domestic hens (Appleby et al. 2004), increased working efficiency of ants in presence of conspecific (Zajonc 1965), and synchronized preening in colonial gulls (Henson et al. 2011). The latter study provided some support to the hypothesis that preening soothed individuals after stress. However, I did not observe any correlation between frequencies of preening and disturbance in scan-hour samples ($r=0.04$, $p=0.64$). The causation of synchronized preening remained unclear. Nonetheless, it served important physiological and social functions, and was influenced by conspecifics (e.g., female preened more in presence of displaying males); thus assuming significance in the light of behavioural microevolution (Henson et al. 2011).

Birds generally formed unisexual flocks and only 4% sightings along transects in the core bustard area were of mixed flocks. Similar observations were reported by Rahmani (1989). Sexually segregated groups are common in sexually dimorphic species such as many ungulates and some birds (Ruckstuhl and Neuhaus 2005), but its evolutionary mechanism is poorly understood (Ruckstuhl and Neuhaus 2000). Several hypotheses have been proposed; the most accepted ones are the 1) *predation risk hypothesis*: if mortality rate differs between gender like higher mortality of females with juveniles (Main et al. 1996); 2) *forage selection hypothesis*: females are less efficient in digestion than males and may select areas with better quality forage while males require more forage quantity to meet absolute metabolic requirements (Main et al. 1996); and 3) *activity budget hypothesis*: sexual dimorphism ensues differences in activity budget making group cohesion difficult (Ruckstuhl 1998a). In GIB, mortality risk might vary between genders. Males being ornamented, bigger, and physiologically stressed after display might be easily targeted by predators; or conversely, females might be more vulnerable with chicks. Hence sexual segregation in flocking could be an adaptation to make life cycle stage specific predation risk uniform across flock members. Although extant natural predators were minimal, how intensely the ghost of past predation influenced current flocking patterns could only be guessed. Sexual segregation in flocking might also imply differences in food and/or habitat requirements. While food size preference could differ between genders (section 5.41), distribution of food sizes was unlikely to differ largely within the core bustard area so as to drive sexual segregation. However, some studies on other bustard species showed female preference towards more cover than males (Morales et al. 2008, Gray et al. 2009). Similar gender differences in microhabitat were also observed in GIB during foraging (section 4.3.2.2) in summer and winter (flock forming

seasons) which could drive sexual segregation in flocking. Activity budgets varied somewhat between genders (section 5.3.1) that could also lead to unisexual flocks. This study does not conclusively explain which (if not all) of these factors influence sexual segregation of GIB flocks and more targeted (preferably experimental) study is required for that purpose.

Although broader scientific interests lie in the mechanistic processes behind these observed patterns, my focus is on drawing conservation inferences from them. Here the conservation message is that flocking plays vital life history roles for bustards. It may improve detection of threats, reduce stress from disturbances, decrease individual vigilance, and assist behavioural microevolution. The first three benefits will provide more time for individual maintenance activities, allowing better utilization of resources and survival prospects to birds. Thus, ongoing fragmentation of patches may have two direct consequences on GIB fitness. It will reduce the potential of patches to hold larger flocks due to resource constraints, and increase the interface of birds with disturbances. Reduction of flock size will pose manifold higher demands on vigilance in presence of more disturbances, and may disrupt the function and evolution of social behaviours.

5.4.3. Courtship behaviour

5.4.3.1. Space-use dynamics

The study extended our prior knowledge on GIB mating system by characterizing their breeding aggregation and discussing the underlying mechanisms. It was not conclusive because of: a) small sample size due to very low bird numbers; b) lack of radio-tracked individuals; c) minimal information on copulations and d) relatively short duration compared to generation time. Synthesis of this and previous studies (Rahmani 1989) revealed the following aspects of GIB mating organization: 1) *Skewed sex-ratio*— adult sex ratio is highly skewed at 1 male per 3–4 females. 2) *Exploded lek*— male defends arena, and two arenas are separated by few kilometers (but two males displayed within 200m in Kachchh during monsoon 2011). Clustering is only noticeable through mapping at larger scales. 3) *Specificity to arenas*— one marked male used the same arena for three consecutive years in Karera, immediately after which a different male occupied it. Arenas were occupied for >15–20 years, longer than a male's breeding duration (Rahmani 1989). 4) *Dominance hierarchy*— several surplus males may be present in a population. Rahmani (1989) observed 24 adult males but three arenas in Rollapadu and eight males but one arena in Nanaj; additionally I observed four males but two arenas in Kachchh. Once the current occupant vacates, arenas are immediately occupied by other males (Rahmani 1989). It is unlikely that males share arenas within

season but this should be confirmed with the help of genetic tools (Ishtiaq et al. 2011). I checked if males were establishing territories in resource rich areas. Insect density, chief food in breeding season, was similar between arena ($4.66_{\text{Mean}} \pm 1.45_{\text{SD}}$, $n=7$) and non-arena (4.06 ± 1.45 , 18) 4-km² grids. Hence resource based territory is unlikely, and the social mating system is perhaps a polygynous dominance hierarchy at traditionally selected arenas in exploded leks.

Where and why such arena clustering occurs are interesting questions. It has been established that male mating strategies are shaped by spatial and temporal distribution of receptive females (Davies 1991). Hotspot model of male settlement driven by female space use (Bradbury and Gibson, 1983) fits into this paradigm. Various predictions of this hypothesis have been formulated and tested in field (Westcott 1997). Leks have been found on regular female movement paths (Apollonio et al. 1990), at high female densities (Clutton-Brock et al. 1988), and where breeding potential is high (Schroeder and White 1993). But some studies have not found any relationship between lek occurrence and female distribution (Balmford et al. 1993). In this study, breeding space use of female GIB was more unpredictable than male occurrence across seasons (also see Rahmani 1989). I tested a simple prediction of hotspot model that male arenas were placed at locations where long-term female encounter rates were consistently high. Based on regular sighting information at the scale of daily bird movements pooled on a seasonal basis, I obtained reasonable support to this prediction. I could not explore other hotspot predictions (Westcott 1997) due to the lack of radio-tracked individuals. However, as pointed out by Beehler and Foster (1988), if female encounter rate was itself influenced by males (e.g., through attraction to display), it would imply a cause-effect reversal. I offer a few observations to counter this possibility. 1) Although males withheld courtship in summer 2009, female concentration was similarly high in arenas. 2) Between seasons, male occupancy of Kalatalao arena was correlated with female encounter rates. Within seasons, vacancy of Kalatalao arena frequently coincided with an extra male, suspected to be the same one, displaying near Naliya arena. 3) During monsoon 2008, a drought season, female concentration shifted to the eastern side of study area since it received relatively higher rainfall than the western side (Dutta et al. 2011). Males, known to display from traditional arenas, showed sporadic displays spread over much wider area to the east. These indicated that male settlement perhaps depended on female use and not the other way round.

Female breeding space use did not depend on insect availability ($r=0.10$, $p=0.58$) or fruiting index ($r=-0.58$, $p=0.007$), but showed some correlation with distance from artificial water

sources in the form of roadside water-pipe leakages ($r=-0.37$, $p=0.04$). Birds were observed drinking water from these sources mostly during mid-summer. Although food resources did not determine female space use, other resource requirements (roosting and resting sites) could have played some role (see chapter 4). Out of 12 nests located in 4 years, 10 were aggregated at the periphery of one arena and one at 2km from another arena (fig 5.6a). Such nesting aggregation could be because of habitat specificity (see section 4.3.2.3) and strong site fidelity (Rahmani 1989), or conspecific attraction and cues from conspecific success (Danchin et al. 1998). Higher arena occupancy and regular territorial rituals in Naliya arena was indicative of its more popularity among males than the Kalatalao arena. This could be because of higher female usage in the surroundings (fig 5.6a) or other hidden reasons. From a conservation perspective, protecting this arena, currently threatened by agricultural encroachment, should be the topmost management priority. Current distribution of GIB arenas are relics of a more populated exploded lek system in the past. Naliya which held one or two arenas in recent times, used to hold many more just about ten years ago (Jhala and Joshua pers. comm.). Historically Naliya and Kalatalao arenas were likely to be connected, but were currently fragmented by the Defense air base and agricultural intensification. This condition can possibly interfere with female movements between arenas which is a crucial process in mate choice of this species. Since nests and arenas are spatially clumped, conservation of habitats within 2–3 km of arena is recommended.

5.4.3.2. Courtship frequency, catalogue and anatomy

Bustards use ornaments and courtship displays to attract females for mating (Johnsgard 1994). The most prominent ornament of *Ardeotis* bustards is their 'balloon' which is formed by inhaling air into a specially evolved chamber, the saccus oralis, within oropharyngeal cavity (Murie 1868, 1869). Courtship display of GIB has been described by previous authors and characterized in this study. Perhaps the most interesting questions about these traits pertain to how they have evolved; whether females cue upon ornaments or behaviour to choose mates; and what is the evolutionary mechanism behind female choice (Zuk et al. 1990). The latter has been alternately explained by the *self reinforcing selection* model (Fisher 1930) and the *indicator* or *handicap* model (Williams 1966). The first hypothesis proposes that if a male trait is preferred by females arbitrarily or based on some survival value, then their offsprings will spread the preferred trait and preference allele in an accelerated *runaway* process (O'Donald 1980). The second

hypothesis contradicts that sexually selected traits may not carry survival value *per se* but indicate better genetic constitution of the actor, thus self imposing a handicap which less viable individuals cannot afford (Trivers 1972, Zahavi 1975). Rahmani (1989) speculated that size of ornament (balloon) depends on age, indicating body condition and influencing female choice, but could not substantiate it because of minimal information on copulations. Female choice can also be influenced by at least two behavioural traits: 1) time investment on rate of courtship, which may indicate better genetic constitution; and 2) quality of display, if females attach aesthetic values to various acts of this complex repertoire. It should be invoked that ornaments are embedded within behaviours in GIB, and the two are inseparable. I characterized courtship from this perspective, by examining if courtship rate and quality were dependent on external environment. I could not test whether courtship traits in turn influenced female choice because of sample size constraints. I observed only three displaying males (at least), based on regular field surveys over four years. Out of these, two were mature with large ornaments (A_K & A_N) and one young with smaller dirty ornament (B_N) possibly due to suspended molting. In monsoon 2011, when A_N and B_N displayed from close proximity (200–1000m), A_N solicited for most of the female attention and also the only copulation that was observed.

Repertoires differed substantially in time allocation to courtship acts, and bouts varied in their lengths and progression. I examined how the probability of courtship occurrence θ changed with environmental conditions, using logistic regression. The constant probability $\hat{\theta}$, calculated under conditions of no female in arena, bright weather, no disturbance and no rival male, was 0.53. Conditional $\hat{\theta}$ did not change under cloud cover (0.51) but increased in dark condition (0.67) and decreased in sunny (0.27) and rainy (0.17) weathers. Influence of weather on courtship rate was most likely mediated through light and temperature effects. Males might prefer cloudy–dark conditions since low light increased the contrast of their white plumage against surroundings, thereby accentuating visual signals. Courtship demands high energy expenditure that can be even higher under severe temperatures (in sage grouse, see Vehrencamp et al. 1989). Preference for bright to cloudy conditions over hot, sunny conditions might be an adaptation to minimize thermal stress. Similar observations were reported by earlier studies on GIB (Rahmani 1989) and great bustard (Trucios and Carranza 1991). Courtship might be withheld in heavy rainfall to avoid physical damage to plumage. In regard to male's biotic environment, $\hat{\theta}$ increased in presence of rival male (0.74). Among observations where two breeding males were <1-km apart ($n=482$

scans), display accounted for 41.5% and territorial rituals 21.4% scans. Territorial rituals consisted of the following sequence: one male approached the other's display spot, both males paced parallel to each other with cocked tail and pendulous balloon, took abrupt turns intermittently, and finally separated out. Outcome of this ritual was sometimes decisive where one male had to leave the arena (monsoon 2007 & 2009), but sometimes indecisive where both males resumed displaying from respective spots (monsoon 2011). The $\hat{\theta}$ changed to 0.61 under mean female radial densities (2.5 km^{-2}) and 0.83 under mean $\pm 2\text{SD}$ female radial density (11.5 km^{-2}), other conditions remaining constant. Results substantiated Rahmani's (1991) observations of more vigorous display by males in proximity of females. I observed males to frequently change positions in arena during display when female concentration was low. Therefore continuous decline in number of female birds can disrupt male mating strategies in at least two ways. 1) It can pose serious consequences on time investment in display. 2) It can disrupt hotspot settlement in traditional arenas by reducing rewards to such prolonged stationary display. Lek extinction has been observed in great bustards (Lane and Alonso 2001). Such *Allee* effects (Stephens et al. 1999) on breeding ecology can worsen GIB's vulnerability to extinction (Dutta et al. 2011). From the perspective of conservation management, regression models on behavioural rates (courtship, vigilance etc.) enabled predictions on which environmental combinations were likely to release or cease behaviour. For example, the combined (but not single) effects of sunny weather and disturbance were likely to cease courtship under normal female distribution in the arena. Such understanding of behavioural thresholds can inform conservation practitioners to favorably manipulate environmental conditions that are manageable. It is advisable to avoid activities such as livestock grazing, tourism or farming near GIB arenas particularly during late morning. Since displaying males have limited mobility and their arenas are mostly known, local managers can implement this task with relative ease than curbing human activity all over the landscape or all through the day.

I performed a rapid content analyses of studies on courtship patterns by searching for keywords "courtship/display + pattern + analysis" in scholar.google.com. It returned 14 relevant publications (out of first 50 results): four on birds (Andrew 1956, Brown 1967, Dane and Kloot 1964, Trucios and Carranza 1991), seven on reptiles (Comuzzie and Owens 1990, Crews 1975, Davis and Jackson 1973, Jackson and Davis 1972, Jenssen 1971 1975, Jenssen and Hover 1976), and three on other taxa (Baerends et al. 1955, Clark 1994, Markow and Hanson 1981). These studies typically classified courtship into structural or functional components and asked the

following questions. Does time apportionment to different components vary between individuals and environmental conditions? Or is there a definite sequence of transition between components? Or does courtship variations influence mate choice? The GIB courtship was a complex repertoire involving many body movements and ornaments. It could be subjectively classified into four components based on prominent traits (balloon, vocalization and tail-position). These were 1) a low-intensity display, characterized by small-medium balloon, flat to partially cocked tail, and no vocalization (observed on 14% of 290 scans); 2) high-intensity display, characterized by large balloon, cocked tail, and no vocalization (56% scans); 3) full display, characterized by large balloon, cocked tail, and vocalization (25% scans); and 4) territorial ritual (described above). Such broad classification, although adequate for some pattern analyses, trimmed the rich assortment of acts leading to information loss. Individuals and conditions might release different assemblages of finer acts, whose sequence and development might be of ethological interest. Objective characterization of body movements against the benchmark *normal posture* (as undertaken in this study) provided much finer description of fixed action patterns. Sampling coverage, calculated from the probability of observing an old act in the next scan (Lehner 1979), was 87%. I identified seven stereotypical patterns occurring regularly in repertoires (described in section 5.3.3.3 and table 5.5). Multivariate analysis on elaboration of traits assigned synthetic scores to discreet acts, which converted them into continuous elements along a quality gradient reflecting energy costs. Average repertoire quality computed from its constituent act scores (NMS 1 & 2) and courtship rate (CR) were strongly correlated ($r_{CR,NMS1} = -0.69$, $p < 0.001$ & $r_{CR,NMS2} = 0.42$, $p = 0.019$, see figure 5.11c). When males apportioned more time of their repertoire to courtship, their display quality tended to be superior. Intuitively, display quality would be similarly influenced by environment as courtship rate. Superior quality displays, involving highly inflated balloon, curving of neck with vocalization and small circular walks, were observed under high female radial density and evening hours. These traits were also observed, although being interspersed with many inferior quality traits, under no or less females in arena and in late but not early morning. Territorial ritual was structurally different from display, and rested between normal posture and high-intensity display along the quality gradient. These results indicated that males' decision to release energy-costlier acts depended on conditions that optimize rewards and visual signaling. Thus, while courtship repertoire was an outcome of sexual selection, its release patterns might have been fine tuned by natural selection forces.

5.4.4. Feeding habits

The study described GIB food utilization on a seasonal basis through fecal pellet analysis, and compared that to natural food abundance in environment across two years. Great Indian bustard had an omnivorous diet (also see Bhushan and Rahmani 1992) which can be considered as a rule among bustards (Johnsgard 1991). At a finer resolution, diet profile shifted from predominantly herbivorous in winter to omnivorous in summer and insectivorous in monsoon. Food resources underwent temporal flux, characterized by rainfall dependent insect population dynamics, seasonal fruiting and crop harvest. Fecal analysis provides a biased representation of animal's diet if food items differ widely in their digestibilities, which is likely to be the case for an omnivore. I tried correcting for the bias by incorporating secondary information on digestibility of food items from comparable large-bodied birds (ostrich, goose and raptors). This technique has been applied to determine avian diet (see Lane et al. 1999) but provides partially correct results. This is because: 1) digestibility of food items can differ between foraging taxa, for e.g., specialized eagles may have better meat digestibility than generalized bustards; and 2) digestibility of a food taxa may not be adequately represented by a single food item, for e.g., dry-matter digestion of dicot plants vary from 20 (blueberry leaves) to 60 (alfalfa) percent in mule deer inocula (Milchunas et al. 1978). Instead of reliance on single food item or foraging taxa, average assimilated mass coefficients of herbage (0.34), fleshy fruits (0.48), insects (0.78), vertebrate (0.58) and cultivated seeds (0.75) were computed from literature review to reduce such discrepancies. Another source of bias could be the assumed equivalence between dry volume and weight of food items. For example, weight per unit volume of beetle would be manifold more than that of cotton. However for common food items, the density of matter was more or less similar. Because of these pit-falls in estimating diet composition, I simultaneously glanced at diet as relative importance of food items synthesized from uncorrected frequency and volumetric measurements. Quantifying diet from multiple perspectives was likely to provide more robust and comprehensive description than earlier standards, albeit not being completely accurate.

Previous studies (Ali and Ripley 1969, Elliott 1880, Hume and Marshall 1879) (Dharmakumarsinhji 1957, Gupta 1974) documented a wide array of food items in GIB diet, such as ants, beetles, grasshoppers, crickets, worms, caterpillars, scorpions, centipedes, mantis, lizards, snakes, eggs, rodents, fruits, crops and grass. I found most of these items to be occasional, while

the bulk of annual nutritional requirements were derived from beetles (29% dry weight in diet), grasshoppers (25%), *Zizyphus* and other seasonal fruits (19%) and particular crops (18%). Plant parts, such as grass blades, leaves and stems occurred in pellets. Their contribution was less in the overall diet (8%), perhaps because they constrain the forager by lignin and tannin intake, low nutrition, slow digestion rate, and gut fill (Stephens and Krebs 1986). Contribution of vertebrate matter was surprisingly low (1%) in spite of their high availability, digestibility and protein content. This could be due to higher foraging costs of searching and handling these preys, or preference for insects since they provide higher proportion of water per unit nitrogen and higher proportion of fat per unit body mass than vertebrates (Konecny 1987). According to the allometric relationship developed by Robbins (1983), body water content of GIB will be about 3.3 (female) and 7.7 (male) kg. This water is essential for physiological functions, such as a solvent, thermoregulation, transport and excretion (Robinson 1957). Since free water is scarce in semiarid landscapes, birds have to procure most of it from preformed water in food. Fleshy fruits although being less digestible (~0.48 AMC, see Karasov 1990) are high in water content (Robbins 1983) and low in foraging costs, which might explain their substantial contribution to the diet. Birds were also observed to drink water more frequently during hot summer mornings to meet additional needs. Results are comparable with Bhushan and Rahmani (1992) which provides the only other quantitative description of GIB diet.

I compared these findings with studies on four other bustards: the great bustard (Lane et al. 1999), little bustard *Tetrax tetrax* (Jiguet 2010), houbara (Tigar and Osborne 2000), and Australian bustard (Ziembicki 2009). The first three studies analyzed fecal pellets and the last one analyzed gizzard samples. Whenever necessary, I used available literature to correct for digestibility differences among major food items (Bell 1990, Halse 1984, Karasov 1990, Withers 1983) to compare results. Diets of all five species were chiefly comprised of plant and insect matter but their relative contributions differed. Corrected dry weight contribution of plant versus insect matter was highest for little bustard and great bustard (94–96% plant and 5–7% insects), nearly equal for GIB and Australian bustard (43–50% plant and 50–55% insects), and least for houbara (24% plant and 76% insects). These differences could have arisen between the species over evolutionary times in response to ecological factors. One of the factors could be aridity gradients that determine trophic resource characteristics; and are arid in houbara habitats, semiarid in Australian bustard and GIB habitats, and relatively wet in Great bustard and little bustard habitats. The latter two

species heavily depend on alfalfa which is much more digestible than many plant feeds (~60% digested in mule deer inocula, see Milchunas et al. 1978) and consume insects seasonally (Jiguet 2010, Lane et al. 1999). Dietary preferences coevolve with structural characteristics of gut (Leopold 1953). Bailey et al.'s (1997) comparison of bustard alimentary morphology with other birds revealed that bustards have: 1) proportionally longer oesophagus (without a crop), proventriculus and ventriculus, which might be an adaptation for food storage (Angel et al. 1996); 2) shorter small intestine than herbivores and granivores (Leopold 1953) which is characteristic of omnivores (Ziswiler and Farner 1972); 3) greater proportion of large intestine than Bantam chicken, which might be an adaptation for better water absorption in semiarid environments; and 4) weaker ventriculus musculature than domestic turkey and fowl, which might explain why several of these species including GIB ingest stones (Surahio 1985, Ziembicki 2009) to grind food.

Seasonal diet composition was perhaps determined by the intersection of birds' seasonal requirements and temporal flux of resources. I found that an accurate representation of the species' diet would require >60 pellets to be analyzed at least for summer and winter. Availability of collectible pellets was low in monsoon since their decomposition rates were higher due to physical action of water and increased dung beetle activity. Importance of *Zizyphus* was higher in winter and summer. This shrub species fruited in natural habitats during winter (November–January) but individuals getting established in agricultural fields, fallowed during winter, fruited late in summer (March–April). Other fleshy fruits were consumed more in monsoon. Among crops, *Sesamum* contributed the most, particularly in winter. However, large quantities of its seeds in fecal pellets might not reflect true dietary contribution since many agricultural seeds contain digestion inhibitors (Bullard and Elias 1979) that decrease their assimilated mass. Importance of *Coleopteran* insects was much higher in monsoon than other two seasons and that of *Orthopteran* insects was higher in summer. Insects are rich sources of protein, greater proportions of which are required by female birds during the egg laying period (Robbins 1983). Breeding coincided with mid-summer and monsoon, therefore its success would be closely linked with protein-rich food resources (Lack 1968). Among vertebrates, lizards were the most consumed taxa. Spiny-tailed lizard formed bulk of the naturally occurring lizard biomass but fecal remains belonged mostly to smaller species, such as *Calotes*, *Sitana* or *Agama* sp.

Higher consumption of a resource type may be because of its high availability in environment or preferential choice made by species. The two possibilities have very different

implications, whereby it is important to explicate resource use in the light of availability (Manly et al. 2002). Resource selection studies have traditionally measured food abundance, considering it (sometimes ambiguously) analogous to availability. More recently, precise measurement of available food resources has been advocated (Hutto 1990) but is fraught with difficulties. For example, if I wished to measure abundance of the burrow-dwelling spiny-tailed lizard for my study, sightings would be biased since lizards evade human presence; whereas an effective way would be to count active burrows since it closely approximates their actual numbers (Dutta and Jhala 2007). However, lizards inside burrows are not available to birds except for two hours a day on average (Dutta and Jhala 2007). Such useful information are absent for most food types, whose availability can depart from abundance in unique and unascertainable ways. For example, crops are perhaps only available to birds during disturbance free times of the harvesting season, which is difficult to measure for a particular crop-field. So I included only the important natural food types (fruits, insects and lizards) in use-abundance analysis, for which sampling was designed to closely approximate availability. Thus, medium to large sized grasshoppers and ground-dwelling beetles were sampled during bird activity hours, and fruits were counted within birds' foraging reach (0-1.5 m from ground). Plant matter (grass, leaf, stem etc.) was not sampled because available proportion of vegetation biomass was not clearly known. Habitat characterization at 10m radius plots estimated 32m^3 shrub-volume/ 100m^2 , and herbaceous dry weight was estimated at $14\text{gm}/100\text{m}^2$ (summer) and $142\text{gm}/100\text{m}^2$ (monsoon) from a subset of this landscape (Dutta and Jhala 2007). Hence an educated guess of plant biomass would be about $500-1000\text{gm}/100\text{m}^2$. Discarding one or more utilizable foods can influence the results of resource selection analyses (Aebischer et al. 1993). Johnson's rank difference method (1980) is less sensitive to this problem, and should be interpreted here as the order of preference within a subset of utilized foods.

In these semiarid ecosystems, rainfall is restricted to three monsoon months (July-September) and exerts an overwhelming influence on productivity (Whitford 2002). Relatively less rainfall, like the one observed in 2008, severely depletes insect biomass till the next wet season, may reduce fruiting of shrub species, and hampers agricultural production. As far as GIB food resources are concerned, erratic rainfall can be hazardous, and consequently affect species' life-history characteristics (Hutto 1990). Thus, I observed females to withhold nesting in monsoon 2008 and arena occupancy by males and females to be least during summer 2009 (fig 5.6). An opposite trend of more rainfall may not necessarily be beneficial to birds because of strong

socioecological impacts. Responding to more rainfall in recent past, local communities in Kachchh shifted to an intensive agro-landuse system that reduced grasslands by 20% within last three years. Natural food resources decreased and heavy pesticide usage reduced insect availability in crop-fields while the impact of pesticides on bird's physiology is unknown. One objective of the study was to estimate the dependency of GIB on human derived resources. Apart from a high level of *Sesamum* consumption in winter, this dependency was lower than that on naturally occurring resources during most of the year. Contrary to my presumption that GIB food biomass would be highest during monsoon, winter provided the maximal food biomass through availability of harvested crops, fleshy fruits and insects. Birds, particularly males after their courtship investments, apportioned most of their time budgets in foraging during this season. *Coleopteran* and *Orthopteran* insects, and *Zizyphus* fruits ranked high in the order of preference within a subset of food array, together composing about 65% of diet. Preference of these food types was probably to meet the necessary protein and water requirements of GIB. Habitat manipulations, so as to provide more of these food items, should be integrated into landuse conservation planning to benefit species' survival and reproductive prospects.

Chapter 6. Pastoralist socioecology

6.1. Introduction

In India about 150 million people depend on resources from natural areas (Kutty and Kothari 2001) that may compete with wildlife resource requirements and compromise conservation objectives. Thus coexistence of local communities in harmony with wildlife has often been questioned (Homewood and Rodger 1984). Global debate on natural resource conservation models has revolved around two dichotomous approaches: sustainable use (IUCN 1991) regulated by traditional institutions (Gadgil 1992) versus preservationism through exclusion of human use (Kramer et al. 1997). Indian Government traditionally follows a preservationist approach through declaration of Protected Areas (hereafter PA), wherein resource extraction is prohibited (Indian Forest Act 1927) and human pressure is reduced through relocation programmes (Rangarajan and Shahabuddin 2006, Shahabuddin and Shah 2003, Sharma 2003). Recently, conservation approach through community involvement has also been legislated, whereby new PA categories like a) Conservation Reserve, b) Community Reserve and c) Ecologically Sensitive/Fragile Area [Section 31A of Wildlife (Protection) Act 1972 as amended on 2002, Section 5 of Environment (Protection) Act 1986] have been included. The GIB requires vast landscapes to complete its life history requirements. Due to the exploded lek mating system and fidelity to display stations, it is possible to protect breeding areas as PAs since they are relatively small (few hundred square kilometers) and critically needed by the species. However in a densely populated country like India, creating landscape size inviolate PAs is not possible on economic and cultural grounds. Therefore coexistence with humans is the only model for conserving GIB. Harmonizing livelihood needs of local community with GIB conservation objectives and mitigating infrastructural development in these landscapes seems to be the only way to conserve this species. Considering these facts, bustard experts have recently reached a consensus on integrated sustainable management of habitats (Anon 2011) which would require comprehensive understanding of local socioecological perspectives (O'Donnell 1992, Saberwal and Rangarajan 2003).

Sedentary and nomadic pastoralism and monsoon farming are important traditional livelihoods of semiarid bustard landscapes. Primary production of these systems is linearly related to growing season precipitation and exhibits high inter annual variability due to stochastic precipitation (Knapp and Smith 2001). High net primary production means increased insect

abundance (Whitford and Creusere 1977) that favours bustards. Livestock grazing may impart several effects on vegetation and soil (Whitford 2002). According to one view, primary productivity reaches maxima at intermediate levels of herbivory (McNaughton 1979) leading to the *grazing optimization conceptual model* (Hilbert et al. 1981). It follows that the survival of grassland species is directly linked with sustainable pasture usage. Theories like *tragedy of commons* (Hardin 1968), *prisoners' dilemma game* (Dawes 1973) and *logic of collective action* (Olson 2002) influence our existing views on pasture management. These theories argue that under exploding human needs, when a pasture is used by many herders, *rational* decisions by individual herders lead to collective irrationality. However, modern research show that many communities evolve institutions through trial and error that can coerce collective rationality and sustainable pasture usage (Ostrom 1990, Ostrom et al. 1999).

Much of the current bustard range in Kachchh is legally unprotected community and revenue lands. These lands have been traditionally used as village pastures and treated as common pool resources (hereafter CPR) over which a group of people share equal rights and can exclude others (Jodha 1986). However, rights over resources are not permanent and evolve with changing power relationships of communities (Commons 1934). Management of CPR under all governance regimes depends on the efficiency of institutional arrangements (Iyengar and Shukla 2002, Marothia 2002), i.e., the collective organization of activities (*sensu* Dietz et al. 2003). They may involve laws, constitutions, traditions, moral or ethical structure, and conventional ways of doing things (Commons 1931, Marothia 2002). The CPRs are important in sustaining rural livelihoods but they are declining due to shrinkage of area, biophysical degradation, and erosion of management systems (Jodha 2002). Some processes held responsible for declining CPRs in India are a) increasing population pressure, b) introduction of land reforms in 1950s ensuing regressive land distributions, and c) introduction of village panchayats that often actively encourage privatization of CPRs (Jodha 1986). Similar trends are continuing in Abdasa tehsil. This region has faced agricultural desertion in drought years and dry rain-fed farming in wet years in the past, much like other low-intensity agro-ecosystems (Gray et al. 2007). But technological advancements such as electricity powered deep bore tube wells, other forms of irrigation, and relatively more rainfall in recent years have made water available in the semiarid remote natural areas. This has attracted massive encroachment of village pastures by local farmers and intensive year-round *Bt*-cotton cultivation by immigrant farmers. The traditional extensive agro-pastoralist

economy (dispersed cropfields, long fallow periods, less use of fertilizer and pesticides) is transforming into an intensive agricultural one (clustered cropfields, short fallow periods, high use of fertilizer and pesticides). Studies have shown that intensive cultivation is detrimental to bustards (see section 4.4.3.3 and Palacin et al. 2012, Simon et al. 2001, Wolff et al. 2001) and the latter's conservation is compatible with traditional landuses. Understanding consequences of these rapid changes on socioecology of traditional livelihood practitioners and their land management systems is important for integrated conservation planning.

I addressed sequential questions that integrate pastoralist livelihoods, grassland resources and bustard conservation. Various aspects of local landuses, such as livestock grazing pressure, concentration of infrastructure, and agricultural use were considered to model GIB habitat use in section 4.3. This chapter specifically asked whether livestock grazing exerted detrimental effect on grass biomass from the correspondence of their spatial gradients. Assessment of vegetation biomass should ideally require measurements on their height and cover. Since cover would also be influenced by other landuses (e.g., cultivation), I focused only on the spatial correlation between grass height and stocking density. Grass biomass will determine insect abundance, a major food item for bustard, and can be predicted to influence the species' space use. So I tested if the intensity of site use by female GIB was influenced by grass height (positive) and stocking density (negative). I restricted this analysis to females since males show strong inertia in space use that is confounded with several other experiential factors. Thereafter I studied the livelihood aspects and institutional arrangements related to pastoralism so that traditional land management systems can be restored. I described the socioeconomics, resource dependency, attitudes and institutional arrangements of resident pastoralist communities through questionnaire surveys. Finally I discussed the current socioecological trends in this region from established theoretical perspectives and their implications on bustard conservation.

6.2 Methods

6.2.1 Sampling grazing pressure, grass height, and female usage

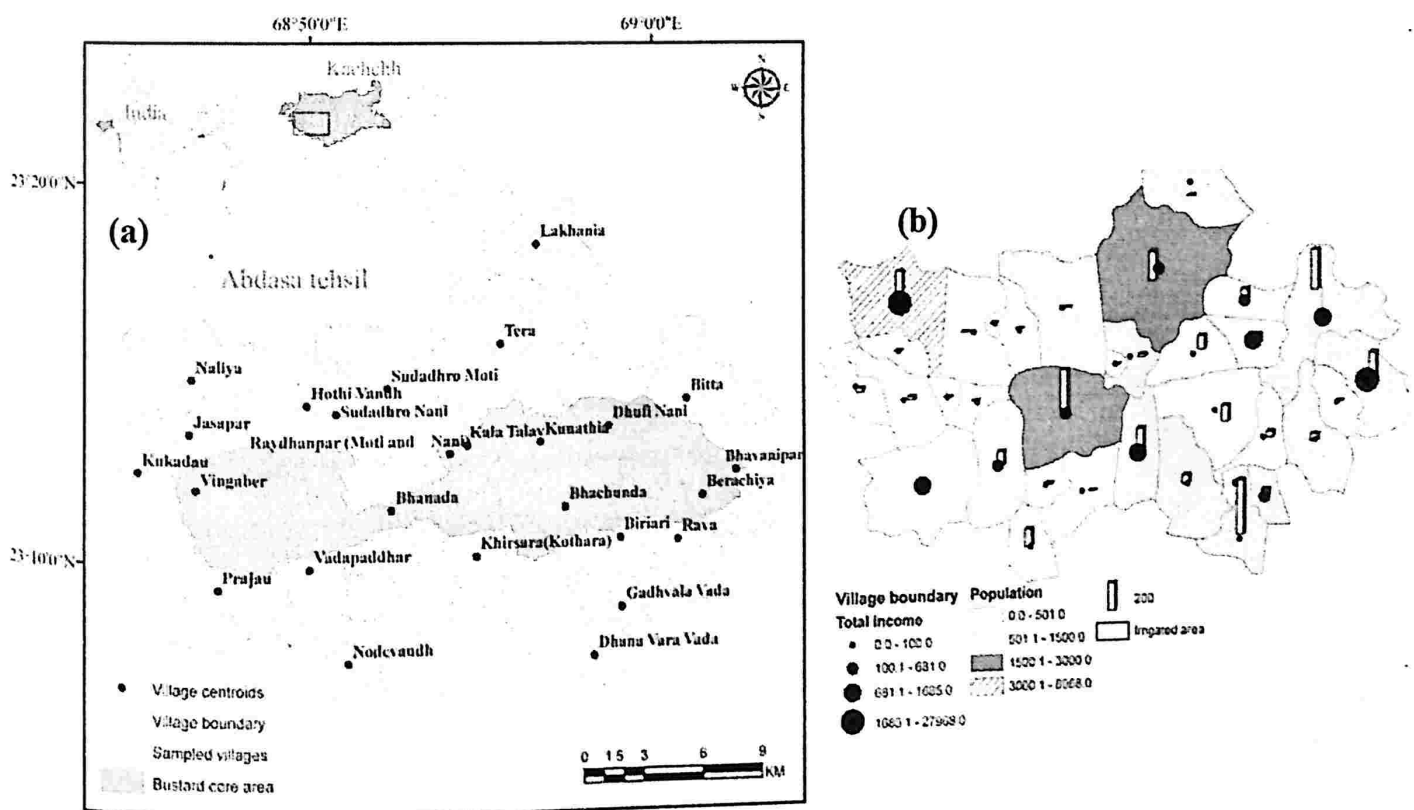
I mapped grazing pressure from livestock population and their impact areas in 20 villages adjoining the core bustard usage. In this region, livestock is owned by pastoralist as well as non-pastoralist households and the latter pay 'wage pastoralists' to herd them. For a comprehensive census of livestock, I first asked multiple pastoralists from each village about their collective herd

size, and averaged their responses. Since the villages were relatively small, herders had accurate knowledge on their collective resources. Then in 18 villages, I corrected these secondary estimates by actual counts of livestock in corals and as they returned from their grazing bouts to the village in evening. Numbers of sheep, goat, cattle and buffaloes were converted into Animal Units (hereafter AU) by standard conversion factors (one unit cattle, buffalo, sheep and goat equaled to 1, 1.25, 0.2 and 0.15 AU respectively, see Pratt and Rasmussen 2001). Grazing intensity was assumed to be uniformly distributed within a certain radius from villages and uniform in all directions (Homewood and Rodgers 1991). This implied that livestock herds spent more time grazing away from village, which was consistent with our field observations. I tracked daily grazing bouts of 34 herds from 10 villages by a handheld Garmin-72 GPS unit during May–August 2009 to capture ranging variability between the driest and wettest months. I estimated the mean herding radius to buffer grazing impact areas of villages. I overlaid AU on grazing impact area of each village to estimate stocking density (AU km^{-2}). I converted the core bustard area into $2 \times 2 \text{ km}^2$ grids and summed stocking densities of all overlapping grazing impact areas within a grid to estimate its combined grazing pressure. I assessed grass height in August 2009 (post monsoon) along 112 systematically distributed transects each $1.1_{\text{Mean}} \pm 0.2_{\text{SD}}$ km in length. At 200m intervals along the transect, I laid 100m radius circular plots to visually assess grass height on five-point scale: 0–5, 5–25, 25–50, 50–80 and 80–110 cm, as the mean assessment at five random points. I estimated the mean grass height of each 4-km^2 grid from mid-values of class intervals in all sample plots falling within the grid. To assess female space use, I made weekly field visits during April–September 2008–2010 and searched birds throughout the study extent. I overlaid visited routes buffered by 250-m (simulating the effective detection width) on the 4-km^2 grids. I considered grids whose $>25\%$ area was exposed to detection during a visit as sampled. Through six consecutive breeding seasons (summer & monsoon 2008–2010), I sampled 27 grids by $12_{\text{Mean}} \pm 7_{\text{SD}}$ (range 2–39) seasonal visits. I generated a detection/non-detection history of grids from bird locations on multiple visits. Based on this, I mapped the seasonal patterns of female space use as numbers detected per visit in a grid. Thereafter I estimated the spatial correspondence between stocking density, grass height and female usage of grids by Pearson's correlation coefficient and Dutilleul's (1993) correction for degrees of freedom. I used programs *ArcMap v 9.2*, *ArcView v 3.2* and *SAM v 4.0* for these analyses.

6.2.2 Socioecological surveys

I studied socioecological aspects of resident pastoralists in villages adjoining the core bustard area by conducting a mixed (open and close ended) questionnaire survey. It was divided into five sets of questions (appendix 6.1): 1) social aspects (household size, caste, religion etc.), 2) economic status (occupations, income, land assets etc.), 3) livestock data (household and village herd sizes, fecundity and mortality rate, supplementary fodder provisioning etc.), 4) ecological attitudes (knowledge on carrying capacity, current vs. past productivity of village pastures, ideal livelihood land cover, threats etc.), and 5) institutional arrangements. On visiting these villages, I obtained information on the number of pastoralist households from multiple herders. I typically surveyed 50% of pastoralist households per village through semi-formal interviews targeting their chief working members. I tested a preliminary set of questions on 10 respondents from two villages (Kunathia and Bitta) following which I restructured the questionnaire and interviewed 97 respondents from 22 villages (fig 6.1).

Figure 6.1 Study area (Abdasa, Kachchh, India) map showing (a) villages adjoining the core bustard usage (n=33) some of which were sampled (n=21) to study pastoralists' socioecology, and (b) village profile in terms of human population, total income and irrigated area during 2007-11



Responses were either on continuous scale (for e.g., annual income, herd size, and supplementary fodder/day/animal-unit), or categorical form (for e.g., major threats to livelihood, and if pastoralists wanted to increase, decrease, or retain the current herd size) later converted into proportion of positive response in different categories. Some responses were synthesized into derived variables, as follows. I computed the caste diversity of pastoralists in a village and diversity of species in their herds using Shannon's diversity index (Shannon 1948) and the proportion of large livestock (in AU) per herd. I estimated the following vital rate parameters of livestock herds: 1) recruitment rate, as the number of youngs surviving from year t to $t+1$ (small livestock) or $t+2$ (large livestock) divided by the average adult population between the two time instances; 2) adult mortality rate, as the number of adults dying between year t to $t+1$ divided by the number of adults in year t ; and 3) intrinsic growth rate, as recruitment rate minus adult mortality rate only for small livestock. I characterized institutional arrangements by assessing: 1) pastoralists' problem reporting and protesting tendency, 2) fidelity to occupation, 3) tendency to exclude 'free-riders' from accessing resources, and 4) organizational ability to enforce land tenure rules. These information were obtained from questions 24, 25, 26 and 28 in appendix 1, whose responses were scored on an ordinal scale. For e.g., I assessed problem reporting and protesting tendency by asking whether pastoralists complained about emerging land tenure problems to any authority, and (if so) to whom. I scored the response "no" as 0, "complained in Panchayats" as 1, and "complained to higher authorities such as revenue and forest departments" as 2. Similarly, I assessed the organizational ability to enforce land tenure rules by asking if pastoralists in a village formed cohesive groups, if land tenure rules existed, and if those rules could be enforced. Each response was scored as 1/0 and averaged into a measure of institutional strength. Finally the four measures of institutional aspects were rescaled between 0-1 and averaged to obtain an overall social capital index for pastoralist community in each village.

To characterize the socio-economy of pastoralists, I reported the mean and standard error of these variables for the overall region, and segregated into villages. To explore the interrelatedness of socioeconomic variables (household size, land holding, herd size, composition and vital rates, supplementary fodder provisioning, and incomes)*, I computed their pair-wise Pearson's correlation coefficients. I classified livelihoods based on combinations of occupations and compared socioeconomics between them in terms of the set of variables listed above (*) using one-way ANOVA. To assess peoples' dependency on grassland resources for livelihood, I

estimated what proportion of total annual income was contributed by pastoralism. I examined if economic viability of pastoralist livelihood was reducing under prevalent scenarios of agricultural encroachment in grazing lands. The major source of pastoralist income was sale of animals along with sale and self-consumption of milk and that of manure, all of which depended on livestock production. So I tested if the intrinsic annual growth rate of herds was significantly positive across all pastoralist households (replicates) by one-mean t-test (Zar 1999). I grouped villages based on similarity of the four institutional measures by cluster analysis (McCune and Grace 2002). Testing for significant difference in the overall social capital index between these clusters, I obtained groups of villages with varying levels of institutional arrangements. Thereafter, I tested if these village groups also differed in social, economic and attitude profile by conducting Kruskal-Wallis test (Zar 1999) on select variables at the village-scale. Finally I tested if natural land-cover (grass and scrub) in village grazing areas was related to the human population density. I obtained human population density of 2001 from the Indian Government's census report published in 2005 (<http://www.censusindia.gov.in>). I calculated the area and proportion of grassland and scrubland within grazing impact areas of villages from a classified vegetation map of the study area (details in chapter 4). I examined if the proportional natural land-cover around villages corresponded with their human population density using Spearman's correlation analysis (Zar 1999).

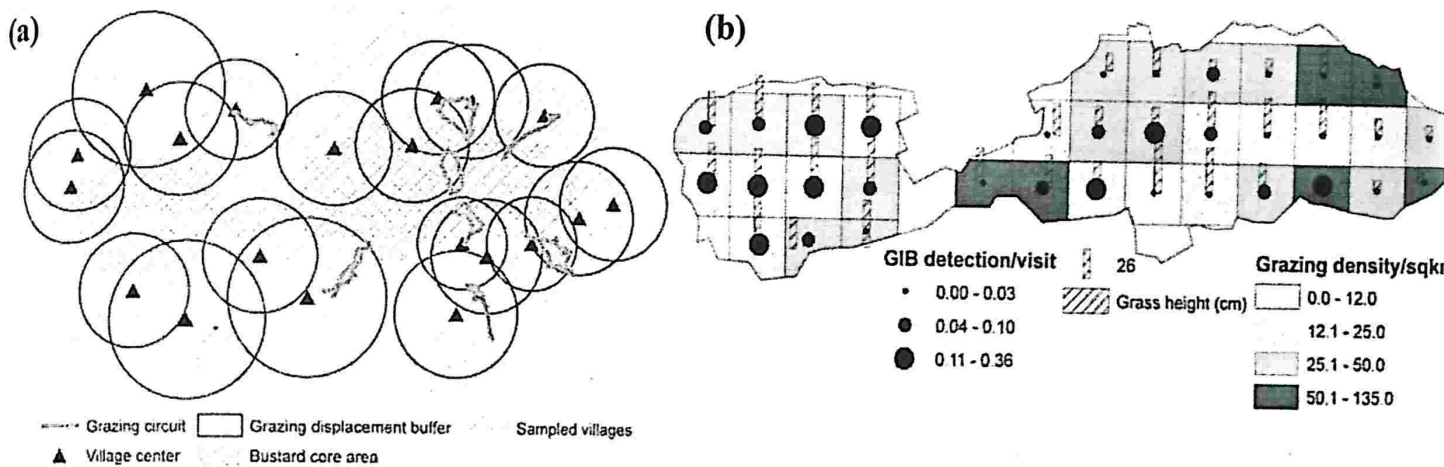
6.3 Result and Discussion

6.3.1 Impact of grazing on bustards

Livestock herds travelled $8.25_{\text{Mean}} \pm 2.21_{\text{SD}}$ ($4.04_{\text{Min}} - 14.44_{\text{Max}}$) km for daily foraging bouts (fig 6.2a). Their linear displacement from village centers was estimated at $3.10_{\text{Mean}} \pm 0.15_{\text{SE}}$ km, ranging from 2.4 (Bhachunda) to 4.2 (Khirsara) km. I buffered sampled villages by their local mean herding radius and non-sampled ones by the global mean herding radius. Stocking density of villages in grazing impact areas was estimated at $24.85_{\text{Mean}} \pm 5.29_{\text{SE}}$ AU km⁻², ranging from 2.6 (Berachia) to 134.6 (Bitta) AU km⁻². Berachia was a sparsely populated village (30 households) where most villagers had abandoned their rural livelihoods post 2001 earthquake. Whereas majority of livestock in village Bitta (90%) belonged to recent immigrants from the village Misriadda, ~75 km away in Banni grasslands, which faced a socioecological collapse about 10 years back. Aforesaid stocking density estimates did not include overlapping use of grazing areas by neighbouring villages. Incorporating this information, stocking density at 4 km² grid-scale was

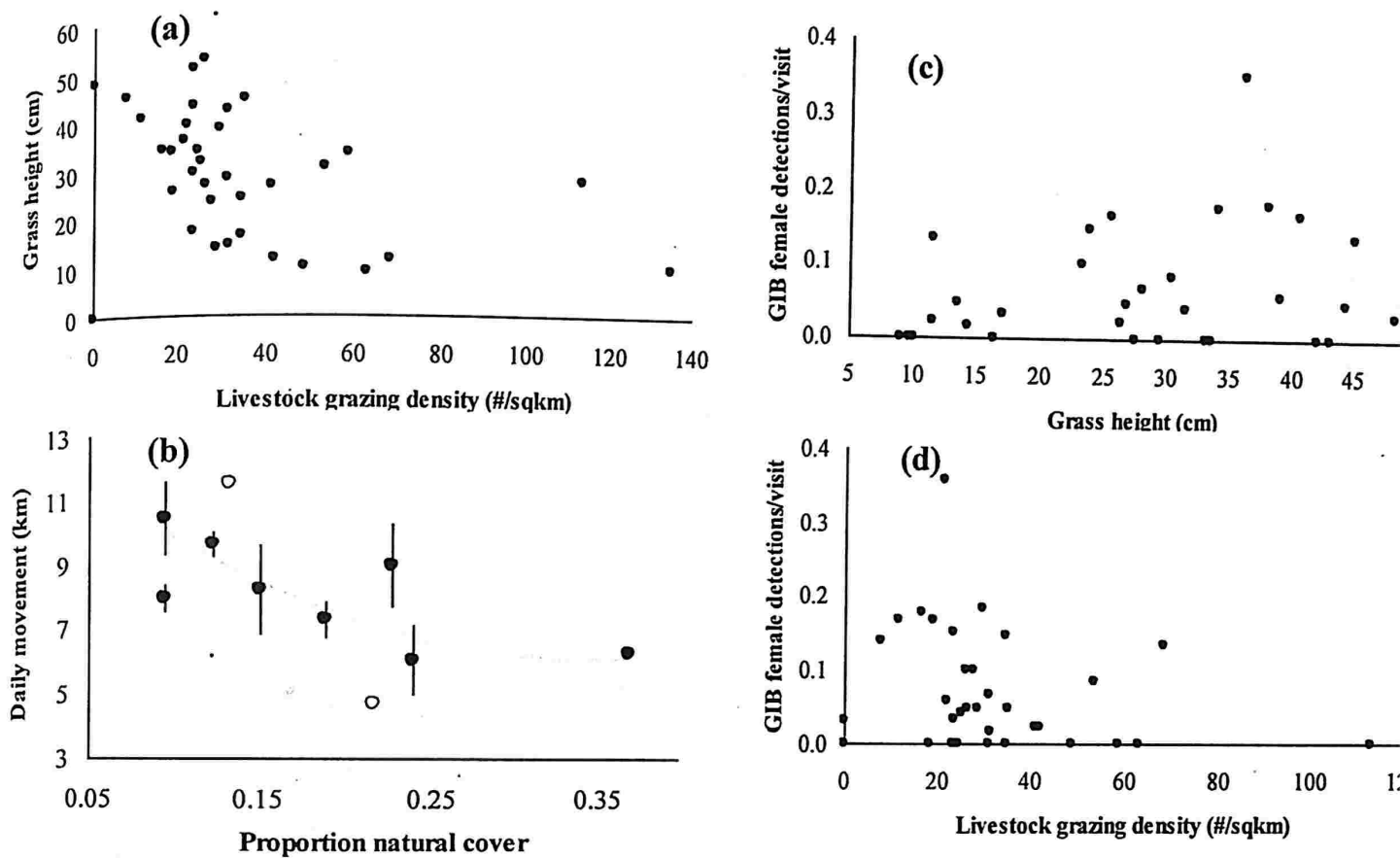
$34.72_{\text{Mean}} \pm 4.59_{\text{SE}}$ ($0_{\text{Min}} - 134.6_{\text{Max}}$) AU km^{-2} (fig 6.2b). This technique of mapping grazing pressure was coarse scaled and simplistic because it ignored the additional influences of palatability of vegetation, distribution of water etc., but was reasonable for my objectives.

Figure 6.2 (a) Livestock herds (n=34) were tracked to map the grazing area of villages around the core bustard area (only 8 grazing circuits shown for clarity). (b) Livestock grazing density, grass height and female great Indian bustard detection/visit mapped at $2 \times 2 \text{ km}^2$ grids in the core bustard area of Abdasa (2007–11)



The carrying capacities of semiarid and arid grasslands have been estimated at 10 AU km^{-2} and $20-50 \text{ AU km}^{-2}$ respectively (Shankar and Gupta 1992). It appears that the current stocking density of this region is within the tolerable range. But this calculation ignores a) additional herds of semi-nomadic pastoralists who visit this region after monsoons, b) forage offtake by wild herbivores (nilgai, chinkara and spiny-tailed lizard), and c) non-utilizable (croplands, unpalatable forage etc.) areas. Since all these will lead to underestimation of true stocking densities, I advocate caution and more conservative interpretation of results. The post monsoon grass height was estimated at 28.5 ± 2.3 (0–53) cm in grids. Grass height was negatively correlated with stocking density ($r = -0.31$, $F = 3.4$, $df = 32$, $p = 0.07$) at the grid-scale. Grid use by female GIB was estimated at 0.05 ± 0.01 (0.0–0.19) detections visit^{-1} . Across grids, female use was not correlated with grass height ($r = 0.32$, $F = 0.9$, $df = 8$, $p = 0.31$) and stocking density ($r = -0.12$, $F = 0.5$, $df = 33$, $p = 0.50$). This was not unexpected since GIB's preferred range of grass height and grazing intensity varied between life history activities, hindering generalizations (fig 6.2 & 6.3).

Figure 6.3 Scatter plots of (a) grass height vs. livestock grazing density, (b) daily distance traveled by livestock vs. proportion of natural cover within village grazing areas, and (c–d) female bustard detections/visit vs. grass height and livestock grazing density in Abdasa (2007–11)



More specifically, habitat models (chapter 4) showed that birds selected plots with moderate grazing pressure for foraging and low grazing pressure for nesting; while short grass height for roosting and moderately tall for resting. Hence livestock grazing is not incompatible with GIB, and can be used as management tool in ways that balance conservation and livelihood benefits.

6.3.2 Socioecology of pastoralists

I characterized the socioeconomics of pastoralists in the important bustard area (tables 6.1 & 6.2). Pastoralists represented the following religion and castes: 63% Muslims (11% Hingora, 6% Mundra, 6% Sumra, 5% Node etc.) and 37% Hindus (22% Darbar–Jadeja, 10% Rabari etc.). Among them, 33% herded sheep ($134_{\text{Mean}} \pm 14_{\text{SE}}$ individuals herd⁻¹), 27% herded goat (59 ± 7), 29% herded cattle (11 ± 3) and 12% herded buffalo (8 ± 2). Hindu households herded more cattle (13.9 ± 4.7 individuals) than Muslim households (4.6 ± 1.1) but equal number of sheep and goat.

(Hindus: 126.7±26.4 and Muslims: 113.08±13.4). Multiple species herds were observed in 58% cases.

Table 6.1. Mean±1SE and range of variables characterizing socio-economy, herd ecology, attitude, threats and institutions of pastoralists at the individual level in Abdasa (2007–2011)

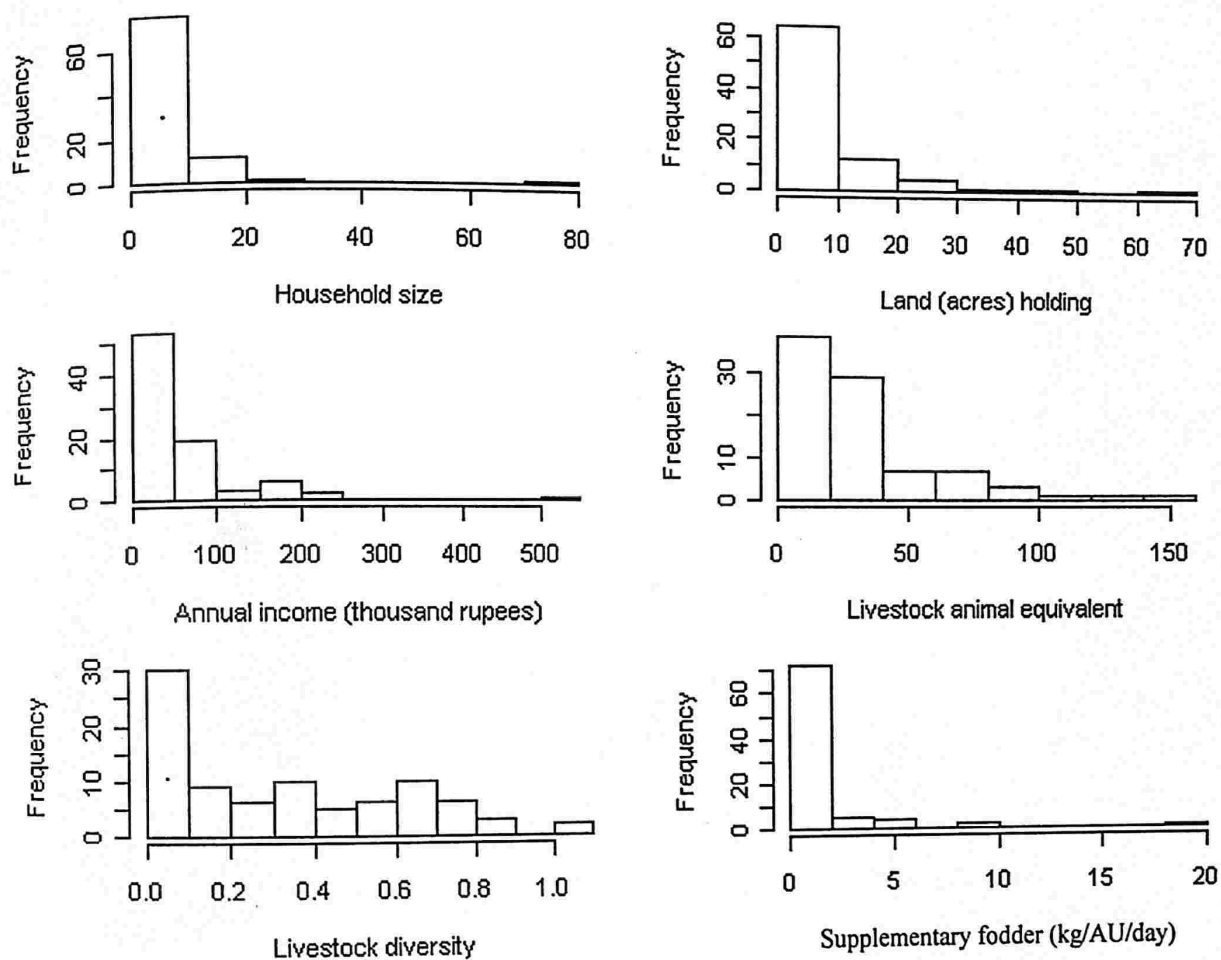
Category	Variables	Mean ± SE	Range
Village characteristics	Number of households in village	220 ± 80	29 – 1781
	Number of village households involved in pastoralism	8.7 ± 1.1	3 – 23
	Number of pastoralist respondents in village	4.5 ± 0.3	3 – 7
	Caste diversity among pastoralists (Shannon's H) in village	0.61 ± 0.12	0 – 1.75
	Village sheep & goat herd size	1349 ± 198	367 – 3429
	Village cow & buffalo herd size	338 ± 43	62 – 846
Pastoralist socio-economy	Pastoralist's household size	7.9 ± 0.7	4.2 – 19.5
	Pastoralist's land holding (acres)	7.5 ± 1.2	0 – 22
	Pastoralists' livestock holding (Animal Unit)	30.8 ± 3.1	4.2 – 69.0
	Supplementary fodder (kg/day/AU) provided by pastoralist	1.1 ± 0.3	0 – 5.5
	Annual income (rupees) from primary occupation	44186 ± 4730	15667 – 97500
	Annual income (rupees) from secondary occupation	20622 ± 4363	0 – 57500
Livestock vital rate parameters	Annual mortality rate of adult sheep & goat	0.15 ± 0.02	0 – 0.32
	Annual recruitment rate of sheep & goat	0.30 ± 0.05	0.14 – 1.22
	Annual instantaneous growth rate of sheep & goat	0.15 ± 0.05	–0.12 – 1
	Annual mortality rate of adult cow & buffalo	0.05 ± 0.02	0 – 0.27
	Annual recruitment rate of cow & buffalo	0.20 ± 0.10	0 – 1.9
How should village lands ideally be for livelihood?	Scrubland (numerical frequency in %)	73 ± 7	0 – 100
	Grassland	65 ± 8	0 – 100
	Cultivation	24 ± 7	0 – 100
What are the major ongoing threats to your livelihood?	Land conversion to cultivation (numerical frequency in %)	57 ± 5	25 – 100
	Land acquisition by Forest Department	19 ± 3	0 – 50
	Land conversion to industrial purpose	13 ± 3	0 – 40
	Other reasons (<i>P. juliflora</i> invasion etc.)	11 ± 3	0 – 36
Do you complaint about land tenure problems? To whom? Do they listen?	Do not complaint (frequency in %)	69 ± 7	0 – 100
	Complaint to Panchayat	22 ± 6	0 – 100
	Complaint to government (Revenue & Forest Dept.)	13 ± 5	0 – 67
	Authorities listened &/or responded to these complaints	30 ± 8	0 – 100
What will you do if such livelihood threats continue?	Solve it among villagers (frequency in %)	8 ± 4	0 – 60
	Change occupation	52 ± 5	0 – 100
	Shift to another village	13 ± 4	0 – 50
Do you allow others to access your resources?	Allows neighbouring villages (frequency in %)	93 ± 2	71 – 100
	Allows remote villages	83 ± 4	50 – 100
	Allows nomadic herders	69 ± 6	17 – 100
Others also allow you us access to their resources (frequency in %)		86 ± 4	33 – 100
Institutional strength (0–1) in terms of cohesiveness, rules & enforcement		0.37 ± 0.05	0 – 0.93

Table 6.2 Mean±SE of socioecological variables characterizing pastoralist communities at the village level in Abdasa (2007–11)

Village	Village livestock details					Livelihood			Herd demography			Attitudes of pastoralist communities		
	Village herd size (AU)	Herd distance (km)	Stocking density AU/km ²	CB (AU) % in herd	CB (AU) per non-pastoralist household	Household herd size (AU)	Suppl. fodder (kg/day/AU)	Total income (th. Rupees)	SG annual intrinsic growth rate	CB annual recruitment rate	Tendency to change herd size (-1 to 2)	Grassland as ideal habitat (% num freq)	Threat from cultivation (% num freq)	Overall social capital index (0–1)
Berachia**	75	3.01	2.6	62	1.67	36.7 (8.9)	3.26 (3.13)	68.1 (29.5)	0.36 (0.09)	1.9 (1.9)	1.5 (0.5)	42 (21)	63 (24)	0.35 (0.02)
Bhachunda	403	2.42	21.9	81	0.68	13.2 (4.5)	3.33 (1.67)	22.5 (2.5)	0.25 (0.14)	0.25 (0.25)	0.33 (0.67)	50 (20)	54 (16)	0.63 (0.03)
Bhanara	592	3.00	21.0											
Bhawanipat*	517	3.00	18.3											
Biriyari*	154	3.01	5.4											
Bitta*	3196	2.75	134.6											
Dhana Vaada	752	3.11	24.7	56	1.73	23.5 (10.0)	5.53 (2.73)	33.5 (8.2)	0.27 (0.11)	0.1 (0.1)	1.33 (0.21)	25 (11)	64 (17)	0.31 (0.05)
Dhufi Nani	298	3.04	10.3	73	0.62	46.7 (36.4)	0.12 (0.08)	91.4 (76.3)	0.14 (0.13)	0.03 (0.03)	0.5 (0.5)	33 (24)	33 (12)	0.34 (0.09)
Gadwara	301	3.32	8.7	58	0.80	26.0 (5.2)	4.53 (1.29)	29.9 (6.7)	0.1 (0.07)	0.17 (0.17)	1.4 (0.4)	67 (21)	23 (10)	0.47 (0.06)
Hamirpar	100	3.01	3.5											
Hotivandh	393	3.01	13.8	100	9.84	17.0 (5.5)	0.6 (0.25)	15.7 (2.3)	0 (0)	0.13 (0.07)	0.5 (0.5)	100 (0)	39 (6)	0.44 (0.09)
Jasapar	247	3.01	8.7	63	2.41	36.7 (21.2)	0.13 (0.13)	80.3 (9.7)	0.08 (0.05)	0 (0)	1.5 (0.5)	67 (17)	75 (25)	0.26 (0.12)
Kalatalao	499	3.01	17.5	22	0.54	19.0 (5.6)	0.06 (0.06)	64.5 (15.4)	0.06 (0.05)	0 (0)	0.4 (0.68)	17 (17)	100 (0)	0.23 (0.03)
Khirsara	820	4.17	15.0	54	1.26	34.5 (13.5)	0.03 (0.03)	67.3 (31.8)	0.12 (0.09)	0.04 (0.04)	0 (0)	39 (8)	67 (21)	0.31 (0.06)
Kukrao	393	3.11	12.9	84	3.47	34.7 (19.1)	0.88 (0.04)	66.7 (17.6)	0 (0)	0.04 (0.04)	0 (0)	83 (17)	83 (17)	0.27 (0.03)
Kunathia	538	3.01	18.9	48	3.32	46.0 (19.4)	0.03 (0.03)	83.7 (43.2)	0.26 (0.11)	0.26 (0.26)	0.5 (0.5)	33 (33)	100 (0)	0.45 (0.04)
Lakhania	251	3.11	8.3	61	1.19	16.0 (2.1)	0 (0)	75.4 (42.4)	0.15 (0.1)	0 (0)	1 (0.41)	25 (25)	63 (24)	0.38 (0.06)
Naliya	1688	4.17	30.9	70	0.25	33.6 (6.9)	0.31 (0.09)	69.0 (20.9)	0.09 (0.1)	0.22 (0.05)	0.67 (0.33)	67 (17)	60 (19)	0.33 (0.04)
Nodebandh	622	3.00	22.0	71	10.68	23.7 (4.5)	0 (0)	28.7 (5.8)	0.02 (0.05)	0 (0)	0 (0)	61 (2)	61 (20)	0.43 (0.04)
Prajau	527	3.01	18.5	86	3.35	12.2 (6.9)	0.94 (0.79)	76.2 (30.9)	0.08 (0.09)	0 (0)	0.5 (0.5)	5 (22)	83 (17)	0.24 (0.03)
Rava	877	2.48	45.4	53	2.88	40.9 (7.1)	0.09 (0.04)	33.6 (3.8)	-0.01 (0.05)	0.05 (0.05)	1 (0)	14 (9)	33 (9)	0.3 (0.04)
Surodhro	1030	2.66	46.4	55	8.47	48.2 (20.1)	0.84 (0.56)	46.0 (18.4)	0.03 (0.03)	0 (0)	0.4 (0.24)	10 (10)	67 (14)	0.22 (0.03)
Tera	1195	3.11	39.3	78	1.48	4.2 (1.7)	0.63 (0.02)	40.3 (6.6)	1.07 (0.99)	0 (0)	2 (0)	0 (0)	100 (0)	0.26 (0.04)
Vadapadar	951	4.17	17.4	43	2.48	32.9 (10.8)	0.54 (0.54)	134.3 (65.6)	0.06 (0.05)	0 (0)	1.2 (0.37)	60 (10)	79 (10)	0.34 (0.05)
Vengaber	542	3.01	19.1	59	4.17	69.0 (17.4)	0.36 (0.14)	126.2 (35.2)	-0.04 (0.03)	0.02 (0.02)	0.5 (0.5)	100 (0)	88 (13)	0.36 (0.04)

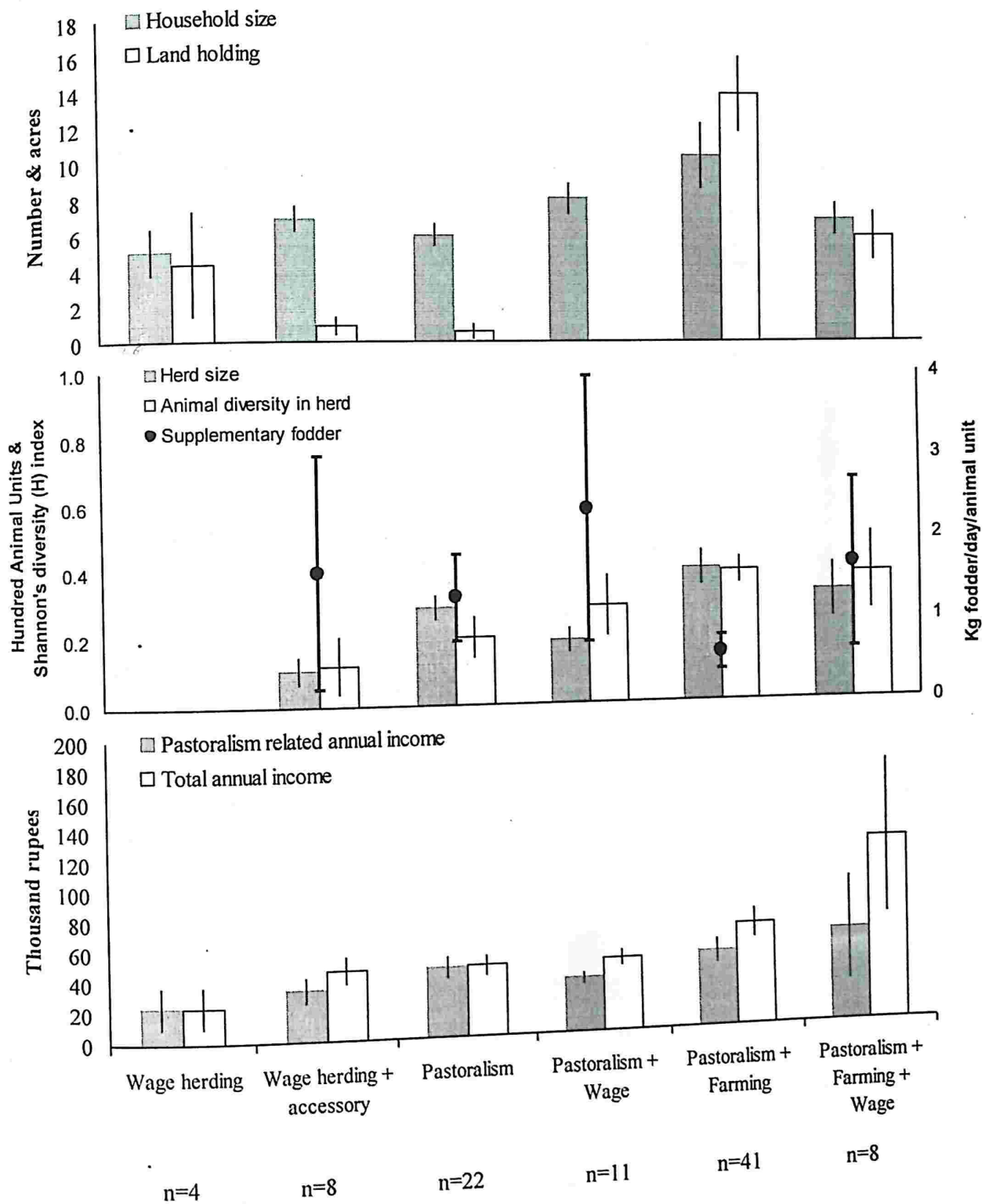
Majority of pastoralist households (~90%) had ≤ 10 members, land holding of ≤ 10 acres, livestock of ≤ 40 AU, and annual income of $\leq 50,000$ Indian rupees (fig 6.4).

Figure 6.4 Distribution of variables characterizing pastoralist livelihoods in Abdasa (2007–2011)



Pastoralist households generated 69% of their total annual income from livestock products: manure, milk products and animals, alongside self consumption of milk. Majority of pastoralists (93%) also practiced dry farming (56%), wet farming (6%), wage farming (3%), wage herding (8%) or wage labour (20%) as accessory occupations. Multiple occupations might have evolved to suit the stochastic environment of this landscape where opportunistic benefits were important for long run sustenance. Based on combinations of occupations, the different livelihood types were: [a] mainly pastoralism (n=22 households), [b] pastoralism and wage herding (11), [c] pastoralism and farming (41), [d] pastoralism, wage herding and farming (8), [e] wage herding (4) and [f] wage herding and accessory occupations (8). Land holding ($F=7.77$, $df=5,84$, $p=0.001$), herd size ($F=2.72$, $df=5,89$, $p=0.025$), species diversity in herd ($F=2.74$, $df=5,89$, $p=0.020$) and income ($F=2.06$, $df=5,84$, $p=0.078$) were higher in pastoralism–farming combined livelihoods (fig 6.5).

Figure 6.5 Socioeconomic status three major (pastoralism, pastoralism & wage and pastoralism & farming) and three minor (wage herding, wage herding & accessory, and pastoralism, farming & wage) livelihoods in Abdasa (2007–2011), in terms of (a) household size and acres of land holding, (b) herd size, animal diversity in herd and supplementary fodder (kg/AU/day), and (c) annual income from pastoralism/herding and total annual income of villagers related to pastoralism



Pastoralists' household size, land holding, herd size and diversity, and income were correlated (table 6.3).

Table 6.3. Correlation plots between pairs of socioecological variables; (a) shows Pearson's correlation coefficients between select livelihood variables measured at the pastoralist-scale, and (b) shows attitude and institutional variables estimated at the village-scale in Abdasa (2007–11)

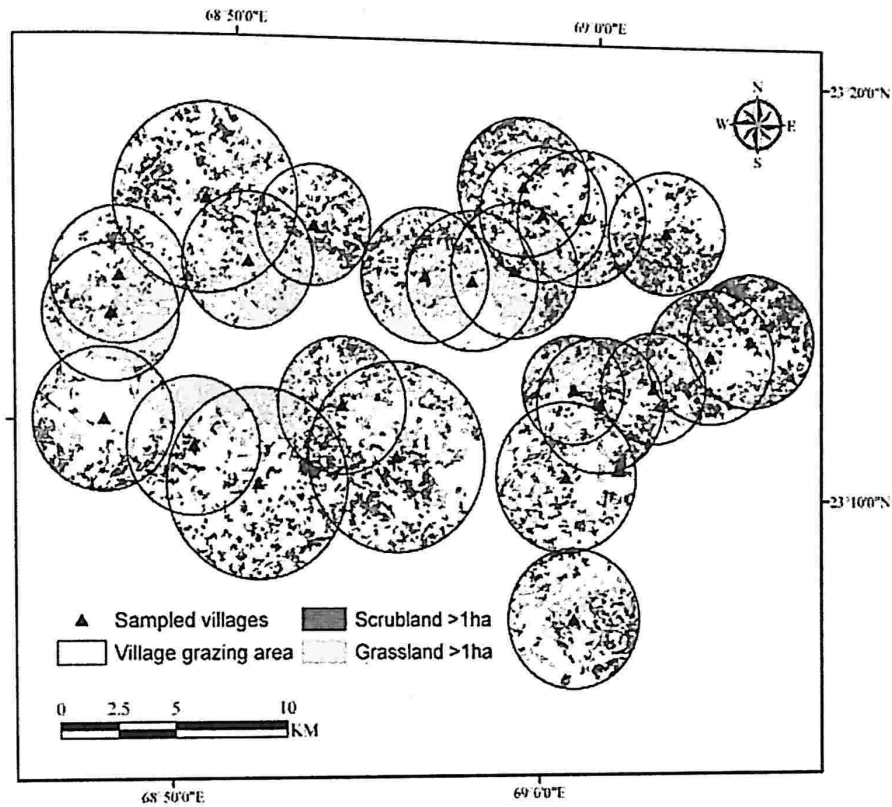
(a) Livelihood variables	HH	LH	PI	TI	HS	CB	HD	SF	GR	MR	RR
Household size (<i>HH</i>)											
Land holding (<i>LH</i>)	0.30										
Pastoralism income (<i>PI</i>)		0.23									
Total income (<i>TI</i>)		0.24	0.89								
Herd size in AU (<i>HS</i>)	0.31	0.56	0.63	0.53							
Proportion cattle & buffalo in herd (<i>CB</i>)											
Herd diversity (<i>HD</i>)	0.33	0.27		0.20	0.29						
Supplementary fodder kg/day/AU (<i>SF</i>)					-0.20						
Sheep & goat intrinsic growth rate (<i>GR</i>)					-0.20	-0.22	-0.21	0.31			
Cattle & buffalo mortality rate (<i>MR</i>)						0.47	-0.27				
Cattle & buffalo recruitment rate (<i>RR</i>)						0.38		0.41			
Animal (sheep & goat) units sold (<i>AS</i>)	0.36		0.51	0.62	0.40	-0.32	0.27			-0.38	-0.33

(b) Attitude and institutional variables	CHS	GIH	ATL	PRT	OCF	RNS	INS
Change (-1 to +2) in herd size (<i>CHS</i>)							
% Respondents consider grassland as ideal habitat (<i>GIH</i>)							
% Respondents consider agricultural conversion as livelihood threat (<i>ATL</i>)							
Problem reporting tendency (<i>PRT</i>)			-0.45				
Occupation fidelity (<i>OCF</i>)							
Resource non-sharing (<i>RNS</i>)							
Institutional strength (<i>INS</i>)			-0.62		0.48		
Social capital index (<i>SCI</i>)			-0.46	0.58	0.58		0.62

Only significant correlation coefficients ($p < 0.05$) have been reported.

I studied pastoralist ecology by assessing population status of herds (primary source of their income) and herders' practices and attitudes at the ecological interface. The estimated human density of villages (population / village area) was 0.48_{Mean} ($63.4\%_{\text{CV}}$, $0.17_{\text{Min}}-1.22_{\text{Max}}$) humans km^{-2} , and that of proportional natural land-cover within village grazing areas was 0.21_{Mean} ($38.6\%_{\text{CV}}$, $0.10_{\text{Min}}-0.38_{\text{Max}}$). Across villages, proportion of natural land-cover in grazing areas was negatively correlated with human population density (Spearman's $\rho = -0.51$, $p < 0.01$, $n=23$). Whilst, mean daily distance traveled by livestock for foraging was negatively correlated with proportion of natural land-cover in grazing areas ($r = -0.62$, $p = 0.056$, $n=10$, fig 6.6). Although expansion of agricultural area in Gujarat as a whole has stagnated post 1980s, agricultural expansion has reduced natural land-cover and grazing lands in Abdasa (Kachchh) by ~30% during 2007–2011. Majority of pastoralists (57%) considered agricultural encroachment into pasture ("Gauchar") lands as the most important threat to their livelihoods. However some farmers allowed livestock grazing in their private lands post crop harvesting season.

Figure 6.6 Distribution of grasslands and scrub(>1 ha) within grazing areas of villages adjoining the core bustard area in Abdasa (2007–11)



But livestock herds showed increasing population change rate ($t=2.81$, $df=72$, $p<0.006$ for sheep and goat, see table 6.1) indicating that pastoralism had retained its economic viability in spite of such odds. For sheep and goat, 46% mortality was caused by contagious disease, 47% by natural reasons or non-contagious disease, and 7% by carnivore depredation. For cattle and buffalo, 13% mortality was caused by contagious disease, 83% by natural reasons or non-contagious disease, and 4% by carnivore depredation. Thus, carnivore depredation accounted for a very low level of livestock mortality. Continued research for 15 years by our team in Kachchh has rarely recorded predation by wolf and hyaena on cattle and buffalo, while the same regularly occurs in Bhal (south Gujarat) region. Pastoralists sold 17.9 ± 2.4 livestock units per year, mostly the new born males. Supplementary fodder was provided by 54% pastoralists at the rate of 2.06 kg/day/AU, and was obtained either from local farmers (36%), local village shops (38%), or shops of other villages (27%). Provision rate of supplementary fodder varied considerably between villages (table 6.3) and was negatively related to the natural land-cover in village grazing areas ($r=-0.39$, $p=0.09$, $n=20$). Intrinsic population growth rate of sheep and goat, and recruitment rate of cattle and buffalo were positively correlated with supplementary fodder provision rate (table 6.2a). It is likely that as natural food resources become scarce, pastoralists substitute them by

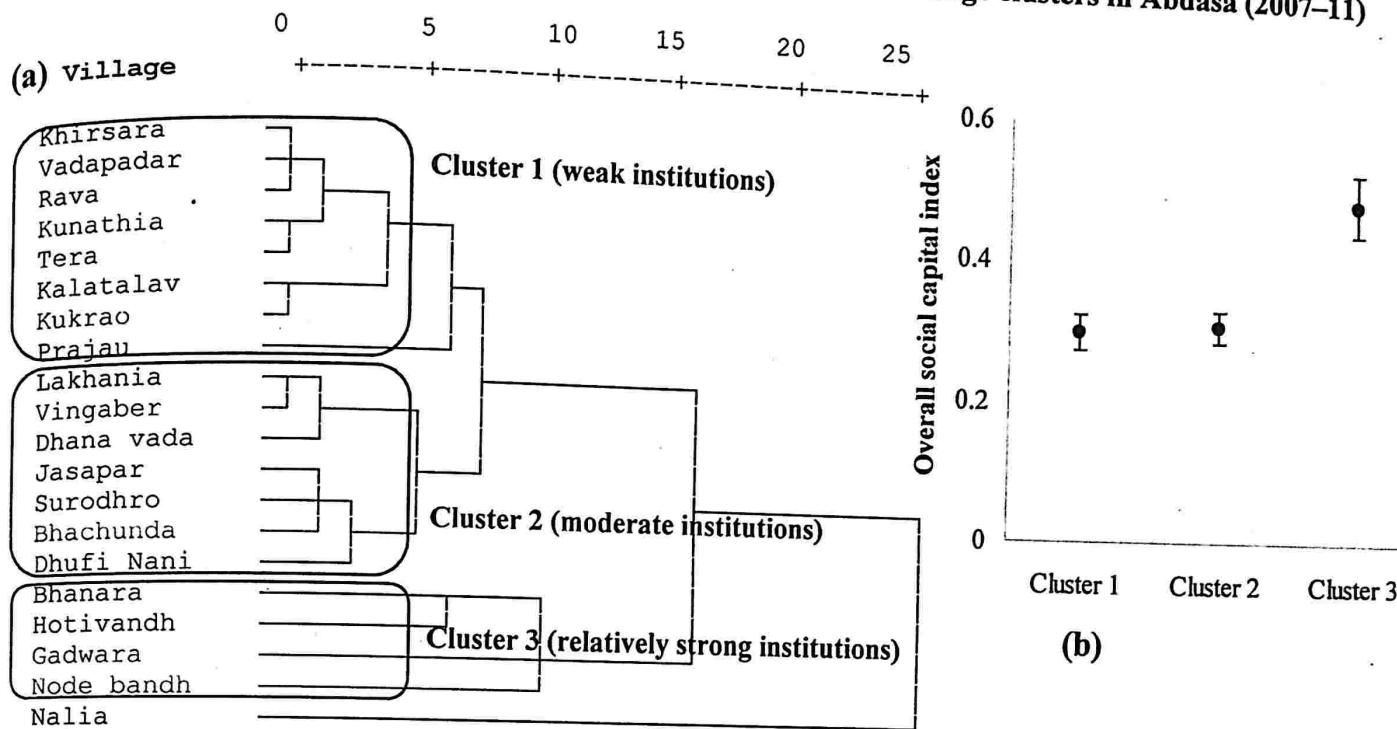
fodder supplements, thereby incurring more expenditure but not suffering livestock loss. When asked about whether they intended to change their herd size, 29% pastoralists responded in negative and 57% answered in affirmative. Among the latter, 22% wanted to increase their stock by buying livestock from outside. This practice has the maximum potential of increasing stocking rates and degrading grassland resources, but has a small number of potential practitioners. On the contrary, a few pastoralists wanted to reduce their stock (4%) and shift to other occupations in light of agricultural encroachment and reduction of grazing lands. Which habitats would pastoralists consider ideal for livelihood should depend on the species composition (grazers vs. browsers) of his herd. Thus pastoralists herding higher proportion of cattle and buffalo showed more tendency of considering grasslands as ideal livelihood habitat ($\rho = 0.38$, $p < 0.001$). They also reported less threat to livelihood from agricultural encroachment ($\rho = -0.28$, $p < 0.01$). Patronizing this group would be important due to their compatibility with bustard conservation.

I investigated how stakes on grassland resources are distributed across the community. This is important as uniform distribution of stakes across the community is a prerequisite for stable management of CPRs (Jodha 2002). I found that only 6_{Mean} ($1.3_{\text{Min}}-14.7_{\text{Max}}$) % households in a village depended on pastoralism for livelihood (table 6.1). This translated into 31 ± 3 AU per pastoralist household. Extrapolating from here the livestock number owned by all pastoralist households in a village and subtracting that from village herd size, I crudely estimated that a non-pastoralist household owned about 4.0 ± 0.9 (0–14) AU. These were mostly herded by pastoralists on wage. Thus economic stakes on grassland resources was skewed, characterized by very high dependence of a small fraction (pastoralist households earning 69% of income) and marginal dependence of the larger fraction (non-pastoralist households not earning much). Furthermore, this small fraction did not represent the socio-economically elite class. For the larger fraction, although the dependence was economically unimportant, it was culturally significant as livestock milk products contributed substantially to self consumption. Apart from their use as pastures, grassland resources were of limited economic value in the past as crop production was constrained by limited period of monsoon rains. While recent agro-infrastructural developments have removed this constraint, marginal stake holders in response to lucrative external economies have expanded and intensified the agricultural use of pastures leading to severe habitat modifications.

I examined the institutional arrangements of land management by resident pastoralist communities. In spite of extensive conversion of grazing lands to agriculture, 69% pastoralists did

not report these problems to any governance authority, reflecting low protesting tendency of the community. Additionally 52% regarded shifting occupation as a viable alternative if such land conversion problems continued, indicating low fidelity to pastoralist livelihood which was also apparent from the maintenance of multiple occupations. About 93% and 83% pastoralists allowed herders of neighbouring and remote villages respectively to access their pastures. Compared to that, fewer respondents (69%) allowed semi-nomadic herders temporary access, and that too for only 2–3 days in their pastures. The semi-nomadic pastoralists are less tied with any particular land and covers large distances to access productive resources after monsoons. They represent a more traditional pastoralist practice which has historically evolved to suit the stochastic environment and rotational use of pastures. With the evolution of modern livelihoods, nomadic herders have to face high tension and conflict over resource use with resident pastoralists due to the latter's perceived legitimacy of land rights. Due to these problems, nomadic herders ("Rabaris") have now bought strategically placed pasture lands so that residents cannot object to them utilizing resources in the vicinity. Rabarais from Anjar tehsil now own several Gauchar lands in Abdasa. But on the whole, the level till which resident pastoralists could exclude *others* from accessing their resources appeared to be low from their responses (table 6.1). Although 77% respondents affirmed that pastoralists of that village were organized, only 50% affirmed the existence of land tenure rules while even fewer (36%) considered that such rules could still be enforced. Thus responses were indicative of generally weak prevalent institutions. I synthesized various aspects of institutional arrangements into one measure of the community's social capital. These institutional aspects showed strong congruence with the overall social capital index (table 6.2b) that was estimated at 0.34 (29.3%CV, 0.22_{Min}–0.63_{Max}) across villages. Villages could be classified into three groups based on institutional arrangements. One of these groups (comprised of Bhanara, Nodevandh, Hotivandh and Gadwara villages) had stronger overall social capital index than the other two (fig 6.7). Pastoralists of this group had lower livestock herd size and lower income level. Higher proportion of them regarded grasslands as the ideal livelihood habitat. There was evidence that pastoralists from villages with stronger institutional arrangements faced less threat from agricultural encroachment (fig 6.7, table 6.2b).

Figure 6.7 (a) Clustering of villages based on institutional aspects and comparison of (b) social capital index, and (c) pastoralists' socioeconomics and attitudes between village clusters in Abdasa (2007–11)



(b) Clustering variables	Mean \pm SD			Kruskal–Wallis	
	Cluster 1	Cluster 2	Cluster 3	χ^2	P-value
Problem reporting & protesting tendency	0.52 \pm 0.47	0.09 \pm 0.25	1.39 \pm 0.71	9.1	0.01
Occupation fidelity	0.48 \pm 0.24	0.40 \pm 0.34	1.07 \pm 0.40	6.4	0.04
Resource exclusion	1.11 \pm 0.14	1.79 \pm 0.35	1.29 \pm 0.21	12.3	0.002
Institutional strength	0.19 \pm 0.15	0.47 \pm 0.14	0.66 \pm 0.20	12.1	0.002

(c) Variables	Mean \pm SD			Kruskal–Wallis test	
	Cluster 1 (n=8)	Cluster 2 (n=7)	Cluster 3 (n=4)	χ^2 -stat	P-value
Number of village households	179 \pm 161.01	99.14 \pm 42.02	186 \pm 239.09	2.09	0.35
% households in pastoralism	7.21 \pm 3.69	8.08 \pm 3.3	8.82 \pm 6.53	0.11	0.95
Pastoralist caste diversity (Shannon H)	0.71 \pm 0.63	0.53 \pm 0.42	0.26 \pm 0.52	1.61	0.45
Village herd size (AU)	748.14 \pm 312.25	526.53 \pm 321.86	481.86 \pm 152.48	3.04	0.22
Income from pastoralism (000. rupees)	50.03 \pm 17.01	52.76 \pm 26.94	21.42 \pm 4.13	7.85	0.02
Total income (000. rupees)	70.81 \pm 30.73	74.44 \pm 30.36	24.22 \pm 6.55	9.14	0.01
Land holding (acres)	4.77 \pm 4.05	12.38 \pm 5.79	7.77 \pm 3.37	6.76	0.03
Personal herd size (AU)	28.04 \pm 14.61	39.55 \pm 17.43	19.98 \pm 5.89	4.15	0.13
% cattle & buffalo in herd	21 \pm 19	18 \pm 13	43 \pm 39	1.69	0.43
Cattle & buffalo/ non-pastoralist family	2.35 \pm 1.12	2.89 \pm 2.7	5.5 \pm 5.51	0.17	0.92
Supplementary fodder (kg/day/AU)	0.4 \pm 0.39	1.46 \pm 2.12	2.12 \pm 2.17	0.98	0.61
Tendency to change herd size (-1 to 2)	0.7 \pm 0.67	0.96 \pm 0.49	0.56 \pm 0.6	2.04	0.36
Considers grassland as ideal livelihood habitat (numerical frequency in %)	37 \pm 27	43 \pm 31	69 \pm 22	3.93	0.14
Considers agricultural conversion as threat (numerical frequency in %)	81 \pm 23	64 \pm 16	44 \pm 17	8.04	0.02

6.4 Conclusion

There are several examples of locally evolved institutions, which aloof from external forces have sustainably managed resources for centuries but have failed under rapid changes (Dietz et al. 2003). This chapter provides another example where traditional agro-pastoralism on common property resources in Kachchh, a compatible landuse with bustard conservation, is being threatened by agricultural intensification. It provides evidence that livestock grazing influences herbaceous vegetation structure and needs to be optimally managed for bustard conservation. Although overgrazing is a serious problem in many dry land ecosystems of India (Raheja 1966, Singh et al. 2006), the prevalent stocking rates in this region can be managed at the carrying capacity through some management interventions. Evidences of low population and weak institutional arrangements of resident pastoralist communities provide link to why these common pool resources are becoming 'open access' and getting encroached by other users, mostly cultivators. Till now, governance intervention has been negligible except for a few incidences where Revenue Department officials have prosecuted agricultural encroachers. Such land management dilution will likely exacerbate the pastoralists' crisis leading to economic non-viability and abandonment of their occupation, ultimately ending in complete landuse conversion. Thus it is important to consolidate the traditional agro-pastoralist livelihood with external aide, such as veterinary service, governance support and Agro-environmental Incentive Schemes. A case study by Homewood et al. (2006) revealed that veterinary provisions in Masailand increased livestock survival and production without any increase in herd size; thereby improving pastoralists' wealth status without affecting wildlife. Stict enforcement of legal ban on agricultural encroachment in Gauchar and revenue lands is the most needed governance intervention in Kachchh. It will consolidate pastoralists' resources, reduce stocking densities and benefit grassland fauna. Another required intervention is to relocate some immigrants from village Misriadda who have settled in village Bitta with 3000 cattle (40% of the total AU in the study region) causing conflict with resident pastoralists and overgrazing in the locale. Intelligent application of Agro-environmental Incentive Schemes can restore habitats in a way that bridges the gap between wildlife requirements and livelihood concerns (Donald and Evans 2006). Some viable schemes in the context of bustard conservation in Kachchh may be 1) shifting to organic farming of seasonal compatible crops such as *Sesame*, groundnut and millets (Bretagnolle et al. 2011), 2) subsidizing

reduced annual cropping frequency, and 3) compensating fodder supplements to livestock in the initial wet season. These schemes will benefit GIB by increasing food supply and decreasing nest damage. Local communities will be benefited from increased pasture productivity in lean-periods. Towards the end of the study, I observed sporadic protests in some villages led by wage herders (herd non-pastoralists' cattle). They surrendered their occupation in protest of agricultural conversion of prime grazing routes that impeded their access to pastures. Subsequently those village panchayats reached a consensus on setting aside some routes and areas for grazing. Conservation managers should patronize cattle herders because of their close link with grasslands and herders with protesting and leadership qualities. Strengthening stakes of marginal grassland users in multiple ways should also be considered. One way would be to donate a scientifically informed quota of livestock to non-pastoralist households for consolidating their cultural stakes on grasslands. This will not contradict bustard conservation goals since moderate intensity grazing is recommended to maintain optimal grass height for GIB. Another way will be to recruit local villagers, keen on wildlife, in conservation jobs, such as eco-tourism guides, Forest Department staff, and assistants in NGO and research organizations. Reviving the Jain-Gandhian cultural reverence to wildlife, rooted in this region, coupled with aforementioned incentives can go a long way in sensitizing local communities for bustard conservation and generating institutional support for traditional land management.

Chapter 7. Conclusion: conservation status and strategies

7.1. Assessment of global conservation status

7.1.1. Population Viability Analysis

To understand the interactions between the inherent *k*-selected demographic traits of GIB with environmental stochasticity, habitat management, anthropogenic influences, and their effects on the viability of different size GIB populations, I conducted Population Viability Analysis (PVA, Boyce 1992) using published demographic parameters of GIB and related species (Alonso and Alonso 1992b, Combreau et al. 2000, del Hoyo et al. 1996, Ena et al. 1986, Hallager and Boylan 2004, Johnsgard 1994, Morales et al. 2005, Osborne et al. 2001, Rahmani 1989, Rao and Javed 2005, see table 7.1). I used program *VORTEX v 9.72* (Lacy et al. 2007) and ran 500 iterations for each of the following scenarios.

Table 7.1 Details of input parameters in Population Viability Analysis models

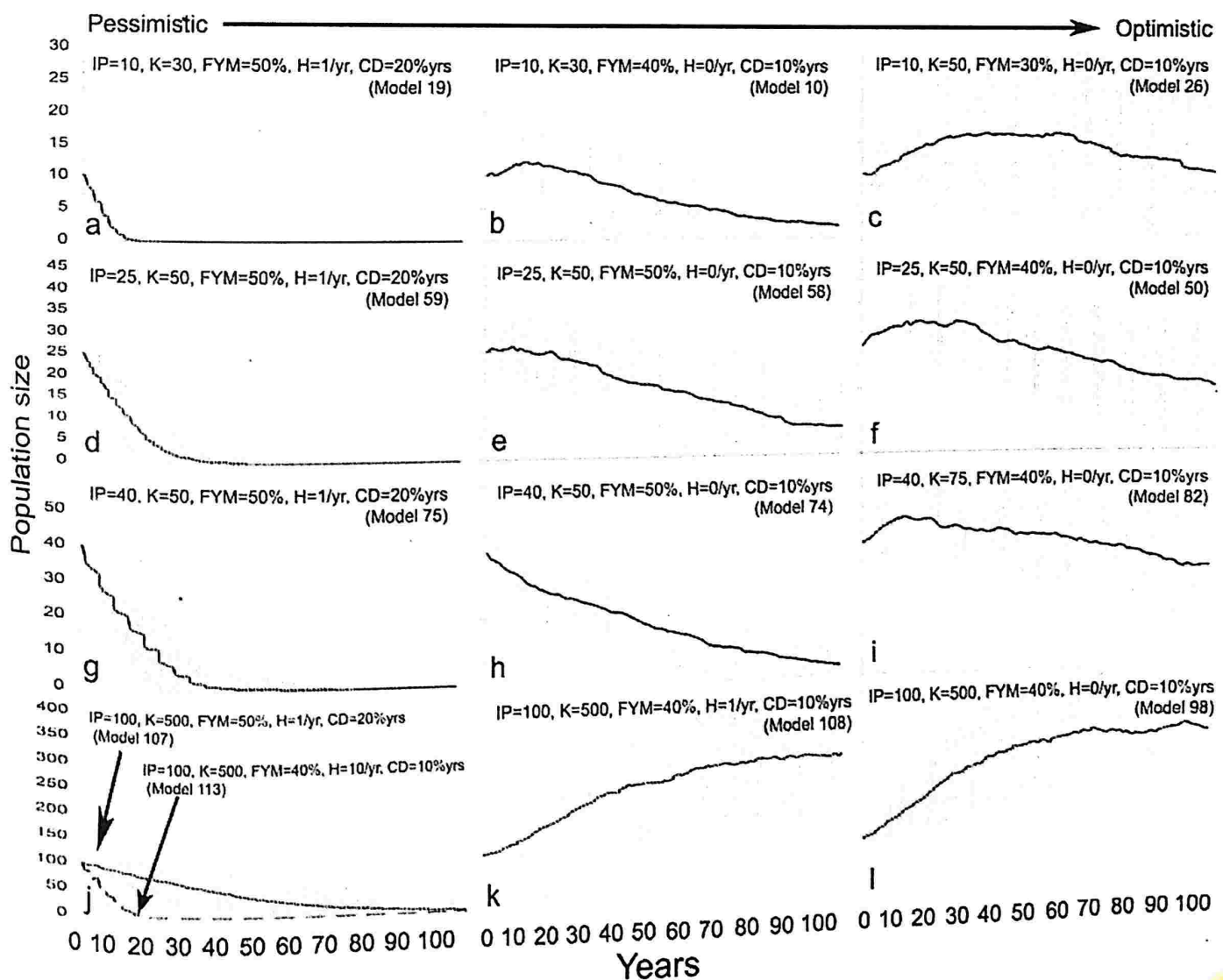
PVA input parameters	Values & Range
Initial population size	(a) 10 (b) 25 (c) 40 (d) 100
Reproductive System & Rate	
Age of 1st offspring	3 years (♀) & 4 years (♂)
Max. age of reproduction	20 years
Max. no of progeny/year	1
Sex ratio at birth	1♀:1♂
% Adult ♀ breeding/year	50 ± 10 §
% ♂ in breeding pool	25
Mortality rate	
1st year	30 ± 6% 40 ± 8% & 50 ± 10%
2nd year	10 ± 2% & 18 ± 4% (♀) & 16 ± 3% & 22 ± 4.5% (♂)
Adults	5 ± 1% (♀) & 8 ± 1.5% (♂)
Catastrophe	
Frequency	(a) 10% & (b) 20% of years
Severity	Fecundity reduced by 80% & survival reduced by 10%
Harvest	(a) nil & (b) 1 adult♂ & 1 adult♀ in 2 years

§ Estimated as the mean ratio of breeding (nesting/chick rearing) females to total females in various populations obtained from published literature (1,2) and field observations during current study. Average sex ratio was used to calculate number of females in cases where there was no separate mention of female and male birds in the population. Literature from where PVA input parameters were obtained: Ena et al. 1986, Rahmani 1989 (1), Alonso and Alonso 1992, Johnsgard 1994, del Hoyo et al. 1996, Combreau 2000, Morales et al. 2001, Osborne and Osborne 2001, Hallager and Boylan 2004, Rao and Javed 2005 (2), current study.

I considered (a) the best case scenario where the initial population was 100 birds mimicking the Rajasthan population, (b) a scenario with the initial population of 40 birds and (c) initial population of 25 birds representing most other populations, and (d) a scenario where the

initial population was 10 birds mimicking the remaining few small, scattered populations. Since some of the life-history parameters were ill-known, I built 'optimistic' and 'pessimistic' models for each scenario to estimate extinction probabilities in 20, 50 and 100 years, using different combinations of first and second year mortality rates, carrying capacities, adult harvests and catastrophic drought incidences occurring once in 5 (20%) years or 10 (10%) years (fig 7.1, see table 7.2). During a catastrophe year the survival and fecundity were reduced by 10% and 80% respectively. GIB though legally protected as a Schedule I species under Wildlife (Protection) Act (1972) has been a prized game bird and is occasionally poached. Poaching and accidental deaths due to human causes were simulated as "harvest" of 1 bird of either sex in alternate years from the modeled population (fig 7.1 and table 7.2).

Figure 7.1 Population Viability Analysis model predictions for Great Indian Bustard populations of initial sizes (IP) 10 (1st horizontal panel: a,b,c), 25 (2nd horizontal panel: d,e,f), 40 (3rd horizontal panel: g,h,i), and 100 birds (4th horizontal panel: j,k,l) under pessimistic (left panel: a,d,g,j) and optimistic scenarios (right panel: c,f,i,l) of various combinations of potential carrying capacity (K), 1st year mortality rate (FYM), human caused adult bird loss (H) and catastrophic drought incidence (CD) during next 100 years



I found that populations of 10 individuals were in imminent risk of extinction (fig 7.1a, see models 1-25 & 27-48 in table 7.2) facing a likely extinction probability of 10% in 20 years, with 43% population trajectories becoming extinct within 50 years and 80% extinction probability in 100 years (fig 7.1b, see model 10 in table 7.2). These populations had low chance of persistence (62% survival probability in 100 years) even under most optimistic (but unrealistic) conditions when first year mortality was below 30%, second year mortality was 10% for females and 16% for males, potential carrying capacity was ≥ 50 individuals, human caused adult loss was totally controlled and catastrophe was less frequent (fig 7.1c, see model 26 in table 7.2).

Populations of 25 individuals also showed high risks of extinction (67-100% extinction probability in 100 years, see fig 7.1d, see models 49, 51-53 & 54-64 in table 7.2). Under realistic conditions, these populations faced extinction probability of 16% in 50 years (fig 7.1e, see model 58 in table 7.2). These populations could only persist (70% survival probability in 100 years) under optimistic but unrealistic conditions when first year mortality was $\leq 40\%$, second year mortality was 10% for females and 16% for males, potential carrying capacity was ≥ 50 individuals, human caused adult loss was totally controlled and catastrophe was less frequent (fig 7.2f, see model 50 in table 7.2).

Populations of 40 individuals had fair chances of persistence ($>80\%$ survival probability in 100 years, see fig 7.1i, see models 82 & 86 in table 7.2) provided first year mortality was $\leq 40\%$, potential carrying capacity was ≥ 75 birds and catastrophe was less frequent. However, when I assumed a pessimistic situation of higher nesting and fledgling mortality (50%) along with more frequent catastrophes, extinction probabilities in 100 years jumped to 37% and 84% respectively (fig 7.1h, see models 89 & 90 in table 7.2). Poaching or accidental additional death of 1 adult every year threatened these populations (extinction probability 6-37% in 20 years) with 99-100% population trajectories facing extinction within 100 years (fig 7.1g, see models 67, 68, 71, 72, 75, 76, 79, 80, 83, 84, 87, 88, 91, 92, 95 & 96 in table 7.2).

The population of 100 individuals had a high probability of persistence ($>70\%$) for the next 100 years even under realistic nesting and fledgling mortality (50%), higher 2nd year mortality rate and more frequent catastrophe (fig 7.1l, see models 97, 98, 100-102, 104, 106 & 110 in table 7.2). But persistence of even this "large" population was sensitive to loss of an additional adult bird every year to human causes (extinction probability 50-100% in 100 years, fig 7.1k,j, models 99, 103, 107, 108, 111 & 112 in table 7.2).

Table 7.2 Population viability model scenarios for Great Indian Bustard populations of initial size (IP) 10, 25, 40 & 100 birds with various combinations of potential carrying capacity (K), 1st & 2nd year mortality rates human caused adult loss, and catastrophic drought incidences with corresponding predictions of population change rate and probability of extinction in 20, 50 & 100 years

ID	IP	K	1 st yr mort	2 nd yr mort	Harvest (2 yrs)	Drought (% yrs)	Mean R (SD)	P(E) 20 yrs	P(E) 50 yrs	P(E) 100 yrs
1	10	30	30	10♀16♂	0	20	-0.011(0.170)	0.15	0.54	0.89
2	10	30	30	10♀16♂	0	10	0.006(0.149)	0.05	0.25	0.58
3	10	30	30	10♀16♂	1♀1♂	20	-0.146(0.256)	0.99	1.00	1.00
4	10	30	30	10♀16♂	1♀1♂	10	-0.124(0.241)	0.98	1.00	1.00
5	10	30	30	18♀22♂	0	20	-0.017(0.179)	0.18	0.62	0.92
6	10	30	30	18♀22♂	0	10	-0.002(0.156)	0.09	0.34	0.75
7	10	30	30	18♀22♂	1♀1♂	20	-0.166(0.264)	0.99	1.00	1.00
8	10	30	30	18♀22♂	1♀1♂	10	-0.146(0.248)	0.99	1.00	1.00
9	10	30	40	10♀16♂	0	20	-0.022(0.175)	0.19	0.68	0.96
10	10	30	40	10♀16♂	0	10	-0.009(0.156)	0.10	0.43	0.80
11	10	30	40	10♀16♂	1♀1♂	20	-0.170(0.26)	0.99	1.00	1.00
12	10	30	40	10♀16♂	1♀1♂	10	-0.138(0.24)	0.99	1.00	1.00
13	10	30	40	18♀22♂	0	20	-0.030(0.185)	0.29	0.79	0.99
14	10	30	40	18♀22♂	0	10	-0.014(0.164)	0.14	0.52	0.90
15	10	30	40	18♀22♂	1♀1♂	20	-0.184(0.272)	1.00	1.00	1.00
16	10	30	40	18♀22♂	1♀1♂	10	-0.263(0.258)	0.99	1.00	1.00
17	10	30	50	10♀16♂	0	20	-0.032(0.177)	0.28	0.84	0.99
18	10	30	50	10♀16♂	0	10	-0.020(0.164)	0.15	0.64	0.95
19	10	30	50	10♀16♂	1♀1♂	20	-0.180(0.267)	1.00	1.00	1.00
20	10	30	50	10♀16♂	1♀1♂	10	-0.162(0.255)	0.99	1.00	1.00
21	10	30	50	18♀22♂	0	20	-0.039(0.183)	0.36	0.91	1.00
22	10	30	50	18♀22♂	0	10	-0.026(0.172)	0.18	0.74	0.99
23	10	30	50	18♀22♂	1♀1♂	20	-0.189(0.263)	1.00	1.00	1.00
24	10	30	50	18♀22♂	1♀1♂	10	-0.183(0.258)	0.99	1.00	1.00
25	10	50	30	10♀16♂	0	20	-0.011(0.166)	0.14	0.49	0.80
26	10	50	30	10♀16♂	0	10	0.010(0.136)	0.03	0.19	0.38
27	10	50	30	10♀16♂	1♀1♂	20	-0.157(0.255)	0.99	1.00	1.00
28	10	50	30	10♀16♂	1♀1♂	10	-0.132(0.249)	0.98	0.99	1.00
29	10	50	30	18♀22♂	0	20	-0.019(0.176)	0.21	0.63	0.91
30	10	50	30	18♀22♂	0	10	-0.002(0.150)	0.08	0.35	0.61
31	10	50	30	18♀22♂	1♀1♂	20	-0.160(0.265)	0.99	1.00	1.00
32	10	50	30	18♀22♂	1♀1♂	10	-0.143(0.254)	0.99	1.00	1.00
33	10	50	40	10♀16♂	0	20	-0.020(0.175)	0.22	0.69	0.95
34	10	50	40	10♀16♂	0	10	-0.005(0.146)	0.10	0.38	0.66
35	10	50	40	10♀16♂	1♀1♂	20	-0.171(0.265)	0.99	1.00	1.00
36	10	50	40	10♀16♂	1♀1♂	10	-0.144(0.249)	0.99	1.00	1.00
37	10	50	40	18♀22♂	0	20	-0.029(0.183)	0.26	0.77	0.98
38	10	50	40	18♀22♂	0	10	-0.016(0.160)	0.13	0.50	0.86
39	10	50	40	18♀22♂	1♀1♂	20	-0.186(0.273)	0.99	1.00	1.00
40	10	50	40	18♀22♂	1♀1♂	10	-0.153(0.255)	0.99	1.00	1.00
41	10	50	50	10♀16♂	0	20	-0.032(0.178)	0.26	0.80	0.98
42	10	50	50	10♀16♂	0	10	-0.020(0.158)	0.17	0.58	0.91
43	10	50	50	10♀16♂	1♀1♂	20	-0.181(0.270)	0.99	1.00	1.00
44	10	50	50	10♀16♂	1♀1♂	10	-0.166(0.248)	0.99	1.00	1.00
45	10	50	50	18♀22♂	0	20	-0.040(0.186)	0.36	0.89	1.00
46	10	50	50	18♀22♂	0	10	-0.026(0.169)	0.22	0.70	0.96

ID	IP	K	1 st yr mort	2 nd yr mort	Harvest (2 yrs)	Drought (% yrs)	Mean R (SD)	P(E) 20 yrs	P(E) 50 yrs	P(E) 100 yrs
47	10	50	50	18♀22♂	1♀1♂	20				
48	10	50	50	18♀22♂	1♀1♂	10	-0.191 (0.260)	1.00	1.00	1.00
49	25	50	40	10♀16♂	0	20	-0.177 (0.260)	0.99	1.00	1.00
50	25	50	40	10♀16♂	0	10	-0.019 (0.151)	0.10	0.24	0.75
51	25	50	40	10♀16♂	1♀1♂	20	0.002 (0.126)	0.00	0.05	0.30
52	25	50	40	10♀16♂	1♀1♂	10	-0.076 (0.189)	0.48	0.96	1.00
53	25	50	40	18♀22♂	0	20	-0.05 (0.166)	0.22	0.86	0.99
54	25	50	40	18♀22♂	0	10	-0.026 (0.160)	0.02	0.35	0.86
55	25	50	40	18♀22♂	1♀1♂	20	-0.008 (0.136)	0.00	0.09	0.51
56	25	50	40	18♀22♂	1♀1♂	10	-0.089 (0.190)	0.58	0.99	1.00
57	25	50	50	10♀16♂	0	20	-0.068 (0.178)	0.32	0.95	1.00
58	25	50	50	10♀16♂	0	10	-0.033 (0.159)	0.04	0.45	0.93
59	25	50	50	10♀16♂	1♀1♂	20	-0.016 (0.137)	0.01	0.16	0.67
60	25	50	50	10♀16♂	1♀1♂	10	-0.098 (0.193)	0.64	0.99	1.00
61	25	50	50	18♀22♂	0	20	-0.075 (0.178)	0.43	0.97	1.00
62	25	50	50	18♀22♂	0	10	-0.039 (0.163)	0.04	0.55	0.97
63	25	50	50	18♀22♂	1♀1♂	20	-0.024 (0.146)	0.02	0.28	0.82
64	25	50	50	18♀22♂	1♀1♂	10	-0.111 (0.197)	0.76	1.00	1.00
65	40	50	40	10♀16♂	0	20	-0.084 (0.183)	0.50	0.99	1.00
66	40	50	40	10♀16♂	0	10	-0.018 (0.148)	0.01	0.15	0.70
67	40	50	40	10♀16♂	1♀1♂	20	0.003 (0.123)	0.00	0.04	0.30
68	40	50	40	10♀16♂	1♀1♂	10	-0.066 (0.177)	0.17	0.94	1.00
69	40	50	40	18♀22♂	0	20	-0.041 (0.158)	0.06	0.73	0.99
70	40	50	40	18♀22♂	0	10	-0.025 (0.154)	0.00	0.25	0.82
71	40	50	40	18♀22♂	1♀1♂	20	-0.006 (0.131)	0.00	0.04	0.41
72	40	50	40	18♀22♂	1♀1♂	10	-0.075 (0.182)	0.23	0.97	1.00
73	40	50	40	18♀22♂	1♀1♂	10	-0.052 (0.162)	0.10	0.84	1.00
74	40	50	50	10♀16♂	0	20	-0.032 (0.152)	0.01	0.32	0.92
75	40	50	50	10♀16♂	0	10	-0.015 (0.133)	0.00	0.11	0.63
76	40	50	50	10♀16♂	1♀1♂	20	-0.081 (0.179)	0.27	0.98	1.00
77	40	50	50	10♀16♂	1♀1♂	10	-0.061 (0.161)	0.13	0.90	1.00
78	40	50	50	18♀22♂	0	20	-0.039 (0.159)	0.02	0.46	0.96
79	40	50	50	18♀22♂	0	10	-0.022 (0.140)	0.00	0.13	0.77
80	40	50	50	18♀22♂	1♀1♂	20	-0.096 (0.184)	0.37	0.99	1.00
81	40	50	50	18♀22♂	1♀1♂	10	-0.071 (0.168)	0.17	0.97	1.00
82	40	75	40	10♀16♂	0	20	-0.015 (0.139)	0.00	0.08	0.51
83	40	75	40	10♀16♂	0	10	0.009 (0.110)	0.00	0.00	0.09
84	40	75	40	10♀16♂	1♀1♂	20	-0.055 (0.167)	0.12	0.76	0.98
85	40	75	40	10♀16♂	1♀1♂	10	-0.030 (0.143)	0.03	0.43	0.91
86	40	75	40	18♀22♂	0	20	-0.024 (0.148)	0.00	0.17	0.71
87	40	75	40	18♀22♂	0	10	-0.001 (0.118)	0.00	0.03	0.19
88	40	75	40	18♀22♂	1♀1♂	20	-0.069 (0.174)	0.14	0.91	1.00
89	40	75	40	18♀22♂	1♀1♂	10	-0.043 (0.153)	0.04	0.59	0.98
90	40	75	50	10♀16♂	0	20	-0.031 (0.147)	0.00	0.24	0.84
91	40	75	50	10♀16♂	0	10	-0.011 (0.122)	0.00	0.05	0.37
92	40	75	50	10♀16♂	1♀1♂	20	-0.082 (0.175)	0.24	0.97	1.00
93	40	75	50	10♀16♂	1♀1♂	10	-0.530 (0.154)	0.05	0.75	0.99
94	40	75	50	18♀22♂	0	20	-0.039 (0.154)	0.01	0.35	0.94
95	40	75	50	18♀22♂	0	10	-0.020 (0.132)	0.00	0.11	0.57
96	40	75	50	18♀22♂	1♀1♂	20	-0.093 (0.182)	0.30	0.99	1.00
97	40	75	50	18♀22♂	1♀1♂	10	-0.068 (0.162)	0.11	0.89	1.00
97	100	500	40	10♀16♂	0	20	-0.002 (0.117)	0.00	0.00	0.03

ID	IP	K	1 st yr mort	2 nd yr mort	Harvest (2 yrs)	Drought (% yrs)	Mean R (SD)	P(E) 20 yrs	P(E) 50 yrs	P(E) 100 yrs
98	100	500	40	10♀16♂	0	10	0.023 (0.091)	0.00	0.00	0.00
99	100	500	40	10♀16♂	1♀1♂	20	-0.025 (0.135)	0.01	0.14	0.57
100	100	500	40	10♀16♂	1♀1♂	10	0.013 (0.096)	0.00	0.01	0.08
101	100	500	40	18♀22♂	0	20	-0.017 (0.125)	0.00	0.01	0.23
102	100	500	40	18♀22♂	0	10	0.008 (0.096)	0.00	0.00	0.01
103	100	500	40	18♀22♂	1♀1♂	20	-0.034 (0.143)	0.00	0.24	0.71
104	100	500	40	18♀22♂	1♀1♂	10	-0.004 (0.109)	0.00	0.03	0.22
105	100	500	50	10♀16♂	0	20	-0.022 (0.126)	0.00	0.01	0.27
106	100	500	50	10♀16♂	0	10	-0.002 (0.092)	0.00	0.01	0.02
107	100	500	50	10♀16♂	1♀1♂	20	-0.052 (0.146)	0.00	0.38	0.93
108	100	500	50	10♀16♂	1♀1♂	10	-0.031 (0.114)	0.00	0.04	0.36
109	100	500	50	18♀22♂	0	20	-0.033 (0.136)	0.00	0.06	0.61
110	100	500	50	18♀22♂	0	10	-0.010 (0.105)	0.00	0.01	0.09
111	100	500	50	18♀22♂	1♀1♂	20	-0.065 (0.151)	0.01	0.60	0.99
112	100	500	50	18♀22♂	1♀1♂	10	-0.036 (0.130)	0.00	0.18	0.77
113	100	500	40	10♀16♂	10♀10♂	10	-0.226 (0.338)	0.98	1.00	1.00

Rows in bold represent realistic situations and shaded rows represent optimistic situations

Sensitivity analysis is often used to assess the relative importance of parameters in model based inference (Heinsohn et al. 2004, McCarthy et al. 1995). Some of our parameter estimates were obtained from related species and some others were not known with reasonable certainty. The number of adult females in the breeding pool each year, second year mortality, frequency of catastrophes and potential carrying capacity were examples of parameters which were fuzzily estimated from literature. I include these along with first year and adult mortality in our sensitivity analysis, wherein each of the parameters was altered by 10% of its original value, and the PVA models rerun to assess its effect on persistence of the GIB population for 50 years. It revealed that persistence was most sensitive to proportion of females breeding each year (table 7.3). This was followed by juvenile and adult mortality as the next most sensitive parameters. The PVA was not sensitive to 10% changes in second year mortality, potential carrying capacity and frequency of catastrophes with population persistence changing marginally by <9%.

Of the above three most sensitive parameters, I had reasonably reliable data on adult and juvenile mortalities. However, proportion of breeding females in the population was not as reliable and was based on anecdotal reports (Rahmani 1989, Rao and Javed 2005) and field data for only two years in Kachchh. An incorrect estimation of this parameter would change our PVA results numerically but our inferences on conservation actions would largely remain unaffected. An underestimation of 10% of the proportion of females in the breeding pool would overestimate the probability of extinction by 30-70%, while an overestimate of 10% of proportion of females in the

breeding pool would underestimate the extinction probability by 31-46%. Similarly, 10% decrease in first year mortality would increase population persistence by 34% and 10% increase in the same would reduce population persistence by 55%; while 10% decrease in adult mortality would increase population persistence by 21% and 10% increase in the same would reduce population persistence by 18%. Interestingly, changes in the potential carrying capacity did not alter model results suggesting that GIB were restricted not by habitat availability but more by direct threats to their survival (table 7.3). This model outcome could be misinterpreted to suggest that ample habitat was available for GIB populations. However, this is not true since crucial habitat requirements for lekking and nesting that are not reflected in the potential carrying capacity would act by limiting breeding success, and survival of juveniles as well as that of adult birds. The potential carrying capacity reflects the size of bustard habitat and food availability which were probably not limiting (Dutta et al. 2011).

Table 7.3 Sensitivity analysis of Population Viability models wherein parameters estimated with less certainty &/or parameters of critical importance were modified by 10% of original values to assess the corresponding percentage change in population extinction over next 50 years [% Δ P(E)50] for initial populations (IP) of 10 25 40 & 100 birds

Modified parameter	Change	IP	% Δ P(E)50	Modified parameter	Change	IP	% Δ P(E)50
Percentage adult female in breeding pool each year	-10%	10	57	Second year mortality	-10%	10	-12
	+10%		-31		+10%		10
	-10%	25	54		-10%	25	-5
	+10%		-44		+10%		10
	-10%	40	30		-10%	40	-4
	+10%		-38		+10%		6
	-10%	100	69		-10%	100	-18
	+10%		-46		+10%		5
First year mortality	-10%	10	-14	Frequency of catastrophes	-10%	10	-10
	+10%		24		+10%		0
	-10%	25	-23		-10%	25	-5
	+10%		36		+10%		5
	-10%	40	-38		-10%	40	-9
	+10%		34		+10%		6
	-10%	100	-62		-10%	100	-13
	+10%		126		+10%		15
Adult mortality	-10%	10	-21	Carrying capacity	-10%	10	5
	+10%		17		+10%		10
	-10%	25	-15		-10%	25	8
	+10%		21		+10%		-5
	-10%	40	-11		-10%	40	-11
	+10%		11		+10%		2
	-10%	100	-38		-10%	100	18
	+10%		23		+10%		-13

Captive breeding to restock depleted natural populations can be a viable strategy for managing endangered species (Pullin 2002). I explored the viability of conservation breeding of GIB by simulating supplementation schemes under different habitat management scenarios. If the program is commenced within 2–3 years, a window of 3–5 years will be required to collect sufficient eggs from wild, and four more years to produce the founder population, i.e., 10–15 years from now before any restocking can begin. For populations of 10, 25 and 100 birds, I selected one optimistic and pessimistic scenario (described before), and supplemented that with alternative combinations of a) one to three adult females per male, on b) each or alternate year, for c) five or eight occasions, starting from d) 10 or 15 years since now. For each scenario, I estimated the deterministic growth rate, population sizes and extinction probabilities after 50 and 100 years.

I found that restocking small GIB populations without effective management interventions that enhance adult and nest survival (see section 7.2) would not be viable in the long run (>0.1 extinction probability and declining population sizes in 100 years, see models 4 and 8 in table 7.4). A viable and economic solution for populations of 10 and 25 birds entailed supplementation of about 15 adult birds over a time of 10 years starting from 15 years since now, with relatively high protection measures by creating disturbance (humans, nest predators and unfriendly infrastructure) free breeding areas (models 2 and 7 in table 7.4). I found that effective management was sufficient by itself for viability of the largest population of 100 birds (model 11 in table 7.4). However, collection of eggs mainly from this population might require restocking it as well. Under this circumstance, supplementation of 20 adult birds over a time of 10 years starting from 15 years since now (model 15 in table 7.4) would be sufficient. Current (2011) population assessments have shown further declines in Kachchh, Maharashtra and Andhra Pradesh–Karnataka populations, each containing ≤ 25 birds. These populations should be targeted for immediate conservation actions so that they retain their potential for restocking after a decade or so. This entails captive breeding of 60–90 birds which will require a founder population of 15–20 adult birds. Hence 30–50 eggs have to be collected from wild considering 50% survival rate from egg to adulthood in captivity. If successfully restocked, the current populations of 175–200 birds will likely increase up to 450–500 birds within 50–100 years (table 7.4).

Table 7.4 Exploring the effects of restocking Great Indian Bustard populations through Population Viability Analysis under scenarios of initial size (IP) 10, 25 and 100 birds with various combinations of potential carrying capacity, 1st year mortality rates, human caused adult loss and catastrophic drought incidences with corresponding predictions of population change rate ($R_{Mean \pm 1SD}$), probability of extinction and estimated population size in 50 and 100 years

Model	IP	Scenario					Supplementation					Extinction probability			Population size (Mean \pm 1SE)	
		Carrying capacity	1st yr mort	Harvest 10 yrs	Drought (% yrs)	F:M	Occ	Int	Start	$R_{Mean \pm 1SD}$	50 yr	100 yr	50 yr	100 yr	50 yr	100 yr
1	10	30 + 5% for 15 yrs	30	0	10	1:1	8	1	10	0.035 \pm 0.11	0.00	0.01	0.00	0.01	46 \pm 1	42 \pm 1
2	10	30 + 5% for 15 yrs	30	0	10	2:1	5	2	15	0.032 \pm 0.125	0.00	0.02	0.00	0.02	40 \pm 1	34 \pm 1
3	10	30 + 5% for 10 yrs	40	0	10	1:1	8	1	10	0.015 \pm 0.125	0.00	0.03	0.00	0.03	34 \pm 1	29 \pm 1
4	10	30 + 5% for 10 yrs	40	0	10	2:1	5	2	15	0.016 \pm 0.139	0.01	0.20	0.01	0.20	30 \pm 1	17 \pm 1
5	25	50 + 5% for 15 yrs	40	0	10	1:1	8	1	10	0.031 \pm 0.094	0.00	0.00	0.00	0.00	77 \pm 1	76 \pm 1
6	25	50 + 5% for 15 yrs	40	0	10	2:1	5	2	15	0.022 \pm 0.104	0.00	0.01	0.00	0.01	65 \pm 1	57 \pm 2
7	25	50 + 5% for 10 yrs	45	1m, 1f	15	1:1	8	1	10	0.002 \pm 0.121	0.01	0.07	0.01	0.07	53 \pm 2	40 \pm 2
8	25	50 + 5% for 10 yrs	45	1 m, 1 f	15	2:1	5	2	15	0.006 \pm 0.115	0.00	0.15	0.00	0.15	48 \pm 2	29 \pm 2
9	100	300 + 5% for 10 yrs	50	2 m, 2 f	20	1:1	8	1	15	0.008 \pm 0.097	0.00	0.04	0.00	0.04	218 \pm 12	241 \pm 13
10	100	300 + 5% for 10 yrs	50	2 m, 2 f	20	3:1	5	2	15	0.007 \pm 0.099	0.00	0.00	0.00	0.00	241 \pm 12	262 \pm 13
11	100	300 + 5% for 10 yrs	50	2 m, 2 f	20	0	0	0	0	0.004 \pm 0.101	0.00	0.06	0.00	0.06	193 \pm 11	219 \pm 15

Varying intensities of management interventions were modeled as 5% increase/year in carrying capacity for 10–15 years, low (30%) to high (50%) juvenile mortality, and human induced loss of adult birds ranging from nil to 2 males and 2 females in 10 years. I simulated restocking schemes by supplementing 1–3 females and 1 male each time for 5–8 occasions on each or alternate year from 10–15 years since now. Most viable solutions are marked in grey.

7.1.2. Genetic analysis

A parallel genetic study, in which I was involved, investigated the diversity of

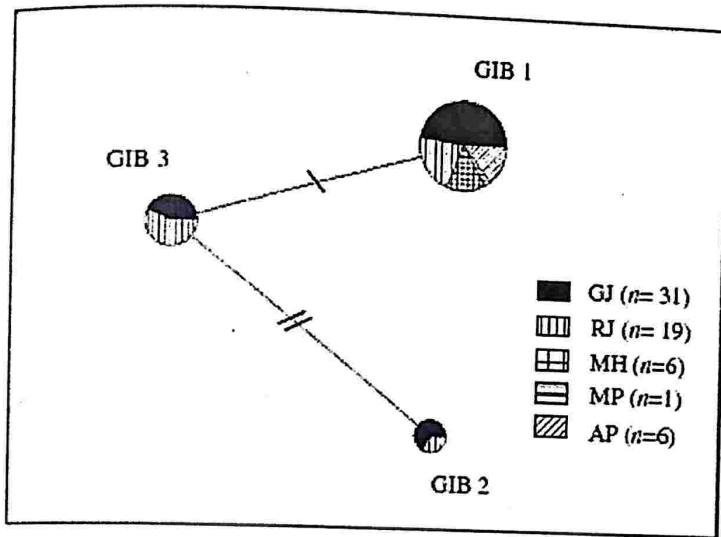


Figure 7.2 Median-joining network for the three Great Indian Bustard haplotypes found in all populations; GJ: Gujarat (Kachchh), RJ: Rajasthan (Desert National Park), MH: Maharashtra (Nanaj bustard sanctuary). MP: Madhya Pradesh (Ghatigaon bustard sanctuary), AP: Andhra Pradesh (Rollapadu wildlife sanctuary). Size of circle reflects relative frequency. Black dash refers to mutational event (Ishtiaq et al. 2011)

mitochondrial DNA (hypervariable control region II and cytochrome b gene) among faecal (25% samples), feather (60%) and egg shell (14%) samples (n = 63) from five states within the distribution range of GIB in India (Ishtiaq et al. 2011). We found just three haplotypes defined by three variable sites, a comparatively low genetic diversity of $p = 0.0021_{\text{Mean}} \pm 0.0012_{\text{SE}}$ for cytochrome b, $0.0008_{\text{Mean}} \pm 0.0007_{\text{SE}}$ for the control region (CR), and $0.0017_{\text{Mean}} \pm 0.0069_{\text{SE}}$

for combined regions. By contrast, a continentwide survey of great bustard *O. tarda* mtDNA showed nine variable sites among 66 combined mtDNA sequences, defining 11 haplotypes (Pitra et al. 2002). The median-joining network showed no evidence for phylogeographic structure (Fig. 7.2). The study suggested that the spatial distribution of fragmented habitat and restricted gene flow between populations could result in low levels of mtDNA diversity and the lack of genetic structure. Alternatively it could suggest female mediated gene flow over a wide geographical range, but this would not account for the low diversity levels. Furthermore, female biased population sex-ratio (Schroeder et al. 1999), sexual bimaturism (Wiley 1974) together with the polygynous exploded lek mating system, in which a relatively small proportion of males on leks perform most copulations, and female breeding failure (Stiver et al. 2008) could reduce genetic diversity due to its negative effects on effective population size. The study obtained evidence of strong population bottleneck in these samples, but was unable to pinpoint the exact timing of population decline because of the low resolution of data. The study indicated that GIB had a small effective female population size with an $N_e(f)$ of $415_{\text{Mean}}, 340-786_{95\%CI}$, and $122-565, 52.5-1313_{95\%CI}$ for Cyt b and CR, respectively. Being a polygynous species, GIB has an extremely female biased sex-ratio, estimated at 3 females per male in Kachchh (section 3.3.1.4), and 5 females per male considering recent information on other populations (Dutta et al. 2011). We used

the latter estimate to convert $N_e(f)$ to N_e total effective population size (number of breeding adults), and found that the estimate (498_{Mean} , $408-943_{95\%CI}$ for Cyt b) is concordant with population estimates of 300–350 individuals (Dutta et al. 2011). Given the underlying uncertainties in parameter estimates, it is necessarily a rough approximation. Even so, given the wide distribution of the species, it is surprisingly low. Although diversity at mtDNA is low for many endangered species populations following known bottlenecks, none have so far shown such low levels of diversity as we report here. The GIB have suffered population bottlenecks affecting genetic diversity throughout their range which should be a key consideration for the development of conservation and management strategies for this species.

7.2. Conservation implications

Based on these assessments, the conservation status of GIB has been recently upgraded to “Critically Endangered” (IUCN, 2011). The Ministry of Environment and Forests, Government of India also is planning to set up a surgical fund for grassland management and the Bustard Task Force for scientific consultation. In the context of conservation planning for GIB, I propose the following actions based on my research. Most of these recommendations have also appeared in the form of a species recovery plan document compiled by the Bustard task Force (Anon 2011).

7.2.1. Protection to core breeding areas

Population viability models show that $\geq 50\%$ nesting and fledging mortalities can jeopardize the persistence of GIB populations. These birds are known to abandon their nests due to human disturbance (Rao and Javed 2005). Since they are extremely site-specific restricted area breeders, it is possible to enhance nesting and fledging success by creating disturbance free zones during the breeding season. In populations of less than 30 birds, additional efforts may be needed to actively control predators (feral dogs, jackals, foxes, cats and wolves) from these sites prior to and during the breeding season. Such predator control though controversial is essential and doable within these small breeding areas. Section 5.3.3 shows the far reaching implications of traditionally selected breeding areas in determining the population persistence of this exploded lek species, while sections 3.4.4 and 4.4.5 show the current levels of threats in some of these areas. Hence, the foremost step should be to consolidate the crucial breeding areas of GIB and make them seasonally inviolate from human interferences. Most extant breeding areas are PAs while

some others occur in unprotected Government lands which should be immediately acquired by the Forest Department. Breeding areas should be enclosed by chain-link-fencing and actively protected by Forest Guards during the 3–5 breeding months. Livestock grazing and other consumptive use of grassland resources should be restricted during this time but allowed under regulations outside of it. Nest predators should be removed prior to breeding from these areas through coordinated efforts of field biologists, Forest Department and veterinary agencies. Removing significant source of mortality during the nesting and fledging stages (most vulnerable life history stage) by providing safe breeding refuge may reverse the species' extinction trajectory (Anon 2011, Dutta et al. 2011).

7.2.2. Protection to adult birds

Population viability models also show that GIB populations are extremely sensitive to removal of adult birds. Even the largest population can plummet to extinction with a constant additional loss of 1 adult to human causes each year. Historically, GIB have been hunted as game bird (Ali 1927, Hume and Marshall 1879, Rahmani 1989) and continue to be hunted in neighbouring Pakistan. Low intensity poaching still persists within India as well. The western Rajasthan and Kachchh populations are probably shared with Cholistan desert and Sindh of Pakistan, where 49 birds were hunted out of 63 that were sighted over a period of 4 years (Khan et al. 2008). Given the life history traits of GIB, this level of removal is unsustainable and threatens the extinction of the largest global western Indian population within next 15–20 years (fig 7.1j, model 113 in table 7.2). Increasing unfriendly infrastructural development within GIB habitats intensifies chances of fatal bird strikes against high tension electric wires, fast moving vehicles and other structures like wind turbines. Such incidents have been reported from Kachchh and Solapur (see section 4.4.3.4). Studies have shown that bustards are particularly prone to these accidents because of their low height flight (exposure to collision risk) as well as a relatively small binocular field and large blind area (inherent susceptibility to collision) that render them blind to the direction of flight while scanning below (Jenkins et al. 2010, Martin and Shaw 2010). Janss and Ferrer (2000) estimated 163 times higher collision rate (number of birds hitting a power line/number of birds crossing a power line) of Great Bustard (0.00634) than common crane *Grus grus* (0.0000393). And Jenkins et al. (2011) extrapolated that about 4000–11900 Ludwig's bustards *Neotis ludwigii* are killed annually across their range by collisions with power lines.

Conservation strategies must try to minimize loss of adult birds from human causes. Therefore, infrastructural development (road and electricity network) and land-use diversion (intensive agriculture, wind turbines, industries and construction) should be completely restricted within 3 km radius of the core breeding areas. Electric lines should be replaced by solar power or underground cables. These areas support high density of GIB during breeding months and may be used to varying degrees in non-breeding months depending on the landscape. Removing the key mortality causes of adult birds from these areas can secure a significant part of their life cycle. While these mortality causes should also be curtailed in other areas that are intensively used within the landscape, we cannot prioritise such areas due to our lack of knowledge on birds' landscape use patterns. Although the bird requires strict protective measures, its wide ranging nature makes implementation of protection difficult without public support (Rahmani 2003). Publicity and awareness campaigns should ensue to generate support among local populace like the ones undertaken by the Bombay Natural History Society, in Rajasthan and Maharashtra (Rahmani 2006). Further, Pakistan Government should be sensitized to initialize conservation practices by diplomatic means and international agencies including the IUCN. This will endorse the measures already recommended by conservationists of Pakistan for controlling GIB hunting there (see Khan et al. 2008).

7.2.3. Landscape conservation planning

Beyond the breeding season, GIB requires vast areas to complete their life history requirements (see section 4.3). Human demands for land are also high in these areas, making it difficult to create PAs that encompass landscapes. Hence their conservation is only possible in coexistence with humans, requiring landscape level planning. Some forms of traditional land uses like dry farming and controlled livestock grazing requires minimal infrastructure and are beneficial to GIB (section 4.4.3). Today's major threat to bustard habitats is the conversion of these traditional landuses into incompatible modern forms, such as intensive agriculture and industry associated with infrastructural developments. Benefits of such landuse changes rarely percolate various social strata of local communities, thus making it easier to introduce reforms which are both economically viable for the general people as well as being GIB friendly. To achieve this dual goal, conservation agencies have to address local livelihood concerns (see section 6.3) by coercing bustard-friendly practices through appropriate incentive driven legislation and policy reforms (see

section 6.4 for Agro–Environmental Incentive Schemes). To make these possible, priority areas within GIB landscapes can be declared as a) Conservation Reserve, b) Community Reserve and c) Ecologically Sensitive/Fragile Area [Section 31A of Wildlife (Protection) Act 1972 as amended on 2002, Section 5 of Environment (Protection) Act 1986]. These new categories of PAs can better protect bustard habitats on government/private mixed ownership lands (Gray et al. 2007) since they do not require land acquisition but allow sustainable use of large areas with participation from local communities and essential intervention of the Government (Rahmani 2006). There is evidence of population recovery among bustards through the implementation of friendly cropping practices (in case of little bustard in France, see Bretagnolle et al. 2011). Many bustard landscapes require habitat restoration to accommodate the species' diverse requirements for daily and seasonal life history activities. Research informed (see sections 4.3 & 4.4) landscape management plans have to be formulated and implemented by State Forest Departments for this purpose. Bustard friendly grassland management regime will not only benefit other threatened fauna (lesser florican, chinkara, wolf, caracal, Indian fox, spiny-tailed lizard etc.) but also local communities in the long run as it will enhance productivity for livestock and prevent overgrazing. A profitable and equitable mechanism to share revenues generated from eco-tourism with local communities (Narain *et al.*, 2005) can also go a long way in harnessing support for GIB conservation. These steps will facilitate in building networks or “Bustard cells” (Anon, 2011) between Forest Department, NGOs and local communities that may be instrumental in reporting and curbing illegal activities in GIB landscapes. Due to their vastness, these landscapes suffer from land encroachment and animal poaching problems, which can not be monitored by conventional means. Lastly, due to the mixed ownership of GIB habitats, their conservation will require cross–sectoral efforts from the State Forest, Revenue and Animal husbandry departments, for which a liaison advisory committee can be formed to facilitate coordinated decision making (Anon, 2011; Dutta *et al.*, 2011).

7.2.4. Research and monitoring

To assess the efficacy of management interventions, systematic assessment of GIB population status needs to be done at local levels along the lines of tiger monitoring (Jhala *et al.*, 2011). Monitoring protocol developed as a part of this study (see chapter 3) can act as a standard model for this purpose. Although GIB requires landscape conservation policy, their space use

patterns, seasonal movements, and cross-country migration (if any) are little known. Without these information, conservation areas cannot be prioritized and management planning will be meaningless. Thus biotelemetry based understanding of ranging patterns of few individuals from each landscape should be treated as high priority research (see chapter 4). This will also improve our understanding of many sociobiological aspects of the species, and refine their status surveys (see chapter 5).

7.2.5. Conservation breeding

In spite of all these measures, owing to the extinction prone *k*-selected nature of GIB and expected lags in field conservation enforcements, there is an urgent need for *ex situ* conservation breeding and subsequent supplementation of existing small *in situ* populations. Conservation breeding is fraught with large financial investments and uncertainties, not advisable if *in-situ* measures are sufficient. A few unscientific attempts to breed GIB in captivity have failed in the past (Putman 1976, Sankhala 1977). However, scientific execution of conservation breeding is possible (Collar 1983) along the lines of successful breeding programs of houbara *Chlamydotis undulata* (Lawrence et al. 2008), great bustard *Otis tarda* (Great Bustard Group 2006–2007), and kori bustard *Ardeotis kori* (Rahmani personal observation). Currently, semiarid grassland habitats of India are facing very high development pressures and the best efforts of *in-situ* conservation plans (Anon 2011) may fall short in decelerating these disruptive forces within time. However, like many other developing countries, there is migration of rural people to urban centers in search of better livelihood and in response to better economies (Gugler 1988). This is likely to reduce human pressures on GIB habitats in the future. At such times in future, it may be possible to restore GIB to their former range provided a captive stock exists, but there is no such stock at present. Conservation breeding is therefore an insurance program against extinction. But it should not be considered as an alternative to effective large scale habitat management and protection to breeding areas which must be the highest priority (Dutta et al. 2011, Ishtiaq et al. 2011).

If we fail to act now in promoting both *in-situ* and *ex-situ* measures for conserving the GIB, we are likely to witness the extinction of this species within a span of 20–40 years (appendix 7.1).

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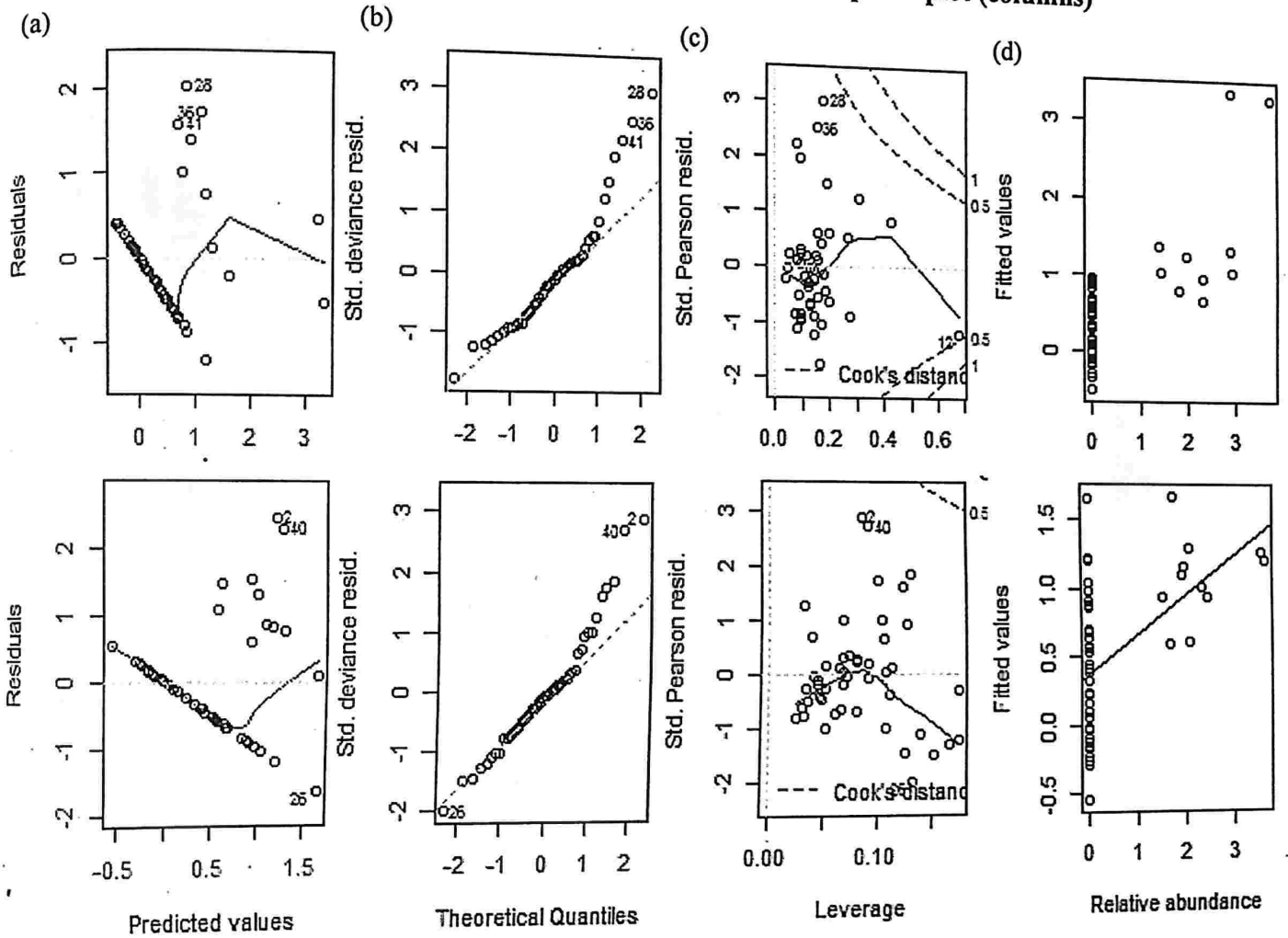
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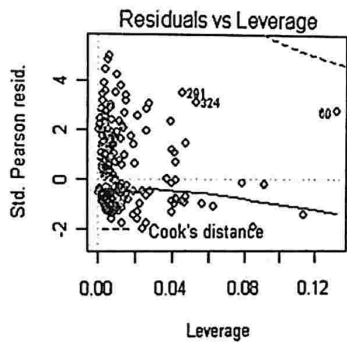
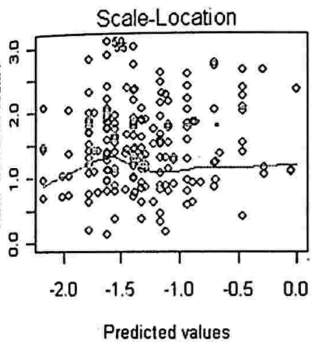
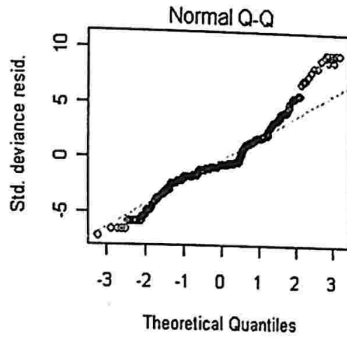
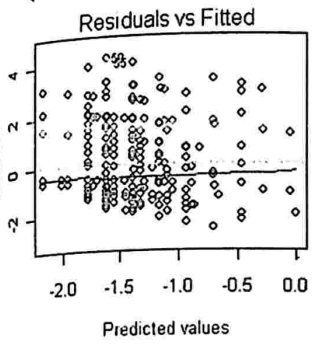
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Appendix 4.1 Diagnosis of the top candidate models for (i) summer and (ii) winter (rows) landscape use by the Great Indian Bustard based on (a) residual vs. fitted plot, (b) normal quantile-quantile plot, (c) residuals vs. leverage plot, and (d) fitted vs. observed response plot (columns)

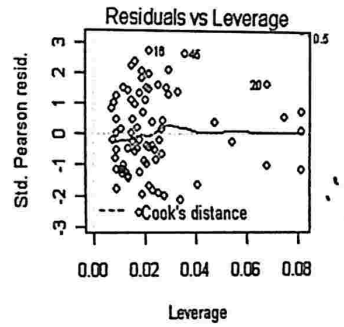
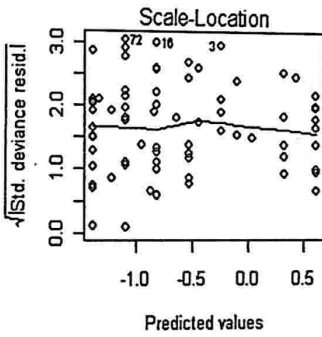
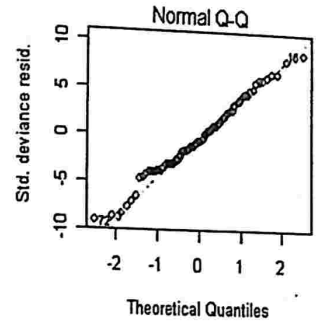
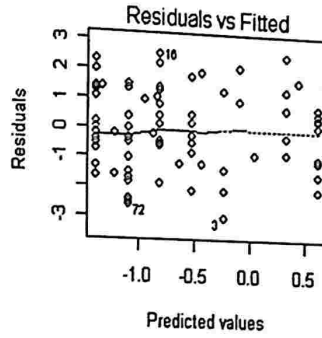


Appendix 5.1 Diagnosis of validity of top models explaining (a) individual vigilance and (b) flock vigilance frequencies using residual plots for the Great Indian Bustard in Kachchh (2007–11)

(a)



(b)



Appendix 6.1 Sample questionnaire to study socioecological aspects of resident pastoralists in villages adjoining the core bustard area of Abdasa during 2007–2011

<u>Social</u>	<u>Livelihood/Economics</u>
Q1. Village: _____	Q7. Primary/year-round Occupation: _____
Q2. Name: _____	Q8. Secondary/Temporary Occupation: _____
Q3. Age: _____ years	Q9. Land: _____ acres & Other assets: _____
Q4. Household size: _____ members	Q10. Annual income: Rs. _____ + _____ + _____ (manure) (milk product) (animal sale)
Q5. Religion: _____	Side profit: Rs. _____ & Loan: Rs. _____
Q6. Caste: _____	Added remarks _____
<u>Livestock data</u>	
Q11. Give details of your livestock holding: _____ Sheep + _____ Goat + _____ Cattle + _____ Buffalo	
Q12. Guesstimate livestock population of your village: _____ Sheep&Goat + _____ Cattle + _____ Buffalo	
Q13. How many adult livestock did you lose every year in last 3 years? _____ Sheep&Goat / _____ Cattle&Buffalo & Cause of loss? a) Disease outbreak <input type="checkbox"/> b) Non-contagious disease/Normal death <input type="checkbox"/> c) Animal depredation <input type="checkbox"/>	
Q14. How many young were born every year in the last 3 years? _____ Fawns & _____ Calves	
Q15. How many of these young survived through the 1 st year? _____ Fawns & _____ Calves How many calves survived till 3 rd year? _____ & How many recruits did you sell in last 3 years? _____	
Q16. Do you provide supplementary fodder to livestock? a) Yes <input type="checkbox"/> / No <input type="checkbox"/> & b) To how many? _____	
Q17. If so, how much do you feed each day? _____ kg/day & where do you procure it from? _____	
Added remarks _____	
<u>Ecological</u>	
Q18. Would you like to increase your stock? a) No <input type="checkbox"/> b) Yes, by natural means <input type="checkbox"/> c) Yes, by adding units from outside <input type="checkbox"/>	
Q19. How many herd animals do you think your <i>village land</i> can <i>ideally</i> support? _____	
Q20. Compared to 10 years back, how productive are <i>village pastures</i> now? a) More <input type="checkbox"/> c) Less <input type="checkbox"/> b) Varies with rain <input type="checkbox"/>	
Q21. Do you remember any past catastrophic event? How did you recover from that? _____	
Q22. How should <i>village lands</i> ideally be? a) Scrubland <input type="checkbox"/> b) Grassland <input type="checkbox"/> c) Crop fields <input type="checkbox"/> d) Mix of all <input type="checkbox"/>	
Q23. Rank <i>threats</i> by their effects, to your <i>village lands</i> that threaten your livelihood: a) Agricultural conversion <input type="checkbox"/> b) Industrial / related development <input type="checkbox"/> c) Land acquisition by Forest Department <input type="checkbox"/> d) Other threats <input type="checkbox"/>	
Added remarks _____	
<u>Institutional arrangements</u>	
Q24. To whom do you complain/address about land tenure issues that threaten your livelihoods? _____ Do they listen to your issues? _____	
Q25. What will you do if such problems persist in future? a) Solve it among villagers <input type="checkbox"/> , b) Shift occupation but not village <input type="checkbox"/> , c) Shift village but not occupation <input type="checkbox"/> , d) Not sure <input type="checkbox"/>	
Q26. Do you allow pasture & water access to livestock of neighbouring villages <input type="checkbox"/> , remote villages <input type="checkbox"/> & Rabari <input type="checkbox"/> If so, what sort of gains/loss do you incur from the allowance? _____	
Q27. Do you access pasture & water of other villages in bad years? <input type="checkbox"/> & do they allow you access? <input type="checkbox"/>	
Q28. Do you have/know of any rule/norm/contract on the use of <i>village lands</i> , which exists? <input type="checkbox"/> & can be enforced? <input type="checkbox"/>	
Added remarks _____	

Appendix 7.1 Current conservatively estimated population sizes of Great Indian Bustard and their probability of extinction in 20, 50 and 100 years under likely pessimistic to optimistic scenarios

Population	Bird number (approx)	Scenario	Carrying capacity	1st yr mort	Adult mort	Harvest (2 yrs)	Drought (% yrs)	Extinction probability		
								20 yrs	50 yrs	100 yrs
Rajasthan (Jaisalmer, Barmer)	100	Pessimistic	200	40	10♀,16♂	10♀,10♂	10	1.00	1.00	1.00
		Realistic	200	50	10♀,16♂	1♀,1♂	20	0.00	0.40	0.96
		Optimistic	200	40	10♀,16♂	0	20	0.00	0.00	0.07
Kachchh (Gujarat)	25	Pessimistic	50	50	10♀,16♂	1♀,1♂	20	0.64	0.99	1.00
		Realistic	50	50	10♀,16♂	0	20	0.04	0.45	0.93
		Optimistic	50	40	10♀,16♂	0	10	0.00	0.05	0.30
Maharashtra (Nasik, Solapur - Ahmednagar)	25	Pessimistic	50	50	10♀,16♂	1♀,1♂	20	0.64	0.99	1.00
		Realistic	50	50	10♀,16♂	0	20	0.04	0.45	0.93
		Optimistic	50	40	10♀,16♂	0	10	0.00	0.05	0.30
Maharashtra (Nagpur - Chandrapur)	10	Pessimistic	30	50	10♀,16♂	1♀,1♂	20	1.00	1.00	1.00
		Realistic	30	40	10♀,16♂	0	20	0.19	0.68	0.96
		Optimistic	50	30	10♀,16♂	0	10	0.03	0.19	0.38
Andhra Pradesh - Karnataka	25	Pessimistic	50	50	10♀,16♂	1♀,1♂	20	0.64	0.99	1.00
		Realistic	50	50	10♀,16♂	0	20	0.04	0.45	0.93
		Optimistic	50	40	10♀,16♂	0	10	0.00	0.05	0.30