Abundance, habitat relationships and behaviour of the semi-fossorial Indian Desert Jird, *Meriones hurrianae*, in Kachchh, Gujarat

Dissertation submitted to Saurashtra University, Rajkot, in partial fulfillment of Master's Degree in Wildlife Science, June 2011

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CERTIFICATE

This is to certify that Ms. Divya Ramesh has carried out original research titled "Abundance, habitat relationships and behaviour of the semi-fossorial Indian Desert Jird, *Meriones hurrianae*, in Kachchh, Gujarat", in partial fulfilment of Master's Degree in Wildlife Science from Saurashtra University, Rajkot. The study was carried out under our supervision from December 2010 to June 2011. We hereby certify that this work has not been submitted for any other degree to any other university.

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Contents

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I also of course thank the jirds themselves, for being mind-bogglingly surprising and annoyingly complicated creatures totally worthy of study.

List of tables

List of figures

Summary

Population sizes, habitat relationships and behaviour are among basic ecological aspects pivotal to demystifying a species and its place in the ecosystem. Numerous in species and number, desert rodents offer immense scope for such investigations. The Indian desert jird, *Meriones hurrianae*, though common, is remarkably little known. This study, conducted in Kachchh, Gujarat, estimates population sizes, examines factors in the habitat likely to influence their occurrence, and elucidates the activity pattern and time budget across 2 land use types, agricultural and natural areas, during winter (December-February) and summer (March-May).

Animals were caught in 9 colonies using Sherman traps and population estimated under closed population Capture-Mark-Recapture framework in Program MARK, using individual covariates (age class, gender, body weight, site). Colony parameters (length, width, number of holes) were regressed against known Mark-Recapture (MR) population estimates to develop predictive models for estimating population size from indices. Population sizes varied from 2 to 10 individuals. Number of holes in a colony provided robust estimates of the number of individuals in that colony ($N=16$, $R^2=0.96$, $t=18.19$, $p<0.001$). Jacknife estimation was performed and population sizes based on this were strongly correlated with MR estimates ($R=0.958$, $p<0.001$).

Habitat variables were recorded in 84 and 75 sample plots in a 4sqkm area each, in agriculture and natural areas respectively. These were tested for multicollinearity using correlation, univariate logistic regression and residual regression. Logistic regression models were run with a final set of predictors, where proportion of clay in the soil ($B=0.116$, $SE=0.036$, $p=0.001$) and presence of agricultural areas ($B=4.216$, $SE=1.515$, $p=0.001$) significantly explained occurrence of jirds.

Behaviour was observed using scan and focal animal sampling methods in 3 and 4 colonies in agriculture and natural areas respectively, during winter and summer. Activity periods were different for the 2 seasons. Irrespective of season and site, major proportion of active time was spent foraging. Vigilance was another key behaviour along with foraging, indicating a trade-off for optimization which requires further testing.

The study delivers baseline information for a trophic level that can impact predators and prey (including vegetation) alike. With the ominous conversion of traditional pastoral land to agriculture in the region in recent times, it is crucial to identify the impacts of this change on the ecosystem.

1. Introduction

Much of Earth has been explored and innumerable organisms discovered and classified. The human brain forever curious, we ask cascades of questions to understand the intricate systems around us. However, we require elementary knowledge and understanding before delving into the mechanisms of it all. Once found, listed and stacked away, some species are forgotten, some abandoned, and some extremely difficult to study. Many a complex model has failed to explain the phenomenon for which it was built because of a lack of basic field data on the species' natural history (Stoddart, 1979).

Fundamental ecology provides information on species' distribution and abundance, species-habitat relationships, behavioural patterns, adaptations and so on. Abundances and densities add perspective to the population of a species. Depending on scale, a population could mean the number of individuals of a species in an area, or throughout its distribution. This has vital conservation significance especially in today's escalating intensity of threats to wildlife globally. However, these figures might adhere to single points in space or time (Wiens, 1976). Simple population sizes monitored over space and time give a glimpse of the population dynamics and this, coupled with how they interact with the environment adds to the population ecology of the species. Species-habitat relationships therefore form another pertinent aspect worth investigating. Habitats being inherently patchy in distribution can have powerful influences on the species' distribution and abundance (Barnard, 1983; Wiens, 1976). Many species make decisions about which habitats to use and which ones to avoid (Bowers, 1995), under different connotations of the phrase 'habitat selection'. As resources become clumped, spatially or temporally, an increasingly larger area is required to ensure an adequate supply, and territory maintenance become difficult, inefficient and energy-demanding (Wiens, 1976). Thus, patches are formed, individuality becomes expensive and social organization becomes localized in a 'central place', a den or a roosting site. Adding a predation risk dimension makes the model more complex and realistic, and the formation of social groups becomes more advantageous as they are known to be better adapted to detect predators, reduce individual risk and advertise resource sites (Brown and Kotler, 2004; Wiens, 1976).

Most theory of population biology and ecology is based on optimization principles governed by the powers of natural selection, where species have to maximize benefits over costs. Optimality theories and their mathematical models indicate that an animal chooses that patch to feed from which provides highest energy return rate and often, these patches have constraints such as increased risk of predation (Bowers *et al.*, 1993; Charnov, 1976; Kamil *et al.*, 1987). Decisions are responses (adaptations in the evolutionary sense) to what the animal perceives, and this could show significant variation not just at the population level, but also within individuals in a population (Bowers, 1995). These responses can be measured by observing and recording behaviour, which is said to be the tool with which an animal uses its habitat (Barnard, 1983). Although it rarely enters models or discussions of demographic evolution, behaviour clearly plays an important role in determining individual fitness. Two important aspects of behavioural evolution are habitat selection and basic features of social organization (Fleming, 1979). Some animals tend to live in groups of conspecific individuals for various reasons. The size of the group is an important aspect of their social organization and tends to be highly variable even within the same species. Combined with the ability to respond to variation in resources and risks through behavioural means such as vigilance (Brown and Kotler, 2004), the model can provide better inferences to explain the system. The facets of ecology described above, i.e., population sizes, habitat use and behaviour, are very important especially during initial investigations into species little known.

1.1. Small mammals, rodents and sociality

In terms of number of species and individuals, small mammals dominate the Class Mammalia, with the diversity of their trophic and ecological adaptations ranging from fossorial grazers to aerial carnivores. Given such an assorted array of lifestyles, it should not be surprising that they have evolved numerous life-history strategies to a wide range of environments (Fleming, 1979). Understanding the population dynamics of animals motivated ecologists in the beginning of the twentieth century and since then, small mammals have been commonly used as model systems because of their convenient size and short generation times (Krebs, 1998; Pocock *et al.*, 2004).

Among small mammals, much time and effort has been spent researching rodent ecology as they often occur in great densities and are frequently referred to as pests in agriculture and human health (Stoddart, 1979). Also, rodents are important components of the diet for numerous carnivorous and scavenging species. They also provide habitat for numerous vertebrate and invertebrate animals as a consequence of their burrowing activity which in turn regulates aeration and water regime of the soil, providing suitable environment for growth of plants (Shenbrot *et al.*, 1999). Models of capture-mark-recapture have been used in the past to estimate population size (Anderson *et al.*, 1983; Otis *et al.*, 1978) and a number of techniques like track plates, chew cards, trapping, etc have been developed to index rodent populations (Whisson *et al.*, 2005).

Social systems in rodents vary from solitary to colonial social kinds so much that hypotheses explaining group-living in rodents are pertinent to only some groups of rodents. This variation is the response or adaptation of the species to the environment. Rodents also show great variation in sociality within species, depending on geographic distribution and habitat characteristics (Ebensperger, 2001; Randall *et al.*, 2005). Abundance of food influences the composition of social groups of some species and does not influence some others. Size of groups is a significant predictor of dispersal in some species but does not influence other species (Ebensperger *et al.*, 2009). Considerable intra-specific variation in number and composition of group members characterizes more social groups (Lott, 1991). The great gerbil, *Rhombomys opimus*, shows variation in sociality and the best reproductive strategy may actually be the flexibility to modify group size according to environmental conditions (Randall, 1994). Such adaptations have also been seen in the Mongolian gerbil (*Meriones unguiculatus*) (Randall *et al.*, 2005) and the Indian gerbil (*Tatera tatera*) (Idris and Prakash, 1985).

1.2. Desert rodents

Deserts are difficult places to live in with extreme and unpredictable environmental conditions. To survive above ground in deserts, rodents must often withstand periods of limited plant growth, resulting in low primary production of vegetation. Such habitats usually have limited cover and so rodents are preyed upon by numerous predators. They also face the problem of maintaining a constant body temperature while minimizing water loss in semi-arid and arid conditions. Semi-fossorial rodents cannot escape extreme temperatures and aridity by living their entire lives underground, as they depend on food sources above ground also.

However, they are a group of highly flexible and opportunistic animals, well-adapted to changing environmental conditions. A majority of them confine their activities to cooler night times (Randall, 1994). They can also retreat into subterranean burrows that are cooler, that act as refuges against predation and also a place to store food (Kinlaw, 1999). Under these conditions of patchy food availability and unpredictable rainfall, group-living is not a surprising adaptation, having its own advantages of efficient resource sharing and early detection of predators (Treves, 2000).

1.3. Study species

The Indian desert jird, *Meriones hurrianae* (Jerdon 1867), Order-Rodentia, Family-Muridae, Sub-family-Gerbillinae, is closely related to the gerbil group and often also referred to as Indian Desert Gerbil. They are found in the arid and semi-arid regions from south-eastern Iran and Pakistan till north-western India. In such arid ecosystems, like other species, they escape the heat of the day by having a comparatively low metabolic rate, an efficient renal system (Goyal, 1988) and utilizing extensive burrow systems. The average weight of the jird is 60-80g, body length 120-125mm and tail length 100-125mm. Their burrows are usually more than 1m deep. They are known to eat seeds from Oct-Mar and switch to insects, mainly grasshoppers and beetles, in summer and green plant parts in monsoon. They breed throughout the year peaking during monsoon and can bear 1-9 young at a time. They live in colonies with varying group sizes (20-40 individuals) (Prakash, 1981). Studies on this species are restricted to one monograph (Prakash, 1981) and a few sporadic investigations into physiological aspects of urine concentration (Goyal, 1988), burrow structure and some laboratory experiments on photoperiod influence and impact of aggressive behaviour on reproductive behaviour (Sinhasane and Joshi, 1998). This common yet little known rodent, being diurnal and/or crepuscular and easy to observe, is an ideal subject for asking fundamental questions in population and behavioural ecology.

1.4. Present study

The current study seeks to gain basic ecological information about the Indian desert jird and look for patterns between 2 land use types (agriculture and natural) across 2 seasons, winter (December-February) and summer (March-May). The study can be divided into 3 aspects;

A) Population ecology

i) To estimate population of jirds in different colonies

ii) To test for differences in mean population size and morphometrics between age-sex classes in 2 land use types

iii) To develop an index for rapid large-scale population estimation

B) Habitat use

i) To identify factors in the habitat that might influence occurrence of jirds

C) Behaviour

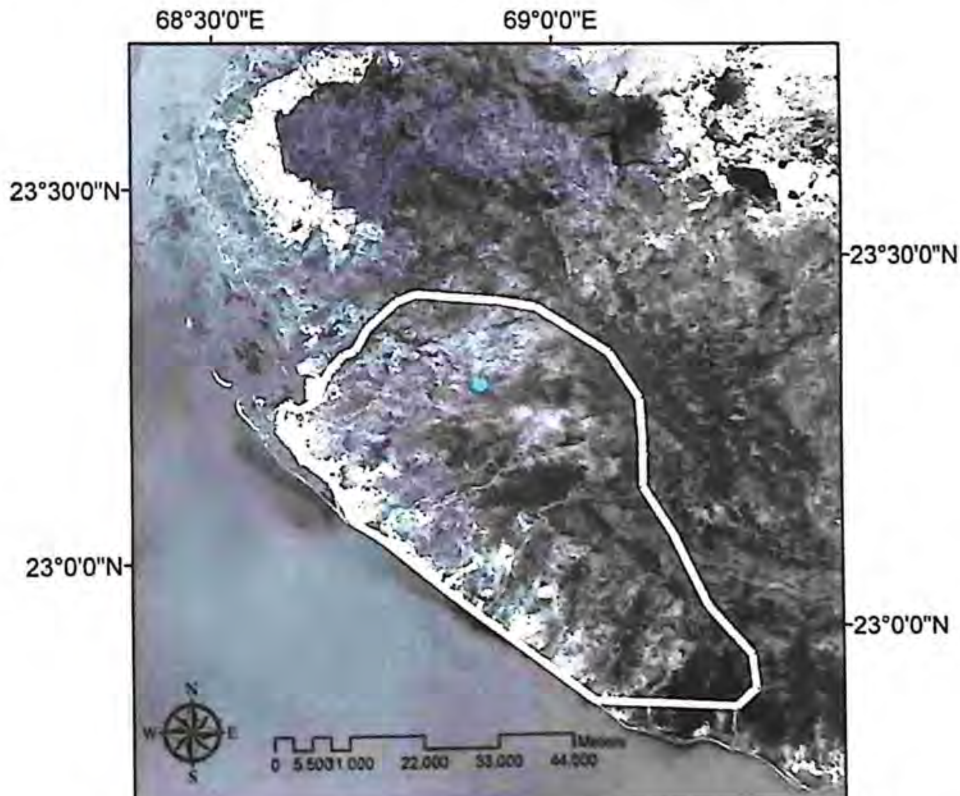
i) To obtain activity patterns of jirds in 2 land use types for 2 seasons

ii) To obtain time budget of jirds in 2 land use types in 2 seasons

2. Study area

The study was conducted in Abdasa taluka, Kachchh district of Northwestern Gujarat, India. Kachchh is surrounded by the Arabian Sea in the west, Gulf of Kachchh in the South and Southeast and Rann of Kachchh in the North and Northeast. The study site is outside the purview of the protected area network of the country.

Classified under biogeographic zone 3B (Rodgers and Panwar, 1988), this semi-desert region experiences summer from March until late June, with May having the highest temperatures (40-45°C). Precipitation is scanty and stochastic with an annual average of 384mm.Winters extend from mid-November to February, with January recording the minimum, while the average temperature remains around 5°C. The terrain is undulating with gullies and ridges, cut by seasonally dry rivers.



Map 1. False colour composite with Abdasa taluka, Kachchh, Gujarat, outlined in white and intensive study area indicated by the blue dot

2.1. Flora and fauna

The vegetation type in the area has been classified as Northern Tropical Thorn Forest (6B) and sub-classified as Desert Thorn Forest (6B/C1) (Champion and Seth, 1968). The arid undulating terrain is dominated by grass species such of *Cymbopogon*, *Chrysopogon*, *Aristida* and *Dicanthium*, along with shrub species of *Acacia*, *Prosopis*, *Salvadora*, *Euphorbia* and *Capparis*. The area supports several faunal species, some of which are protected under the Schedule I of Indian Wild Life (Protection) Act, 1972, such as the Indian Peninsular Wolf (*Canis lupus*), striped hyena (*Hyaena hyaena*), golden jackal (*Canis aureus*), caracal (*Caracal caracal*), desert cat (*Felis libyca ornate*), chinkara (*Gazella gazelle*), Great Indian Bustard (*Ardeotis nigriceps*), lesser florican (*Sypheotides indica*), white-backed vulture (*Gyps bengalensis*), spiny-tailed lizard (*Uromastix hardwickii*). Other species include nilgai (*Boselaphus tragocamelus*), wild pig (*Sus scrofa*) and jungle cat (*Felis chaus*).

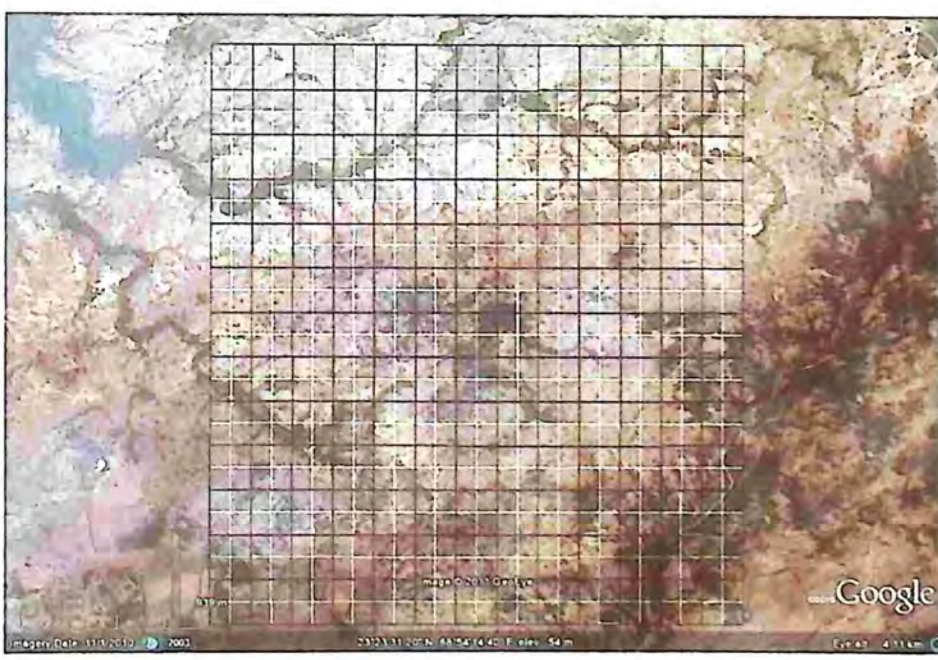
2.2. Land use practices

Pastoral grazing, nomadic and settled, dominates the traditional land use practices. Cattle (*Bos taurus indicus*), goat (*Capra aegagrus hircus*), sheep (*Ovis aries*), buffalo (*Bubalas bubalis*) and camel (*Camelus dromedaries*) constitute the livestock and the grazing action over centuries has moulded the landscape to its current form and all faunal and floral components adapted to this system. However, in the last 2 years, land is being converted rapidly to make way for agriculture. While immigrants from states like Punjab and Haryana have extensive Bt cotton farms throughout most of the year, residents harvest one-time short duration crops like til (*Sesamun indicum*), groundnut (*Apios americana*), tomato (*Solanum lycopersicum*) and chili (*Capsicum frutescens*).

2.3. Intensive study site

Two study sites of approximately 4sqkm each were located in Abdasa tehsil for the study. One was agriculture-predominant and the other was relatively untouched except for traditional pastoral grazing. During the study period, most fields had been harvested and were fallow, few having crops of tomato and chili. Henceforth, these sites will be referred to as 'agriculture' and 'natural'.

Map 2. Image of agriculture study site of 4sqkm, converted into 4 ha grids (black), each subdivided into 1ha grids (white) in Kachchh, Gujarat, 2011. (Courtesy: Google Earth)



Map 2. Image of natural study site of 4sqkm, converted into 4 ha grids (black), each subdivided into 1ha grids (white) in Kachchh, Gujarat, 2011. (Courtesy: Google Earth)

3. Methodology

3.1. Field Methods

3.1.1. Population estimation

Nine colonies were selected for estimating population sizes, 5 in agriculture and 4 in natural areas. Parameters such as number of holes, length and width of each colony were recorded. Colonies were saturated with Sherman traps (H. B. Sherman Inc., Tallahassee, Flor.) in order to capture as many individuals as possible. Traps were placed 1-3m apart in a systematic coverage of burrow entrances and therefore trap numbers varied from 25-60, but were kept constant across trapping sessions in a particular colony. They were covered with mud/grass/twigs to help in camouflaging and heat reduction (Plate 1). Traps were baited with a paste made of biscuit crumbs mixed with jaggery syrup. Initially bait trails were laid in some colonies with jaggery syrup on small twigs, from burrow entrances to the trap but this was not necessary in most colonies as the animals quickly found the bait. A minimum of 6 trapping sessions were conducted at each colony with 2-3 sessions/day. Initially, trap sessions lasted 2 hrs but by mid-February, the metal traps heated up quickly. So trap sessions were reduced to 1 hr to avoid heat stress and mortality. Traps were checked at the end of each session and animals were removed from the trap by holding a cone-shaped cloth at the trap door with a small hole at the other end. The trap door was gently pushed open and the animals rushed into the cone bag, after which they were handled. Measurements such as weight, hind limb length and tail length were collected using a spring balance (PESOLA, Switzerland; metric, 600gm) and Vernier calipers. Gender and age category (based on genitals and teats) were also noted. A unique consecutive identification number was written with a non-toxic marker pen on the inner hind limb of each animal. Handling time was kept less than 5 minutes to minimize stress to the animals, which were then released near a burrow entrance.

3.1.2. Habitat use

Both study sites were converted into 4-ha grids, 28 grids in the agricultural area and 25 grids in the natural study site. Systematic sampling was done by selecting alternate grids that were in turn sub-divided into four 1-ha sites, of which any 3 were sampled. Google Earth and a handheld GPS (Garmin GPS 72) unit were used to find sampling units. A 20m radius circular plot was laid at the center of each of these sites. Four perpendicular axes cut the plot into 4 quadrants (Figure 1). While the observer walked from the center outwards in each quadrant, another person recorded the data. Broad habitat type was recorded by visually estimating percentage shrub cover within the 20m radius into dense scrub (>50%), open scrub (20-50%), open grassland (<20%), riverine and agriculture field. Using the Robel Pole method, a 1m stick marked at heights 10cm, 25cm, and 50cm was placed every meter from the center and data on habitat structure was collected (Robel *et al.*, 1970). Variables that were recorded include bare ground, rock and vegetation height classes of 0-10cm, 10-25cm, 25-50cm and above 50cm.

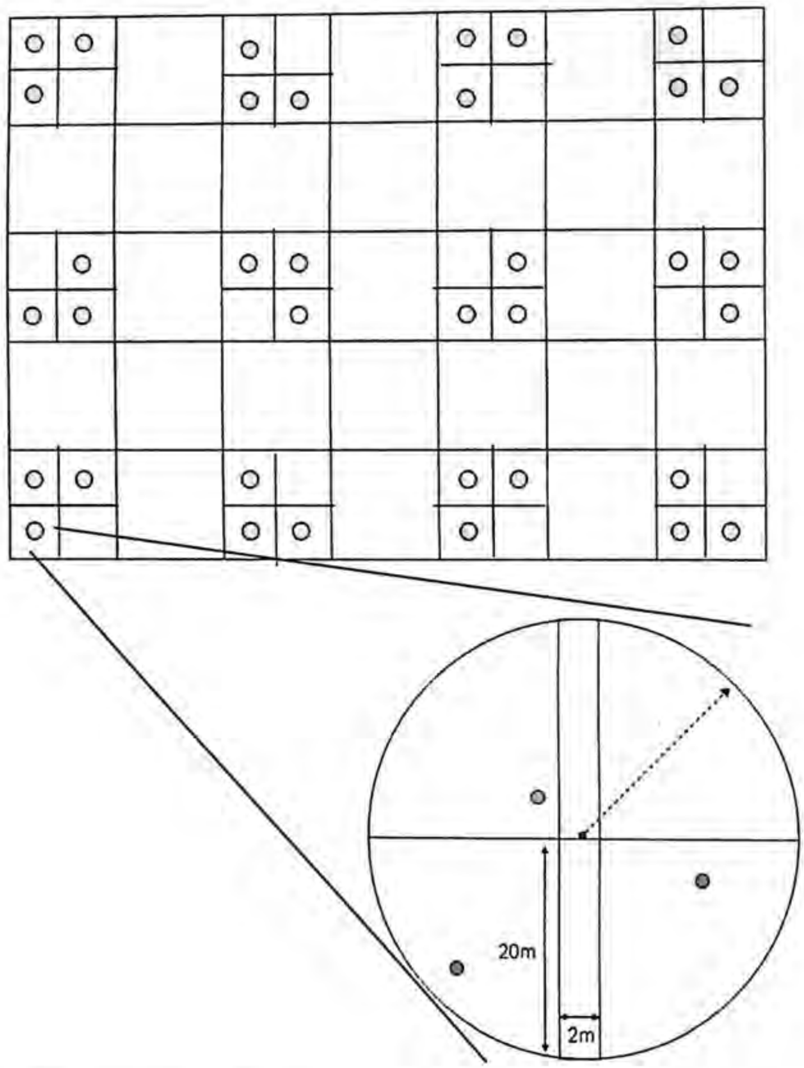


Figure 1. Systematic grid-based sampling design to quantify habitat relationships of jirds in Kachchh, Gujarat 2011. Blue dots indicate the sample plots. Dotted line shows direction of walk using Robel Pole method, done in all 4 quadrants. Brown dots indicate soil sample collection sites. Central rectangle shows belt transect for pellet groups (40x2m).

A 40m x 2m belt transect was laid across the diameter for livestock pellet/dung count (Neff, 1968). Pellet groups of livestock including goat, sheep, cattle and camel were counted. Anthropogenic activity intensity was given a subjective score from 0 (least) to 3(maximum), based on distance to village, water body, grazing signs and wood cutting with increasing intensity Also, 3 soil samples of fixed volume were collected at 3 independent points within each plot, from a depth of 15-20cm below ground using a small crowbar. These samples were stored in labeled plastic bags for further analysis. All sites were visited twice with a gap of 35days in between, and all data except soil was collected following the methods mentioned above. Soil samples were sieved through 3 layers using standard mesh sizes (BSS) to get composition of clay, silt, sand and coarse particles (Fisher and Anthony, 1980).

3.1.3. Behavioural observations

Seven of the 9 colonies whose abundance was estimated, were observed using scan and focal animal sampling, and a pair of binoculars (Bushnell, 8x40) and a voice recorder were used to record behaviour. After reconnaissance, behavioural states were grouped under 6 main categories namely foraging (eating, moving, climbing), vigilance (standing, drumming), digging, resting, maintenance (grooming), interaction and rubbing (rubbing ventral side of the body on the ground, scent marking).Observations were made from 2-3m elevated natural and man-made hides at distances of 10-15m from the colony. Observations were started 10-15mins after reaching the colony, in order to allow the animal to return to its normal state of behaviour. As part of a trial, individuals in agriculture were marked with combinations of shapes and colours using non-toxic paint, and therefore focal animals were 'known' during winter. The marks did not last more than two weeks and marking was not done thereafter. A scan was conducted every 10mins and all individuals had equal probability of being focal individuals between 2 successive scans. An individual was randomly chosen as the focal animal. If the individual went into a burrow during the focal sample, then another individual was randomly selected and observed. If no individual was present above ground, the colony was scanned every minute for focal individuals. All behavioural events/states were recorded throughout the activity period.

3.2. Analytical methods

3.2.1. Population estimation

All 9 colonies were combined and provided with a grouping variable to get a pooled estimate because of inadequate sample size. Program MARK (version 6.0), was used to estimate population size (N) using Huggins fully closed capture models with variations in capture (p) and recapture (c) probabilities as this allows incorporation of individual covariates (White and Burnham, 1999). The Huggins models are also known to provide more reasonable estimates of N when nearly all the population is captured. Eight models were constructed including the null model (Mo), heterogeneity models (Mh) with and without variation across behaviour (Mb) and time (Mt). Individual covariates included were gender, body weight (gm) and age category with a block effect of land use type. Multi-model averaging was done with the first 5 models since the ΔAIC was very small (Burnham and Anderson, 2002) and thus population estimates were obtained for each colony.

Also, body weights and hind limb lengths of all captured individuals belonging to each age (sub adult/adult)-gender (male/female) class were compared between agriculture and natural areas using Mann-Whitney U-test. Colony dimensions and number of holes were regressed with their estimated population sizes to obtain a correction model by which population size of colonies with known dimensions can be estimated without intensive Capture Mark Recapture sampling. For more robust analysis, historical data of colonies from the same area (see Home, 2005) was added to data from this study, which gave a total sample size of 16 colonies for this regression analysis.

3.2.2. Habitat use

While species distribution is a complex ecological process requiring collection of inherently correlated variables, such multicollinearity can complicate interpretation of regression results (Graham, 2003). Pearson's correlation coefficients between pairs of habitat variables (Zar, 1999) were computed. From substantially correlated variable-pairs ($|R|>0.4$, $p<0.05$), univariate logistic regression models were run and the variable with smallest AICc was retained. Number of pellet groups was converted into a categorical score (0 for 0 pellet groups, 1 for 1-2 pellet groups, 2 for 3-5 pellet groups, 3 for more than 5 pellet groups) and added with the subjective score for disturbance since they were highly correlated but provided different perspectives on disturbance. Alternative hypotheses on proximate habitat determinants of jird distribution were then tested using logistic regression by modeling the probability of jird occurrence with alternative linear combinations of habitat variables. The model with the smallest AIC was selected for interpretation of jird-habitat relationships.

3.2.3. Behaviour

Focal samples from seven colonies in two land use types during summer and winter were divided into half-hour intervals across the day. Average proportion of time spent performing each of the above behaviours was calculated across colonies and plotted against time of day to obtain the time budget. Scan samples were also grouped similarly for the land use types and for summer and winter, within half-hour intervals, such that every half hour comprised 3 scans at 10min intervals. The average proportion of active individuals performing each behaviour during each of the half hour intervals was obtained across seven colonies. This was plotted against time of day to get an activity pattern.

All analysis was done using SPSS 16.0 (SPSS Inc., Chicago, IL), NCSS 5.1 (Hintze, 2001) and Microsoft Excel 2003 (Microsoft Corporation).

4. Results

4.1. Population estimation

In all, 38 individuals were captured from 9 colonies. Number of individuals caught, ratios of different age-sex classes and other parameters are given in table 1. The male to female ratio is 1 in both agriculture and natural areas. The sub-adult (male and female) to adult female ratio is 2.63 times less in agriculture than in the natural area.

Habitat	M	F	S	Ad	Ad_F	F:M	S:Ad_F	Var (S:Ad_F)
Agriculture	10	10	6	14	7	1	0.86	0.227
Natural	9	9	9	9	4	1	2.25	1.828

Table 1. For each habitat type (Habitat), number of males (M), females (F), sub-adults (S), adults (A) and number of adult females (Ad_F) are listed with ratios of F to M (F:M) and S to Ad_F (S:Ad_F), in Kachchh, Gujarat, 2011

Colony-specific population sizes were estimated using different models, including the null model (*Mo*) where capture probability (*p*) equals recapture probability (*c*) and is kept constant (.) for all colonies and across trapping sessions. The model *Mt* assumed equal *p* and *c* but allowed them to vary across trapping sessions but not with colony. *Mb* was the behaviour model with *c* unequal to *p*, but constant over all trapping sessions and colonies. *Mh* was the heterogeneity model which assumed the population to be a mixture of two sub-populations having different *p* which may (*Mbh*) or may not differ from *c*, and may (*Mth*) or may not vary across trapping sessions (Table 2). In these models, '*pi*' was the probability of an individual belonging to one sub-population versus the other, which was estimated implicitly by likelihood approach, or allowed to vary across colonies, or explicitly modeled with individual covariates, such as age, gender, weight and site. Multi-model averaging was done over models having ΔAICc <3, which summed up to 0.82 Akaike weight (*Wi*) or, had >80% confidence of including the actual best model. This procedure estimated average population size and the unconditional standard error for each colony (Table 3). Mean population size in a colony did not differ between the agriculture and natural area (Mann-Whitney U=6.00, p=0.325).

Model name	Parameters	L	K	AICc	ΔAICc	Wi
Mbh2mixture	pi(site+gender)p(.)c(.)	1.00	7	303.23	0.00	0.48
Mbh2mixture	pi(site)p(.)c(.)	0.49	6	304.65	1.42	0.23
Mbh2mixture	pi(.)p(.)c(.)	0.24	5	306.09	2.86	0.11
Mbh2mixture	pi(colony)p(.)c(.)	0.15	13	307.07	3.84	0.07
Mbh2mixture	pi(age)p(.)c(.)	0.09	6	308.15	4.92	0.04
Mbh2mixture	pi(wt)p(.)c(.)	0.09	6	308.16	4.93	0.04
Mh2mixture	pi(.)p=c(.)	0.04	3	309.58	6.35	0.02
Mb	P(.)c(.)	0.01	2	313.45	10.21	0.00
Mh2mixture	pi(colony)p=c(.)	0.00	11	313.97	10.74	0.00
Mo	P=c(.)	0.00	1	315.40	12.17	0.00
Mt	P=c(colony)	0.00	6	317.19	13.19	0.00

Table 2. Competing models for population estimation of jirds in Kachchh, Gujarat, 2011, with their corresponding model likelihood (L), number of parameters (K), AICc scores, differences in AICc scores between the *i*th model and the model with the lowest AICc score (Δ_i) and Akaike weights (W_i).

(.) = constant probabilities across colonies
(colony) = probabilities varying with colony
b = behaviour
t = time
h = heterogeneity
site = agriculture or natural
gender = male or female
age = adult or sub-adult
wt = weight

Colony	N-*hat*	SE	LCL	UCL
1	2.23	0.57	1.12	3.34
2	4.46	0.87	2.75	6.17
3	3.38	0.78	1.85	4.90
4	9.99	1.50	7.05	12.94
5	2.23	0.57	1.12	3.34
6	9.06	1.59	5.95	12.18
7	3.39	0.79	1.85	4.94
8	3.45	0.88	1.72	5.18
9	4.62	1.11	2.45	6.79

Table 3. Estimated population size (N-hat) of Jirds, for each colony with standard error (SE) and 95% lower (LCL) and upper confidence limits (UCL) using the model averaging estimate in Kachchh, Gujarat 2011.

However, morphometric measurements of individuals differed between agricultural and natural areas but the difference was limited to certain age-sex classes (Table 4). Body weight and hind limb length of adult and sub-adult females significantly differed between natural and agricultural areas. Sub-adult males also showed a significant difference in hind limb length between the 2 areas. Body weight of adult females was greater in natural than agricultural area (mean=80, SE=2, N=4; mean=70, SE=2.19, N=7 respectively). Sub-adult females also weighed more in natural than in agriculture areas (mean=59, SE=1.869, N==5; mean=45, SE=2.88, N=3 respectively). Adult and sub-adult females in natural area had longer hind limbs (Adult: mean=7.725, 6.2875; SE=0.655, 0.89; N=4, 7; Sub-adult: mean=7.16, 4.9; SE=0.671, 0.381; N=5, 3 respectively). Sub-adult males in natural area had longer hind limbs (mean=5.3, 4.6; SE=0.34, 0.306, N=4, 3 respectively). Adult males did not show any significant difference in any morphometric character.

Age-sex category	Body Weight		Hind Limb Length		Number of individuals	
	U	p	U	p	Agriculture	Natural
SF	0.000	0.024	2.000	0.101	3	5
AF	4.000	0.035	6.000	0.089	7	4
SM	3.500	0.354	1.000	0.007	3	4
AM	12.500	0.420	4.000	0.476	5	7

Table 4. Results of Mann-Whitney U-tests, U with p-value (p), to test for difference between sub-adult females (SF), adult females (AF), sub-adult males (SM) and adult males (AM) in the 2 land use types in Kachchh, Gujarat, 2011.

Number of holes in a colony increased linearly with the estimated population size (N=16, $R^2 = 0.9594$, t=18.1947, p<0.001, Figure 1). Length (N=16, $R^2 = 0.7645$, t=6.7420, p<0.001) and breadth (N=16, $R^2 = 0.8104$, t=7.7366, p<0.001) also showed a strong linear relationship with population size. However, since the regression with number of holes had the highest R^2, this was considered the best predictor. The estimated model was Population size = 2.38(SE=0.75) + 0.013(SE=0.0007) * Number of holes. The ability of the index to predict population size was assessed using a Jack-knife analysis where each population estimate was dropped, best regression model re-computed and used to predict the population size of the excluded colony (Jhala *et al.*, 2011; Krebs, 1989). The predicted estimates based on Jacknife analysis were strongly correlated with the original mark-recapture based estimates (R=0.958, p<0.001, Figure 2) implying reasonable predictability of population size from number of holes in colony as the index.

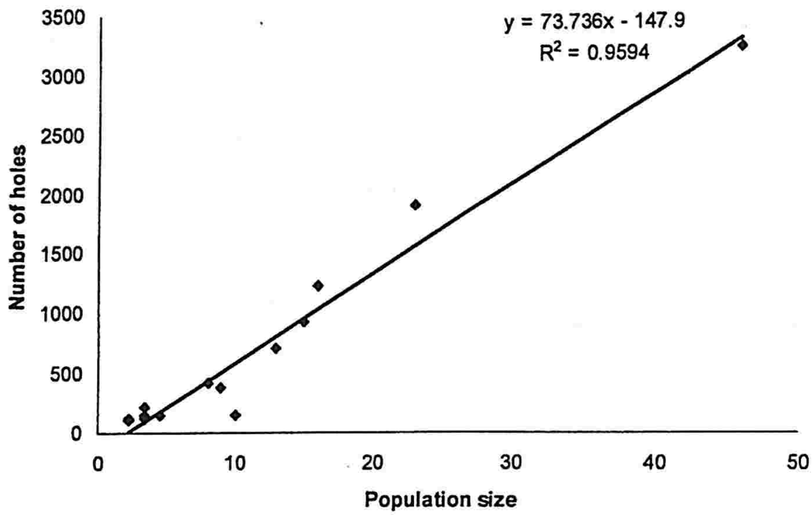


Figure 2. Mark-recapture based population size for 16 colonies of jirds in Kachchh, Gujarat, 2011, plotted with number of holes at each of the colonies. Also given is the equation of the line with the corresponding coefficient (R^2) value.

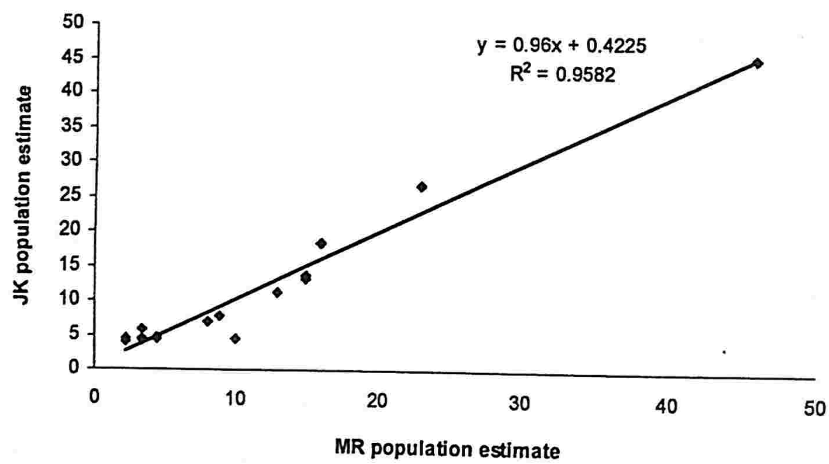


Figure 3. Mark-recapture (MR) based population estimate of jirds in Kachchh, Gujarat, 2011, plotted with Jack-knife (JK) predicted estimates for all 16 colonies. Also given is the equation of the line and the correlation coefficient (R^2) value.

4.2. Habitat use

Habitat relationships of jirds were quantified by modeling their occurrence with combination of predictor habitat variables. Preliminary processing of habitat variables revealed that percentage of clay and percentage of coarse soil were significantly correlated (R=-0.724, p<0.001), but were also significant predictors. This was determined from the univariate logistic regressions (Clay: β=0.065, SE=0.018, p<0.001, AIC=93.27; Coarse: β =-0.069, SE=0.021, p=0.001, AIC=93.86). Hence, they were used in separate logistic regression models. Among the variables describing vegetation structure, average frequency of occurrence of 0-10cm and 10-25cm vegetation height classes were significant predictors (β=0.245, SE=0.143, p=0.09, AIC=109.07; β=-0.72, SE=0.356, p=0.04, AIC=106.38 respectively) but were also correlated (R=0.115, p=0.151).Although 10-25cm vegetation height class had smaller AIC value, my behavioural observation suggested that the 0-10 cm height class formed the major forage for jirds. Hence the 10-25 cm height was regressed against 0-10cm height and the residuals from the regression were used in the subsequent models. Eleven ecological models were run as meaningful combinations of the final set of variables (Table 5) and the results of the smallest AIC model has been presented in table 6.

Model	AIC	ΔAIC	df	R^2	GOF-*p*	% cc
Clay+Veg (0-10) + Veg (res10-25) + Dist + Hab	79.15	0	8	0.50	0.98	91.2
Clay+Veg (0-10)+Veg (res10-25)+Dist + Hab(Field)	80.98	1.83	5	0.48	0.96	90.6
Clay+Veg (0-10)+ Veg (res10-25) + Dist	96.93	17.78	4	0.32	0.93	87.4
Clay+Veg (0-10)+ Veg (res10-25)	97.42	18.27	3	0.31	0.95	88.1
Hab	99.21	20.05	4	0.18	1.00	89.3
Coarse+ Veg (0-10)+ Veg (res10-25)	100.12	20.97	3	0.28	0.59	88.7
Clay+ Veg (0-10)+ Dist	105.14	25.99	3	0.23	0.50	89.3
Clay+Veg (0-10)	105.26	26.11	2	0.23	0.84	89.3
Clay	105.27	26.12	1	0.23	0.84	89.3
Coarse	105.86	26.70	1	0.22	0.88	89.3
Veg(0-10)+Veg(res10-25) + Dist	112.52	33.37	3	0.14	0.51	89.3
Veg (0-10) + Veg (res10-25)	112.56	33.41	2	0.14	0.48	89.3

Table 5. Competing ecological models of jird occurrence in Kachchh, Gujarat, 2011, as a function of predictor variables (average frequency of occurrence of vegetation height class 0-10cm (Veg(0-10)), residuals of 10-25cm on 0-10cm (Veg(res10-25)), overall score for anthropogenic activity/disturbance (Dist), habitat type (Hab) and field (Hab(Field)), with associated -2LogLikelihood values (-2LogL), model degrees of freedom (df), AIC values, difference between the AIC value of *i*th model and the model with smallest AIC score (Δ_i), Nagelkerke's R-square value (R^2), goodness-of-fit (GOF-*p*) and classification rate (%CC).

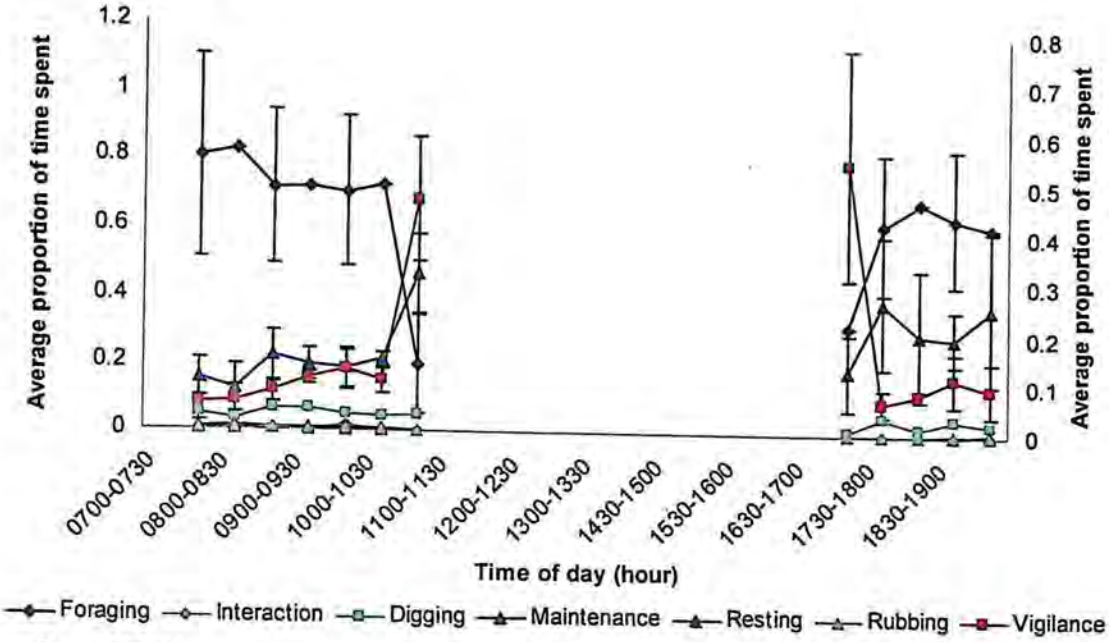
Variable	*B*	SE	df	*p*-value
Constant	-13.164	3.305	1	.000
Clay	.116	.036	1	.001
Vegetation 0-10cm	.179	.219	1	.415
Disturbance score	.460	.266	1	.084
Residuals of 10-25cm	-.231	.476	1	.628
Habitat type			4	.022
Habitat type(riverine)	-12.924	1.292	1	.999
Habitat type(open scrub)	.174	1.351	1	.897
Habitat type(dense scrub)	1.687	1.495	1	.259
Habitat type(field)	4.216	1.515	1	.005

Table 6. Variables in the final model with associated β values (B), standard error values (SE), degrees of freedom (df), and p-values.

4.3. Behaviour

Activity periods showed a clear difference between winter and summer. While in winter time of activity ranged from 0830-1330hrs and 1430-1930hrs, in summer, activity period was restricted to 0700-1100hrs and 1730-1930hrs. The time budget, i.e., average proportion of time spent performing each behaviour, calculated from focal samples, is presented for agriculture in summer and natural in summer (Figure 4) and winter (Figure 5). Foraging is calibrated in the primary Y-axis while the other behaviours are calibrated on the secondary Y-axis. Irrespective of site or season, it was found that individuals spent most of their time foraging when compared to other activities. Average proportion of time spent vigilant peaked where foraging dipped. Average proportion of time spent digging was more in the forenoon than in the afternoon. More time was spent resting when compared to being vigil. Average proportion of time spent in maintenance, interaction and rubbing was less than 0.1 in all cases.

A. Agriculture



B. Natural

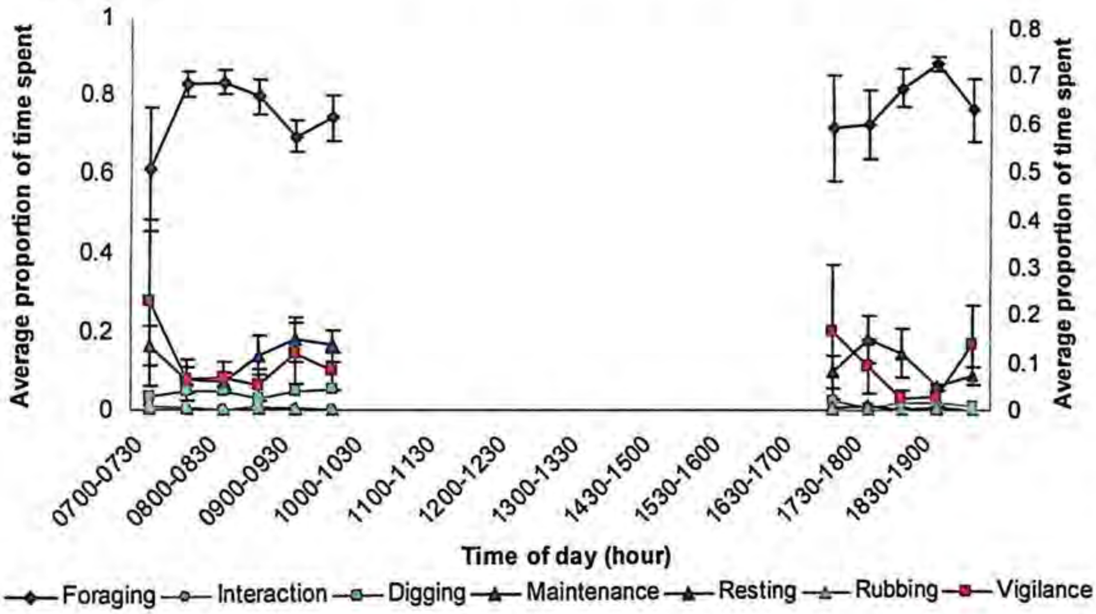


Figure 4. Time budget of jird behavioral activities from focal samples in agricultural landscapes (A) and natural landscapes (B) during summer (March-May) in Kachchh, Gujarat, 2011; foraging calibrated on primary Y-axis and rest on secondary Y-axis.

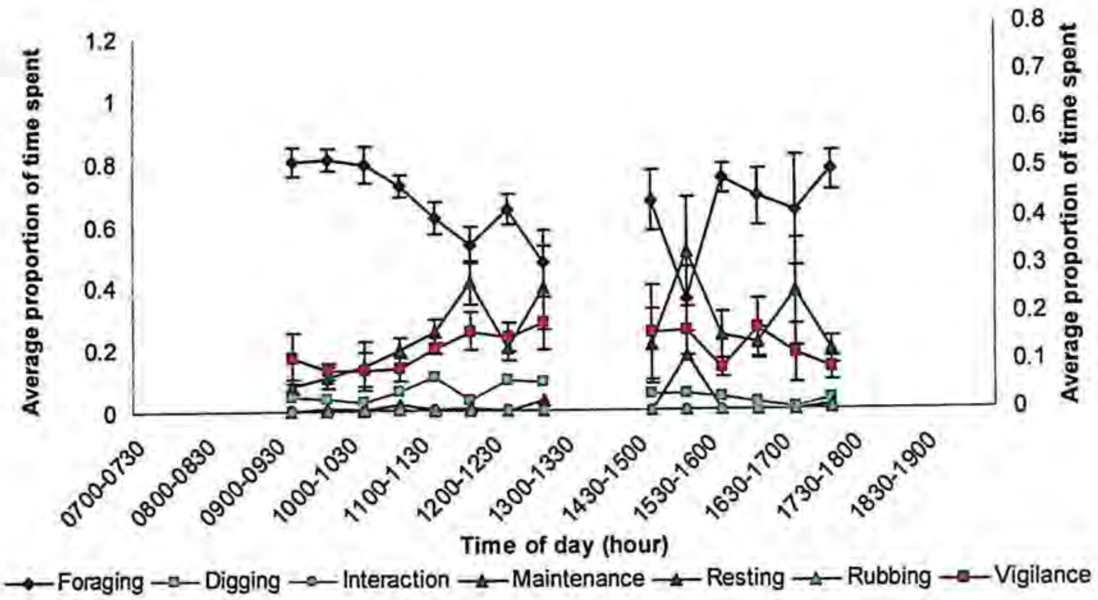


Figure 5. Time budget of jird behavioural activities from focal samples in natural area during winter (Dec-Feb) in Kachchh, Gujarat, 2011; foraging calibrated on primary Y-axis and rest on secondary Y-axis.

Activity patterns obtained from scan samples, i.e. the average proportion of individuals performing each behaviour, are presented for agriculture in summer and natural in summer (Figure 6) and winter (Figure 7). Foraging is calibrated on the primary Y-axis, with the other behaviours on the secondary Y-axis. Irrespective of site and season, the average proportion of individuals foraging was always higher than individuals performing any other behaviour. Foraging peaks in natural area in winter occurred between 0900-0930hrs and 1800-1830hrs while in summer, foraging peaked between 0800-0830hrs and 1900-1930hrs. The average proportion of individuals vigilant peaked when those foraging dipped. Vigilance was greater in the evening than the forenoon in agriculture during summer. The average proportion of individuals digging was higher during the forenoon than in the afternoon on both sites during summer. However, this was not the case in natural area during winter. Resting, maintenance and interaction were rare when compared to the other behavioural states and average proportion of individuals exhibiting these remained less than 0.1.

The number of individuals averaged across colonies, performing each behaviour, from scan samples, is represented for agriculture in summer and for natural in summer and winter (Figure 8). This is a measure of the frequency of each behaviour across site and season. In natural area during winter, foraging was the most frequently performed behaviour followed by vigilance, resting, digging, maintenance and interaction. In summer however, frequency of resting was marginally higher than vigilance in both natural and agriculture sites.

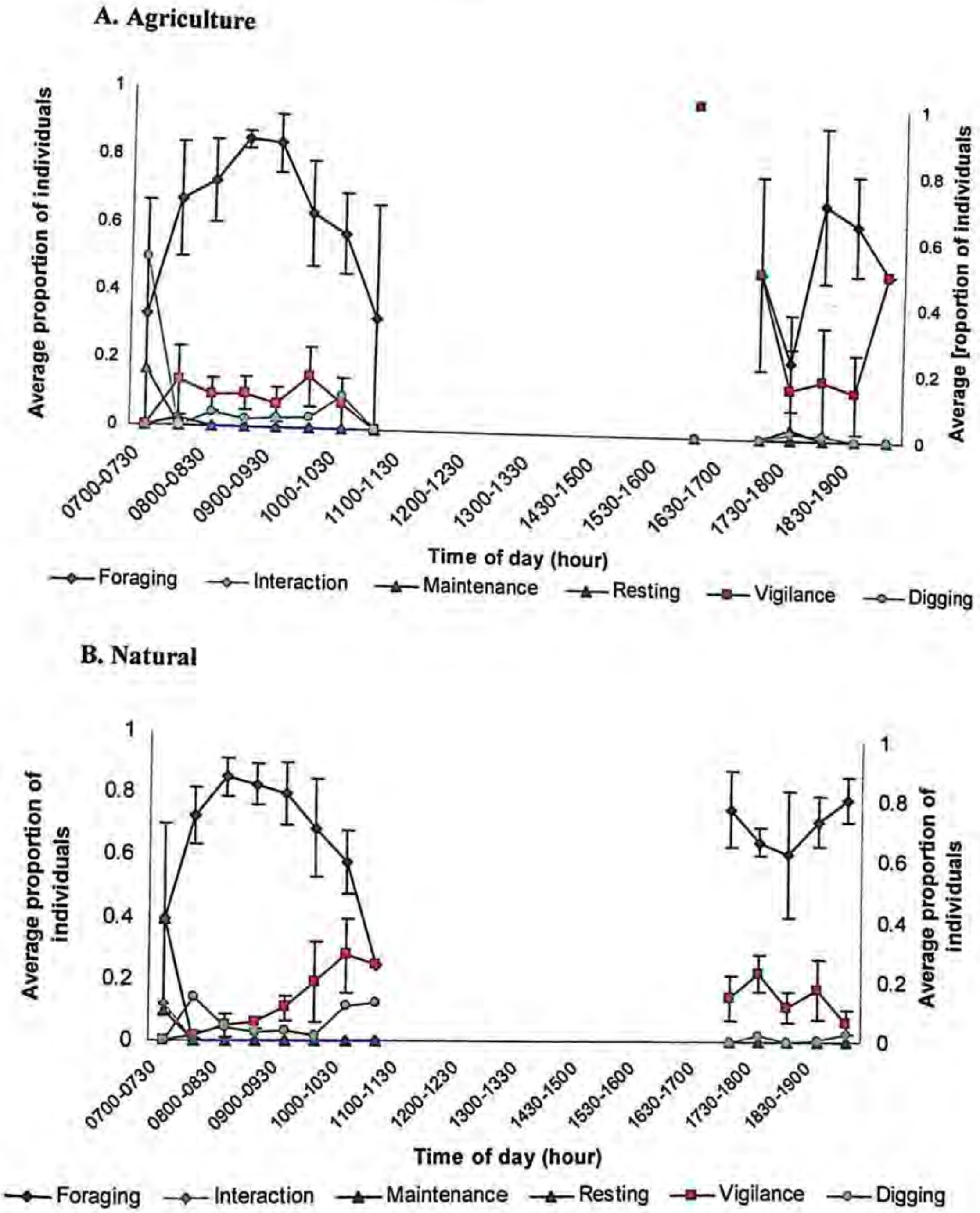


Figure 6. Activity patterns of Jirds from scan samples, in agriculture (A) and natural (B) during summer (March-May) in Kachchh, Gujarat, 2011; foraging calibrated on primary Y-axis and rest on secondary Y-axis.

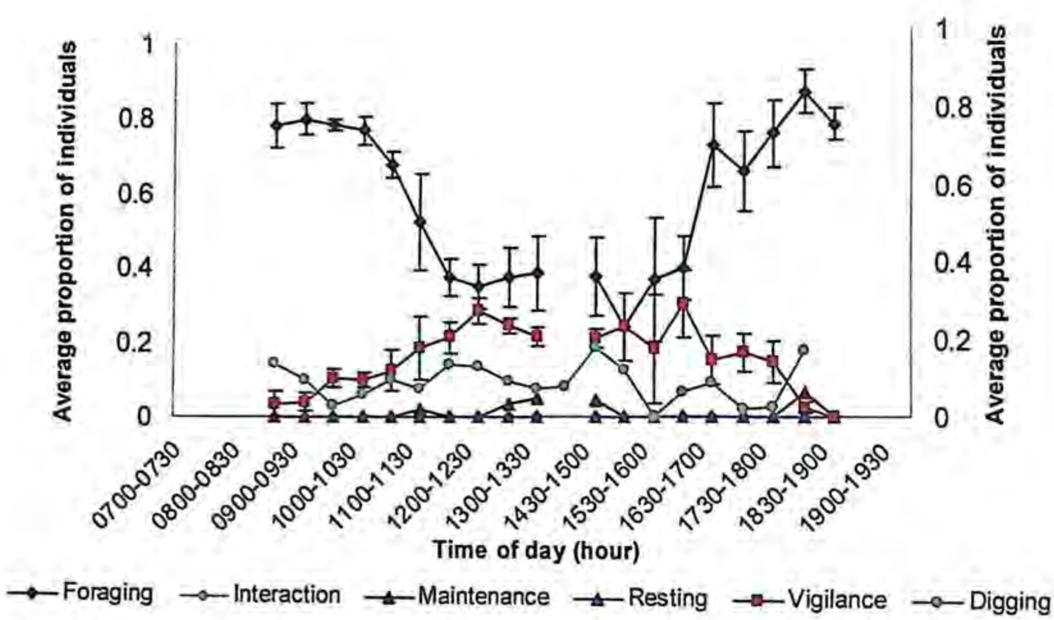


Figure 7. Activity pattern of Jirds from scan samples, in natural area during winter (Dec-Feb) in Kachchh, Gujarat, 2011; foraging calibrated on primary Y-axis and rest on secondary Y-axis.

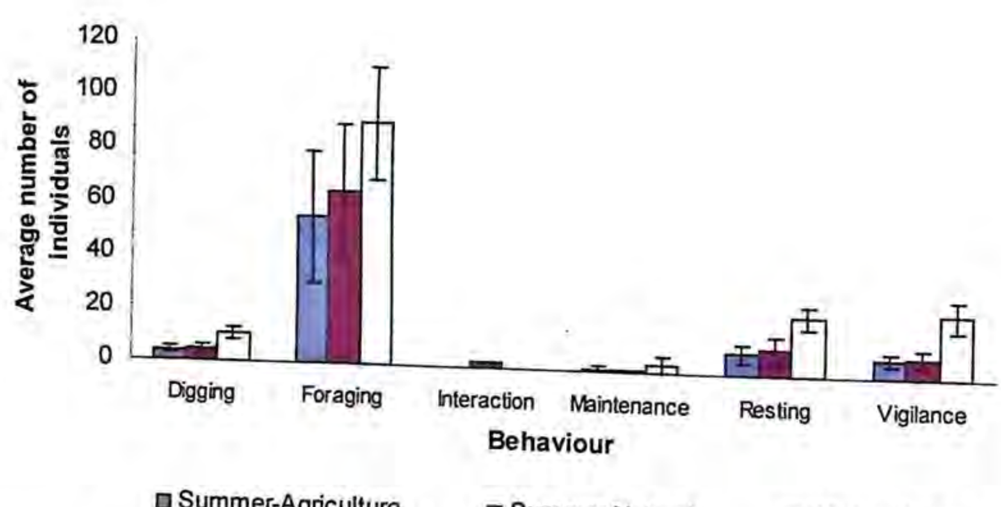


Figure 8. Overall time budget for each behaviour from scan samples, in agriculture and natural area during summer (March-May) and natural in winter (Dec-Feb) in Kachchh, Gujarat, 2011.

5. Discussion

5.1. Population estimation

The demographic data from 9 colonies for 38 individuals show that the male to female ratio is equal to 1 in both agriculture and natural areas. However, the sub adult (male and female) to adult (female) ratio is 2.63 times more in the natural area than in agriculture. This is interesting in that it could indicate higher recruitment in colonies in natural areas than in agriculture. Fields act as storehouses of food for many animals and rodents are often considered pests because of their ability to breed prolifically when food is aplenty. However, in the study site, crops (mostly til and groundnut) were harvested 2-3 months prior to trapping, thus taking away the major source of food. Therefore, despite hoarding, it is possible that food availability in the area was limiting and individuals had little access to natural patches. Although the species is known to breed throughout the year, the peak littering period coincides with monsoon (Prakash, 1981). Rain-fed agriculture, as is practiced in Kachchh probably causes a population explosion in jirds, where during the lean period food is a limiting factor, in comparison to natural areas that are likely to be more stable in terms of food resources. For example, food resources in an agricultural field could be taken away by ploughing overnight. This is also reflected in the larger body weights of adult females in natural areas as compared to the ones in agriculture.

Mark-recapture based population estimates indicate a range from 2 to 10 individuals. An earlier study (Home, 2005) recorded population sizes of up to 46 but such large-sized colonies were not found even after extensive search at the start of this study. Arid and semi-arid regions are known to experience drastic fluctuations in natural phenomena such as rain and drought. However, animals and plants in these landscapes are equally flexible and have the ability to survive such stochasticity (Kotler and Brown, 1988). The region had received good rainfall over the last 4 years (2007-2010) and it has been well established that population dynamics of rodents follow rainfall fluctuations (Brown and Heske, 1990; Shenbrot and Krasnov, 2001). There is also evidence for a strong inverse relationship between precipitation and population growth rates (Liu *et al.*, 2007). Hence, rodent-rain relationships are complex and cannot be adequately explained by a simple bottom-up trophic model (Brown and Ernest, 2002).

Good rainfall could also be one of the reasons for the sudden rapidly expanding agriculture. Although fields represent localized abundant food resources, the crop season lasts only for a short duration, by which time the land is cleared of the natural forage. Desert rodents have been described as opportunists, feeding on items that give highest rate of return when foraging costs are increased and becoming more selective when resources are abundant (Brown *et al.*, 1979; Kotler and Brown, 1988). Despite these foraging strategies, such drastic land conversions and the sporadic nature of forage availability could have caused a reduction in colony sizes. Decline in densities post-harvest has been reported in earlier studies (Mills *et al.*, 1991). The study site also has other rodent species that are primarily nocturnal and solitary and changes in the ecology of these competitive species could also have caused a change in jird colony size. This provides one explanation for smaller colony sizes but will apply only to those in agriculture. From the young to female adult ratio discussed earlier, this could mean that since natural areas have higher recruitment, colonies in Home's study expectedly had 2.63 times higher recruitment than now, since most of the area covered in that study are now under agriculture. It is likely that rainfall bears a negative relationship with colony size but has caused higher densities of colonies (Utrera et al., 2000). However, this is not conclusive as densities were not estimated in the current study.

The minimum population size was found to be 2 individuals in 2 colonies, each having 1 male and 1 female individual. These could be mating pairs or individuals establishing a new colony. Since Jirds are social, colonial animals, they are likely to benefit if they belong to a colony with enough individuals such that vigilance is enhanced, predation risk reduced and foraging more efficient. This has been demonstrated and tested under vigilance hypotheses across taxa, including desert rodents (Roberts, 1996; Tchabovsky *et al.*, 2001). Therefore, these 2 colonies might have been trapped when the colony was being established as they also had least number of holes.

Developing indices for abundance estimates have proved useful in monitoring change over time, particularly for endangered and cryptic species, being cost effective and practical (Jhala *et al.*, 2011). From this study, we find that number of holes predicts population size with significant accuracy as compared to length and width of the colony. This index can be used for further investigation and also for rapid assessments of the population status of this species, considering very little is known about them.

Variation in body weight among conspecifics has been recorded in rodents and causes for this variation have been explored by many. For example, individuals of some species, born in late summer can remain immature over winter (Hansson, 1990; Lidicker, 1979). The Chitty effect (Chitty, 1967; Hansson, 1992; Krebs, 1996) suggests that small rodent weight is a genetically determined characteristic, also influenced by nutrition and this has been tested in a few species. While comparing land uses and their effects on species ecology, body size is often tested as one of the variables (Nupp and Swihart, 2000). This study shows that body weight of adult and sub-adult females is significantly higher in natural areas than in agriculture-dominated landscape. While trapping, some young individuals/juveniles (not sub adults) were caught but not marked, and young were also seen during the behavioural observations. Since resource requirements are higher for adult females with young, this combined with the stability of natural areas as opposed to the stochasticity of the agricultural area discussed earlier, might explain the greater body weights in natural areas.

Hind limb lengths and ratios of other morphometrics have often been used to explain escape speed and dispersal abilities especially in many lizards and mammals (Calsbeek and Irschick, 2007; Garland and Janis, 1993; Phillips *et al.*, 2006). A difference in hind limb lengths between adult females in agriculture and natural areas, also sub-adult females and males, is intriguing. Since we do not know the social system governing this species, we cannot be sure that only sub-adult males disperse, as is the case amongst most other mammals. Female-biased dispersal is usually associated with monogamous systems with many examples among birds (Favre *et al.*, 1997). Evidence from studies in 2 species of rodents show heavy female-biased dispersal (Favre *et al.*, 1997; Ribble, 1992) but both these species are known to be monogamous. Nunes *et al.* (1997) found female-biased dispersal in a group-living diurnal rodent, Belding's ground squirrel, and propose that juvenile females may emigrate from the natal site to increase access to areas with lower densities of conspecifics. Since agriculture is a fairly recent affair, it is unlikely that the species has adapted to the change so quickly. However, this characteristic is primarily genetically controlled, but is also enhanced by nutrition. Therefore, individuals in natural areas, having larger body weight, which is often used as a surrogate for body size, are likely to have longer hind limbs.

5.2. Habitat use

Factors in the surrounding habitat play important roles in the ecology of a species, some more influential than others. Animals occupy a certain habitat for its high energy return rate and low risk of predation among other factors. Loosely translated, these are food, cover, shelter and so on. In order to survive, they must make the most of that available, or take a risk, leave the refuge and search for better habitat. Substrates including soil type, vegetation aspects like composition and percent ground cover characterize a desert rodent's world and these animals are known to experience striking changes with respect to microclimate, predatory risk, resource availability and substrate (Kotler and Brown, 1988). This study tried to identify which factors in the environment are likely to influence occurrence of Jirds and the model that best answers this includes soil parameters, vegetation structure, and a measure of anthropogenic activity.

The Indian desert jird, like many other semi-fossorial mammals, digs burrows and actively maintains them. Burrows act as refuges, larders and heat sinks (Kinlaw, 1999). Soil is a dense and cohesive medium and burrowing is definitely energetically expensive, a necessary evil. Costs of burrowing have been shown to vary with soil types such as clay, loam, sand, etc (Fisher and Anthony, 1980; Massawe *et al.*, 2008), and these are far higher than costs of locomotion on the surface (Liu *et al.*, 2007; Vleck, 1979). Some species have been found to avoid stony substratum (Rhodes and Richmond, 1985), some prefer loose clay mixed with rocks (Shenbrot *et al.*, 1997) while some others prefer a certain amount of sand (Feldhamer, 1979). Depending on soil type, burrowing can require 300-3400 times as much energy as moving the same distance above ground (Vleck, 1979). Other soil parameters like moisture and temperature are also known to influence occurrence of fossorial rodents (Collis-George, 1959; Rhodes and Richmond, 1985).

In the current study, soil type was recorded and classified into 4 types, out of which, clay and coarse soil significantly explained occurrence of jirds but also acted antagonistically. Clay positively influenced the occurrence of jirds while coarser the soil, lesser was the chance of occurrence. Frequency of occurrence of different vegetation height classes was recorded, with 0-10cm class likely to be the main food source and higher classes contributing to cover. Depending on the species life history, some were found to prefer dense vegetation (Nel, 1978), some open areas (Shenbrot *et al.*, 1997). From the univariate logistic regression, vegetation height classes of 0-10cm and 10-25cm were significant, although selected but not statistically significant in the full model. This is probably an artifact of multicollinearity. The lower height class could be considered their major food source, while 10-25cm vegetation height class likely provides cover, both vital for survival. One category of broad habitat type, namely agriculture field, was the only other variable explaining a significant amount of information in the model. This means that in an agriculture field, there was greater chance of jird occurrence. Ploughed and fallow fields were grouped under this category for the analysis. Ploughed fields recorded all absences, obviously. The number of occupied sites was very few in comparison with unoccupied sites and therefore data from both study sites were combined. However, the natural area recorded only 4 occupied sites and 71 unoccupied. The other 13 sites with jird presence were in the agriculture area. This questions the contribution of the variable in explaining occurrence of jirds. Also, clay content is generally higher in fields in dry areas, as clay holds soil better. This could cause an autocorrelation between 'field' and 'clay'.

Agricultural farming is known to have direct impacts on species decline through habitat destruction, at the same time acting as centres of food, especially for rodents. However, it is also known to allow behavioural modifications of indigenous species and even changing the predator-prey natural balance (Jacob, 2008; Shapira et al., 2008). Studies on rodent ecology in agricultural matrices indicate occurrence of seasonal dispersal of animals to hedgerows or bunds between fields, from where recolonisation takes place (Ouin et al., 2000). In the current study, jird colonies in agriculture were found to undergo changes in the number of holes over time as compared to natural areas. Similar habitat data collected after 30 days in each site showed that 7 colonies in agriculture had an increase or decrease in number of holes while only 2 colonies in the natural area showed a change in number of holes. Therefore, the proportion of occupied sites in agriculture can be an artifact of frequent shifts in colonies and colonies persisting even after being vacated by jirds. It is also indicative that colony-shifting occurs more often in agricultural areas than in natural ones, a likely cause being the fluctuation in available food resource in agricultural areas.

The landscape is fast turning into an agriculture-dotted matrix, with mining explorations also simultaneously taking place. When the fields are ploughed, what happens to these burrowing animals? Do they detect early and shift colony or are they killed? More extensive surveys, temporally and spatially, will help provide a better understanding of factors that might influence occurrence of jirds.

5.3. Behaviour

The concept that animals make decisions about foraging behaviour in a way that leads to long-term fitness has generated much debate and formed the basis of optimal foraging theory (Pyke, 1984; Stephens and Krebs, 1986). One out of 4 aspects of optimal feeding strategies includes optimal feeding period where the basic components are metabolic costs of activity under varying food, climatic and predator conditions (Schoener, 1971). Trade-offs between foraging and vigilance are made differently depending on seasonal variability in nutritional status, requirements and forage availability (Brown *et al.*, 1988) and even this may change under predatory conditions (Kie, 1999). Many animals show bimodal feeding periods during summer and unimodal in winter as a response to the climate, avoiding the harshest periods of the day. Our study concurred with this and showed a clear difference of activity period between winter and summer, indicating that animals avoided the hottest parts of the day by moving underground and ceased activity above ground soon after sunset.

Many studies have investigated optimal foraging strategies and variations in activity periods with particular reference to predation risk (Dall *et al.*, 2001; Lima and Dill, 1990). In our study area, known predators of jirds and gerbils are Indian fox, jungle cat, raptors, golden jackal and snakes, each with varying activity peaks and different methods of capturing prey. While foxes have been observed to dig and modify jird colonies for denning (Maurya, pers. comm.), snakes can move through their colonies. Western black cobra (*Naja oxiana*) and black-headed royal snake (*Spalerosophis atriceps*) were observed on many occasions creating a furore among the jirds during our study. Individuals drummed the ground with either hind feet or both, sometimes 2 individuals taking turns. This behaviour has been reported earlier (see (Prakash, 1981) as an alarm call when raptors were detected by jirds. Variations of this behaviour were observed, suggesting that jirds have a diverse array of signals for different threats and for varying intensities of threat. In the presence of snakes, instead of taking refuge, individuals even moved towards the predator on 1 occasion and drummed. This has also been observed in kangaroo rats (*Dipodomys* spp.) (Randall and Boltas King, 2001). On most occasions, only 1-2 individuals remained above ground, while the rest ran into the nearest hole. Prakash (1981) reports that individuals below ground also thump the ground. Drumming can communicate messages of territorial ownership, competitive superiority, readiness to mate and presence of predators and foot drumming patterns are known to be species specific, ranging from single thumps to individual foot drum signatures (Randall, 2001). The behaviour has been most extensively studied in kangaroo rats but still requires further understanding of the context in which the signals are generated. Much has been investigated on this front in solitary species, while social species might be limited to drum only in predation risk situations (Randall, 2001; Randall *et al.*, 2000).

The more common vigilance behaviour was demonstrated when an individual stood still in a fully erect posture, mostly perpendicular to the ground, similar to vigilance exhibited by ground squirrels. This state has been classified as a high-cost, high-quality overt vigilant posture (Lima and Bednekoff, 1999; Tchabovsky *et al.*, 2001). However, vigilance is also expressed in less-expressive bi-pedal semi-upright postures and horizontal quadrupedal postures (Arenz and Leger, 1999). In our study, behavioural state was recorded as vigilant only in bi-pedal and upright and semi-upright postures. When on all 4 limbs, it was difficult to differentiate whether the animal was resting or vigilant. Apparently vigilant animals do not always show scanning movements of the head and a resting individual can still survey its surroundings, unless its eyes are closed. Many animals including gerbils can do this while handling or chewing food, therefore the level of alertness may be misinterpreted (Tchabovsky *et al.*, 2001). Hence, motionless quadrupedal behavioural states, when not handling food, were grouped under 'resting'. It is also probable, however unlikely, that as day temperatures increased, individuals stood on 2 feet as a thermoregulatory adaptation.

The interplay between foraging and vigilance suggest the existence of a trade-off that is the central theme of all optimality theories and with further exploration, this can be drawn out. Vigilance peaks coincided with activity periods of raptors and it is possible that individuals were overtly vigilant in an attempt to detect these aerial predators. Since quadrupedal vigilance was not easily perceivable, it should not be concluded that jirds sense terrestrial predators any lesser. They could use olfactory and tactile receptions to detect predators. This however requires further examination.

Scent-marking was also observed a few times during the study and is evident when the animal moves from hole to hole along the edge of the colony, rubbing the ventral portion of the body on the ground/grass/twigs near the hole. Since individuals were not marked, it was difficult to distinguish between males and females as both sexes are reported to perform this behaviour (Prakash, 1981). Individuals were not perturbed by doves feeding alongside them during early hours of the day. This is in concurrence with Prakash (1981) but in our study, jirds were intolerant of babblers, stonechats, and bulbuls. Babblers were chased on many occasions, and individuals were vigilant in the presence of other birds.

This study provides baseline information on population sizes, habitat influences and behavioural patterns of the Indian desert jird, thus extending a platform to challenge, test and understand the myriad mechanisms underlying desert ecology. It also delivers insight at a trophic level which can influence both higher and lower levels, in this case predators such as foxes and raptors, and prey including vegetation. Impacts of the dramatic change in land use have not yet been studied and rodents are prospective subjects for examining this, which will be pertinent in the conservation of predators whose role in an ecosystem cannot be undermined.

6. Conclusion

The results from this study shows that population sizes of jirds vary from 2 to 10 individuals per colony, using closed population estimators. Pooling all colonies and indicating each colony as a grouping variable allows handling of small sample sizes. The development of an index for estimating population size, crucial for rapid assessments, is a methodological advancement and the study suggests that number of holes in a colony can predict the population size of that colony with good accuracy. This will allow a rapid assessment of the population status of jirds in the region, information of economic significance. Also, adult females weighed significantly more in natural areas than in agriculture, and this is also reflected in the higher young to adult female ratio in natural area, thus showing that natural areas are better habitats.

The study also shows that occurrence of jirds was higher in agricultural fields indicating that this land use type could provide favourable habitat for jirds. However, the total number of sites unoccupied (142) was proportionately greater when compared to those occupied (17) by jirds. Also, shifting of colonies might be more prevalent in agriculture than in natural areas because of fluctuating food resources and remnants of abandoned colonies might have influenced the higher number of 'occurrences' in agriculture. Therefore, this aspect of jird-habitat relationship requires a more extensive survey, spatially and temporally.

Activity patterns and time budgets are concordant in that irrespective of season and site, individuals spent a major proportion of active time foraging. Vigilance was higher when foraging activities were at a low, particularly in the afternoon and evening. This is supported by the general theory of hurried eating at the start, progressively becoming satiated and allowing more time for other activities later in the day. The trade-off between vigilance and foraging, both very vital to the survival of individuals is tremendous opportunity for testing the optimal foraging theory in field conditions.

a.

b.

c.

d.

e.

f.

Plate 1. Photographs from Kachchh, Gujarat; from a-f: Sherman traps at colony in agriculture, jird going towards trap, elevated hide for behavioural observation, one of the vigilance postures of jirds, cattle and sheep, agricultural field

7. Appendix

Classification of jird behaviour for the current study, under group heads:

Foraging:

Eating – movement of limb to mouth, followed by chewing; head down, the mouth, if seen, is open and animal is chewing

Moving – slow movement of head/body/both, in search of something to eat and the mouth, if seen, is closed and the animal is not chewing

Running – fast saltatory movement across the colony, to and from a hole, with or without food in limb or mouth

Climbing – animal climbs vegetation and either takes a part of it and climbs/jumps/falls down, or eats the food item on the vegetation itself

Vigilance:

Standing – standing on hind limbs, forelimbs extended from the body or not, looking steadily in one direction

Drumming – thumping the ground with one or both hind limbs, forelimbs on or off the ground, looking steadily in one direction

Digging – using 1 or more limbs and /or mouth to excavate soil at any hole in the colony

Resting – sitting on all 4 limbs, no movement of head/body, animal may be scanning for predators or simply resting

Maintenance:

Grooming – scratching or biting any part of body of self, with 1 or more limbs

Interaction – contact with 1 or more individuals; includes allogrooming, displaying aggression, probable mating

Rubbing – stretching the ventral portion of the body over the ground/on twigs/grass; animal may be scent-marking

8. References

Anderson DR, Burnham KP, White GC, Otis DL, 1983. Density Estimation of Small-Mammal Populations Using a Trapping Web and Distance Sampling Methods. Ecology 64:674-680.

Arenz CL, Leger DW, 1999. Thirteen lined Ground Squirrel (Sciuridae: Spermophilus tridecemlineatus) Antipredator Vigilance: Monitoring the Sky for Aerial Predators. Ethology 105:807-816.

Barnard CJ, 1983. Animal behaviour: ecology and evolution. Beckenham, Kent: Crook Helm Ltd.

Bowers MA, 1995. Use of Space and Habitats by the Eastern Chipmunk, Tamias striatus. Journal of Mammalogy 76:12-21.

Bowers MA, Jefferson JL, Kuebler MG, 1993. Variation in Giving-Up Densities of Foraging Chipmunks (Tamias striatus) and Squirrels (Sciurus carolinensis). Oikos 66:229-236.

Brown JH, Ernest SKM, 2002. Rain and Rodents: Complex Dynamics of Desert Consumers. BioScience 52:979-987.

Brown JH, Heske EJ, 1990. Temporal changes in a Chihuahuan Desert rodent community. Oikos 59:290-302.

Brown JH, Reichman OJ, Davidson DW, 1979. Granivory in Desert Ecosystems. Annual Review of Ecology and Systematics 10:201-227.

Brown JS, Kotler BP, 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999-1014. doi: 10.1111/j.1461-0248.2004.00661.x.

Brown JS, Kotler BP, Smith RJ, Wirtz WO, 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76:408-415.

Burnham KP, Anderson DR, 2002. Model selection and multimodel inference: a practical information-theoretic approach: Springer Verlag.

Calsbeek R, Irschick DJ, 2007. The Quick and the Dead: Correlational Selection on Morphology, Performance, and Habitat use in Island Lizards. Evolution 61:2493-2503.

Champion HG, Seth SK, 1968. A revised survey of forest types of India. Delhi: Government of India publications.

Charnov LE, 1976. Optimal foraging theory: the marginal value theorem. Theoretical Population Biology 9:129-136.

Chitty D, 1967. The natural selection of self-regulatory behaviour in animal population. Proc Ecol Soc Aust 2:51-78.

Collis-George N, 1959. The physical environment of soil animals. Ecology 40:550-557.

Dall XRS, Kotler BP, Bouskil A, 2001. Attention, 'apprehension' and gerbils searching in patches. Ann Zool Fennici 38:15-23.

Ebensperger LA, 2001. A review of the evolutionary causes of rodent group-living. Acta Theriologica 46:115-144.

Ebensperger LA, Chesh AS, Castro RA, Tolhuysen LO, Quirici V, Burger JR, Hayes LD, 2009. Instability rules social groups in the communal breeder rodent Octodon degus. Ethology 115:540-554.

Fagerstrom T, Moreno J, Carlson A, 1983. Load size and energy delivery in birds feeding nestlings: constraints on and alternatives to energy-maximization. Oecologia 56:93-98.

Favre L, Balloux F, Goudet J, Perrin N, 1997. Female-biased dispersal in the monogamous mammal Crocidura russula: evidence from field data and microsatellite patterns. Proceedings of the Royal Society of London Series B: Biological Sciences 264:127-132.

Feldhamer GA, 1979. Vegetative and edaphic factors affecting abundance and distribution of small mammals in southeast Oregon. Western North American Naturalist 39:207-218.

Fisher AR, Anthony RG, 1980. The effect of soil texture on distribution of pine voles in Pennsylvania orchards. American Midland Naturalist 104:39-46.

Fleming HT, 1979. Life-history strategies. In: Stoddart MD, editor. Ecology of small mammals London: Chapman and Hall. p. 1-61.

Garland T, Janis CM, 1993. Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? Journal of Zoology 229:133-151.

Goyal SP, 1988. Field urine concentration of two Indian desert gerbils. Journal of Mammalogy 69:418-421.

Graham MH, 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84:2809-2815. doi: doi:10.1890/02-3114.

Hansson L, 1990. Ultimate factors in the winter weight depression of small mammals. Mammalia 54:397-404.

Hansson L, 1992. Fitness and Life History Correlates of Weight Variations in Small Mammals. Oikos 64:479-484.

Author. 2001. NCSS and PASS. . Kaysville.

Home C, 2005. Masters thesis: Resource utilization and parental investment in the Indian fox (Vulpes bengalensis) in Kutch, Gujarat: Saurashtra.

Idris M, Prakash I, 1985. Social and scent marking behaviour in Indian gerbil, Tatera tatera. Biological Behaviour:31-39

Jacob J, 2008. Response of small rodents to manipulations of vegetation height in agro ecosystems. Integrative Zoology 3:3-10.

Jhala Y, Qureshi Q, Gopal R, 2011. Can the abundance of tigers be assessed from their signs? Journal of Applied Ecology 48:14-24. doi: 10.1111/j.1365-2664.2010.01901.x.

Kamil AC, Krebs JR, Pulliam HR, 1987. Foraging behavior: Plenium Press / Plenum: New York, NY (USA).

Kie GJ, 1999. Optimal foraging and risk of predation: effects of behaviour and social structure in Ungulates. Journal of Mammalogy 80:1114-1129.

Kinlaw A, 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. Journal of Arid Environments 41:127-145.

Kotler PB, Brown SJ, 1988. Environmental heterogenieity and coexistence of desert rodents. Annual Review of Ecology and Systematics 19:281-307.

Krebs CJ, 1989. Ecological methodology: Harper & Row New York.

Krebs CJ, 1996. Population cycles revisited. Journal of Mammalogy 77:8-24.

Krebs CJ, 1998. Whither small rodent population studies? Researches on Population Ecology 40:123-125.

Lidicker WZ, 1979. Analysis of two freely-growing enclosed populations of the California vole. Journal of Mammalogy 60:447-466.

Lima SL, Bednekoff PA, 1999. Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? Animal Behaviour 58:537-543.

Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Liu W, Wan X, Zhong W, 2007. Population dynamics of the Mongolian gerbils: Seasonal patterns and interactions among density, reproduction and climate. Journal of Arid Environments 68:383-397. doi: 10.1016/j.jaridenv.2006.07.002.

Lott DF, 1991. Intraspecific variation in the social systems of wild vertebrates: Cambridge University Press.

Massawe AW, Rwamugira W, Leirs H, Makundi RH, Mulungu L, Ngowo V, Machang'u R, 2008. Soil type limits population abundance of rodents in crop fields: case study of the multimammate rat Mastomys natalensis Smith, 1834 in Tanzania. Integrative Zoology 3:27-30.

Mills JN, Ellis BA, McKee KT, Maiztegui JI, Childs JE, 1991. Habitat Associations and Relative Densities of Rodent Populations in Cultivated Areas of Central Argentina. Journal of Mammalogy 72:470-479.

Neff DJ, 1968. The pellet-group count technique for big game trend, census, and distribution: a review. The Journal of Wildlife Management 32:597-614.

Nel J, 1978. Habitat heterogeneity and changes in small mammal community structure and resource utilization in the southern Kalahari. Bull Carnegie Mus Nat Hist 6:188-131.

Nunes S, Zugger PA, Engh AL, Reinhart KO, Holekamp KE, 1997. Why Do Female Belding's Ground Squirrels Disperse Away from Food Resources? Behavioral Ecology and Sociobiology 40:199-207.

Nupp TE, Swihart RK, 2000. Landscape-Level Correlates of Small-Mammal Assemblages in Forest Fragments of Farmland. Journal of Mammalogy 81:512-526.

Otis DL, Burnham KP, White GC, Anderson DP, 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs.

Ouin A, Paillat G, Butet A, Burel F, 2000. Spatial dynamics of wood mouse (Apodemus sylvaticus) in an agricultural landscape under intensive use in the Mont Saint Michel Bay (France). Agriculture, ecosystems & environment 78:159-165.

Phillips BL, Brown GP, Webb JK, Shine R, 2006. Invasion and the evolution of speed in toads. Nature 439.

Pocock MJO, Searle JB, White PCL, 2004. Adaptations of Animals to Comnensal Habitats: Population Dynamics of House Mice Mus musculus domesticus on Farms. Journal of Animal Ecology 73:878-888.

Prakash I, 1981. Ecology of the Indian desert gerbil, Meriones hurrianae. CAZRI Monograph.

Pyke HG, 1984. Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics 15:523-575.

Randall JA, 1994. Environmental constraints and the evolution of sociality in semi-fossorial desert rodents. In: Wolff JO, Sherman PW, editors. Rodent societies: an ecological & evolutionary perspective. p. 368.

Randall JA, 2001. Evolution and function of drumming as communication in mammals. American Zoologist 41:1143.

Randall JA, Boltas King DK, 2001. Assessment and defence of solitary kangaroo rats under risk of predation by snakes. Animal Behaviour 61:579-587.

Randall JA, Rogovin K, Parker PG, Eimes JA, 2005. Flexible social structure of a desert rodent, Rhombomys opimus: philopatry, kinship, and ecological constraints. Behavioral Ecology 16.

Randall JA, Rogovin KA, Shier DM, 2000. Antipredator behavior of a social desert rodent: footdrumming and alarm calling in the great gerbil, Rhombomys opiums. Behavioral Ecology and Sociobiology 48:110-118.
Rhodes DH, Richmond ME, 1985. Influence of Soil Texture, Moisture and Temperature on Nest-site Selection and Burrowing by the Pine Vole, Microtus pinetorum. American Midland Naturalist 113:102-108.
Ribble DO, 1992. Dispersal in a Monogamous Rodent, Peromyscus Californicus. Ecology 73:859-866.
Robel RJ, Briggs JN, A.D.Dayton, Hulbert LC, 1970. Relationships Between Visual Obstruction Measurements and Weight of Grassland Vegetation. Journal of Range Management 23.
Roberts G, 1996. Why individual vigilance declines as group size increases. Animal Behaviour 51:1077-1086.
Rodgers WA, Panwar HS, 1988. Planning a protected area network in India. Dehradun: Wildlife Institute of India.
Schoener TW, 1971. Theory of Feeding Strategies. Annual Review of Ecology and Systematics 2:369-404.
Shapira I, Sultan H, Shanas U, 2008. Agricultural farming alters predator–prey interactions in nearby natural habitats. Animal Conservation 11:1-8.
Shenbrot G, Krasnov B, 2001. Rodents in desert environment: is density dynamics really correlated with annual rainfall fluctuations. Ecology of desert environments Festschrift for professor JL Cloudsley-Thompson Scientific Publishers, Jodhpur:405–421.
Shenbrot G, Krasnov B, Khokhlova I, 1997. Biology of Wagner's gerbil Gerbillus dasyurus (Wagner, 1842)(Rodentia: Gerbillidae) in the Negev Highlands, Israel. Mammalia 61:467-486.
Shenbrot GI, Krasnov, Boris R., Rogovin KA, 1999. Spatial ecology of desert rodent communities: Springer.
Sinhasane SV, Joshi NB, 1998. Impact of aggressive encounters on reproductive behaviour in the Indian desert gerbil, Meriones hurrianae (Jerdon). Journal of Biosciences 23:633-639.
Stephens DW, Krebs JR, 1986. Foraging Theory. Princeton, New Jersey: Princeton University Press.
Stoddart MD, editor 1979. Ecology of small mammals: Chapman and Hall.
Tchabovsky AV, Popov SV, Krasnov BR, 2001. Intra- and interspecific variation in vigilance and foraging of two gerbillid rodents, Rhombomys opimus andPsammomys obesus : the effect of social environment. Animal Behaviour 62:965-972. doi: DOI: 10.1006/anbe.2001.1833.
Treves A, 2000. Theory and method in studies of vigilance and aggregation. Animal Behaviour 60:711-722. doi: 10.1006/anbe.2000.1528.
Utrera A, Duno G, Ellis BA, Salas RA, Manzione Nd, Fulhorst CF, Tesh RB, Mills JN, 2000. Small Mammals in Agricultural Areas of the Western Llanos of Venezuela: Community Structure, Habitat Associations, and Relative Densities. Journal of Mammalogy 81:536-548.
Vleck D, 1979. The Energy Cost of Burrowing by the Pocket Gopher Thomomys bottae. Physiological Zoology 52:122-136.
Whisson DA, Engeman RM, Collins K, 2005. Developing relative abundance techniques (RATs) for monitoring rodent populations. Wildlife Research 32:239-244.

White GC, Burnham KP, 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study Supplement 46:120-138.
Wiens JA, 1976. Population Responses to Patchy Environments. Annual Review of Ecology and Systematics 7:81-120.
Zar JH, 1999. Biostatistical analysis.