# Habitat Relationships and Resource Partitioning in a Lizard Community of the Thar Desert

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# Certificate

This is to certify that Mr. Ishan Agarwal, student of the Wildlife Institute of India has carried out original research titled **"Habitat Relationships and Resource Partitioning in a Lizard Community of the Thar Desert"** for the partial fulfillment of the M.Sc. (Wildlife Science) degree from Saurashtra University, Rajkot, India. These investigations were carried out under our supervision from November 2006 to June 2007. We also certify that this research has not been submitted for any other degree to any university.

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**SUMMARY**

A lizard community in the Thar Desert was studied in relation to habitat relationships, resource partitioning and community niche patterns. The study was carried out in parts of the Desert National Park, Jaisalmer District, Rajasthan. Stratified sampling was used, and 12 one hectare grids, with 16 25m X 25m subplots each, were sampled in summer. Four habitat types were recognized, barren dunes, stabilized dunes, grassland and rocky hills. A visual encounter survey was used to sample lizards within grids. Seven synthetic variables from a principal components analysis describing soil and vegetation structure were used to analyze relationships among lizard species.

A total of 14 species of five lizard families were observed during the study. Winter activity was considerably lower than summer. 1039 sightings of 12 species were recorded in summer sampling, and results are based on summer data. Seven species were restricted to a single habitat type, and four species were found in all habitat types. The stabilized dunes had highest abundance of lizards, followed by grassland. Barren dunes and rocky hills had the lowest abundances of lizards. Species richness and diversity (Shannon's index) was highest in the rocky hills, followed by barren dunes, grassland, and finally stabilized dunes. *Tropiocolotes persicus euphorbiacola* is a new record for India, *Hemidactylus persicus* a new record for Rajasthan.

Logistic regression was used to identify determinants of species presence. Two to three factors determined presence for most species. Substrate was the main gradient to which species and the community as a whole responded, with two distinct groups, psammophiles and sclerophiles.

Spatial overlap was low among most species pairs, and the spatial organization of the community appears well structured, with partitioning at different scales between sympatric species.

Canonical correspondence analysis was used to examine community patterns and quantify niche measures including breadth and position. Niche overlap along the first two canonical axes was high for sclerophilous and psammophilous species separately. There was a strong negative correlation between niche breadth and position, and strong positive correlation between abundance and occupancy. Niche breadth did not have strong correlations with abundance, occupancy, or body size. Niche position was weakly negatively correlated with body size, occupancy.

# 1. INTRODUCTION

## 1.1 The Desert Ecosystem

Desert ecosystems are characterized by extreme conditions with highly patchy and temporally variable resources. These systems are fragile and highly vulnerable to change. Immense anthropogenic pressures on the Thar in the form of grazing, irrigation projects and mining are drastically altering the distinctive desert landscape (Prakash 2001). True desert species are closely bound with their habitats and are extremely susceptible to change (e.g. Hawlena and Bouskila 2006). Studies on various faunal groups have found replacement of desert species by generalist species (e.g. Prakash 2001; Hawlena and Bouskila 2006).

Any conservation efforts in such a biologically irreplaceable and fragile landscape must be based on knowledge of the ecology of desert organisms (Hawlena and Bouskila 2006). It is vital to understand the relationships and dynamics of this unique assemblage in the wake of imminent change, so that conservation efforts can be prioritised. Accordingly, this study aims to investigate habitat use, and resource partitioning in a desert lizard community of the Thar, besides examination of general community and niche patterns.

## 1.2 Desert lizards

Desert lizards provide an excellent system in which to test habitat relationships, resource partitioning and more general ecological processes. This is due to three reasons, firstly that lizards are ectotherms and are thus physiologically (and behaviourally) constrained, and highly habitat specific (Pianka 1986). Secondly, the desert provides a simple system in which to validate or explore ecological questions and hypotheses (Pianka 1986; Kotler and Brown 1988). Third, lizards are relatively diverse, and easier to study than other reptiles such as snakes as they occur in relatively higher abundance and are easily detectable (Toft 1985).

The ecology and natural history of desert lizards have been studied across four continents – Africa, North America, Asia and Australia (e.g. Pianka 1986; Shenbrot *et al.* 1991; Shenbrot and Krasnov 1997). Inter-continental comparisons have provided insights into convergent evolution, and helped identify some of the factors responsible for the evolution and maintenance of high diversity, such as spatial and temporal heterogeneity, species-area relationships, and historical factors. (Pianka 1986; Colli *et al.* 2006).

**1.3 Lizards of the Thar Desert**

India has a diverse saurian fauna, with at least 190 species known from within its political boundaries (Das 1997). The main centres of lizard diversity in mainland India are the Western Ghats and Northeastern India; though the arid northwest is also species-rich. The affinities of this diverse assemblage are almost exclusively Palearctic (Afro-Mediterranean and Turkomanian-Central Asian), with a few Oriental genera (Tibeto-Yunnanese) (Das 1996).The saurian fauna of the Thar is unique within India, with very little overlap in species with other regions, apart from a few wide ranging species (Das 1996). Studies on lizards in the Thar Desert have been limited primarily to taxonomic and basic distributional studies (e.g. Sharma 1996, 2002) with only anecdotal natural history observations. Community studies of herpetofauna are rare in India and have been limited to areas with diverse assemblages such as the Western Ghats (e.g. Vasudevan *et al.* 2000;

Ishwar *et al.* 2003). Desert lizards provide a simple system with reasonable diversity to investigate patterns in communities and consequently inferences can be made more conclusively (Pianka 1986).

### 1.4 Habitat selection

Habitat is most basically defined as the place an animal inhabits. A more rigorous definition, that ties habitat with a particular species, is that it must possess a set of resources and environmental conditions that allow occupancy, survival and reproduction of that particular species (Morrison *et al.* 1992). This implies that habitat is species-specific; however terms such as habitat type are often used interchangeably with forest type, biotope or ecotope.

Habitat selection can be most easily defined as use of resources disproportionate to their availability. Habitat selection is assumed to operate in a hierarchical manner (Johnson 1980), and could hypothetically operate at four spatial levels: geographical range, macrohabitat, microhabitat and finally a specific resource or space within the microhabitat. Selection may be across habitats (i.e. based on broad differences in physiognomy) or within habitats (i.e. based on specific microhabitat cues, regardless of overall structure). Within the hierarchy of habitat selection is a complex interplay of historical factors, phylogeny, evolutionary and biological dynamics (Morrison *et al.* 1992; Buskirk and Millspaugh 2003). However, any current interpretations of habitat relationships are based largely on habitat attributes and extant faunal relationships. Habitat selection and use; and the specific attributes that determine species presence and abundance are highly species-specific and scale dependent. Studies aiming to determine habitat selection must have basic natural history data in order to select the scale of the study or patterns may be obscured.

Of the habitat attributes that contribute to general desert lizard diversity, structural complexity and spatial heterogeneity are the most important (Pianka 1967, 1986); while autoecological studies have demonstrated explicitly the habitat requirements of the focal species with regard to habitat structure and resources (e.g. Fisher *et al.* 2002).

Habitat use is one aspect of resource partitioning, relating to the spatial resource. Much of the current knowledge on resource partitioning comes from studies on herpetofauna (for a review see Toft 1985). Lizards, in particular highly speciose genera such as *Anolis* (e.g. Lister 1981) and *Ctenotus* (e.g. Pianka 1969) are among the most extensively studied groups.

**1.5 Resource partitioning**

Resource partitioning and niche partitioning are terms often used synonymously. An understanding of these requires a basic knowledge of what the niche of a species is. The niche can be broadly defined as the position and function of an organism in the environment (Smith 1990). A more useful working definition was that put forward by Hutchinson (1957). The fundamental niche is simply the set of environmental factors (abiotic and biotic) within which a species is able to survive, while the realized niche is that subset of the fundamental niche that a species is restricted to by other factors including competition, predation, or disturbance (Hutchinson 1957).

That two species with identical niches, or relying on the same resources cannot coexist was first spelt out in laboratory experiments by Gause (1934). Gause's exclusion principle is based on the premise that resources are limited, and communities, or more specifically sympatric species can only coexist through resource partitioning (Schoener 1974). It is understood that most natural communities demonstrate resource partitioning to at least some extent (Schoener 1974). Besides competition for resources, other factors such as differential predation risk and adaptation to certain microhabitats or resources may drive resource partitioning among species. This spacing out of niches along a particular axis is related to the realized niche (Hutchinson 1957); in that species with similar fundamental niches (for example, closely related species of a genus) may each be restricted to different realized niches when in sympatry.

All measurements of the niche are only approximate, estimating a multidimensional hypervolume (Hutchinson 1957) along some important dimensions; usually food, space and time. What is considered important for a species is biased by what can be measured, as well as our perception; and may not in fact be reflective of actual processes. Additionally, niches are often conserved, and the niche is thus a complex interplay of phylogenetically determined and derived evolutionary elements (Wiens and Graham 2005). Approximations of species niches have been facilitated with computerized methods. Recent studies on the niche have made explicit use of multivariate ordination methods that seek to approximate the multidimensional niche of a species with regard to a set of environmental variables (e.g. Dueser and Shugart 1979; Carnes and Slade 1982; Semenov *et al.* 2001). GIS (Geographical Information System) based techniques have made it possible to approximate the species niche in geographical space based on a set of geophysical variables (e.g. climate, altitude) and vegetation types (e.g. Stockwell and Peterson 1999; Hirzel *et al.* 2001; Phillips *et al.* 2006).

Studies on the niche and resource partitioning in sympatric desert lizards usually examine any or all of three major axes: space, food and time. These are further divided (after Schoener 1974; Toft 1985) into macro and microhabitat; food size and type; diel and seasonal activity. Spatial or habitat occupancy is measured at various scales ranging from geographic location to more detailed descriptors of microhabitat. Analyses of the dietary niche are usually made through gut content analysis (e.g. Huey and Pianka 1977; Dusen and Oz 2001) and more recently through faecal analysis (e.g. Rissing 1981; Hodar *et al.* 1996, 2006). Separation in time may be either within a day or across seasons. Toft (1985) mentions that variation in daily activity is the least important axis for lizards. It is unclear if temporal separation truly implies resource separation or merely lack of interference (Jaksi 1982). Additional aspects investigated include morphology (as a proxy for specialization for habitat use, foraging behaviour, prey selection; e.g. Pianka 1986; Schoener 1974; Vanhooydonck *et al.* 2000; Verwaijen *et al.* 2002), thermoregulatory behaviour (related to microhabitat use, diel activity pattern, physiological adaptations; Huey and Pianka 1977; Tracy and Christian 1986; Melville and Schulte 2001).

**1.6 General abundance and niche relationships**

An important generalization in ecology is the range-abundance theory (Brown 1984). This states that a wide-ranging species is likely to have greater abundance than a range-restricted species. Intuitively appealing, there are various mechanisms that may explain such patterns (Seagle and McCracken 1986).

Niche metrics are measures of a species niche that reflect its ecological characteristics in relation to the community. Niche position refers to the distance of a species centroid from the centroid of the community as a whole (Gregory and Gaston 2000). It reflects the marginality of the resources used by the species; a species whose niche position is low uses the resources most widely available in the community, while a species with high niche position uses atypical resources (Gregory and Gaston 2000). It follows, that if sampling of habitats is representative of the landscape, species occupying atypical habitats are specialists or range-restricted species. Niche breadth is a measure of the tolerance of a species to varying environmental conditions. Generalist species are likely to have high niche breadths and specialist species low niche breadths.

## 1.7 OBJECTIVES

**1. To identify the habitat attributes that determine lizard species presence**

**2. To identify patterns of resource partitioning among sympatric lizard species in different habitat types**

a) What are the patterns of resource partitioning between sympatric lizard species?

b) What is the degree of niche overlap between sympatric lizard species?

**3. To examine niche patterns within the lizard community, and its relationship with abundance and occupancy**

# 2. STUDY AREA

## 2.1 The Thar Desert

The Thar is one of the smallest deserts in the world (Islam and Rahmani 2005), with a geographical extent of about 1.3 million km$^2$ across western India and Pakistan; the area in India about 278,330 km$^2$ (Gupta 1986; Fig. 2.1 a). The boundaries of the Thar are the Aravallis in the east, Indus River and Nara Valley in the west; the salt flats of Kutch in the south and the flood plains of Punjab and Haryana (in India and Pakistan) in the north (Gupta 1986). The Thar Desert is of relatively recent origin, thought to have originated 5000 years ago (Gupta and Prakash 1975a). It has been variously considered to be of anthropogenic origin, though recent evidence based on the aeolian sedimentation record has confirmed this is not the case (Singhvi and Kar 2004).

The 3162 km$^2$ Desert National Park (DNP) in the Thar Desert, is spread across western parts of Jaisalmer and Barmer Districts (Fig. 2.1 b), and is pending final notification. To protect representative habitats within the DNP, the forest department set up and maintains several large exclosures to prevent grazing and other human pressures. The fauna of the Thar Desert includes species with palearctic, northwestern and oriental affinities (Minton 1966; Das 1996). Though there are only a few animals endemic to the Thar Desert – the Hairy-footed Gerbil *Gerbillus gleadowi*; the reptiles *Bufoniceps laungwalansis* (Laungwala Toad-headed Agama), *Lytorhynchus paradoxus* (Sindh Awl-headed Snake); and Stolickza's Bushchat *Saxicola macrorhyncha* approaches endemicity; many other species are represented in India from only this region (Corbett and Hill 1992; Das 1996; Grimmett *et al.* 1998; Whitaker and Captain 2004; Macey *et al.* 2006).

The northern part of the DNP and adjacent areas in Jaisalmer District was chosen as the study site, as it has landforms representative of the Thar Desert (Gupta and Prakash 1975b). Working in a protected area meant that anthropogenic disturbances were likely to be minimized. Fieldwork was based around Sam village for logistic reasons.

**2.2 Location, area and physical features:**

Jaisalmer District is the western-most district of Rajasthan, falling entirely within the bounds of the Thar Desert (Fig. 2.1). With an area of 38,401 $km^2$ this is the largest district in Rajasthan. Jaisalmer shares a border with Pakistan in the north and west, and is bound by Bikaner and Jodhpur districts in the east, Barmer in the south. Altitudes are low, ranging from 210-300m (320m) above mean sea level (Govt. of India, 1994). Kar (1989) classified the landforms in Jaisalmer into eleven terrain categories; the predominant forms being sand dunes (44.77% of the area), and flat buried pediments/pavements/structural plains (28.38 %). More ecologically relevant is the classification of natural desert habitats into sandy, gravelly, and rocky (Prakash 1962). Sandy areas dominate the western parts of Jaisalmer district, while gravelly and rocky areas are scattered throughout central and eastern areas.

The study area lies close to Sam Village (26.82757° N, 70.50554° E), in the western part of Jaisalmer District (Fig. 2.3). Sam is about 45 km southwest of Jaisalmer, close to the northern boundary of the DNP. Areas around Sam village include sand dunes, interdunal plains, gravelly pediments, rocky/gravelly pediments with isolated hills, and high level structural plains (Kar 1989). All these landforms are well represented in the northern part of the DNP except rocky areas. The two exclosures at Sam protect an area of about 1,100 ha (Islam and Rahmani 2001).

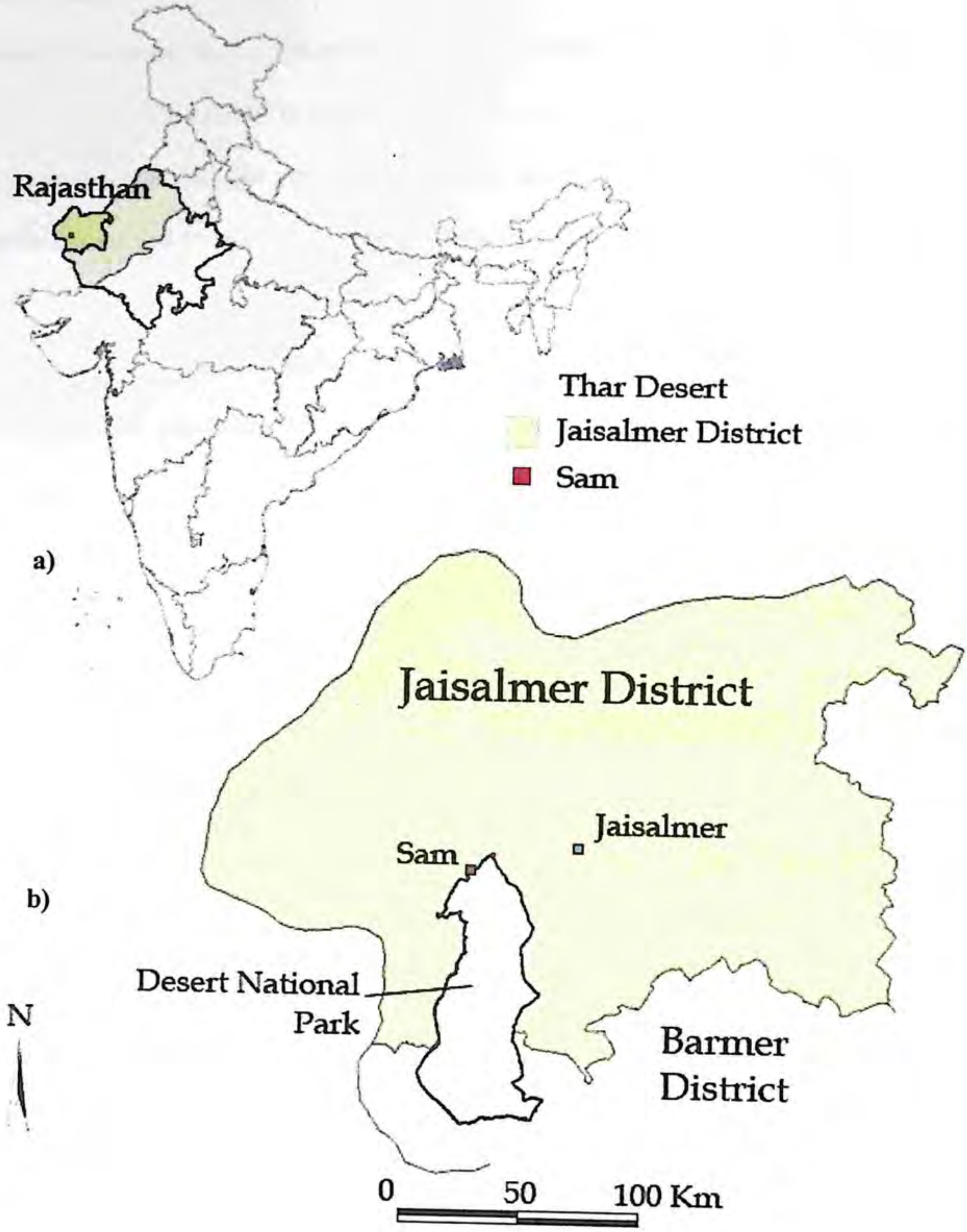


**Figure 2.1 a)** Location map of study area in India.
**b)** Jaisalmer District, with the outline of the DNP. The intensive study area was around Sam

## 2.3 Climate

*Rainfall*: Jaisalmer District has an average annual rainfall of 164 mm with 7.7 rainy days (Gupta 1986). The rainfall is very unpredictable, with very high variation from year to year and frequent drought years and occasional heavy rains. There is a distinct rainfall gradient from east to west, from about 200 mm to 100 mm in the west (Chaterji and Kar 1992).

*Temperature*: This area experiences a distinct winter and summer. Winter begins in November and continues till the end of February. Early March is transitional, and summer is from late March onward till the onset of the monsoon in July. The average temperatures during the study period range from a minimum of 7.9°C and maximum of 23.6°C in January, to a minimum of 25.8 °C and a maximum of 41.6°C in May (Meena 2000). Daily temperature variation is high throughout, about 15°C on average. Figure 2.2 shows temperature data from a Central Arid Zone Research Institute (C.A.Z.R.I.) field station about 55 km from the study area.

*Wind*: This region records the highest wind speeds in western Rajasthan (Chaterji and Kar 1992). Average wind speeds are light to moderate through winter (5.5 – 8.6 km/h), March and April have moderate average wind speeds of between 10.9 – 12.7 km/h that gradually build up to a peak in June with an average speed of 27.2 km/h (Sehgal, 1973).

*Clouds*: Winter skies are periodically overcast. In early summer (March-April) skies are generally clear except for occasional disturbances or dust storms, the frequency of which increase into May and June.

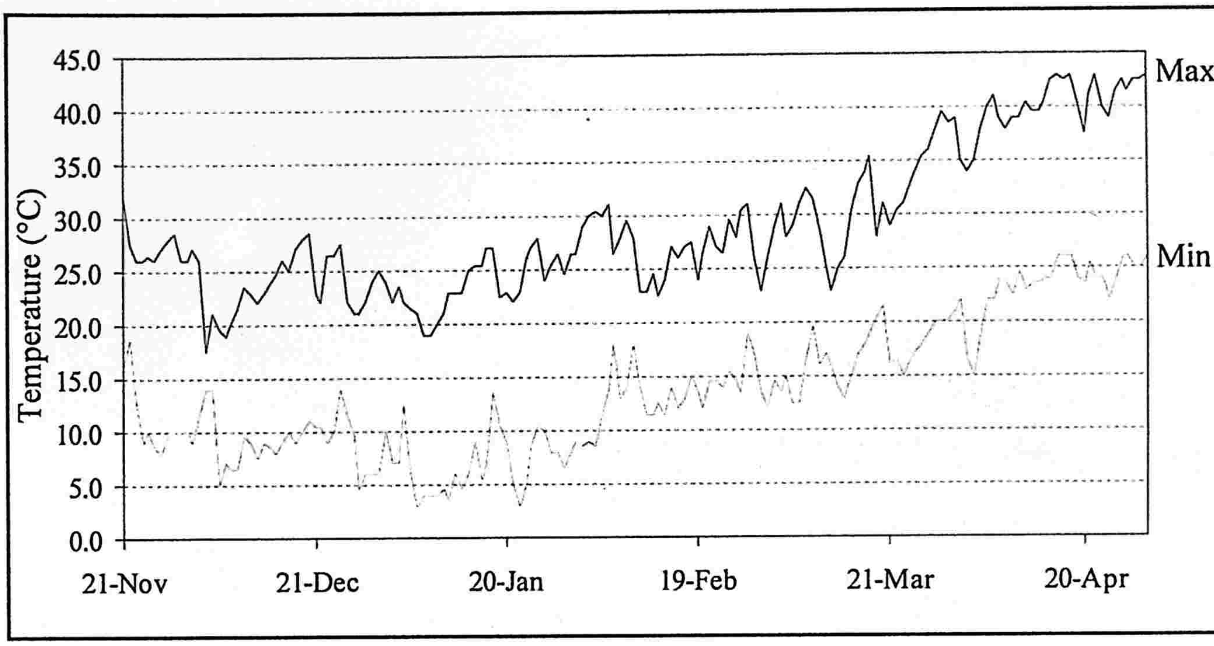


**Figure 2.2** Maximum and minimum temperatures during the study period

### 2.4 Intensive study area

The study area includes areas within the A and B exclosures at Sam (inside DNP), as well as the rocky ridge around Nabh Dongar (outside DNP; Figure 2.3). All sites are within a 20km radius of Sam, and the furthest two sites are 25 km apart, with a rectangular area of about 250 $km^2$. Within the study area, I recognized four main habitat types that were subsequently sampled: barren dunes, stabilized dunes, grasslands, and rocky hills. An additional habitat type that could not be sampled was rocky outcrops. Opportunistic observations indicate that these areas contain a subset of species from other habitats, depending on the surrounding soil type (sand or gravel).

Descriptions of each habitat given below are based on observations made in winter through summer and though there were rains every month from November to March, a large part of desert flora consists of annuals. Most of these would not have been present during the study period.

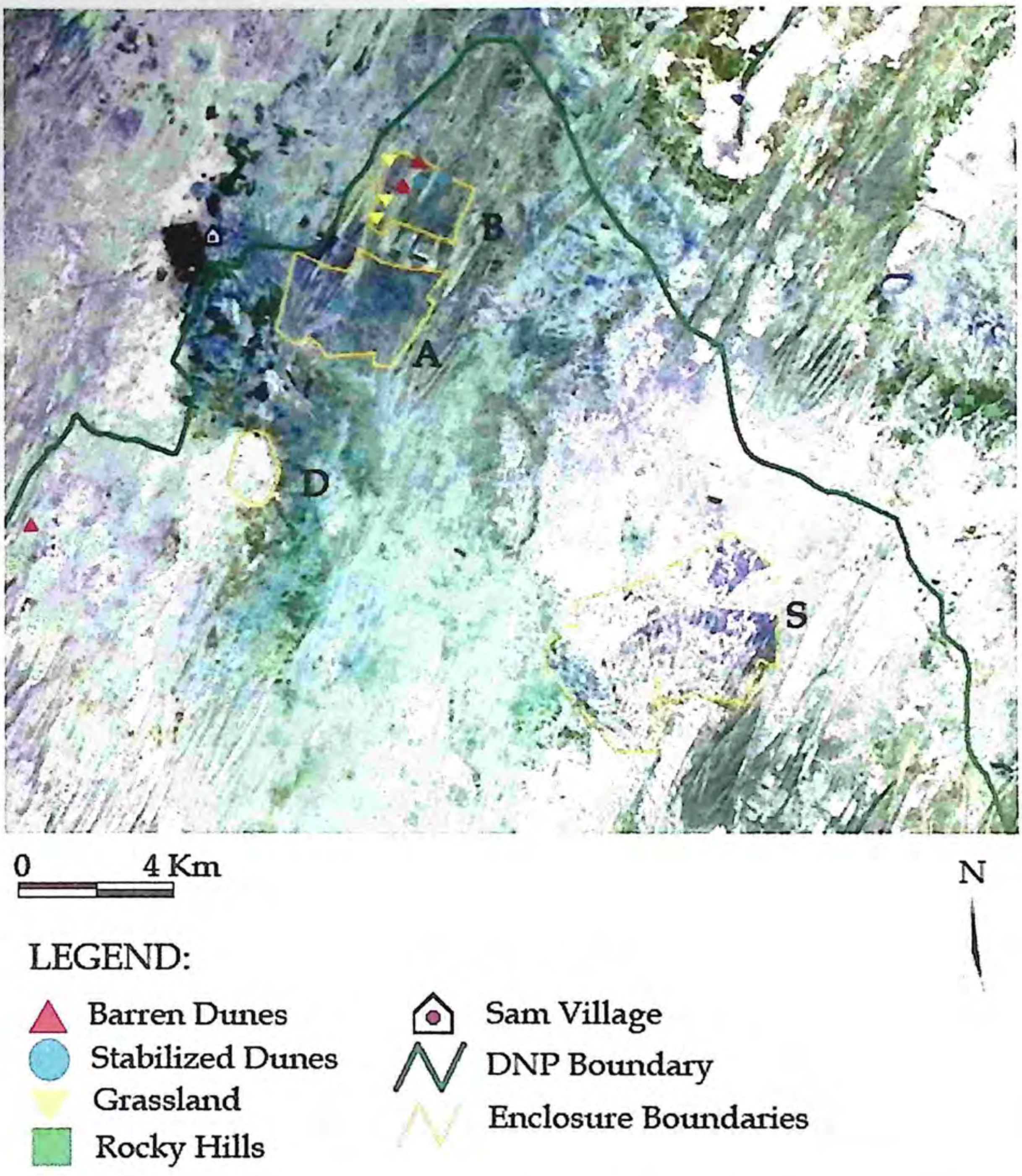


**Figure 2.3:** Map of intensive study area. The 12 one ha plots sampled in summer are shown, along with exclosures at Sam (A, B, D); and Sudasiri (S).

### 2.4.1 Barren dunes (BD)

Also known as shifting dunes, these mobile sand dunes are characterized by very low vegetation cover <2% (Fig 2.4). The soil is uniformly >95% sand, and very loose in all areas except interdune areas. I use the term interdunal areas to refer to hard depressions within the dune field. These are usually the only areas in this habitat with permanent vegetation, but may occasionally be barren. The sparsely distributed vegetation on the barren sand dunes consists mainly of the grass *Stipagrostis plumosa*; and scattered herbaceous growth of *Indigofera cordifolia, Cyperus* arenarius. Interdunal areas support more vegetation including the grass *Panicum turgidum* and shrubs *Aerva spp*., *Calligonum polygonoides*, *Crotolaria burhia*, *Fagonia cretica*, and *Haloxylon salicornium*. *Calatropis procera*, *Capparis decidua* and *Leptadeina pyrotechnica* may occasionally be found along the edges of dune fields. Rodent burrows and hummocks are mostly restricted to the vegetated interdunal areas and edges of dune fields. Though grazing is minimal in this habitat due to lack of fodder species, the vegetated interdunal areas are often grazed.

The shifting sand dunes in the Sam area can be classified according to shape and size into barchans and other minor sand streaks (2-6 m high), barchanoids (8-10 m) and megabarchanoids (15-40 m; Kar 1989). The dune fields around Sam are generally small, a few kilometers long and less than a kilometer wide; while further west are much larger dune fields.

### 2.4.2. Stabilized sand dunes (SD)

Also called vegetated dunes, these stationary undulating sand dunes are characterized by low vegetation cover (7-11%) and uniformly sandy (>95%), loose soil (Fig. 2.5). Dominant grasses include *Lasiurus sindicus*, *Cenchrus bifloris*, and *Panicum turgidum*. Shrubs include *Aerva spp*., *Calligonum polygonoides*, *Crotolaria burhia*, *Haloxylon salicornium*, *Indigofera cordifolia*. Trees are few and scattered; the only species present is *Capparis decidua*. This habitat has the highest number of rodent burrows, with extensive colonies of the Indian gerbil (M*erriones hurrianae*) reaching burrow (opening) densities of greater than 125/100$m^2$ (personal observation). Hummocks are a distinctive part of this habitat. Grazing pressures are high due to availability of palatable grasses such as *Lasiurus sindicus* and *Panicum turgidum*.

### 2.4.3 Grassland (GG)

Both grasslands with gravelly (up to 30% gravel) and sandy soil (up to 95% sand) were included under this category (Fig. 2.6). These were clubbed together because this combination occurs frequently in the areas between dune fields ("interdunal habitat" *sensu* Mukherjee 1999). Vegetation cover is moderate (31-50%) with high grass cover (up to 44%). The sandy areas are dominated by the grasses *Lasiuris sindicus* and *Cenchrus bifloris* and shrubs *Aerva spp*,.*Calligonum polygonoides*,,*Crotolaria burhia* and *Haloxylon salicornium*; while gravely areas are dominated by *Dactyloctenium scindicum*,

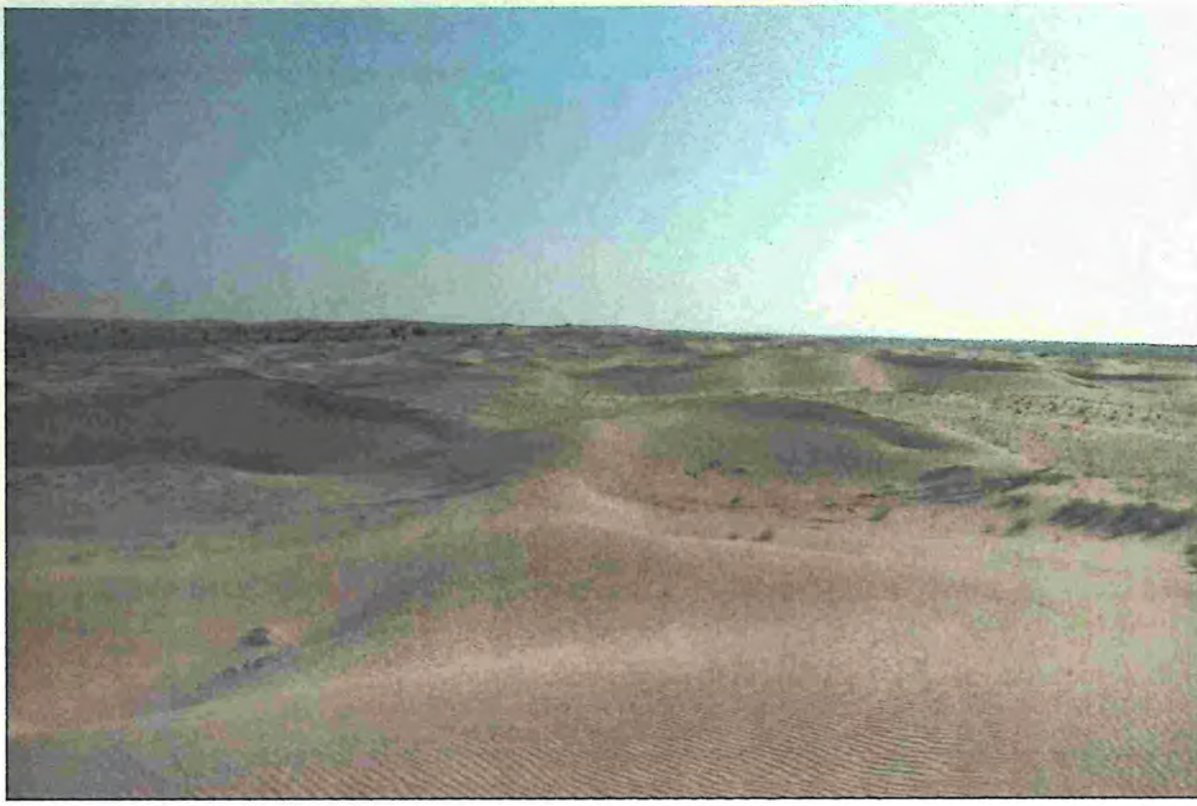

**Figure 2.4:** Typical barren dunes in the study area

**Figure 2.5:** The stabilized dune habitat

**Figure 2.6:** Grassland habitat. A gravely expanse is seen in the foreground, sandy areas behind. In the distance are barren dunes

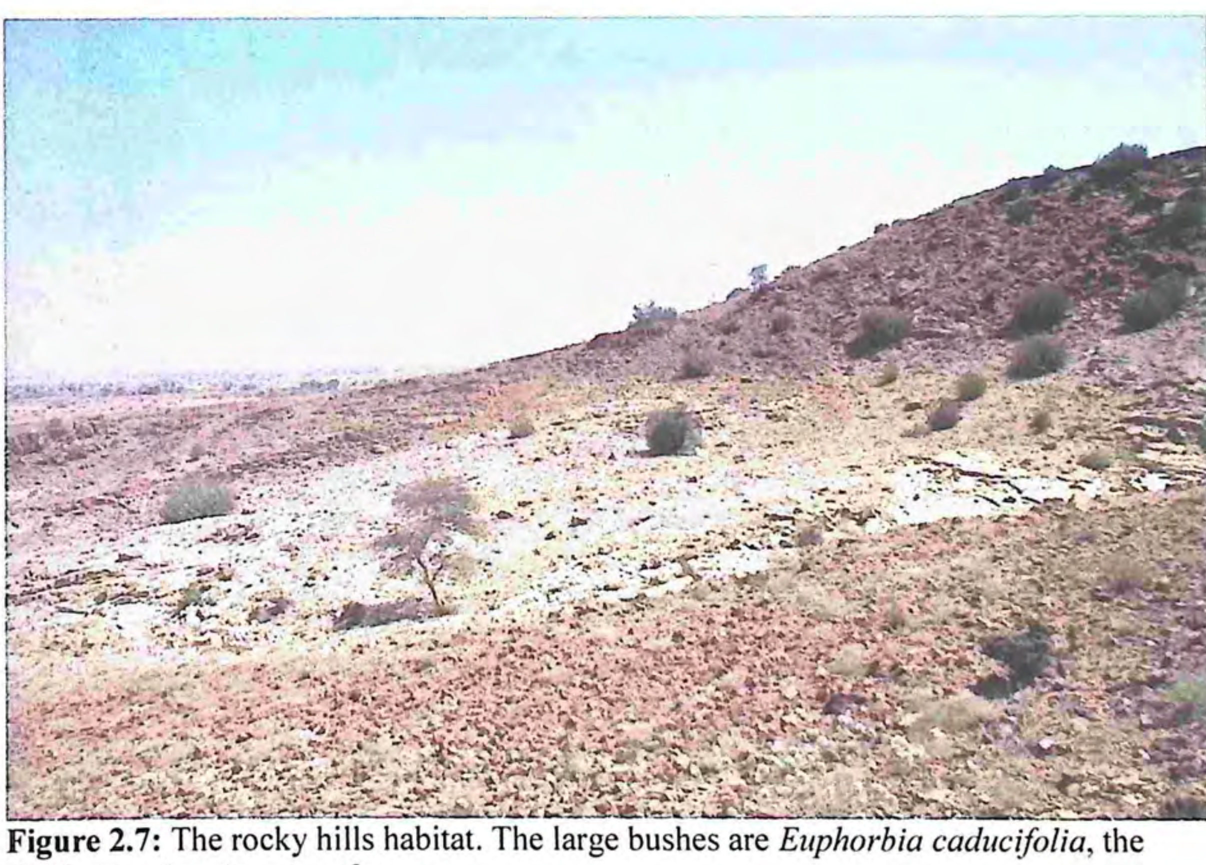

**Figure 2.7:** The rocky hills habitat. The large bushes are *Euphorbia caducifolia*, the single tree *Acacia senegal*

*D. aristatum*, *Indigofera cordifolia* and *Fagonia cretica*. Gravely areas also have a number of ephemerals that sprout during rains including *Cleome brachycarpa*, *Erodium cicutarium*, and *Indigofera spp*. This area has a fair number of trees, most common of which is *Capparis decidua*, and occasional *Zizyphus nummularia*. Rodent burrows are prominent in the sandy areas, while hummocks are also restricted to these areas but are rare. Grazing pressure is high as a result of high % cover of *Laisurus sindicus*.

### 2.4.4 Rocky hills (RH)

These are also known as rocky and gravelly pediments (Kar 1989; Fig. 2.7). These mildly undulating hills are below 290 m in this area and are composed of sandstones and limestone. The soil is rocky with occasional sand deposits and there is low vegetation cover (9-23%). Though streams are ephemeral, drainages are a prominent feature of these rocky hills. There are various forms of rocks depending both on the underlying structure and amount exposed, including sheet rock, rock faces formed by large rocks breaking away at the crest of slopes, and various sizes of rubble. Trees are restricted mainly to drainages and depressions, while *Euphorbia caducifolia* clumps are scattered across most areas but are concentrated on slopes and in drainages. Grasses include *Cenchrus pennisetiformis*, *Aristida sp*., and *Dactyloctenium scindicum*. Dominant shrubs are *Aerva spp*., *Fagonia cretica*, and *Grewia tenex* (in dwarf form). Trees include *Acacia senegal*, *Capparis decidua*, *Grewia tenax* and *Salvadora oleoides*. *Euphorbia* cover may be as high as 20 %. Rodent burrows and hummocks are absent in all areas except where there are very extensive sand deposits. Grazing pressures are fairly high in vegetated areas, and are likely to be more extensive in the post-monsoon season (based on dry dung deposits in barren areas). A more serious cause of anthropogenic disturbance in these areas is small-scale mining and rubble collection. The rocky hills are outside the DNP as a result of which there is increasing commercial exploitation.

**2.5 Saurofauna**

A total of 21 species are reported from Jaisalmer District (Sharma 2002). Of these, the record of *Phrynocephalus euptilopus* is questionable (see Prakash 1972). 12 species are reported from the DNP (Das and Rathore 2004). Specific accounts are listed for these 12 species, and an additional two species found around Sam. Table 2.1 summarizes time of activity, foraging mode, size and weight for these 14 species.

***Bufoniceps laungwalansis*** (Fig 2.8a) is a small lizard well adapted to a psammophilous life and is restricted to barren sand dunes. This species is very swift across the sand and leaves distinct tracks. Tracks can run as far as 130m (pers obs). The escape behaviour is characteristic- the animal rapidly buries itself in the sand by rapid shivering movements of its body. This diurnal species is active through winter during periods of sunshine, and activity peaks in summer. This small lizard can be found on sand hotter than 50°C (pers. obs.). This species is likely to be a sit and wait forager, either remaining partially buried or exposed while 'waiting' (pers. obs.). This species is endemic to the Thar Desert, restricted to a few localities in Jaisalmer District and adjacent Pakistan (Macey *et al.* 2006).

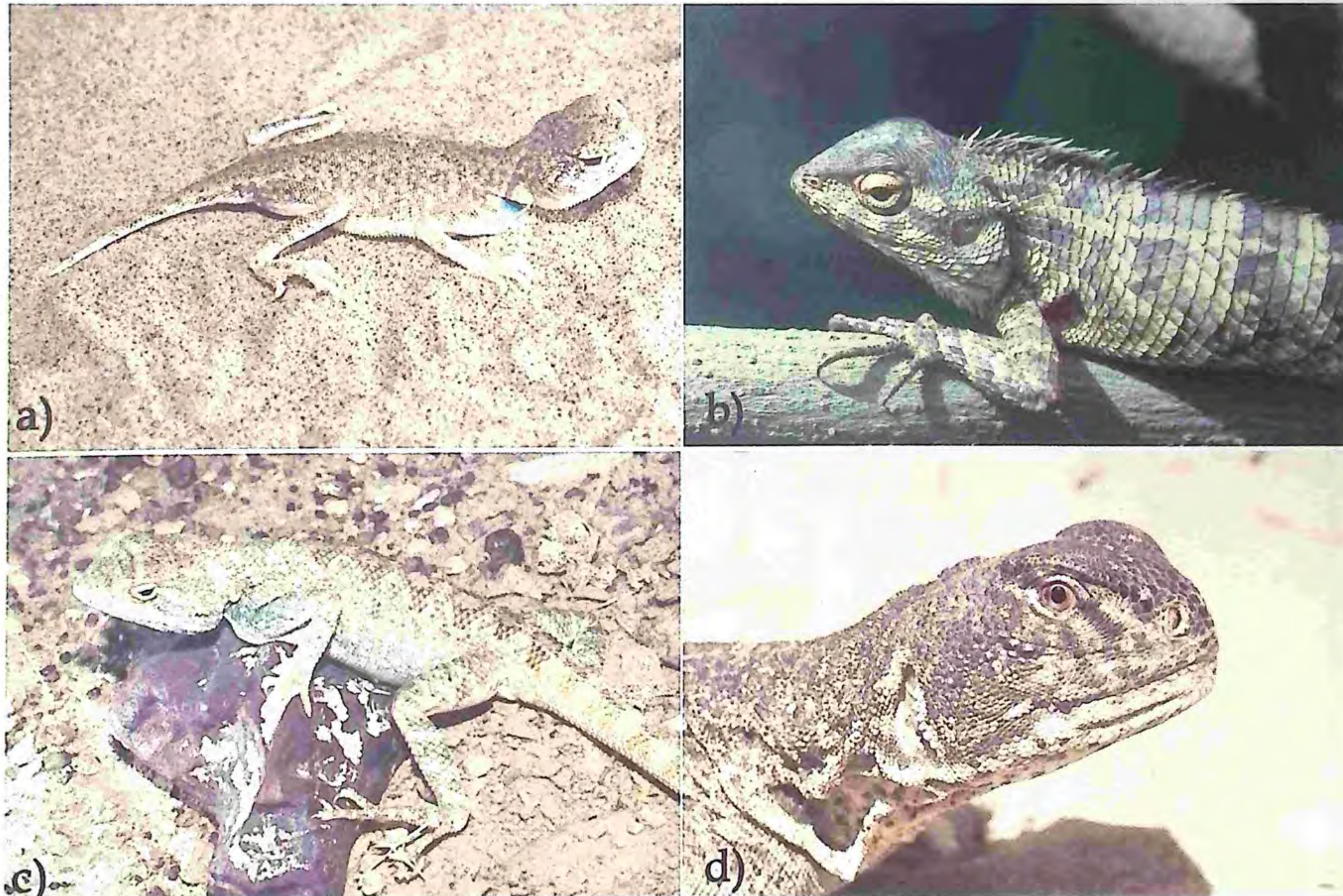


**Figure 2.8 a)** *Bufoniceps laungwalansis*; **b)** *Calotes versicolor*; **c)** *Trapelus agilis*; **d)** *Uromastyx hardwickii*.

***Calotes versicolor*** (Fig. 2.8b) is widely distributed across the Indian subcontinent, and is a common lizard in urban, rural and undisturbed settings. This species is likely to be an active forager (S. Mukherjee pers comm.).

***Trapelus agilis*** (Fig 2.8c) is widely distributed across the Thar and is most abundant in sandy habitat (pers. obs.) though Minton (1966) found it most common in rocky and gravely areas. The foraging mode is likely to be sit and wait ("sit and wait under shrubs"; Shenbrot *et al.* 1991). Adults of this species show rapid metachroic colour change (Minton 1966) and breeding males are bright blue with yellow tails. *Trapelus* emerges at least three hours after sunrise and is active at very high temperatures (up to 42°C air temperature, substrate >50°C; pers. obs.). Winter activity is low. This is the easternmost limit for this genus, and *T. agilis* is is widely distributed from western India eastward till Iran, north to Russia, Turkmenistan and China; and is considered a species complex (Macey *et al.* 2006, Minton 1966).

***Uromastyx hardwickii*** (Fig 2.8d) is the most unique of the species in the Thar as it is almost entirely herbivorous, though juveniles are known to take small arthropods (Minton 1966). This species tends to live in colonies or aggregations and is found in areas with compact soil and cover of *Dactyloptenium spp. Uromastyx* digs its own burrows that are easily recognizable. This is the easternmost limit for this genus, with *U. hardwickii* ranging from western India into Pakistan.

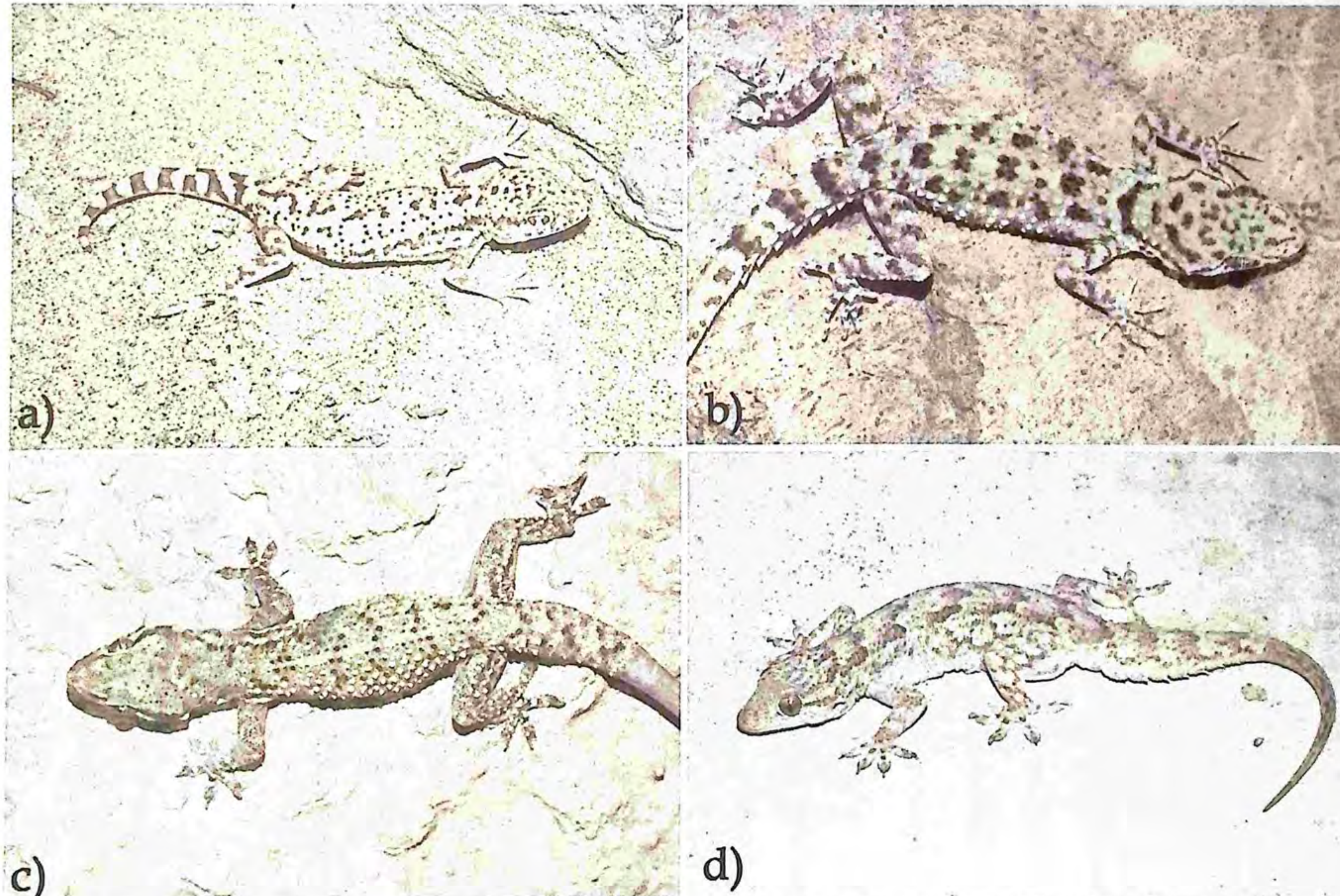


**Figure 2.9 a)** *Crossobamon orientalis*, **b)** *Cyrtopodion scaber*, **c)** *Hemidactylus persicus*, **d)** *Hemidactylus flaviviridis*

***Crossobamon orientalis*** (Fig 2.9a) is found closely associated with sand (Das 2002). This terrestrial gecko is the only gecko in sandy habitats in this area and is fairly abundant. Winter activity is low. It is distributed in the Thar and Sindh Deserts (Minton 1966).

*Cyrtopodion scaber* (Fig 2.9b) is restricted to rocky habitats including both small rocky outcrops as well as more extensive rocky hills. Individuals can be seen close to the ground as well as up to 2 m high, on horizontal and vertical substrates. Individuals are also found among buildings though usually away from habitation (e.g. boundary/ tank walls; Minton 1969; pers. obs.). Individuals may be found under and within rock crevices in the day. Winter activity is limited to warm nights. *C. scaber* is distributed from South Asia, Egypt, Ethiopia, and the Middle East; till Western Rajasthan (Minton 1966).

***Hemidactylus flaviviridis*** (Fig 2.9c) is a familiar house gecko, found on trees as well as among rocks. Winter activity is limited. This species is widely distributed through India, as well as from Northern Africa through the Middle East to South Asia (Das 2002).

***Hemidactylus persicus*** (Fig 2.9d) is poorly known within India, and has only been previously reported once from India, in Jassore Wildlife Sanctuary, Gujarat (Vyas *et al.* 2006). This is the second record of this species from India and the first record from Rajasthan. *H. persicus* is known to frequent rocky desert areas. Winter activity is low. This species is distributed up to Eastern Arabia and Southern Iran (Minton 1966).

***Tropiocolotes persicus euphorbiacola*** (Fig 2.10a) is known from localities in Pakistan, and though found in adjacent parts of the Thar Desert, has not earlier been recorded from India. This is the first record for this genus from India. This small gecko is found in rocky areas up to about 250 m and its distribution closely follows the distribution of the large shrub *Euphorbia caducifolia* (Minton *et al.* 1970).

***Ophiomorus raithmai*** (Fig 2.10b) is a nocturnal, fossorial species found closely associated with sand. Winter activity is fairly consistent, though summer activity is considerably higher. This species is probably an active forager, based on the length of its distinctive sinuous tracks (>30 m; pers obs). This is the easternmost limit for this genus; *O. raithmai* ranges from western Rajasthan to southern Pakistan (Anderson and Leviton 1966).

***Acanthodactylus cantoris cantoris*** (Fig 2.10c) is a diurnal, widely foraging species. This species is restricted to sandy areas and is the most common lizard seen in such situations (Das 2002). It is the only species in this area active throughout winter, and in summer is the first species to emerge after sunrise. This is the easternmost limit for this genus; the species is distributed from northern and northwestern India to eastern Afghanistan (Minton 1966).

***Ophisops jerdoni*** (Fig 2.10d) is found in rocky, arid areas (Das 2002). This small species is active in winter though activity is considerably lower than in summer. This species is an active forager. It is distributed through northern India down to at least Maharashtra (pers. obs); ranging into Pakistan and eastern Afghanistan (Minton 1966).

***Varanus bengalensis*** is the most common monitor in the Indian subcontinent and most of South Asia, but is rarer than *V. griseus* in many parts of the Thar (Minton 1966). This large species is known to take vertebrate prey including mammals, birds, snakes and even lizards (Das 2002).

***Varanus griseus koniecznyi*** or the desert monitor is the smaller relative of the common monitor. This species also takes vertebrate prey including other lizards. The distribution ranges from Western Rajasthan and Gujarat up to the Middle East (Das 2002).

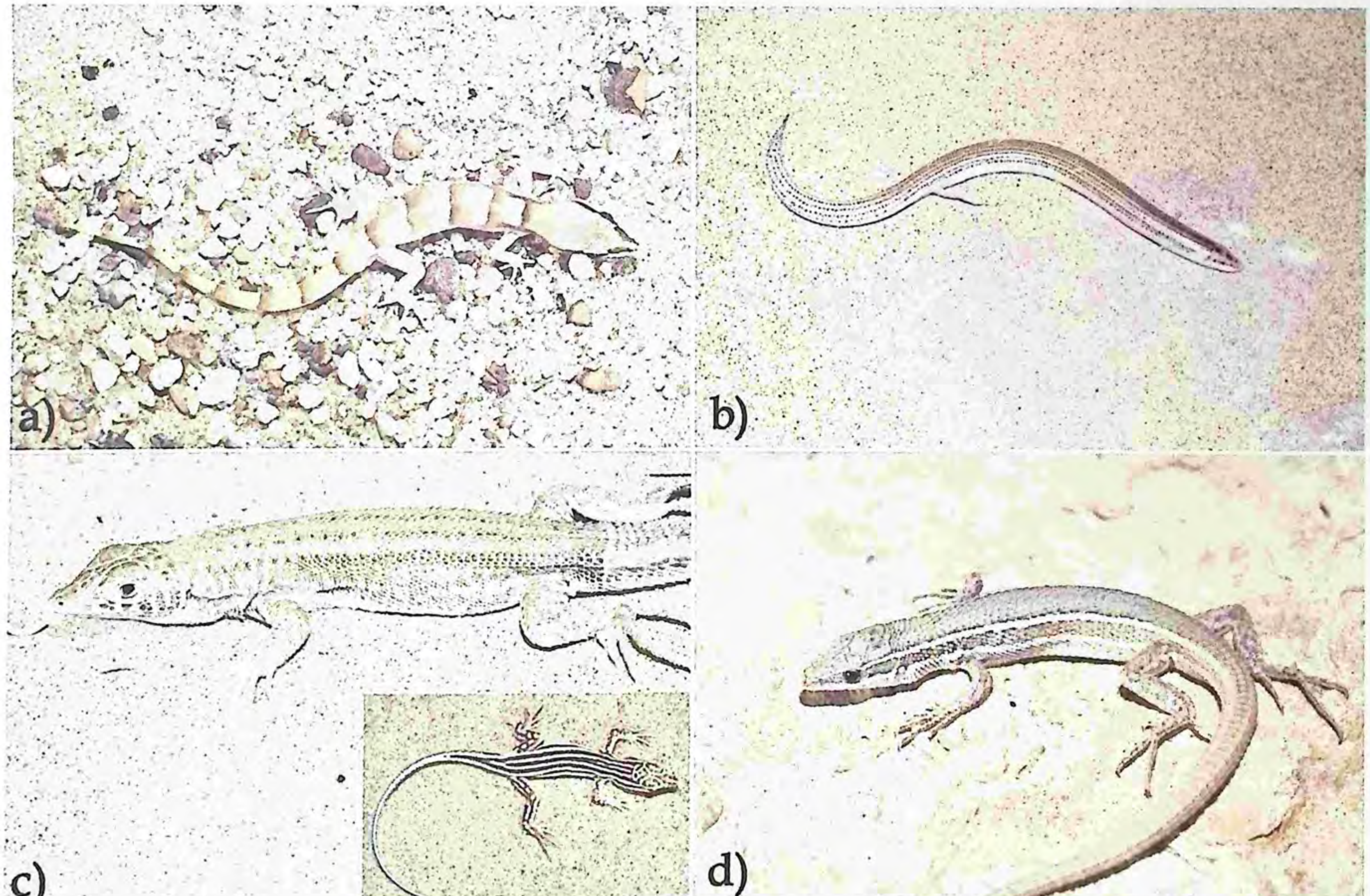


**Figure 2.10 a)** *Tropicolotes persicus*, **b)** *Ophiomorus raithmai*, **c)** *Acanthodactylus cantoris* (juvenile inset), **d)** *Ophisops jerdoni*

**Table 2.1** Species recorded from the study area along with activity pattern, snout vent length (SVL) and weight.

| Family: | Species | Common Name | Activity period | Foraging mode[a] | SVL[b] (mm) | Wt.[c] (g) |
|---|---|---|---|---|---|---|
| **Agamidae** | *Bufoniceps laungwalansis* (Sharma 1978) | Laungwala Toad-headed Agama | Diurnal | Sit and wait | 70 | 9.5 |
| | *Calotes versicolor* (Daudin 1802) | Garden Lizard | Diurnal | Active forager | 450 | ? |
| | *Trapelus agilis* (Olivier 1807) | Brilliant Agama | Diurnal | Sit and wait | 106 | >19.5 |
| | *Uromastyx hardwickii* Gray 1827 | Spiny-tailed Lizard | Diurnal | Active forager | 250 | >270 |
| **Gekkonidae** | *Crossobamon orientalis* (Blanford1876) | Sindh Sand Gecko | Nocturnal | Sit and wait | 55 | 6 |
| | *Cyrtopodion scaber* (Heyden 1827) | Keeled Rock Gecko | Nocturnal | Sit and wait | 60 | >3 |
| | *Hemidactylus flaviviridis* Ruppell 1835 | Northern House Gecko | Nocturnal | Sit and wait | 90 | ? |
| | *Hemidactylus persicus* Anderson 1872 | Persian Gecko | Nocturnal | ? | 66 | >6.5 |
| | *Tropiocolotes persicus euphorbiacola* Minton, Anderson & Anderson 1970 | Sindh Dwarf Gecko | Nocturnal | ? | 33 | 1 |
| **Scincidae** | *Ophiomorus raithmai* Anderson & Leviton 1966 | Indian Sandfish | Nocturnal | Active forager | 100 | >8 |
| **Lacertidae** | *Acanthodactylus cantoris* Gunther 1864 | Indian Fringe-toed Lizard | Diurnal | Active forager | 80 | >7 |
| | *Ophisops jerdoni* Blyth 1853 | Snake-eyed Lacerta | Diurnal | Active forager | 45 | >1 |
| **Varanidae** | *Varanus bengalensis* (Daudin 1802) | Indian Monitor | Diurnal | Active forager | 750 | ? |
| | *Varanus griseus* (Daudin 1803) | Desert Monitor | Diurnal | Active forager | 525 | >270 |

[a] personal observations, personal communication (S. Mukherjee)
[b] Minton 1961; Minton *et al.* 1970; Das 2003
[c] based on field measurements. For specimens smaller than maximum reported SVL, minimum wt. based on largest specimen personally examined presented.
? indicates information unavailable

## 3. METHODS

The lizard community of the Thar Desert was studied between November 2006 and April 2007. Stratified sampling was used to investigate patterns of diversity, habitat relationships and resource partitioning by a lizard community.

### 3.1 Definitions

'Grid' refers to any of the twelve one ha grids set up in summer, 'plot' to any of the sixteen 25m x 25m subdivisions within each grid, and 'habitat plot' to the 5m radius circular plot laid within each plot for habitat variables. I use 'habitat', 'habitat types' or 'strata' to refer to any or all of the four habitat types recognized in this study. 'Walk', 'VES' (Visual encounter survey), 'session' and 'transect' are used interchangeably in reference to a particular sampling session. 'T1' to 'T4' refer to transects, while a 'replicate' or 'repeat' is a repeat sample of T1, T2, or T4 within the same grid. 'Diurnal' walks include T1, T2, and T3; while T4 is the only 'nocturnal walk'. 'Microhabitat category' refers to the spatial position occupied by an undisturbed lizard at the time of sighting, while 'microhabitat' refers to the specific subcategory of a habitat in which a species is found. Species may occupy the same microhabitat with differential spatial use; while spatial use may be similar in distinct microhabitats.

### 3.2 Reconnaissance and selection of sampling methods

Winter was spent surveying the area and delineating different habitat types. I also evaluated sampling methods during this period. Systematic sampling was restricted to the sandy habitats and to a lesser extent grasslands. Sampling was tested in grids of different sizes ranging from 0.25 ha to 1ha, as well as transects of varying length (50 m to 350 m). Activity patterns of some species of lizards, and the commonly occupied microhabitat categories were studied. This period was used to familiarize and train both observers (my field assistant and I) in recognizing and locating lizards, essential to maximize detections. Finally, the placement and size of habitat sampling plots, and the type of variables to measure for summer sampling were selected based on results from winter sampling.

### 3.3 Defining habitats and grid selection

A grid size of 1ha was selected based on preliminary sampling. Regardless of size, only a single grid can be sampled during a particular activity period, as moving between grids is only possible on foot, and thus sampling many, smaller grids was not feasible. One ha is suitable as the entire grid can be sampled within about 90 minutes with conditions remaining relatively constant in that time frame, the number of lizard sightings is reasonable, and the size is large enough to capture habitat heterogeneity.

The sampling scheme used in this study was essentially stratified sampling. Strata were identified using broad categories that were defined in field on the basis of distinctive physiognomic characters of soil and vegetation structure. Within each habitat type, the selection of grids can be best described as "arbitary but without preconceived bias" (McCune and Grace 2002), as no true randomization process was used. In summer twelve sampling grids of 1ha size were set up, three each in the four major habitat types: barren dunes, stabilized dunes, grassland and rocky hills. I chose the location of grids within each based on three criteria; habitat diversity, disturbance, and distance to other grids. Grids were placed to capture the major gradients in habitat structure, vegetation composition and cover within each habitat (visually determined). As the entire region is heavily grazed, I attempted to minimize the disturbance factor by selecting grids within exclosures of DNP as far as possible. The final constraint was that grids were at least 400 m apart, to ensure individual lizards did not move between grids. Table 3.1 summarizes the habitat diversity represented in each grid.

**Barren dunes:** The main source of variability I could identify in barren dunes was the size and slope of dunes, relative proportion of interdunal area, vegetation cover, as well as surrounding habitat type. Thus in this habitat, I selected two grids with almost no vegetation and a combination of steep and moderate sloped dunes (20-45°) with some barren interdunal area; one in the middle of an extensive dune field, and the other in a much narrower dune field bordered by grassland and stabilized dune The third grid had a larger proportion of vegetated area.

**Stabilized dunes:** The stabilized dunes do not have much structural diversity, most being uniformly undulating with similar soil. However, there is a distinct change in vegetation structure from one area to the next, and it was this variation that I tried to capture. The three plots had dominance of *Cenchrus bifloris* and *Panicum turgidum*, *Haloxylon*, and *Panicum turgidum* and *Aerva* respectively.

**Grassland:** The grassland area is perhaps the most variable, depending on the surface and underlying soil type. The grassland grids were laid to reflect the diversity of soil types and vegetation seen in the habitat, from >95% sand to >30% gravel. The third grid has >90% sand overall but is distinct in including a large number of *Capparis decidua* trees.

**Rocky hills:** The rocky area is the most structurally diverse habitat. There are distinct gradients in vegetation cover, rock size and rock type. After selecting the general area for a grid in this habitat, I aligned the majority of the plot with the predominant slope for ease of sampling. I laid a grid in an almost entirely barren flat area with mainly sheet rock, another in an area with high *Euphorbia* cover with diversity of rocks and soil, and the last grid partially containing a drainage with some trees and high *Euphorbia* cover.

**Table 3.1** Details of sampling grids across habitat types

| | Barren Dunes | Stabilized dunes | Grassland | Rocky Hills |
|---|---|---|---|---|
| **Grid 1** | Vegetation cover very low, moderate slope, barren interdunal area, in small dunefield | Dominance of *Cenchrus bifloris* and *Panicum turgidum* | Sandy with equal amount of gravel area | High cover of Euphorbia, slope, high rock diversity, sand deposits |
| **Grid 2** | vegetation cover higher, low slope, vegetated interdunal area, in small dunefield | Dominance of *Haloxylon salicornium* | Sandy with some gravel | High cover of Euphorbia, few trees, slope + drainage, high rock diversity |
| **Grid 3** | Vegetation cover very low, moderate slope, barren interdunal area, in extensive dunefield | Dominance of *Panicum turgidum* and *Aerva spp.* | Sandy, with many *Capparis decidua* trees | Vegetation cover very low, flat, mainly sheet rock |

Grids were physically laid out using a compass and laser rangefinder in flat terrain or 25m rope in undulating terrain. Each 1 ha grid was subdivided into sixteen 25m x 25 m plots that formed the sampling unit for habitat and lizards. Thirteen sticks were used to mark the boundaries of plots (Fig. 3.1); eight along the perimeter spaced every 50 m, one in the centre and four between the centre post and the four corners of the 1 ha grid. Prior to sampling for lizards these sticks were replaced by split bamboo poles 3-4m in height that were colour coded with a ribbon and radium strips (for night visibility). These had to be installed just before sampling to prevent them from being stolen as livestock herders frequent these areas. Poles that were stolen were replaced by sticks temporarily, and by a coded pole before the next sampling session.

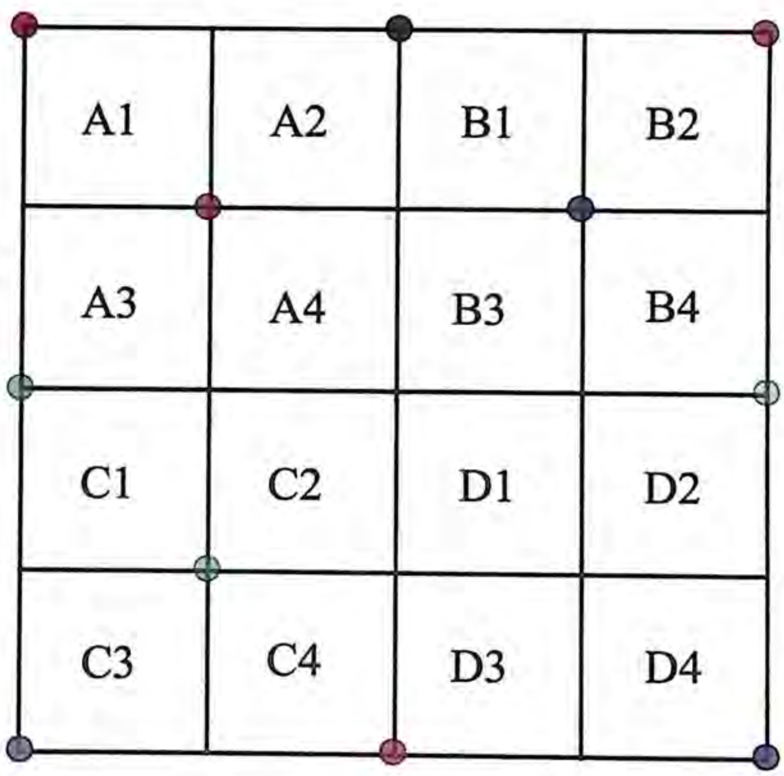


**Figure 3.1** Representation of sampling grid. Letter codes indicate 25mX25m plots, coloured dots represent bamboo markers

### 3.4 Sampling methods

#### 3.4.1 Sampling units

Square 25m X 25m plots within 1 ha grids formed the units for vegetation and animals. Quadrats were selected as the unit of sampling over linear transects because habitats are fairly spatially heterogeneous. The use of a linear transect meant that lizards may be sighted a considerable distance from the habitat plot. Thus, the relationship between lizard sightings and the habitat variables may not be as clear as in a quadrat, where all sightings are closer to the habitat plot.

### 3.4.2 Sampling lizards

Each grid was sampled by the same two observers using the same equipment, eliminating any observer biases between grids. Torches were used at night and geckos were spotted by eye-shine or body-shine. Both observers had spent a considerable 'training' period getting acquainted with the habitats and learning to locate and visually identify all the lizard species in them. Levels of skill in detecting lizards were similar by the end of this training period. To confirm visual identifications, an initial sample of at least 5 individuals of most species was keyed out from literature (Smith 1935; Anderson and Leviton 1966; Minton 1966; Minton *et al.* 1970).

Two common methods used in studies on lizards are visual encounter surveys (Crump and Scott 1994) and pitfall trapping. Though pitfall traps have proven effective in studies of herpetofauna (e.g. Shenbrot and Krasnov 1997; Fisher *et al.* 2002), I chose not to use pitfall sampling as the time and effort investment required for pitfall trapping could not be met under the logistic constraints of this study.

A visual encounter survey was used within grids to sample lizards. The VES technique used in this study deviates from some VES approaches (e.g. Crump & Scott 1994; Persons 2005) in that it was not time constrained but only area constrained (Doan 2003). Observers walked at a similar pace through each of the sample grids, but used as much time as was necessary to visually scan the entire area comprehensively. Thus the time taken across the same walks (T1, T2, T3 or T4) in different grids varied, depending on the structural complexity and detectability within that particular grid - the main factors influencing search time. These were however generally similar within a habitat. Similarly, nocturnal walks were longer than diurnal walks in most grids (Figure 3.2). Thus rather than an area and time constrained search, the VES used here was to visually conduct a repeatable count representing the maximum number of animals seen in the 1 ha grid.

During preliminary sampling, almost all sightings fell within 2-3 m from observers. Accordingly, the observers were spaced 5 m apart to avoid missing any animals. Grids were sampled in the form of a zigzag VES, equivalent to ten 100m x10m belt transects,

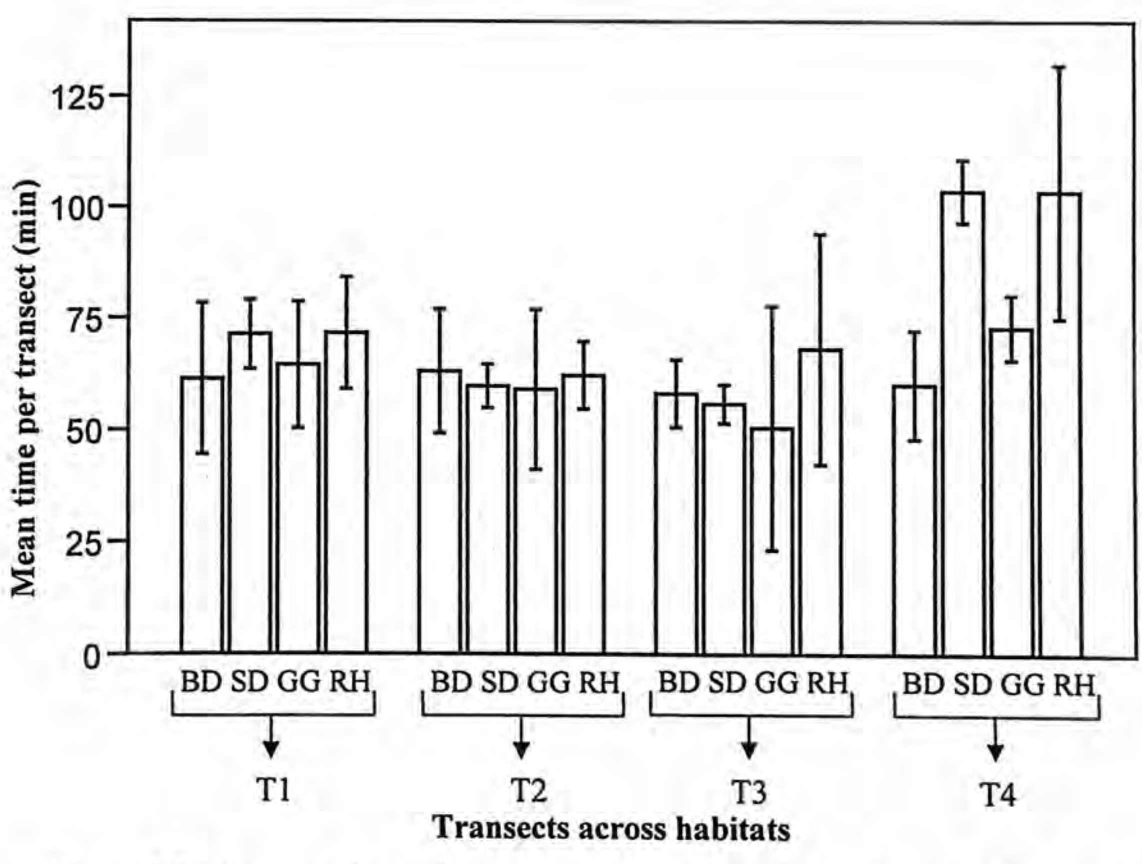


**Figure 3.2**: Average time taken per transect across habitat types. Error bars represent 95% CI.

with each subsequent transect shifted by 10 m (Fig 3.3). The starting points were 2.5m and 7.5m (observers 1 and 2) from a randomly selected corner, finally ending at 92.5m and 97.5m respectively. The direction of walk was reversed on the second day of sampling to account for minor time and temperature differences between the first and last sampled plots in a given sampling session. Even though the time between subsequent passes through the same area was short, between 5-9 min, there was a possibility of double count since observers passed within 5 m of previously sampled areas. However, this was minimal for all species except *Acanthodactylus*, which was very abundant in some grids and moves considerably more than other species. Even for this species, the occurrence of four distinguishable classes based on size and pattern made keeping track of double count of individuals easier. The other species are relatively uncommon, move less and could be kept track of.

**Figure 3.3** A barren dune grid after sampling. The hard interdunal area is seen in the foreground, a bamboo marker on the top right. Footprints were generally obscured by the wind within a few hours. (Photograph courtesy V. Mistry)

### 3.4.3 Sampling schedule

Though the basic sampling unit was a 25 m plot, an entire grid was sampled in a session. Grids were sampled for lizards between 22.3.7 and 29.4.7. The average maximum temperature during this period was 40° C and the average minimum 22 °C. Grids were sampled in sets of three or four grids within 7-8 days and I attempted to sample grids from different habitats simultaneously. However, due to logistic constraints the rocky hills grids had to be sampled together and so I placed them in the middle of the sampling period (Table 3.2). Each grid was sampled twice, with three to five days between replicates (except two transects that were repeated a month later).

**Table 3.2** Sampling schedule of the twelve 1 ha grids sampled in summer

| Habitat | Grid number | Date 1 | Date 2 |
|---|---|---|---|
| Barren Dunes | 1 | 30.3.7 | 29.4.7 |
| | 2 | 20.4.7 | 24.4.7 |
| | 3 | 22.3.7 | 26.4.7 |
| Stabilized | 1 | 19.4.7 | 23.4.7 |
| Dunes | 2 | 31.3.7 | 4.4.7 |
| | 3 | 22.4.7 | 25.4.7 |
| Grassland | 1 | 21.4.7 | 27.4.7 |
| | 2 | 29.3.7 | 1.4.7 |
| | 3 | 23.3.7 | 3.4.7 |
| Rocky Hills | 1 | 14.4.7 | 17.4.7 |
| | 2 | 13.4.7 | 16.4.7 |
| | 3 | 12.4.7 | 15.4.7 |

The time during which grids were walked was determined based on prior sampling to determine peak times of lizard activity. There were four sampling sessions (three daytime and one nighttime; Fig 3.4) on the first day: T1, start time 8:00hrs to 8:40 hrs (between 1 hr 30min to 2 hrs since sunrise); T2, start time 09:30 hrs to 10:10 hrs (between 2 hrs 45 min to 3 hrs 30min after sunrise); T3, start time 17:00 to 17:15 (two hrs before sunset); and T4, 20:00 to 20:25 (about one hr after sunset). T1, T2 and T4 were repeated on the second day a grid was sampled. The evening session (T3) was least productive and was only walked once.

Wind and sky conditions were noted at the start of each transect; air (shaded bulb, ~ 1 m height) and soil (surface) temperature were recorded at half hour intervals using a digital probe thermometer.

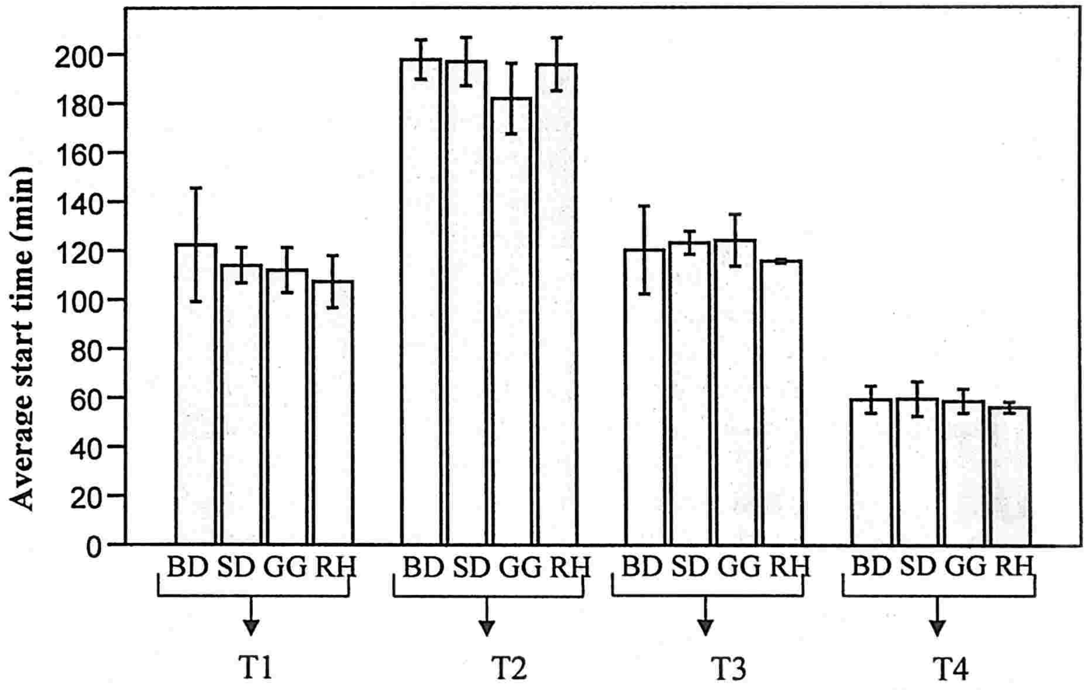


**Figure 3.4** Average start times for transects across strata. Error bars represent 95 % CI. For T1 and T2 start time is expressed in minutes after sunrise, for T3 as minutes before sunset, and T4 minutes after sunset

Lizards could easily be identified visually from a distance. Those that were seen fleetingly or heard were located either in vegetation or occasionally in rodent burrows and identified. A few that escaped definite identification were not recorded, but these account for less than 1 % of overall sightings. Species, (subjective) size/age category, time of sighting, 25 m plot ID, substrate, and rock size (in rocky hills habitat) were recorded for all lizards. For undisturbed lizards, microhabitat category (Table 3.3), distance to and type of closest vegetation; slope, aspect and dune position (crest, slope, edge or interdune; for barren dunes only) were also recorded. *Ophiomorus* tracks were recorded as present or absent (with no measure of abundance) during each transect and wiped out subsequently to prevent double counts.

A few lizards were captured during opportunistic searching or at the end of a sampling session for morphometric data.

**Table 3.3** Microhabitat categories and their definitions, used in classifying undisturbed lizard sightings. Modified after Pianka (1986)

| Sr. No. | Microhabitat Category | Definition |
|---|---|---|
| | **Diurnal** | |
| 1. | Fossorial | Includes burrowing individuals |
| 2. | Open Sun | Lizards in open sun |
| 3. | High Sun | Lizards in the sun, perched above 100cm |
| 4. | Low Sun | Lizards in the sun, perched below 100cm |
| 5. | Bush | Any lizards within a bush |
| 6. | Bush Shade | Any lizards using the shade of a bush (but not within it) |
| 7. | Grass | Any lizards within grass |
| 8. | Grass Shade | Any lizards using the shade of grass (but not within grass) |
| 9. | Rock Shade | Lizards using the shade of a rock |
| 10. | Rodent Burrow | Lizards in a rodent burrow when first sighted |
| | **Nocturnal** | |
| 11. | Fossorial | Burrowing lizards |
| 12. | Terrestrial | Found on the ground |
| 13. | Rupicolous | Found on rocks |

### 3.4.4 Habitat sampling

Habitat variables were recorded between 20.2.7 and 10.3.7. The final variables derived from original measurements are listed in Table 3.4. Vegetation sampling was carried out in each of the 25 m plots. A soil sample of approximately 300 g and 5 cm depth was collected from the centre of each plot for texture analysis. Soil analysis was done using a SS-94 Mechanical Sieve Field Analysis Kit (Keck Instruments Inc., Michigan, U.S.A.), and soil was sorted into four categories – pebbles (>20mm), gravel (2-20mm), sand (0.1-2mm), fine sand+silt+clay (0.1< mm). A circular 5 m radius plot was used to enumerate

**Table 3.4** List of habitat variables quantified

| Sr. No. | Variable | Abbreviation | Units |
|---|---|---|---|
| 1. | Dung (presence-absence) | Dung | Number/ plot |
| 2. | Hummocks (large/medium/small) | Hum (L/M/S) | Number/ plot |
| 3. | Rodent burrows (large/small) | RB_ (L/S) | Number/ plot |
| 4. | Percent pebbles in soil sample | %peb | % |
| 5. | Percent gravel in soil sample | %grav | % |
| 6. | Percent sand in soil sample | %sand | % |
| 7. | Percent silt + clay in soil sample | %silt | % |
| 8. | Percent grass cover | %Grass | % |
| 9. | Percent shrub+herb cover | %Sh_Hrb | % |
| 10. | Percent barren ground | %Barren | % |
| 11. | Average shrub+herb species rank | Hrb_Sh_rk_av | Unitless |
| 12. | Average grass species rank | Gr_rk_av | Unitless |
| 13. | Grass Volume up to 25 cm ht category | Gr_Vol1 | $cm^3$ |
| 14. | Grass volume in 25 cm to 50 cm ht category | Gr_Vol2 | $cm^3$ |
| 15. | Grass volume in >50 cm ht category | Gr_Vol3 | $cm^3$ |
| 16. | Shrub Volume up to 25 cm ht category | Sh_Vol1 | $cm^3$ |
| 17. | Shrub volume in 25 cm to 50 cm ht category | Sh_Vol2 | $cm^3$ |
| 18. | Shrub volume in >50 cm ht category | Sh_Vol3 | $cm^3$ |
| 19. | Grass percent cover | Gr_Cov | % |
| 20. | Shrub percent cover | Sh_Cov | % |
| 21. | Euphorbia cover$^{\dagger}$ | Eu_COV | % |
| | Rock size classes$^{\dagger}$: | | |
| 22. | Soil | Soil | - |
| 23. | Small rubble (<0.1m) | SR | - |
| 24. | Medium rubble (0.1-0.3m) | MR | - |
| 25. | Small rocks (0.3-1m) | SmRk | - |
| 26. | Moderate rocks (1-3m) | ModRk | - |
| 27. | Rock face + large rocks (3-5m, any dimension) | LRk | - |
| 28. | Sheet rock | Sheet | - |

$^{\dagger}$ only used within rocky hills habitat

hummocks (three categories – large, medium and small), rodent burrows (two categories – large and small), and estimated number of dung groups (camel, cow or goat; old or new). Within the same plot, height and cover at crown height were measured for all discrete vegetation units at least 15 cm high and 15 cm on the two longest axes, using a measuring tape. Similarly, height and cover at crown height were measured for all trees and *Euphorbia* clumps taller than 0.75m within the entire 25m plot. Cover was calculated crudely by measuring the longest axis of a vegetation unit and an axis perpendicular to that and multiplying both axes; and volume from the product of height and cover. A weighted average of height using area as a weight was calculated and used instead of average height to better represent the spatial distribution of vegetation. In cases where one of the vegetation units of the 25m plot, a tree or *Euphorbia* clump, fell within the 5 m habitat plot, the area that fell inside was estimated. This vegetation unit was excluded from the 5 m plot, and the cover and volume of other discrete vegetation units in the plot were multiplied by a correction factor. The correction factor was calculated as

$$\left[\frac{\text{area of 5m circular plot}}{(\text{area of 5m circular plot - area occupied by 25m unit})}\right]$$

Ground cover was sampled using a 0.5m x 0.5m quadrat. %grass cover, %herb + shrub cover, %barren ground, and species rank abundance for up to 5 species were estimated visually; and five heights were measured at random within this quadrat. Additionally, to further describe the barren dune habitat, the following were visually estimated for each plot – position on the dune (from interdunal, edge, slope, crest), type of dune (three categories – gentle, medium and steep), and proportion of interdunal area. Eight values for slope and aspect were recorded from the centre of the plot at 45° intervals, visually determining the predominant values for each sector. Slope and aspect were recorded, and a point count to describe rock diversity was carried out for each plot in the rocky hill grids. Rock size was estimated every 1m for 25 points along a tape passing through the centre of the plot. The tape was aligned against the slope to capture maximum rock diversity within the plot.

### 3.5 Data analysis

25m sample plots were considered as the unit of sampling. For single species comparisons, and comparisons between diurnal species, the total number of sightings in a plot summed over all sampling sessions was used as a measure of abundance. To account for the different effort spent in searching for diurnal and nocturnal species, the highest number seen in a grid during any single sampling session, summed across the two days of sampling, was used for comparisons including abundances of nocturnal and diurnal species.

#### 3.5.1 Patterns of diversity

All habitat variables and plot-wise species registrations were summarized from original measurements using Microsoft Excel 2002 (Microsoft Inc. 2001). Species accumulation curves and diversity indices were calculated using the program EstimateS (Version 8.0.0; Colwell 2006). Cluster analysis with group average linkage and Jaccard's distance measure was performed on species occurrence and abundance data to visualize species co-occurrence patterns, using program PC-ORD (Version 4.0; McCune and Mefford 1999).

### 3.5.2 Habitat relationships

A subset of variables representing soil and vegetation structure were selected. These were entered into a principal components analysis (PCA) in SPSS to reduce the dimensionality of the dataset and group the original variables that contributed similar information. Varimax rotation was used for ease of interpretation.

Sampling plots were plotted against the first two factors from PCA to graphically represent the distribution of plots from different habitats in two dimensions of environmental space.

I used logistic regression to explore relationships between species and habitat. This was done both across habitats and within habitats. Binary logistic regression in SPSS (Version 14.0; SPSS Inc. 2005) was used to identify determinants of species presence. PCA factors were entered as independents in a forward stepwise binary logistic regression with probability (*p*) of f to enter 0.05, to remove 0.10; only for species with adequate unique plot registrations. Different values of classification cutoff were used, the final combination determined by the optimal correct classification of occupied plots with examination of predicted group memberships. These relationships were examined both across habitats and within habitats.

### 3.5.3 Resource partitioning:

Resource partitioning was examined as a hierarchical process, operating most broadly at the scale of occurrence within and between habitats, to overlap at the 25m plot level, and at the finest scale spatial use within plots in relation to microhabitat categories and habitat specific spatial resources.

Niche overlap with regard to spatial co-occurrence, use of microhabitat categories, distance to vegetation, time of activity, air-temperature, substrate use (in grasslands), spatial use of dunes (barren dunes), rock size use (rocky hills) was calculated based on Pianka's (1973) and Czechanowski's (Feinsinger *et al.* 1981) measures in the program EcoSim700 (Version 7.0; Gotelli and Entsminger 2001). Pianka's niche measure is a modification of the measure proposed by MacArthur and Levins (1967) but is normalized to make it symmetric. Czechanowski's measure corresponds to the area of intersection between the use histograms of species pairs. Both measures range from 0-1 and are symmetric between pairs. EcoSim uses Monte Carlo randomizations to generate 'pseudo-communities' (Pianka 1986) that approximate the organization in a community in the absence of competition, or simply without constraints. A comparison with the real data allows evaluation of whether observed niche overlap is greater or lesser than that expected by chance. EcoSim was run with 2500 iterations, and equiprobable resource states. The custom settings used in the program were niche breadth retained and zeroes reshuffled, retaining the degree of specialization for the species but allowing possible use of other available states. This corresponds to algorithm RA3, which besides intuitively corresponding to an ecologically meaningful null model with which to compare real data, has been shown to be most reliable in detecting non-random overlap patterns (Willenmier and Pianka 1990). An additional option available in the program is the option of setting 'hard zeroes'. These correspond to resource states a species cannot occupy, and are not reshuffled in the randomization process. I used this for species restricted to a particular habitat type or types, with hard zeroes in plots of the other habitat type(s). $Chi^2$ tests for some of the data used in calculating niche overlap were used to examine which variables contributed to differences between pairs and to determine statistical significance.

A species presence-absence matrix and a set of environmental variables were used in PC-ORD for CCA (canonical correspondence analysis). I used CCA to obtain a graphical representation of species occurrence and co-occurrence in multivariate space, in essence a representation of each species niche in multivariate space formed by the habitat variables used in analysis. Though discriminant analysis is often used in such analyses (e.g. Carnes and Slade 1982; Shenbrot *et al.* 1991; Rogovin *et al.* 2000), I selected CCA because it characterizes the distribution of sample plots in a multivariate space formed by linear combinations of environmental variables, constrained by a species abundance matrix. This direct gradient analysis technique focuses only on community structure that is related to environmental variables (McCune and Grace 2002). CCA assumes a hump shaped or unimodal species response to environmental gradients (McCune and Grace 2002). Nine species, including tracks of *Ophiomorus* were used in this analysis because other species had few presence points, and abundance measures were not appropriate. I used scores generated from linear combinations of habitat variables, with row and column scores standardized by centering and normalizing, and scaled ordination scores to optimize species distribution. CCA scores for the first two axes were paired with species registrations and imported into ArcView (v 3.2a; ESRI Inc. 2000). The Animal Movement extension (Hooge *et al.* 1999) was used to represent the species distribution in canonical space. 95% and 50% confidence ellipses were made using the Jennrich-Turner method (assuming a bivariate normal distribution; Jennrich and Turner 1969). I chose to use this method with the assumption that even though sampling was not carried out in areas covering the entire range of conditions reflected in canonical space, a given species would be expected to occupy regions intermediate to extremes of occupied regions. A measure of niche breadth was calculated based on the standard deviation of each species registration from the centroid of that species in canonical space (Carnes and Slade 1982; Gregory and Gaston 2000), calculated as the root of the mean of squared standard deviations across the first two canonical axes (Gregory and Gaston 2000). Niche position of a species was calculated as the Euclidean distance of species centroids from the centroid of the community as a whole (Shenbrot *et al.* 1991; Gregory and Gaston 2000). The community centroid was calculated using the arithmetic mean of centroids of all species in the community. Niche position reflects the specialization of a species in resource use within the community space (Shenbrot *et al.* 1991).

## 4. RESULTS

A total of 14 lizard species were recorded during study. Only two of these species were represented in sampling during winter, while 12 were represented in sampling during summer. *Tropiocolotes persicus* is a new record for India, *Hemidactylus persicus* for Rajasthan

### 4.1 Seasonal variations in abundance

#### 4.1.1 Winter

Grids of 0.25 ha (15, with two to three repeats each) and 1 ha (five, with two repeats each), and belt transects (eight, two repeats each) of 10 m width, from 100 to 250 m long were sampled in the three sandy habitats (barren dunes, stabilized dunes, grassland) during the daytime in winter with a total of 124 lizard sightings of only two species. The total systematic search effort was about 54 man hours. Additional unsystematic daytime and nighttime walks were periodically carried out for lizards, including a total of about 100 man hours of effort. Lizard activity was poor throughout, further affected by rains every month. Only two diurnal species were consistently active through most of winter, *Acanthodactylus cantoris* and *Bufoniceps laungwalansis*. Opportunistic sightings of other species showed that a few species were also active. *Ophiomorus raithmai* was active throughout, except during the coolest part of winter, determined by its distinctive tracks. *Cyrtopodion scaber* was also active in winter on relatively warm evenings, soon after sunset. The coolest air temperature I observed this species at was 20° C, though they were active in cooler weather (temperature unrecorded). Even though only these four species were regularly active, and only *Acanthodactylus* and *Bufoniceps* were represented in sampling, I had opportunistic sightings of 12 lizard species in winter (Table 4.1). The two species I added in summer (*Calotes* and *Tropiocolotes*) were both in the rocky hills habitat, where I spent little time in winter.

**Table 4.1** Total number of sightings in relation to habitat during winter

| Species | Number of sightings | Habitats/ areas |
|---|---|---|
| *Bufoniceps laungwalansis* | >50 | Barren dunes |
| *Trapelus agilis* | 10 | Rocky hills, Stabilized dunes, Sam village |
| *Uromastyx hardwickii* | >10 | Sam village |
| *Crossobamon orientalis* | 1 | Sam village |
| *Cyrtopodion scaber* | >10 | Rocky hills, rocky outcrop |
| *Hemidactylus flaviviridis* | >10 | Rocky hills, Sam village |
| *Hemidactylus persicus* | >10 | Rocky hills (inside buildings) |
| *Acanthodactylus cantoris* | >50 | Stabilized dunes, barren dunes, grassland, Sam village |
| *Ophisops jerdoni* | 3 | Rocky hills |
| *Ophiomorus raithmai* | 3 | barren dunes (tracks observed in stabilized dunes, at Sam) |
| *Varanus bengalensis* | 1 | rocky outcrop |
| *Varanus griseus* | 2 | Stabilized dunes, Sam |

### 4.1.2 Summer

A total of 12 1ha grids were sampled, including 192 sample plots in all, with a total of 84 sampling sessions equivalent to 194.2 man-hours. 1039 sightings of 12 species were recorded. Of the 192 plots, each sampled seven times; 17 plots had no species, 65 had one species, 48 recorded two species, 33 had three species, 27 had four species and only two plots had five species (considering only direct sightings, excluding tracks of *Ophiomorus* and *Varanus* sp.). Table 4.2 summarizes abundances of species across habitats. Abundance was determined as the maximum number of lizards seen in any one given sampling session, representing a lower bound of actual densities (Shenbrot and Krasnov 1997; McNair 2003). Consistency in sampling was maintained by a fixed start time (Fig. 3.4), and temperature conditions were similar for most transects (Fig. 4.2) Rarefaction curves indicate all habitats had adequate sample plots ensure all species represented, with the species accumulation curve stabilizing between 12-30 plots across habitats (Fig. 4.3).

Subsequent results are based on summer sampling, except where specified.

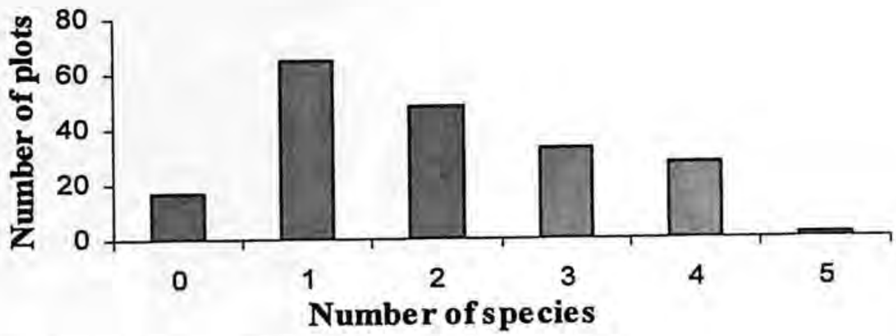


**Figure 4.1** Histogram of number of species per plot

**Table 4.2** Abundance (ind./ha), species richness and diversity of lizards across grids sampled in summer. 1, 2, 3 refer to separate grids within each habitat. The range across habitats is presented for abundance of lizards with the mean in parentheses.

| | Barren Dune | | | Stabilized Dune | | | Grassland | | | Rocky Hills | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **1** | **2** | **3** | **1** | **2** | **3** | **1** | **2** | **3** | **1** | **2** | **3** |
| *Bufoniceps laungwalansis* | 10 | 12 | 8 | - | - | - | - | - | - | - | - | - |
| *Calotes versicolor* | - | - | - | - | - | - | - | - | - | 1 | 1 | 1 |
| *Trapelus agilis* | 0 | 4 | 1 | 8 | 3 | 9 | 9 | 1 | 0 | 1 | 2 | 1 |
| *Uromastyx hardwickii* | - | - | - | - | - | - | - | 1 | 1 | - | - | - |
| *Crossobamon orientalis* | 0 | 10 | 1 | 23 | 18 | 23 | 14 | 5 | 1 | 2† | 0 | 0 |
| *Cyrtopodion scaber* | - | - | - | - | - | - | - | - | - | 10 | 2 | 0 |
| *Hemidactylus flaviviridis* | - | - | - | - | - | - | - | - | - | 1 | 0 | 0 |
| *Hemidactylus persicus* | - | - | - | - | - | - | - | - | - | 10 | 2 | 0 |
| *Tropiocolotes sp.* | - | - | - | - | - | - | - | - | - | 1 | 5 | 0 |
| *Acanthodactylus cantoris* | 0 | 12 | 1 | 21 | 23 | 50 | 16 | 18 | 28 | - | - | - |
| *Ophisops jerdoni* | - | - | - | - | - | - | - | - | - | 7 | 3 | 8 |
| *Ophiomorus raithmai* | 0 | 2 | 0* | 0* | 0* | 0* | 0* | 0* | 0* | 0†* | 0 | 0 |
| Abundance range | 10 – 40 | | | 44 – 82 | | | 25 – 39 | | | 10 – 31 | | |
| Mean abundance | 20.3 | | | 59.3 | | | 31.3 | | | 19.3 | | |
| Species richness# | 1 - 5 | | | 3 (4) | | | 3 (4) - 4 (5) | | | 3 – 8 (9) | | |
| Species Diversity+ | 1.23 | | | 0.84 | | | 0.89 | | | 1.57 | | |

Dashes indicate species not recorded from a particular habitat type
† only found where there are extensive sand deposits
* tracks recorded in grid
# *Ophiomorus* added to species richness based on indirect signs, in parentheses
+ Shannon's index of diversity

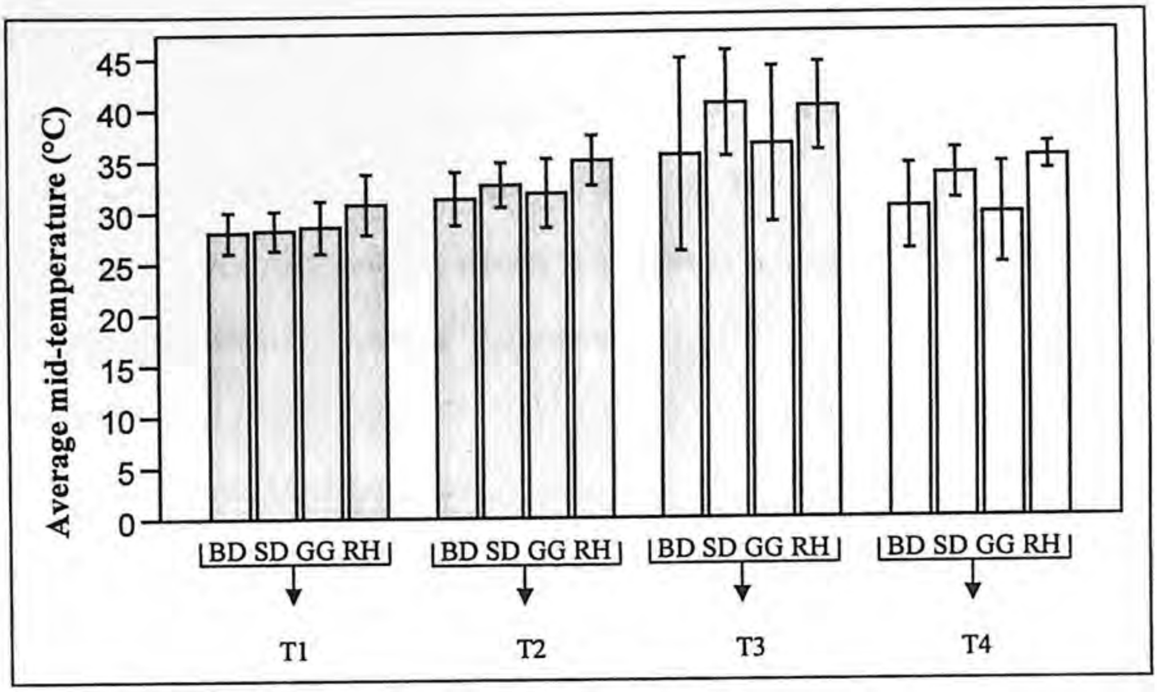


**Figure 4.2** Average temperatures recorded during the middle of transects across habitat types with 95% CI. BD-barren dunes, SD-stabilized dunes, GG-grassland, RH-rocky hills. T1 to T4 are transects

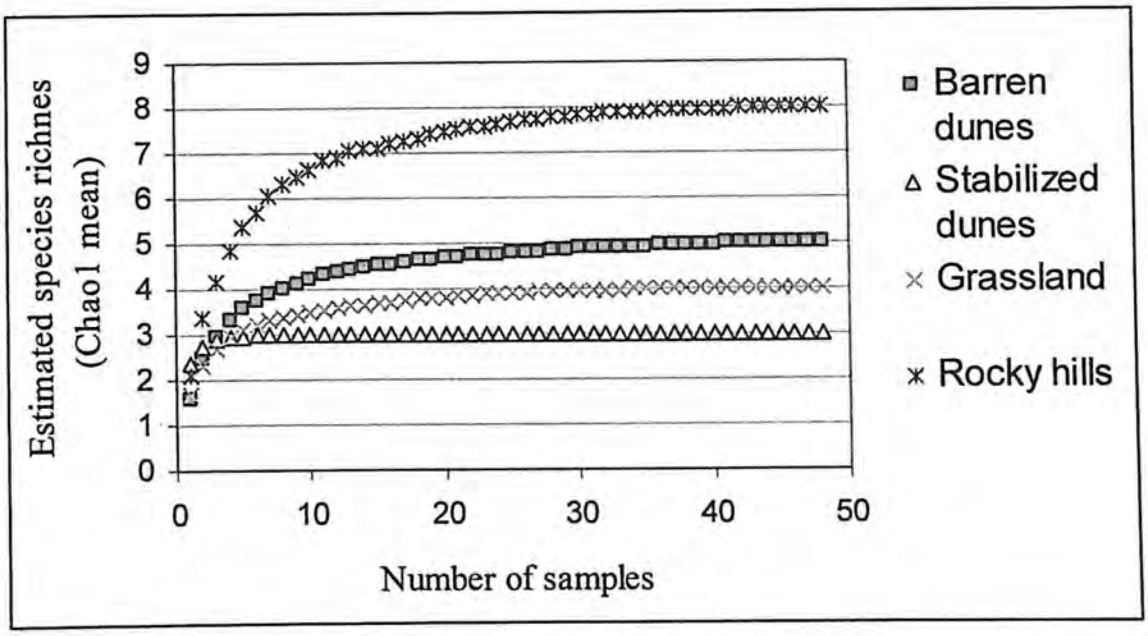


**Figure 4.3** Species accumulation curves across different habitat types

### 4.2 Range extensions

The closest records of *Tropiocolotes persicus euphorbiacola* are from the Thar Desert in Thar Parkar district, Pakistan (Minton *et al.* 1970; Khan 2006). The present finding represents the first record of this species and genus from within the political boundaries of India. *Hemidactylus persicus* was recently reported from India from Banskantha District, Gujarat (Vyas *et al.* 2006). This is the second report of this species from India and the first record from Rajasthan.

### 4.3 General patterns of abundance and dominance across habitats

*Acanthodactylus* was the most widely distributed (71.5 % of sample plots occupied) and abundant lizard on sand (for abundances see Table 4.2), followed by *Crossobamon* (49.3%) which was the most abundant nocturnal species, and finally by *Trapelus* (32%).

Barren dunes were characterized by dominance of *Bufoniceps* (68.8% of sample plots); with *Acanthodactylus* (25%) and *Crossobamon* (29.2%) as subdominants in vegetated grids. *Bufoniceps* is entirely restricted to this habitat. Nine sample plots in this habitat had no lizard sightings, though *Bufoniceps* tracks were observed on all plots in this habitat (not used in analysis).

Stabilized dunes had just four species (including *Ophiomorus* presence from its tracks). *Acanthodactylus* (100%) and *Crossobamon* (81.3%) were the dominant species, with *Trapelus* (50%) as a subdominant. All 48 plots had at least one species.

Grasslands additionally had the herbivorous *Uromastyx*, found only in gravely areas of this habitat. In other respects, the sandy parts of this habitat are similar to stabilized dunes in species composition, except that *Acanthodactylus* was dominant (89.5%) across all grids, with *Trapelus* (31.3%) and *Crossobamon* (37.5%) as subdominants. The first grid with a high proportion of gravel had these three species in similar abundance. Only two plots had zero species registrations.

The rocky hills had the highest species richness (nine; Table 4.2) and were characterized by low abundance of all species. Overall *Ophisops* was dominant (66.7%), though *Cyrtopodion* (27.1% overall in this habitat) and *H. persicus* (31.3%) were dominant in one grid, and in another grid *Tropiocolotes* (16.7% overall) was dominant. Six sample plots were unoccupied.

### 4.3.1 Nocturnal and diurnal species

Nocturnal lizards were represented by five species of geckos and a skink. The two nocturnal species in sandy habitats are *Ophiomorus* and *Crossobamon*, with three more species found in the rocky areas; *Hemidactylus flaviviridis*, *H. persicus* and *Tropiocolotes persicus*. The rocky habitat was unique in the proportion of nocturnal lizards, both in terms of species as well as proportionate abundances. In the barren dunes the proportion of nocturnal species is 0.4, stabilized dunes 0.5, grassland 0.4, and rocky hills 0.7. If total proportions are considered in terms of abundance (from least count abundances, Table 4.2) of nocturnal lizards vs. diurnal lizards, the difference is even more evident: 0.21 in barren dunes, 0.36 stabilized dunes, 0.21 grassland, and 0.57 in the rocky hills (Table 4.3)

**Table 4.3** Proportions of nocturnal species across different habitat types

| | Barren dunes | Stabilized dunes | Grassland | Rocky hills | Overall |
|---|---|---|---|---|---|
| Proportion of nocturnal species | 0.4 | 0.5 | 0.4 | 0.7 | 0.5 |
| Proportion of nocturnal lizards | 0.21 | 0.36 | 0.21 | 0.57 | 0.3 |

### 4.3.2 Cluster analysis

Cluster analysis of lizard species co-occurrence across plots clearly separates species found in the rocky area from psammophilous species (Fig 4.4). *Crossobamon* and *Acanthodactylus* cluster together, reflecting their similar distribution, while *Trapelus* forms the next cluster as most of the sightings were in sandy habitats. *Bufoniceps* is separated from these species but still clusters in the sandy group. *Uromastyx* and *Ophiomorus* have too few sightings to comment, however their position in the sand group fairly accurately represents their distribution. The rocky area had too few sightings of most species to make any definite statements, however some initial trends are apparent. *Ophisops*, ubiquitous in this habitat, clusters in the centre of this group. *Cyrtopodion* and *H. persicus* were observed in many of the same plots in the field, this relationship mirrored in the cluster.

A cluster of sample plots based on similarity in species composition (Jaccard similarity measure, group average linkage; not shown due to size constraints) reveals a similar pattern of co-occurence. Plots from the barren dunes separate almost completely. The grassland and stabilized dunes plots are indistinguishable in species composition and form a distinct group, along with a few barren dunes plots. The rocky area plots are a distinct unit, with one grassland plot (with only a single record of *Trapelus*) clustering with that group. There are no distinct groups within either main group.

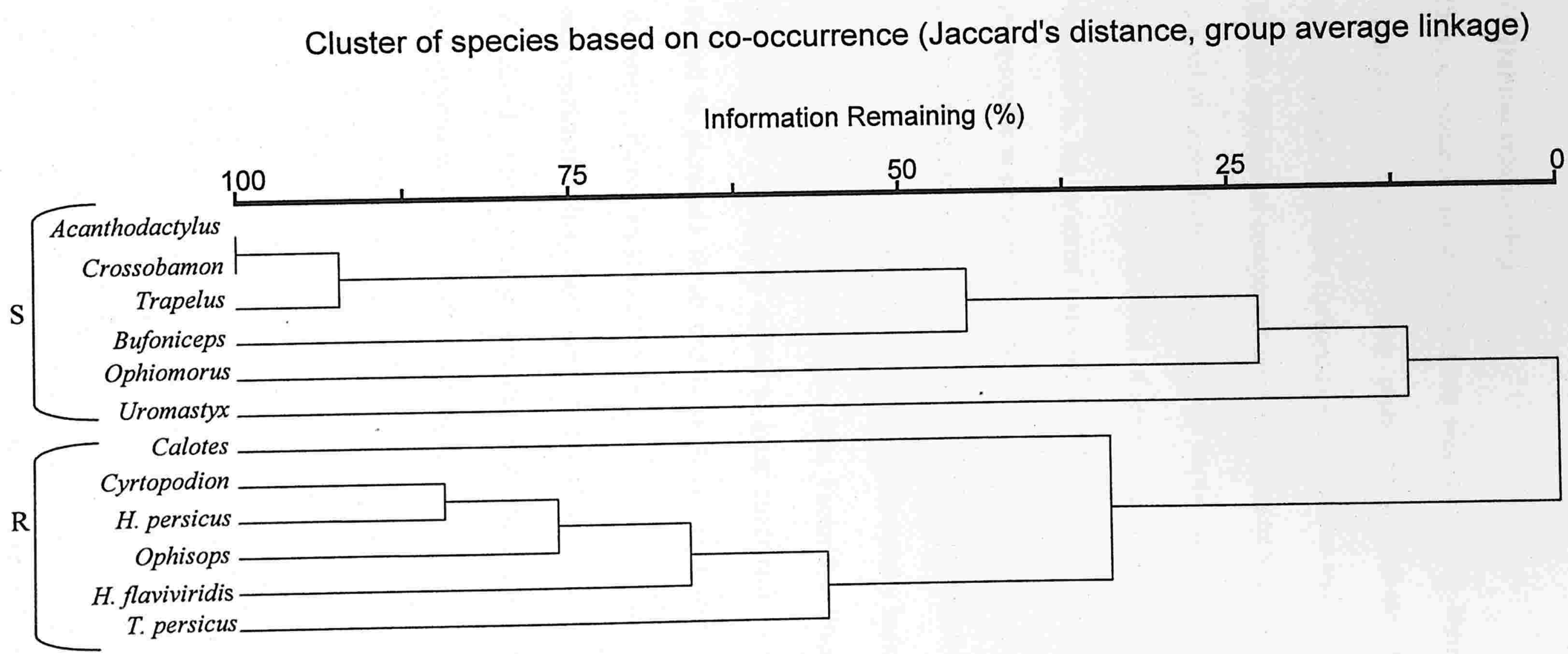


**Fig 4.4** Cluster of species based on abundance and co-occurrence across sample plots, with group average linkage and Jaccard's distance measure. S refers to psammophilous (sand associated) species, R to sclerophilous (rock associated) species.

#### 4.4 Habitat relationships

Presence-absence logistic regression was statistically significant only for species with registrations on at least nine plots. These include *Acanthodactylus, Bufoniceps, Crossobamon, Ophisops, Cyrtopodion, H. persicus* and *Trapelus*.

Results of principal component analysis of habitat variables are summarized in Table 4.4. A total of seven factors were extracted explaining 87.7% of the variance in the original data set of 17 variables. A total of seven factors were extracted explaining 87.7% of the variance in the original data set of 17 variables. Each of these factors was readily interpretable in ecological terms.

Factor 1 is formed by components of soil, indicating negative sand content and increasing pebbles, gravel and silt in the soil. Factor 2 essentially indicates increasing grass % in the ground cover and decreasing barren area. Factor 3 is linked to shrub cover and volume above 0.25m. Factor 4 is related to grass cover and volume above 0.25m. Factor 5 is related to increased shrub and herb % in the ground cover, and to a lesser extent decreasing barren area. Factor 6 is associated with grass volume below 0.25m in height and vegetation volume (grass and shrub) in the 0.25m – 0.50m height category. Factor 7 is related only to shrub volume below 0.25m in height. Table 4.5 summarizes contributing variables for the seven factors.

**Table 4.4** Factor loadings for 7 factors extracted from PCA of habitat variables. Shown are Eigen values, percentage of variation explained by each factor, cumulative variation explained, and correlations between original variables and extracted factors. Only variables with absolute value >0.3 are shown. All variables are significant at $p<0.01$ Varimax rotation was used.

| | FAC1 | FAC2 | FAC3 | FAC4 | FAC5 | FAC6 | FAC7 |
|---|---|---|---|---|---|---|---|
| Eigen Value | 3.50 | 2.55 | 2.36 | 2.33 | 1.83 | 1.30 | 1.04 |
| Variation explained (%) | 20.58 | 15.02 | 13.85 | 13.73 | 10.78 | 7.65 | 6.12 |
| Cumulative (%) | 20.58 | 35.59 | 49.45 | 63.18 | 73.96 | 81.61 | 87.72 |
| **Pearson's correlations** | | | | | | | |
| %sand | -0.97 | - | - | - | - | - | - |
| %grav | 0.88 | - | - | - | - | - | - |
| % peb | 0.85 | - | - | - | - | - | - |
| % silt | 0.81 | - | - | - | - | - | - |
| % Grass | - | 0.96 | - | - | - | - | - |
| %Barren | - | 0.91 | - | - | -0.35 | - | - |
| Gr_rk_av | 0.43 | 0.75 | - | - | - | - | - |
| Sh_Cov | - | - | 0.94 | - | - | - | - |
| Sh_Vol3 | - | - | 0.86 | - | - | - | - |
| Sh_Vol2 | - | - | 0.71 | - | - | 0.37 | - |
| Gr_Vol3 | - | - | - | 0.94 | - | - | - |
| Gr_Cov | - | - | - | 0.93 | - | - | - |
| Gr_Vol2 | - | - | - | 0.57 | - | 0.48 | - |
| ShHrb_rk_av | - | - | - | - | 0.89 | - | - |
| %Sh_Hrb | - | - | - | - | 0.87 | - | - |
| Gr_Vol1 | - | - | - | - | - | 0.89 | - |
| Sh_Vol1 | - | - | - | - | - | - | 0.92 |

**Table 4.5** PCA factors, their abbreviations and main contributing variables.

| FACTOR | Abbreviation | Positive variables | Negative variables |
|---|---|---|---|
| FAC1 | Peb_Grav | %grav, %peb,%silt | %sand |
| FAC2 | Gr_per | % Grass, Gr_rk_av | % Barren |
| FAC3 | Sh_Cov_Vol2-3 | Sh_Cov, Sh_Vol2, Sh_Vol3 | - |
| FAC4 | Gr_Cov_Vol2-3 | Gr_Cov, Gr_Vol2, Gr_Vol3 | - |
| FAC5 | Sh_Hrb | ShHrb_rk_av, %Sh_Hrb | - |
| FAC6 | Gr_Vol1_Veg2 | Gr_Vol1, Gr_Vol2, Sh_Vol2 | - |
| FAC7 | Sh_Vol1 | Sh_Vol1 | - |

### 4.4.1 Distribution of sampling plots

A scatter diagram of sampling plots against the first two PCA axes separates habitat types fairly clearly (Fig 4.5). Axis 1 (Peb_Grav) is related positively to pebble, gravel and silt content and negatively to sand; while axis 2 (Gr_per) is related positively to % grass in ground cover and negatively to % barren area. Sandy plots are clustered on the left and rocky, gravely plots to the right. Barren dunes separate from other sandy habitats based on low grass cover, while rocky hills separate on account of high rock content in soil. Stabilized dunes and grasslands overlap, along with a few barren dunes plots, based on soil and ground cover. Most grassland plots separate along axis 2 due to high ground cover, and a few plots are close to the rocky hills plots, reflecting similarity in soil structure.

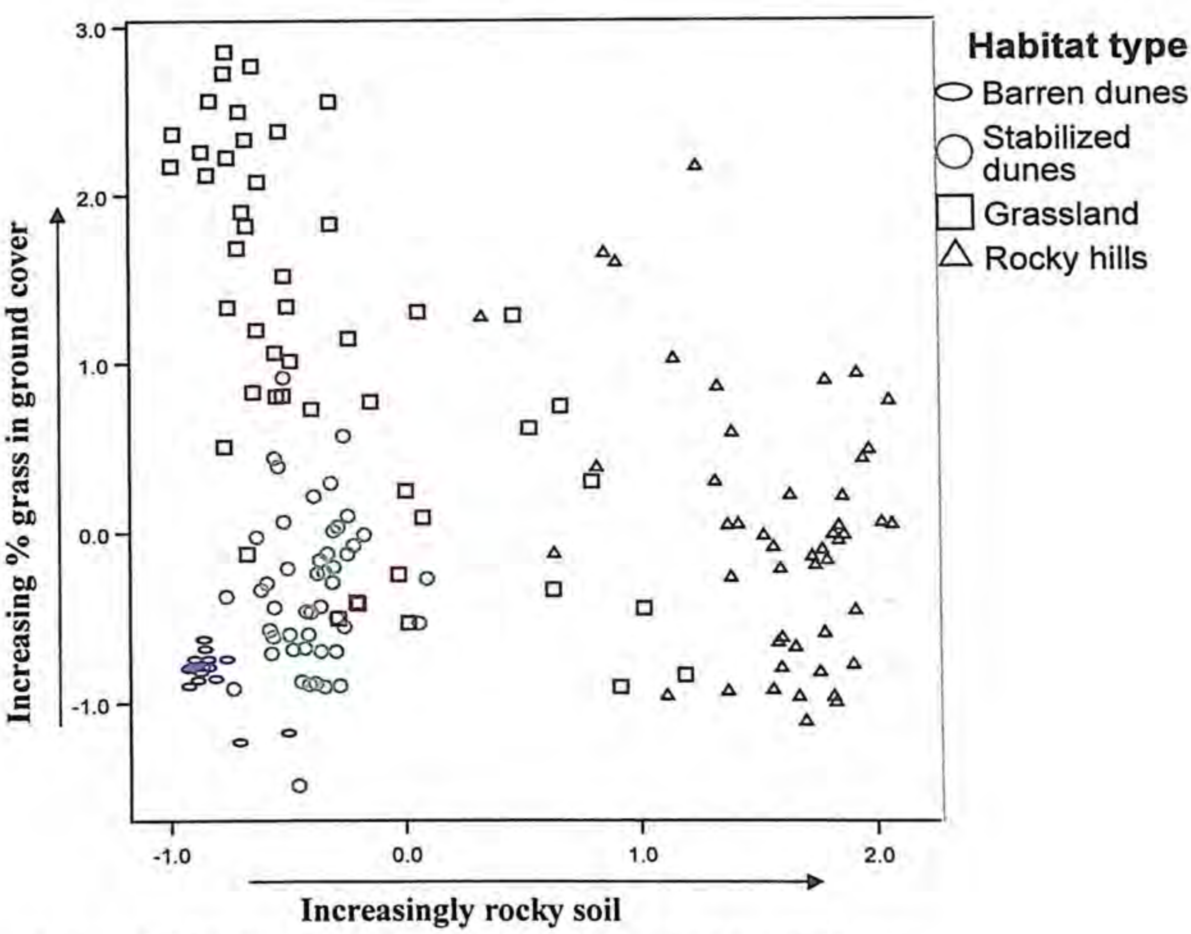


**Figure 4.5** Scatter diagram of plots against the first two PCA axes.

### 4.4.2 Specific accounts

***Acanthodactylus cantoris*:**

A total of 556 sightings of this species were recorded on 103 plots (Table 4.6). This species was widespread in the three sandy habitats (barren and stabilized dunes, grassland), and was not recorded from the rocky hills habitat. The model in logistic regression predicted species presence-absence well ($R^2$=0.81), with an overall correct classification rate of 92.7 % (with 88.3 % of occupied plots correctly classified). A cutoff value of 0.5 gave a fairly good model with predictions conforming to field observations. The strongest variables contributing to this species presence were found to be high vegetation (volume and cover >25 cm in height (Sh_Cov_Vol2-3, Gr _Cov_Vol2-3), low pebbles, gravel and silt (negative association with Peb_Grav), and herbs and shrubs in the ground cover (Sh_Hrb).

When analysis was restricted to the sandy habitats the same variables were picked up ($R^2$=0.74), though the order changed slightly with shrub volume and cover (Sh_Cov_Vol2-3, ShVol1) becoming the most important variable, followed by grass volume and cover (Gr_Cov_Vol2-3, GrVol1), herbs and shrubs in ground cover (Sh_Hrb) and sand (– Peb_Grav).

Large rodent burrows alone predicted absence of this species well (98.9%, cutoff 0.5), but did not predict presence as well (76.7%).

**Table 4.6** Summary of binary logistic regression showing model parameters and variables contributing to species presence across all habitat types for eight species. Standard error (S.E.) is given for each variable. AC- *Acanthodactylus cantoris*, BL- *Bufoniceps laungwalansis*, CO- *Crossobamon orientalis*, OR- *Ophiomorus raithmai*, TA- *Trapelus agilis*, OJ- *Ophisops jerdoni*, CS- *Cyrtopodion scaber*, HP- *Hemidactylus persicus*

| | AC | BL | CO | OR | TA | OJ | CS | HP |
|---|---|---|---|---|---|---|---|---|
| No. of occupied plots | 103 | 33 | 75 | 43 | 55 | 32 | 13 | 9 |
| Nagelkerke $R^2$ | 0.81 | 0.75 | 0.32 | 0.27 | 0.17 | 0.66 | 0.45 | 0.46 |
| Proportion of total plots occupied | 0.54 | 0.17 | 0.39 | 0.22 | 0.29 | 0.17 | 0.07 | 0.05 |
| Classification cutoff | 0.5 | 0.3 | 0.3 | 0.3 | 0.25 | 0.3 | 0.12 | 0.06 |
| Overall classification rate | 92.7 | 93.8 | 72.4 | 81.8 | 64.6 | 91.7 | 91.7 | 86.5 |
| Occupied plot classification rate | 88.3 | 100.0 | 77.3 | 65.1 | 61.8 | 93.8 | 92.3 | 100.0 |
| **Significant Variables** | | | | | | | | |
| Peb_Grav | –3.09 | –14.56 | –7.22 | - | - | 2.61 | 1.55 | 1.47 |
| S.E. | 0.60 | 4.72 | 0.21 | - | - | 0.46 | 0.43 | 0.47 |
| Gr_per | - | –1.88* | - | - | - | 0.71* | 0.82* | - |
| S.E. | - | 1.07 | - | - | - | 0.38 | 0.49 | - |
| Sh_Cov_Vol2-3 | 3.84 | - | 0.58 | 0.70 | - | - | - | - |
| S.E. | 1.27 | - | 0.17 | 0.18 | - | - | - | - |
| Gr _Cov_Vol2-3 | 3.78 | - | 0.46 | 0.68 | 0.54 | - | - | - |
| S.E. | 1.07 | - | 0.16 | 0.17 | 0.16 | - | - | - |
| Sh_Hrb | 2.68 | - | 0.41 | - | 0.38 | - | –1.21 | –2.45 |
| S.E. | 0.56 | - | 0.16 | - | 0.16 | - | 0.59 | 0.71 |
| GrVol1_Veg2 | - | - | 0.49 | 0.43 | 0.47 | - | - | - |
| S.E. | - | - | 0.21 | 0.19 | 0.19 | - | - | - |
| ShVOL1 | - | - | - | - | - | - | - | - |
| S.E. | - | - | - | - | - | - | - | - |

* significant at $p<0.1$ level. Other variables significant at $p<0.05$

***Bufoniceps laungwalansis*:**

This species was recorded on 33 plots and is restricted to the barren dunes habitat. The model in logistic regression had high $R^2$= 0.75 and correctly classified 93.8% of plots overall and 100% of occupied plots. A cutoff of value of 0.2 was tested (corresponding roughly to observed occupancy) but this model overpredicted considerably and a cutoff of 0.3 gave the best predictions with no predictions outside the barren dunes area. The strongest predictors of this species presence were sandy soil (– Peb_Grav), and high % barren area (–Gr_per; significant at $p<0.1$ level), which represents the characteristics of the barren dunes habitat in general.

When comparisons were limited to within the barren dunes habitat, the model was poor ($R^2 < 0.20$). Slope was not significant in explaining presence and absence of this species.

***Crossobamon orientalis*:**

This gecko was ubiquitous in areas with surface sand deposits, across all habitat types. The model performed poorly overall ($R^2=0.32$, overall classification=72.4%, occupied=77.3%). The strongest variable determining presence was sandy soil (–Peb_Grav), followed by shrub volume (>25 cm height) and shrub cover (Sh_Cov_vol2-3), grass volume (Gr _Cov_Vol2-3, GrVol1_Veg2), %herb and shrub in ground cover (Sh_Hrb).

For sandy habitats alone the model did not improve, ($R^2= 0.21$, overall classification=76.4%, occupied=77.5%). Significant predictors were sandy soil (–Prb_Grav), shrub volume (>25 cm height) and cover (Sh_Cov_vol2-3), decreasing grass in ground cover (–Gr_per).

***Ophiomorus raithmai*:**

Indirect signs of this species indicated it is ubiquitously distributed in sandy tracts. The logistic regression model for all habitats was poor $R^2=0.27$, and could not predict presence well (81.8%, 65.1%; cutoff 0.3). Shrub volume and cover (Sh_Cov_vol2-3), as well as grass cover and volume (Gr _Cov_Vol2-3, GrVol1_Veg2) were significant variables. Sand was not selected as a significant variable.

Within sandy habitats the prediction improved slightly ($R^2$=0.35; 77.8% overall, 71.1 occupied; cutoff 0.3). Additional to the previously selected variables, %grass in ground cover was selected as the strongest (negative) variable (–Gr_per).

***Trapelus agilis*:**

This species is widely distributed, occurring in all the habitat types with highly variable microhabitats. This apparently poor environmental determination at this scale was reflected in the model with a low $R^2$ (0.17), and poor classification (64.6% overall, 61.8% occupied; cutoff=0.25). The only significant predictors were grass volume (Gr _Cov_Vol2-3, GrVol1_Veg2) and % of herbs and shrubs in ground cover (Sh_Hrb; Table 4.6).

When analysis was restricted to the sandy habitats the model still performed poorly ($R^2$=0.20; 66.7% and 67.4%; cutoff 0.3), and sandy soil (–Peb_Grav) was added as a predictor. For just stabilized dunes and grassland $R^2$ = 0.22 (70.1%, 74.4%), and presence was associated negatively with %grass in the ground cover (–Gr_per) and positively with shrub volume >25 cm and shrub cover (Sh_Cov_Vol2-3).

***Ophisops jerdoni*:**

Widely distributed throughout, and restricted to the rocky habitat, this species had few predictors for presence (Table 4.6). Prediction accuracy was high ($R^2$=0.66; 91.7%, 93.8%; cutoff 0.3). Pebbles and gravel content in soil (Peb_Grav) was the strongest positive factor, followed by percent grass in the ground cover (Gr_per; significant at $p$<0.1 level).

When analysis was restricted to the rocky habitat (Table 4.7), the model could not predict presence well ($R^2$=0.16; 68.8% overall, 87.5 occupied; cutoff 0.5) with shrub volume >25 cm in height and shrub cover (Sh_Cov_Vol2-3), herbs and shrubs in the ground cover (Sh_Hrb) as the only significant variables. Addition of rock size categories did not improve prediction

**Table 4.7** Summary of binary logistic regression showing model parameters and variables contributing to species presence within the rocky habitat for four species. Standard error (S.E.) is given for each variable. CS – *Cyrtopodion scaber*, HP- *Hemidactylus persicus*, OJ- *Ophisops jerdoni*, TA- *Trapelus agilis*

| | CS | HP | OJ | TA |
|---|---|---|---|---|
| Logistic regression method | forward | forward | backward | backward |
| No. of occupied plots | 13 | 9 | 32 | 9 |
| Nagelkerke R2 | 0.59 | 0.78 | 0.16 | 0.20 |
| Proportion of total plots occupied (in this habtat) | 0.27 | 0.19 | 0.67 | 0.19 |
| Classification cutoff | 0.3 | 0.2 | 0.55 | 0.2 |
| Overall Classification Rate | 85.4 | 89.6 | 81.3 | 72.9 |
| Occupied plot classification rate | 76.9 | 88.9 | 70.8 | 66.7 |
| **Significant Variables** | | | | |
| Peb_Grav | - | - | - | 2.89$^+$ |
| S.E. | - | - | - | 1.84 |
| Gr_per | 1.52 | - | - | - |
| S.E. | 0.66 | - | - | - |
| Sh_Cov_Vol2-3 | - | 7.93 | 2.46 | - |
| S.E. | - | 3.43 | 1.18 | - |
| Sh_Hrb | - | - | 1.20* | - |
| S.E. | - | - | 0.62 | - |
| Large rocks | 0.34 | - | - | 0.24* |
| S.E. | 0.12 | - | - | 0.13 |
| Small & medium rubble | - | -0.28 | - | |
| S.E. | - | 0.13 | - | |
| Sheet | - | - | - | 0.10* |
| S.E. | - | - | - | 0.05 |

* significant at $p$<0.1, $^+$significant at $p$<0.12; other variables significant at $p$<0.05

*Cyrtopodion scaber*:

The overall model for this species was poor ($R^2$= 0.45; Table 4.6) and over predicted presence (91.7, 92.3; cutoff 0.12) with some plots in the grassland predicted as having this species. The significant variables were rocky soils (Peb_Grav), and decreasing shrub and herb in ground cover (– Sh_Hrb). Grass % in ground cover (Gr_per) was significant at the $p$>0.1 level.

When considered within the rocky habitat alone (Table 4.7), only grass percent in ground cover (Gr_per) and large rocks were selected as significant positive predictors ($R^2$=0.59; 85.4%, 76.9%; cutoff 0.3).

*Hemidactylus persicus*:

Only nine plot registrations of this species were recorded and so a cutoff level of 0.07 was selected, with an overall classification rate of 86.5%, occupied classification rate of 100.0% ($R^2$=0.46; Table 4.6). Shrub and herb cover was negatively related and rocky content positively related.

Within the rocky habitat (Table 4.7), the model was considerably improved with $R^2$= 0.78 (89.6%, 88.9%; cutoff 0.2). Different variables explained presence within this habitat, shrub volume >25 cm in height and cover, and a negative association with medium rubble.

## 4.5 Resource partitioning

### 4.5.1 Habitat co-occurence

Of the 12 species observed, only *Trapelus* and *Crossobamon* were found in all habitat types, though *Crossobamon* was linked to the presence of surface sand. *Acanthodactylus* was found in the three sandy habitats (BD, SD, GG), while *Bufoniceps* was restricted to - the barren sand dunes. *Uromastyx* was only found in the grassland habitat, and *Ophisops*, *Tropiocolotes*, and the two *Hemidactylus* geckos were restricted to the rocky habitat. *Ophiomorus* was only observed directly in the barren dunes, but tracks were observed in sandy tracts in all habitats. Opportunistic sightings did not change the observed pattern of habitat specificity. Table 4.8 summarizes species composition of different habitat types.

**Table 4.8** Species occurrence in different habitats.

| **Species** | **BD** | **SD** | **GG** | **RH** |
|---|---|---|---|---|
| *Bufoniceps laungwalansis* | ■ | | | |
| *Calotes versicolor* | | | | ■ |
| *Trapelus agilis* | ■ | ■ | ■ | ■ |
| *Uromastyx hardwickii* | | | ■ | |
| *Crossobamon orientalis* | ■ | ■ | ■ | ■ * |
| *Cyrtopodion scaber* | | | | ■ |
| *Hemidactylus flaviviridis* | | | | ■ |
| *Hemidactylus persicus* | | | | ■ |
| *Tropiocolotes sp.* | | | | ■ |
| *Acanthodactylus cantoris* | ■ | ■ | ■ | |
| *Ophisops jerdoni* | | | | ■ |
| *Ophiomorus raithmai* | ■ | ■ | ■ | ■ * |
| Total no. of species (no. of species unique to the habitat) | 5 (1) | 4 (0) | 5 (1) | 9 (6) |

* only where there are extensive sand deposits

### 4.5.2 Spatial overlap

Spatial overlap at the level of the 25m plots across all habitats was moderate only for three pairs: *Acanthodactylus-Crossobamon* (Piankas measure 0.59, Czechanowski's measure 0.48), *Acanthodactylus-Trapelus* (0.48, 0.36), and *Crossobamon-Trapelus* (0.36, 0.32). The observed niche overlap was not much higher than expected (Pianka's mesure, $p$=0.32; Czechanowski's measure, $p$=0.52). Overall spatial overlap is summarized in Table 4.9 Cluster analysis of species composition revealed a similar pattern of co-occurrence (Fig. 4.3).

When only diurnal species were considered with cumulative registrations of all species, the absolute values of overlap did not change markedly (*Acanthodactylus-Trapelus*= 0.52, 0.40), however the observed overlap was significantly higher than expected ($p$=0.99, both measures).

**Table 4.9** Overall spatial overlap for 192 plots. Pianka's measure shown in the right half, Czechanowski's measure on the bottom half. AC- *Acanthodactylus cantoris*, BL- *Bufoniceps laungwalansis*, CO- *Crossobamon orientalis*, OJ- *Ophisops jerdoni*, TA- *Trapelus agilis*

| | AC | BL | CO | OJ | TA |
|---|---|---|---|---|---|
| **AC** | - | 0.09 | 0.59 | 0 | 0.48 |
| **BL** | 0.03 | - | 0.06 | 0 | 0.03 |
| **CO** | 0.48 | 0.05 | - | 0.01 | 0.36 |
| **OJ** | 0 | 0 | 0.01 | - | 0.05 |
| **TA** | 0.36 | 0.06 | 0.32 | 0.05 | - |

### 4.5.3 Microhabitat categories and distance to vegetation

Some trends were evident across species with regard to microhabitat category. *Acanthodactylus* was most often seen in the open sun (53%, n=216). 93% of active *Bufoniceps* (n=44) were seen in the open sun, while 48% of undisturbed *Bufoniceps* were buried (fossorial; n= 86). 57% of *Trapelus* were seen either inside or on a bush (bush and high sun categories combined; n=68). *Ophisops* was closely associated with rocks and 50% of sightings were associated with rock shade. Of six sightings of *Calotes*, five were associated with vegetation above 1.5m high.

For nocturnal species defining microhabitat categories was difficult. Among nocturnal species only *Crossobamon* was abundant, with 100% of sightings on the ground (nocturnal terrestrial; n=167). The two sightings of *Ophiomorus* were both while the animals were buried (nocturnal fossorial) and this species is almost entirely fossorial, though occasionally coming above ground (pers. obs.). All sightings of *Cyrtopodion*, *Hemidactylus persicus*, *Hemidactylus flaviviridis*, and *Tropiocolotes* were associated with rocks (nocturnal rupicolous).

Distance to closest vegetation was not considered for *Ophisops* because the rocky habitat generally has much lower vegetation cover, and escape cover is usually among crevices. *Acanthodactylus*, *Bufoniceps*, *Crossobamon* and *Trapelus* show significantly different spatial use when measured as distance to closest vegetation ($Chi^2$ test, $p<0.001$). *Bufoniceps* was found further than 3m from vegetation more than expected, while *Trapelus* was found within 25 cm more often than expected, *Acanthodactylus* within 1m, and from 0.25m-1m..

### 4.5.4 Habitat-specific comparisons

**Barren dunes**

When the barren dunes were considered independently at the 25 m plot level (Table 4.10), overlap was moderate for all species pairs except *Bufoniceps-Trapelus* (0.10, 0.06). The observed overlap was significantly less than expected ($p< 0.005$, both measures). Overlap was highest between *Acanthodactylus*, *Trapelus* and *Crossobamon* (Table 4.10). *Bufoniceps* had low overlap with all other species (0.06-0.32). At a finer scale this species further separates with different spatial use of the dunes in two respects, dune position (Fig. 4.6, 4.7) and distance to closest vegetation. 56% of *Bufoniceps* sightings (n=86) were more than 5 m away from the closest vegetation, and only 15% less than 1m from vegetation. On the other hand 77% of *Acanthodactylus* sightings (n=13) and 63% of *Crossobamon* sightings (n=19) were within 1m of vegetation.

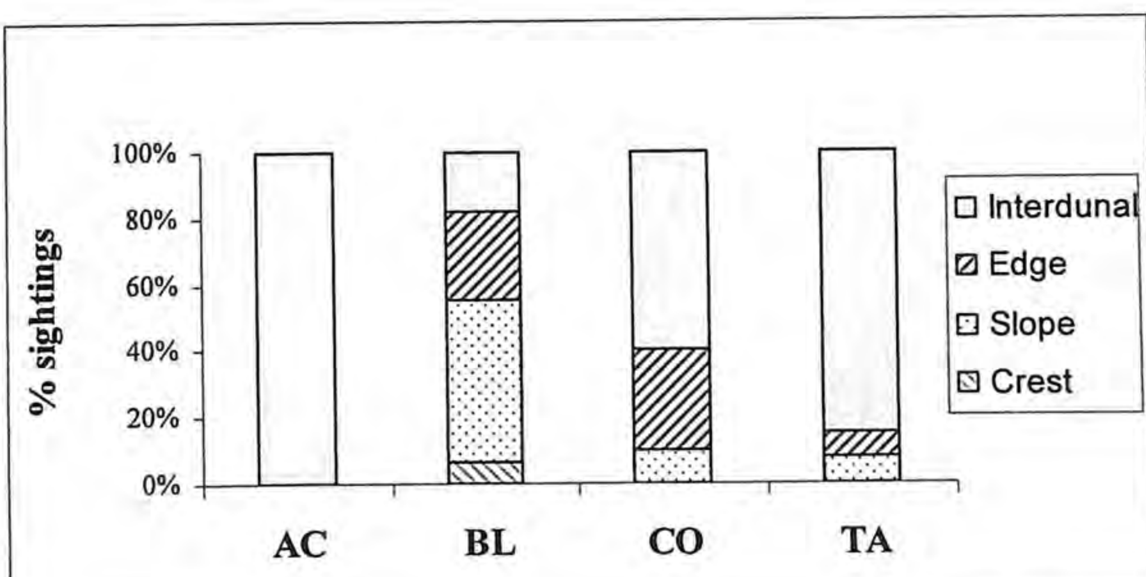


**Figure 4.6** Spatial use by four species in the barren dunes*Acanthodactylus* (AC; n=40), *Bufoniceps* (BL; n=89), *Crossobamon* (CO; n=20) and *Trapelus* (TA; n=13).

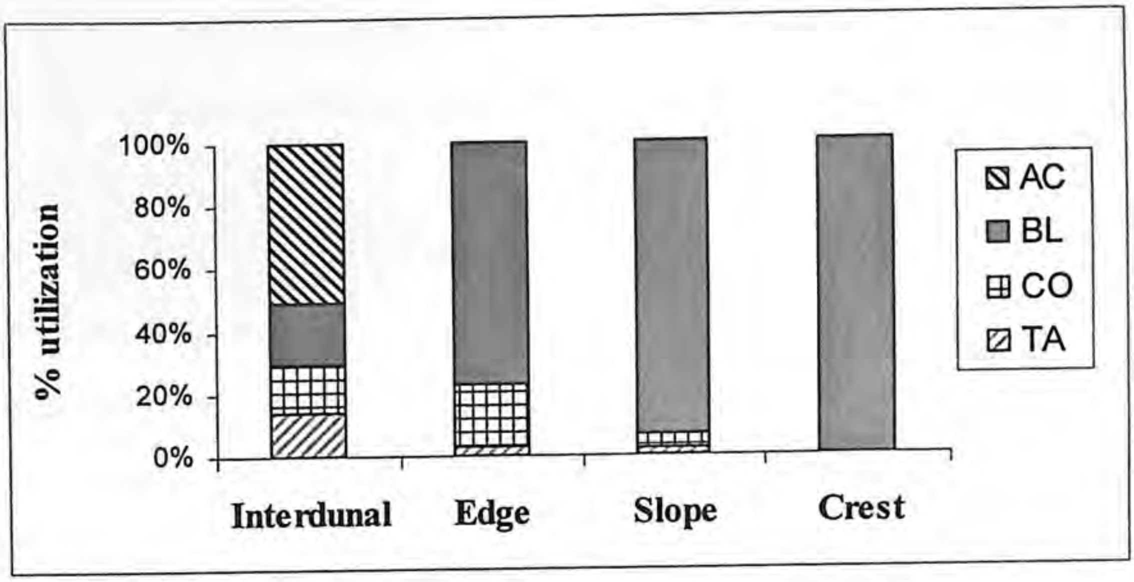


**Figure 4.7** Spatial use of barren dunes by four species. AC- *Acanthodactylus* (n=40), BL- *Bufoniceps* (n=89), CO- *Crossobamon* (n=20) and TA- *Trapelus* (n=13).

**Table 4.10** Spatial overlap within sandy habitats. Pianka's measure shown above, with Czechanowski's measure beneath. AC- *Acanthodactylus cantoris*, BL- *Bufoniceps laungwalansis*, CO- *Crossobamon orientalis*, TA- *Trapelus agilis*

| | AC-BL | AC-CO | AC-TA | BL-CO | BL-TA | CO-TA |
|---|---|---|---|---|---|---|
| **BD** | 0.32 | 0.39 | 0.45 | 0.25 | 0.10 | 0.65 |
| | 0.29 | 0.29 | 0.27 | 0.23 | 0.06 | 0.40 |
| **SD** | - | 0.69 | 0.60 | - | - | 0.31 |
| | - | 0.60 | 0.49 | - | - | 0.33 |
| **GG** | - | 0.30 | . | - | - | 0.51 |
| | | 0.19 | 0.19 | - | - | 0.36 |

**Stabilized dunes**

This habitat had only three species, but each of these was in its highest abundance in this habitat (Table 4.2). Overlap at the level of 25 m plots (Table 4.10) was highest for *Acanthodactylus-Crossobamon* (0.69, 0.60) and *Acanthodactylus-Trapelus* (0.60, 0.49);

and low for *Crossobamon-Trapelus* (0.31, 0.33). Substrate is constant within this habitat, so the only way in which species separate is based on microhabitat categories and distance to vegetation.

A Chi² test comparing distance to closest vegetation across these species was significant ($p$=0.006), indicating that *Trapelus* was found disproportionately often within 0.25m of vegetation (89% of sightings in this habitat; n=28), while the other two species were found approximately in proportion (*Crossobamon, Acanthodactylus*: 51,52% <0.25m; 24,26% 0.25-1m; 24,21% 1-3m ). 52.5 % of *Acanthodactylus* sightings (n=139) were in open sun, 22.3 % in bushes and 19.4 % in shade of vegetation. *Trapelus* (n=25) had 40.0% of sightings in bushes and a further 32% sightings on bushes between 0.3m to 1.5 m high (low and high sun).

**Grassland**

Patterns of overlap at plot level are slightly different within this habitat (Table 4.10). Only *Trapelus-Crossobamon* show moderate overlap (0.51. 0.36), while other pairs are below 0.3 (both measures). These species are further separated in this habitat by use of substrate. *Acanthodactylus* used gravel significantly less and sand more than expected , *Crossobamon* used gravel more, and sand less than expected, while *Trapelus* used gravel more, and sand in proportion (chi-square test, $p$<0.001; Fig. 4.8). However in terms of the proportion of total lizards using these substrate categories, *Crossobamon* was clearly highest in gravel and *Acanthodactylus* highest on sand (Fig. 4.9).

43.2 % of *Acanthodactylus* (n=88) sightings were in grass, and 38.6% in the open sun. *Trapelus* (n=26) on the other hand had 46.2% sightings on bushes (low and high sun), and remaining sightings were equally divided between bushes and grass (19.3% each), and open sun (15%).

The <0.25m distance to vegetation category had 83.0% of *Acanthodactylus* sightings, 54.2% of *Crossobamon* sightings (n=24), and 88.5% of *Trapelus* sightings. However, the majority of *Acanthodactylus* sightings were close to grass and *Trapelus* sightings close to bushes, as mentioned above.

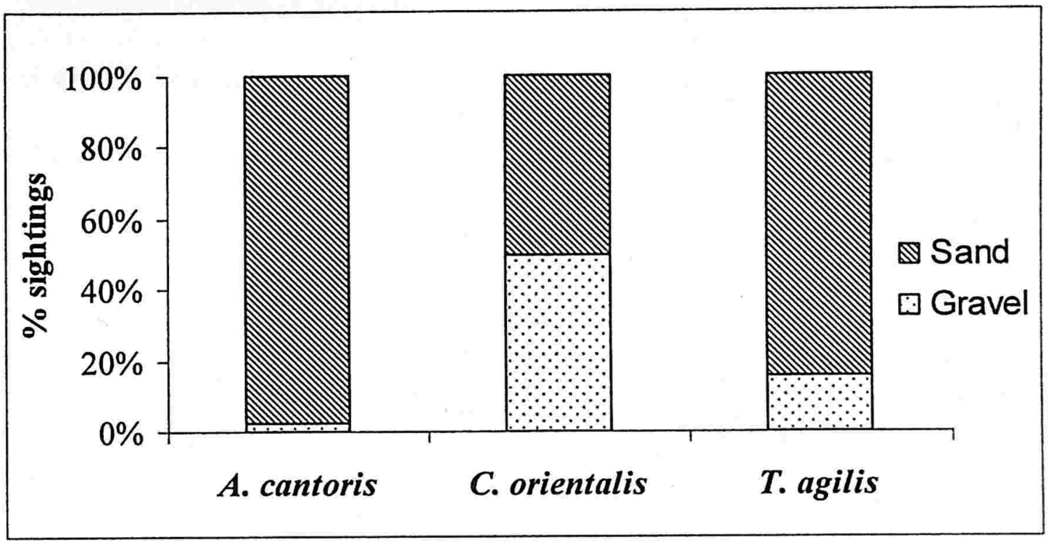


**Figure 4.8** Substrate use by three species in grasslands. *A. cantoris* (n=196), *C. orientalis* (n=33), *T. agilis* (n=35)

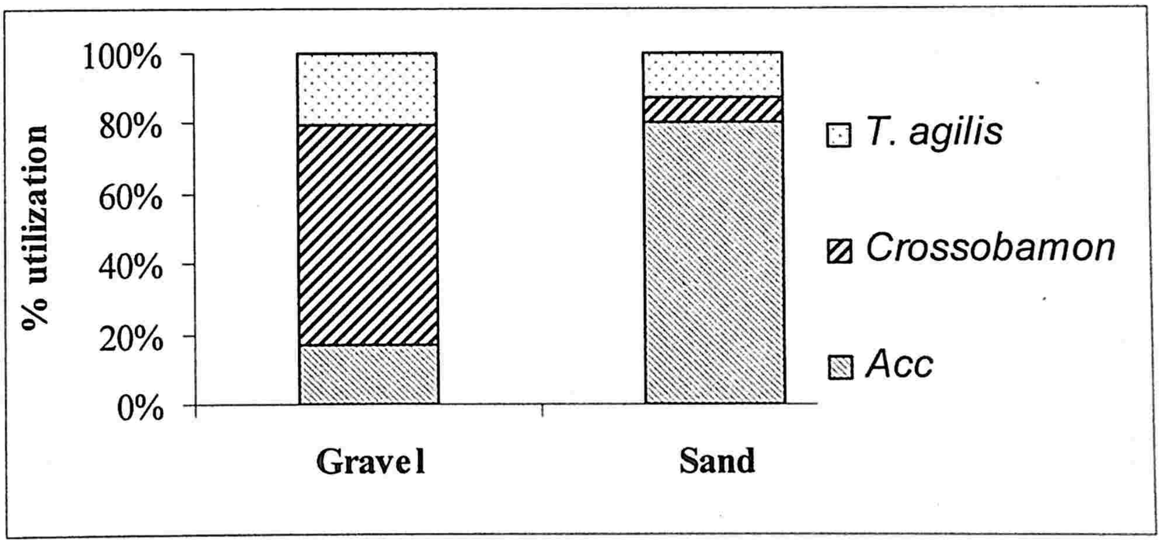


**Figure 4.9** Substrate use in grasslands by three species. *A. cantoris* (n=196), *C. orientalis* (n=33), *T. agilis* (n=35)

**Rocky Hills**

The rocky hills were characterized by high species richness and low abundance of all lizards. Spatial overlap was low (Table 4.11) but considerably higher than expected ($p>0.8$, both measures). *Crossobamon* was restricted to sand deposits which were not used preferentially by other species. *Ophisops* was by far the most abundant species in this habitat (6ind/ha), and along with *Trapelus* (1.3ind/ha) and *Calotes* (1/ha) found on all 3 grids. *Cyrtopodion* and *H. persicus* (4ind/ha), and *Tropiocolotes* (2/ha) were found on the same two grids with higher vegetation and *Euphorbia* cover. *Crossobamon* (0.7ind/ha) and *H. flaviviridis* (0.3ind/ha) were both restricted to one grid.

**Table 4.11**: Spatial overlap within the rocky habitat. Pianka's measure shown in the right half, Czechanowski's measure on the bottom half. CO-*Crossobamon orientalis*, CS-*Cyrtopodion scaber*, HP- *Hemidactylus persicus*, TA- *Trapelus agilis*, TP- *Tropiocolotes persicus*

| | CO | CS | HP | OJ | TA | TP |
|---|---|---|---|---|---|---|
| **CO** | - | 0.21 | 0.79 | 0.11 | 0.00 | 0.12 |
| **CS** | 0.17 | - | 0.33 | 0.37 | 0.27 | 0.18 |
| **HP** | 0.53 | 0.31 | - | 0.22 | 0.11 | 0.10 |
| **OJ** | 0.06 | 0.27 | 0.19 | - | 0.23 | 0.04 |
| **TA** | 0.00 | 0.21 | 0.13 | 0.12 | - | 0.00 |
| **TP** | 0.13 | 0.17 | 0.13 | 0.03 | 0.00 | - |

### 4.5.5 Temporal and thermal patterns of activity

Overall, activity of most diurnal species was predominantly unimodal, with a smaller peak in activity in the evening (Fig. 4.1). The unimodality was more pronounced in winter (Fig. 4.10). Times of activity in winter are different from summer, peak activity being between 4 ½ to 7 ½ hours after sunrise. In summer, activity was maximal for most species between 2 ½ hours to 4 hours after sunrise (72.8 % of all sightings). No sampling was carried out between 5-10 hrs after sunrise.

Different species had distinct trends in activity in summer (Table 4.12), with *Acanthodactylus* the first species to emerge with maximal activity in T1, followed by *Bufoniceps* with maximal activity in T2. *Trapelus* was the most variable, peaking in activity in either T2 or T3. Activity of *Ophisops* did not show any specific trends.

The air temperatures at which peak activity were noted varied across species (Fig. 4.11). *Acanthodactylus* shows a peak at lower temperatures than the other species. *Trapelus* and *Ophisops* show peaks in activity at very high air temperatures (>40°C).

**Table 4.12** Activity of the four most abundant diurnal species across transects. Data are % of sightings for each species during transects. T1, T2 were repeated once each and T3 was not repeated. The total number of sightings in T1 and T2 was halved for comparisons. Sample size in parentheses.

| Transect | *A. cantoris* (303) | *Bufoniceps* (46) | *Ophisops* (43) | *Trapelus* (67) |
|---|---|---|---|---|
| T1 | 50.3 | 15.4 | 30.6 | 23.1 |
| T2 | 33.2 | 56.0 | 22.4 | 30.6 |
| T3 | 16.5 | 28.6 | 47.1 | 46.3 |

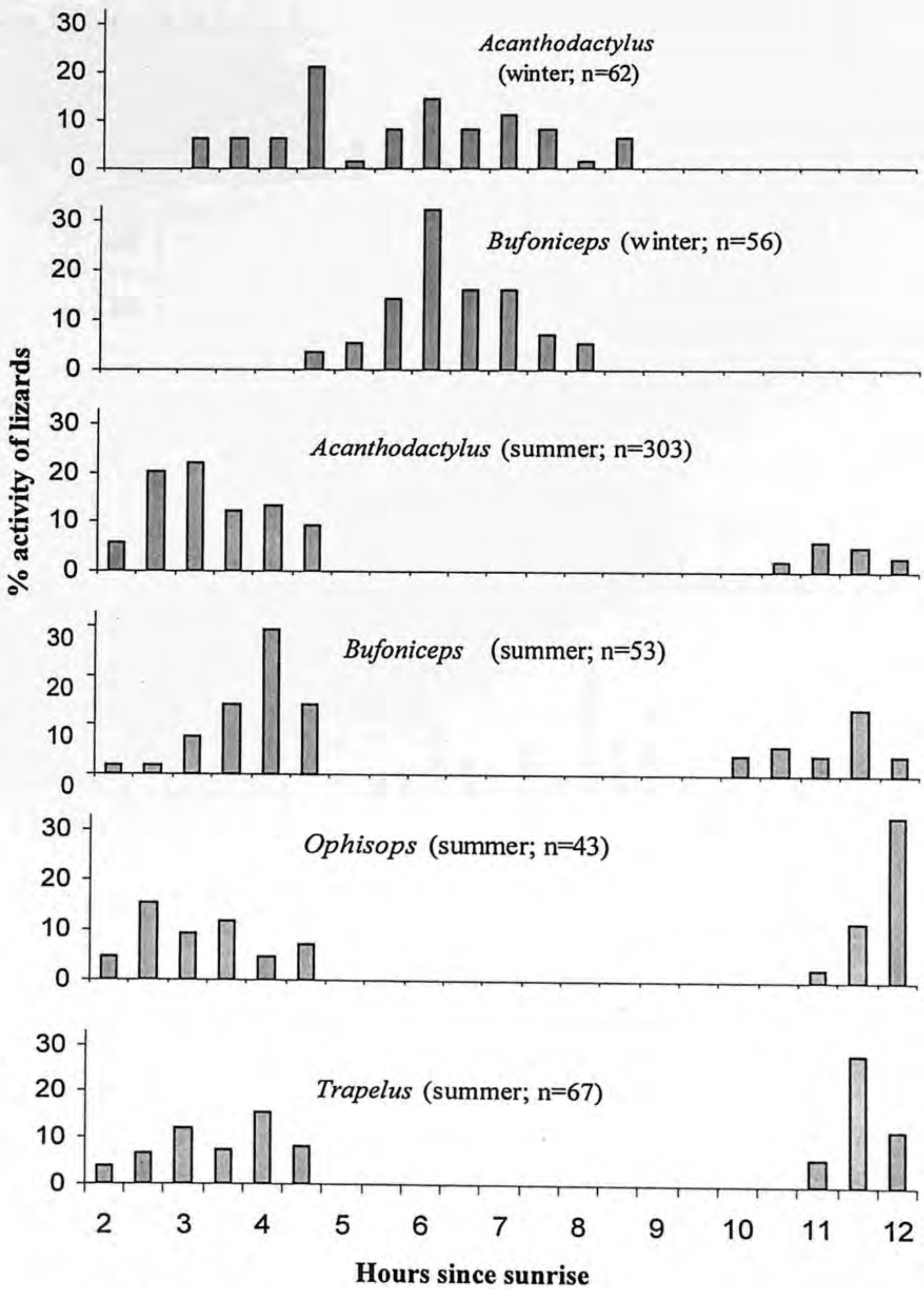


**Figure 4.10** Frequency distributions of % lizard activity through different times of the day. Half-hourly data, expressed as hours since sunrise. Sampling not carried out before 3 hours and after 9 hrs in winter; between hours 5-10 during summer. Summer data is corrected for differential sampling effort (Table 4.12)

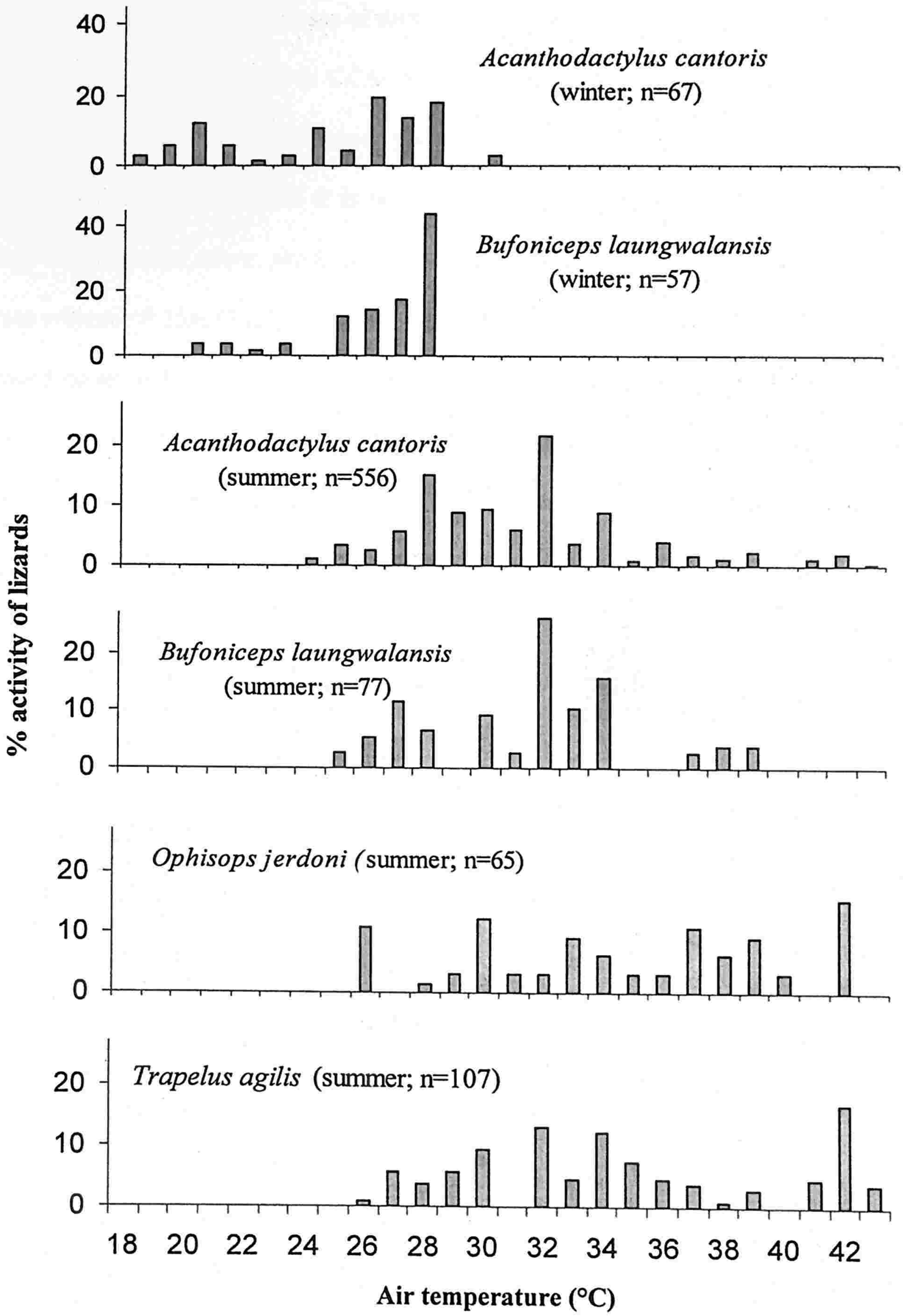


**Figure 4.11** Frequency distributions of active lizards at different ambient air temperatures.

### 4.5.6 Multidimensional analyses of niches

Three axes were constructed in CCA for the 175 occupied plots (Table 4.13). Axis 1 is most highly related to soil structure, positively with sand content and negatively with gravel, pebbles and silt. Axis 2 is positively related to grass cover >0.25m, herb and shrub % in ground cover, shrub cover and volume >0.25m and to a lesser extent with grass volume <0.25m (Table 4.14; Fig. 4.12). Axis 3 is strongly related to % grass in the ground cover and weakly negatively related with all other factors. I used only the first two axes as the information contributed by the third axis is low. Centroids of all species are included in a biplot in Fig. 4.12. The bilpot separates two species groups along the first axis, psammophiles (on the right half of the graph) and sclerophiles (on the left).

**Table 4.13** Summary of the first three axes from CCA. Eigen value, % of variance explained by each axis, cumulative variance, and species environment correlations are listed for each axis.

| | Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|
| Eigenvalue | 0.665 | 0.387 | 0.109 |
| Variance in species data: | | | |
| % of variance explained | 14.7 | 8.6 | 2.4 |
| Cumulative % explained | 14.7 | 23.2 | 25.6 |
| Pearson correlation* | 0.893 | 0.732 | 0.503 |
| Kendall correlation* | 0.563 | 0.593 | 0.378 |
| Total variance ("inertia") in the species data: 4.5275 | | | |

*Correlations are between species and environment

**Table 4.14** Intraset correlations between PCA factors of habitat variables and CCA axes. Factor abbreviations from Table 4.5

| Variable | Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|
| Peb_Grav | -0.982 | 0.062 | -0.139 |
| Gr_per | -0.209 | 0.41 | 0.815 |
| Sh_Cov_Vol2-3 | 0.006 | 0.379 | -0.218 |
| Gr_Cov_Vol2-3 | 0.151 | 0.401 | -0.371 |
| Sh_Hrb | 0.243 | 0.498 | -0.228 |
| Gr_Vol1_Veg2 | 0.084 | 0.206 | -0.251 |
| ShVOL1 | -0.05 | 0.091 | 0.237 |

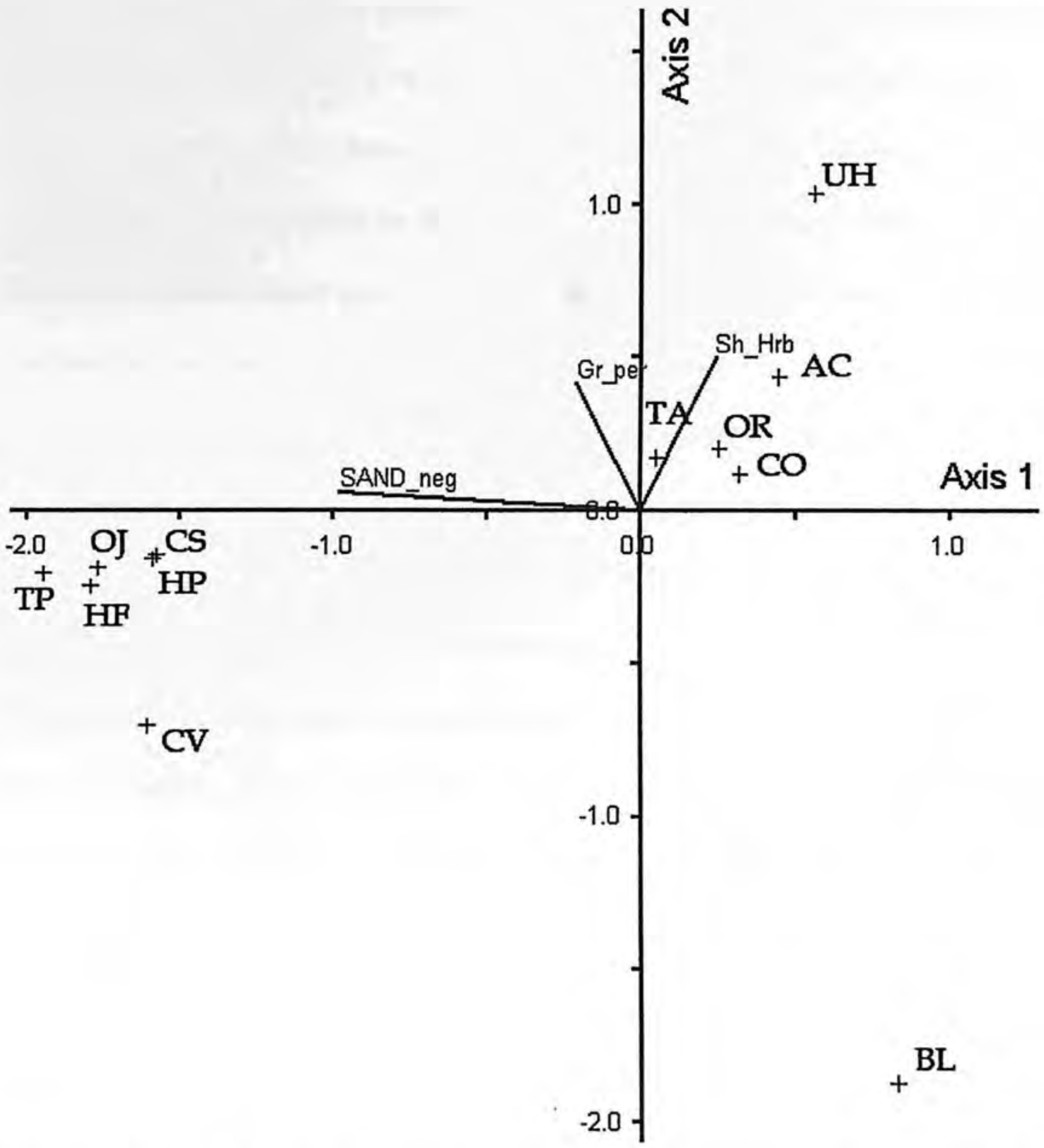


**Figure 4.12** Biplot of species centroids against the first two canonical axes. The length of the biplot indicates the strength of the relationship and the angle of the biplot indicates the direction of relationship. Raw scores are plotted with a bilpot cutoff of $R^2$=0.14. AC- *Acanthodactylus cantoris*, BL- *Bufoniceps laungwalansis*, CO- *Crossobamon orientalis*, CS- *Cyrtopodion scaber*, CV- *Calotes versicolor*, HF- *Hemidactylus flaviviridis*, HP- *Hemidactylus persicus*, OJ- *Ophisops jerdoni*, OR- *Ophiomorus raithmai*, TA- *Trapelus agilis*, TP- *Tropiocolotes persicus*, UH- *Uromastyx hardwickii*

95 % confidence ellipses are shown for eight species in Fig. 4.13, 50 % ellipses for the same set of species in Fig. 4.14. 95 % ellipses encompass almost the entire range of species' occurrence, while 50% ellipses are more conservative, reflecting only the core area. The width of the niche on the X-axis reflects the tolerance of the species to soil type, while vertical spread indicates the distribution of the species with regard to aspects of vegetation cover and volume.

It is clear that *Bufoniceps* has the narrowest niche, followed by *Cyrtopodion* and the other rocky area species (Fig 4.13 4.14). There is considerable overlap in the niches of the species inhabiting the rocky area. The niches of *Crossobamon, Ophiomorus* and *Trapelus* almost entirely encompass that of *Acanthodactylus*.

Table 4.15 summarizes niche breadth and niche position for nine species. Niche breadth was significantly negatively correlated with niche position (-0.93; $p<0.001$), while abundance and occupancy were significantly positively correlated (0.99; $p<0.001$). The correlation of average abundance (abundance of a species averaged across only habitats in which it is present) and occupancy approached significance (0.71; $p=0.05$).

There are strong nonsignificant negative correlations between niche position and body size, occupancy, and density; though these approach significance (Table 4.16). Niche breadth had nonsignificant positive correlations with these factors. Average density had weak relationships with both niche position and breadth.

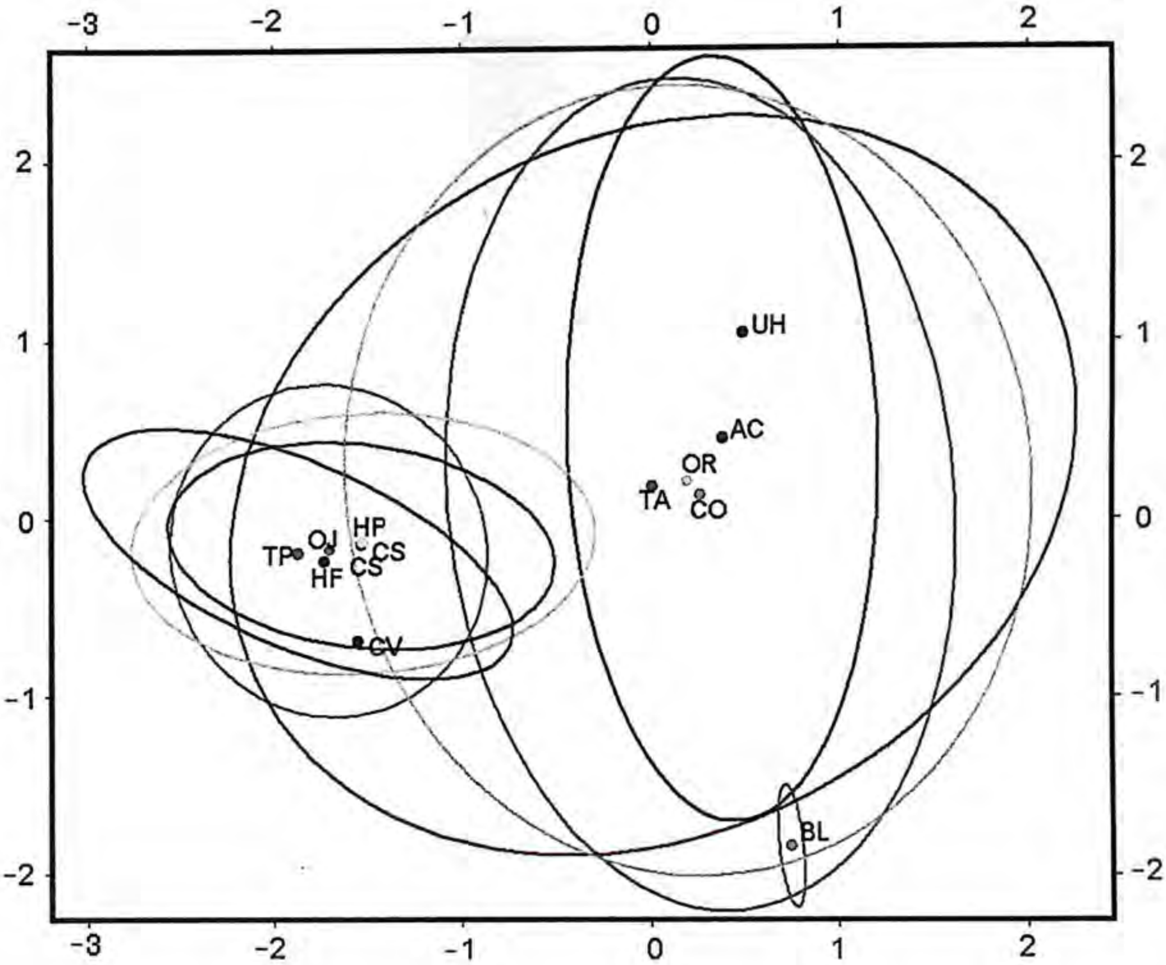


**Figure 4.13** 95% confidence ellipses for species scores on the first pair of canonical axes (Axis 1, Axis 2). Ellipses are colour-coded with species centroids, black centroids are species for which ellipses were not constructed due to low sample size. AC- *Acanthodactylus cantoris*, BL- *Bufoniceps laungwalansis*, CO- *Crossobamon orientalis*, CS- *Cyrtopodion scaber*, CV- *Calotes versicolor*, HF- *Hemidactylus flaviviridis*, HP- *Hemidactylus persicus*, OJ- *Ophisops jerdoni*, OR- *Ophiomorus raithmai*, TA- *Trapelus agilis*, TP- *Tropiocolotes persicus*, UH- *Uromastyx hardwickii*

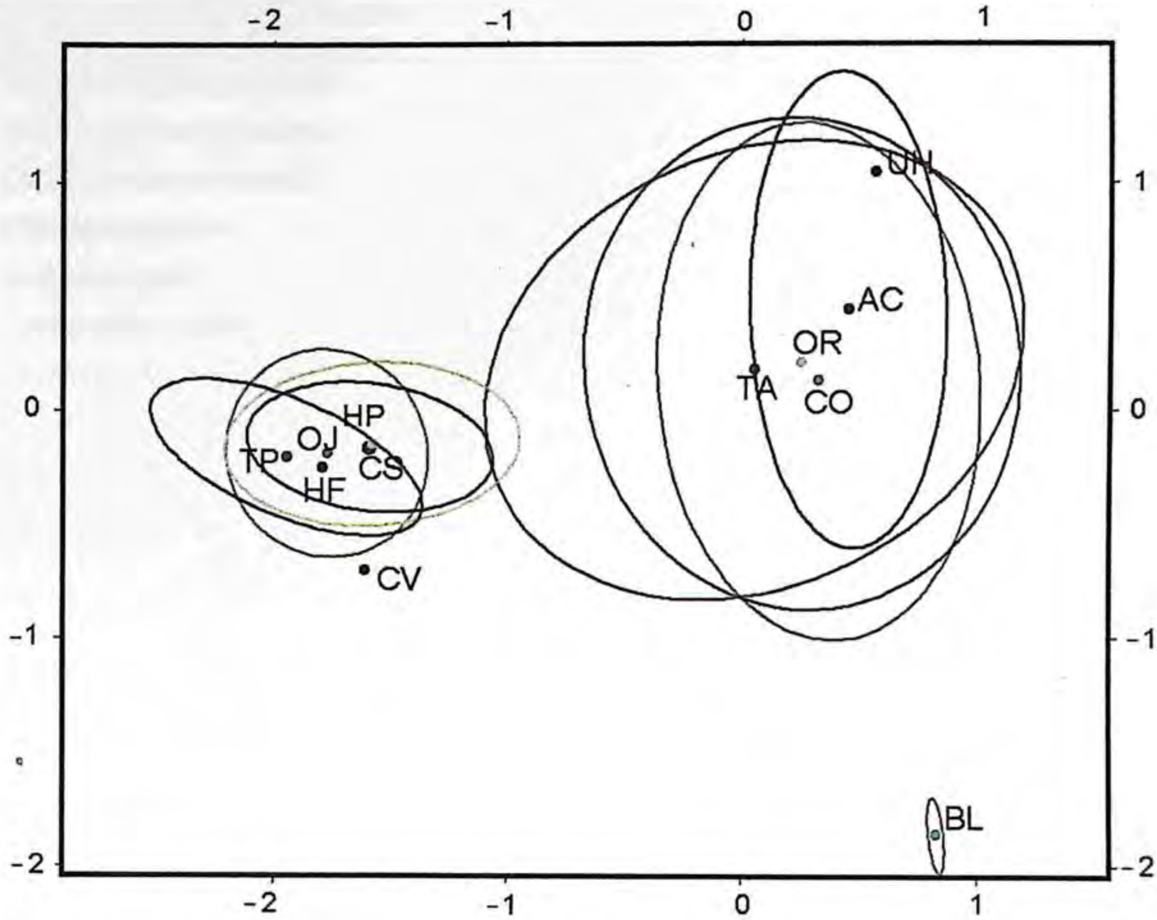


**Figure 4.14** 50 % confidence ellipses for species scores on the first pair of canonical axes (Axis 1, Axis 2). Ellipses are colour-coded with species centroids, black centroids are species for which ellipses were not constructed due to low sample size. AC- *Acanthodactylus cantoris*, BL- *Bufoniceps laungwalansis*, CO- *Crossobamon orientalis*, CS- *Cyrtopodion scaber*, CV- *Calotes versicolor*, HF- *Hemidactylus flaviviridis*, HP- *Hemidactylus persicus*, OJ- *Ophisops jerdoni*, OR- *Ophiomorus raithmai*, TA- *Trapelus agilis*, TP- *Tropiocolotes persicus*, UH- *Uromastyx hardwickii*

**Table 4.15** Niche breadth and position for nine species.

| Species | Niche position | Niche breadth |
|---|---|---|
| *Acanthodactylus cantoris* | 0.73 | 0.67 |
| *Bufoniceps laungwalansis* | 1.98 | 0.10 |
| *Crossobamon orientalis* | 0.43 | 0.80 |
| *Ophisops jerdoni* | 1.73 | 0.38 |
| *Trapelus agilis* | 0.29 | 0.92 |
| *Cyrtopodion scaber* | 1.54 | 0.36 |
| *Hemidactylus persicus* | 1.53 | 0.44 |
| *Tropiocolotes persicus* | 1.90 | 0.41 |
| *Ophiomorus raithmai* | 0.42 | 0.86 |

**Table 4.16** Kendall's rank correlation of niche breadth and position against measures of abundance and occupancy. *Ophiomorus* excluded from measures involving abundance

| Measure of abundance or distribution | Niche position | | Niche breadth | |
|---|---|---|---|---|
| | r | *p* | r | *p* |
| Average abundance[a] | 0.01 | 0.978 | -0.13 | 0.756 |
| Overall abundance[b] | -0.59 | 0.126 | 0.51 | 0.192 |
| Occupancy[c] | -0.62 | 0.077 | 0.55 | 0.125 |
| Body size (SVL)[d] | -0.63 | 0.067 | 0.53 | 0.139 |

[a] abundance averaged across only those habitats in which a species is found
[b] average abundance across all habitats
[c] proportion of sites occupied
[d] SVL from Table 2.1

## 5. DISCUSSION

### 5.1 Seasonal variations in abundance

There are clear differences in activity between summer and winter, both within and across species (Tables 4.1, 4.2). The only two species active in winter, *Acanthodactylus* and *Bufoniceps* are both diurnal species that inhabit open, sandy habitats. Sand heats up faster than rocks and it is likely that these species gain heat primarily through thigmothermy (contact with substrate), besides heliothermy (basking) in winter. Another pattern observed for these species was that much smaller individuals were active in winter, consistent with other lizard faunas (Huey and Slatkin 1976; Huey and Pianka 1977). Besides that juveniles would have been more abundant in winter, the largest size class recorded for both these species in summer was not seen at all in winter. There are two purported theories to explain this, one that a smaller body size has higher surface area to volume ratio, and thus smaller individuals would be able to gain heat from the environment more easily than adults (Cowles 1941; Huey and Slatkin 1976). Alternately juveniles are likely to have lower fat reserves, necessitating activity in winter (Huey and Pianka 1977).

The abundance of lizards, and number of species seen daily in a given area was considerably higher in summer, where on any given day in the appropriate habitat, all species could be seen. There were no differences in occurrence across habitats between summer and winter, except that *Trapelus* was not recorded from the barren sand dune habitat in winter. Other species had too few sightings for any patterns to emerge.

## 5.2 Range extensions

Range extensions were reported for two species during this study. The range extension for *H. persicus* is approximately 300 km to the north from the closest locality in Jassore Wildlife Sanctuary, Gujarat; and this is the second report of this species from India and the first from Rajasthan. The range extension for *T. persicus euphorbiacola* is about 275 km northeast from the closest locality, in Thar Parkar District, Pakistan; and this represents the first record from India. Both *H. persicus* and *T. p. euphorbiacola* are known from contiguous areas with similar climate and terrain (Khan 2006; Vyas *et al.* 2006), and their occurrence at Sam is not significant from a biogeographic point of view. Rather, this reflects how little is known of the reptilian fauna of the Thar Desert, and India in general. While *Tropiocolotes* was uncommon and difficult to spot, *H. persicus* was common and is a large, easily distinguishable lizard. It remains to be seen how widespread these species are in other rocky areas across the Thar, and what species remain undiscovered in these poorly explored areas.

## 5.3 General patterns of abundance

Of 12 species recorded during sampling in this study, eight were restricted to a single habitat type (six to the rocky hills, two to the barren dunes), one to the sandy habitats and only three were found in all habitat types (Table 4.8). Highest values of abundance were in sandy habitats, and the lowest in rocky habitats, a pattern consistent with observations in the Ramon cirque (Shenbrot and Krasnov 1997), Bukhara and Chihuahua (Shenbrot *et al.* 1991).

Absolute values of abundance observed in this study (Table 4.2) compared to other desert systems are lower than the Bukhara (Shenbrot *et al.* 1991), Australia (Morton and James 1988); similar to the Gobi (Rogovin *et al.* 2000); and considerably higher than those reported from Israel (Ramon cirque; Shenbrot and Krasnov 1997), Chihuahua (Mexico; Shenbrot *et al.* 1991), and North America (Pianka 1967).

The North American, Gobi, Bukhara and Ramon study areas are similar to the study area in average annual precipitation (<150mm), though the Australian and Chihuahuan study sites have annual rainfall >230mm. Altitudes are similar for the Ramon and Bukhara, while the Chihuahuan study site is at a higher altitude (>1000m). There are also latitudinal differences between these deserts, and a true comparison cannot be made without selecting very similar sites in different deserts.

**5.4 Patterns of species richness and diversity**

**5.4.1 Species richness and diversity**

Species richness based on the species recorded during the study period was moderate (14), similar to that observed in the Ramon Erosion Cirque, Israel (14; Shenbrot & Krasnov 1997), the Chihuahuan (17) and Bukhara Deserts (15; Shenbrot *et al.* 1991). The Kalahari Desert has between 12-18 species in sympatry (Pianka 1971), sites in desert regions of Australia between 18-40 species (Pianka 1986) and North American desert sites from 4-10 (Pianka 1967). However, such comparisons are of limited use because of the difference in spatial and temporal extents of investigation. For example, at least seven species, additional to the 14 recorded in this study, are reported from Jaisalmer District (Sharma 2002).

Species richness was highest in the rocky habitat, similar to the Ramon cirque, but other studies reported the lowest values in rocky areas (Shenbrot *et al.* 1991). Conversely, sandy habitats in this area have low species richness. The possible reasons for the high richness and diversity in the rocky areas can be explained by the high diversity of available microhabitats (rock types, different areas of slopes, sandy tracts) and considerable horizontal and vertical heterogeneity. Lizards in the rocky areas in this study included both sclerophilous species and a few psammophilous species where there were sand deposits (Table 4.8). Sandy habitats lack a vertical component altogether and are spatially homogenous. Additional reasons for the low richness in sandy areas may be due to the overall geographic position of the sandy areas of the Thar, forming the easternmost limit of sandy deserts in the horse latitudes (Singhvi and Kar 2004).

Proportions of nocturnal species (43% of the 14 species found in the area) are similar to those observed in Australia (36%) and the Kalahari (35%; Pianka 1986), Israel (29%; Shenbrot and Krasnov 1997), and higher than those seen in the Bukhara (13%) and Chihuahua (12%; Shenbrot *et al.* 1991)

Arboreal species are conspicuously absent from this study, largely because of the lack of trees in all habitats but the rocky hills. The only two arboreal species are *Calotes* and *Trapelus*. *C. versicolor* can at most be termed semi-arboreal, as it is often found associated with trees and shrubs, but juveniles and subadults are often terrestrial (pers. obs.). *Trapelus* on the other hand was not observed on shrubs higher than 2 m, and I am unsure whether the use of shrubs is for display behavior or actual foraging. Elsewhere, the arboreal component of diversity may be high (Australia – 18%, Kalahari – 24%; Pianka 1986)

### 5.4.2 Generic and higher order diversity

Generic and higher order diversity was relatively high in this study (Table 5.1), and is reflective of desert lizards in India (Das 1996). 12 genera are represented from five lizard families, with only two congeneric pairs. If the entire Thar Desert is considered, there are likely to be five additional genera (*Chamaeleo*, *Eublepharis*, *Eumeces*, *Mabuya*, *Mesalina*) and about twelve additional species (Sharma 2002). In other desert areas, these patterns are considerably different. The Bukhara has five genera with 12 species in all, Mapimi nine with 12 species (Shenbrot *et al.* 1991), Kalahari 13 genera and 23 species (Pianka 1971), while the entire desert regions of Australia have 24 genera and 61 species, with 14 species in a single genus, *Ctenotus* (Pianka 1986). The Ramon erosion cirque shows a similar pattern to this area, with 13 genera and 14 species. This is attributed in part to the isolated location of the sand dunes in this area, as a result of which many congeneric species are excluded from the area (Shenbrot and Krasnov 1997).

It is likely that higher order richness can be explained based on the overall geographic distributions of the genera and species recorded in this work. Of the 14 species, three species - *Calotes versicolor*, *Hemidactylus flaviviridis* and *Varanus bengalensis* are widely distributed across the subcontinent. *Ophisops jerdoni* is distributed across northern India. Of the other 10 species, only *Bufoniceps laungwalansis* is endemic to the Thar, while *Crossobamon orientalis* is restricted to the Sindh and Thar Deserts (Minton 1961). *Uromastyx hardwickii* ranges till Pakistan, while the remaining seven species range widely into Pakistan, Iran and even up to the Middle East. The arid regions of western India are the easternmost limit for these species; and for the genera *Acanthodactylus*, *Crossobamon*, *Ophiomorus*, *Trapelus*, *Tropiocolotes* and. *Uromastyx*. These six genera are represented in India by a single species each.

**Table 5.1** Numbers of species of lizards from different families found in sympatry on desert study sites. Modified after Pianka (1986). Values in parentheses indicate total number of different species in each family. ? indicates not known.

| Family | North America [a] | Kalahari [a] | Australia [a] | Gobi [b] | Israel [c] | Bukhara [d] | Thar (this study) |
|---|---|---|---|---|---|---|---|
| Agamidae | | 1 (1) | 2-8 (11) | 1 (1) | 1-2 (3) | 2-3 (5) | 2 (4) |
| Chamaelonidae | | 1 (1) | | | | | |
| Gekkonidae | 1 (1) | 4-7 (7) | 5-9 (13) | 1 (1) | 1-4 (4) | 1-3 (3) | 1-5 (5) |
| Helodermatidae | 1 (1) | | | | | | |
| Iguanidae | 3-8 (9) | | | | | | |
| Lacertidae | | 3-5 (7) | | 1-2 (2) | 1-4 (4) | 2-4 (5) | 1 (2) |
| Pygopodidae | | | 1-2 (3) | | | | |
| Scincidae | | 3-5 (6) | 6-18 (28) | | 1-3 (3) | 1 (1) | 1 (1) |
| Teiidae | 1 (1) | | | | | | |
| Varanidae | | | 1-5 (5) | | | 1 (1) | 1-2 (2) |
| Xantusidae | 1 (1) | | | | | | |
| **Total** | 4-11 (13) | 12-18 (22) | 18-42 (61) | 1-3 (4) | 3-11 (14) | ? (15) | 5-10 (14) |

[a] Pianka (1986)
[b] Semenov *et al.* (2000)
[c] Shenbrot & Krasnov (1997)
[d] Shenbrot *et al.* (1991)

### 5.5 Habitat relationships

Each of the habitats sampled is considerably different from the others, with no intermediate areas represented. Species were generally only found in one or a few of these habitats, and the variables picked up by logistic regression were generally between habitat variables rather than within habitat variables (such as soil, overall vegetation cover etc., which are similar within a habitat, but differ across habitats). Habitats appear generally homogenous, and the differences between adjacent plots in terms of species composition may not be reflected in terms of habitat variables. Potential species composition is likely to be similar, but differences in occupancy may be responsible for these patterns. An additional confounding factor is that the surrounding habitat type will determine to some extent the species found in a habitat. The patchiness of habitats was not taken into account.

Five of the eight species for which presence-absence habitat relationships were investigated showed fairly strong environmental determination, the exceptions being *Trapelus*, *Crossobamon* and *Ophiomorus*. These five species are all restricted to either one or a few similar habitats. Of these, the presence/absence of *Acanthodactylus*, *Bufoniceps* and *Ophisops* appears to be determined at the habitat level, for two reasons. These species are widespread within the habitats in which they are found, and the same variables that explain presence between habitats cannot adequately separate occupied and unoccupied sites within each habitat.

### *Acanthodactylus cantoris*

Though *Acanthodactylus* was the most widely distributed and abundant species, it had fairly strong determinants of presence. This indicates its wide distribution may be a function of the availability of suitable habitat, rather than a very broad niche (Table 4.15). The possible reasons for the strong relationship between absence of burrows and absence of *Acanthodactylus* can be explained by the significant correlation ($p<0.01$) between large burrows (of the gerbil *Merriones hurrianae*) with %sand (0.39), shrub cover (0.34) and grass cover (0.65). *Acanthodactylus* was present in 98.7% (77/78 plots) of plots with large rodent burrows, but additionally present in another 26 plots with no burrows. These burrows are found only in sandy, vegetated areas, similar to areas that *Acanthodactylus* uses, though *Acanthodactylus* uses additional areas. Though this species was observed to use burrows (large and small) as escape cover, other species of the genus are known to dig their own burrows (Zaady and Bouskila 2002). It is unlikely this pattern indicates a cause-effect relationship between burrows and *Acanthodactylus*, and is more likely that the gerbils occupy very similar microhabitats that make up a subset of the niche of *Acanthodactylus*.

***Bufoniceps laungwalansis***

The model for this species incorrectly predicted presence in many plots within the barren dunes with no direct sightings, though no predictions indicated use of plots outside this habitat. These predictions conform to field observations of tracks, from which it is clear that this species used all plots in the barren dunes girds. Thus, there are no specific determinants of presence within the barren dunes habitat. The strong difference between this habitat and other habitats is reflected in the rigid habitat preference of this species. Slope was not significant in explaining presence and absence of this species within the barren dunes, but data on the use of slope by *Bufoniceps* shows a clear preference for low (<10°) and flat areas (30.9%, 51.5% of 68 sightings). This lack of correspondence is probably because of the difference in scale of use by the species and measurement of the variable.

***Trapelus agilis***

Poor classification results for this species (Table 4.6) are related to two possible aspects of the ecology of this species, besides the possibility that relevant habitat variables were not examined. The first of these may be poor environmental determination at the scale of the study, or in relation to the variables considered. The second factor may be low occupancy (indicating that all preferred sites are not occupied). Field observations indicate the species is widespread in diverse microhabitats and is not abundant in any specific area. The factors explaining the presence and absence of this species may operate at a broader scale, and are likely to include factors of climate and general geographic location.

*Crossobamon orientalis*

Field observations and literature indicate this species is closely associated with sand and sand deposits (Das 2002). The reason the presence/absence predictions for this species were poor (Table 4.7) is probably because sand deposits would not have shown up in the habitat variables quantified. Additionally, this species is found in many habitats and varied microhabitats, indicating intrinsically low environmental determination at this scale.

*Ophiomorus raithmai*

This species is very similar to the previous species, and seems to be widespread, with the primary determinant for presence being sand. % barren ground, which was statistically significant only within sandy habitats, was a common factor noted for most observations of tracks of this species. This may reflect true use of these microhabitats by this species, or that tracks are detected more easily in barren areas. Long term studies with pitfall trapping or more extensive observations on tracks are required to understand the factors influencing the presence and absence of this species.

*Ophisops jerdoni*

The classification for this species was good between habitats, as the habitat it occupies is very different from other habitats in both soil composition and vegetation structure. However, the within habitat classification was poor. This could be because this small lizard is distributed more widely through this habitat than sampling revealed. Personal observations indicate this species inhabits a wide range of open, rocky areas in other parts of its range. The scale of habitat selection may thus be at a much broader level. All sites the species can possibly use may not have been in use (low occupancy) during the time scale of the study (only two days per grid). This species is also considerably difficult to detect, due to its small size and habit of moving in and out of crevices and rubble.

*Cyrtopodion scaber*

This species was only found in the rocky hills habitat during sampling, though opportunistic searching revealed this species also occurs on isolated rocky outcrops and stone structures. This was the only species from the rocky area (besides *Trapelus* and *Hemidactylus flaviviridis* which were widely distributed) that was found outside this habitat. Though sometimes terrestrial, this species is most often found on rocks larger than 0.5 m. Large rocks (3-5m) are also associated with other, smaller rock categories (>0.5m) and this explains the positive relationship between this species presence and large rocks.

*Hemidactylus persicus*

There were just nine plots with this species and any results are preliminary. This species is mainly associated with rocks larger than 0.5 m, and the negative relationship of this species presence with medium rubble can be interpreted as increased availability of larger rock resources.

### 5.6 Resource partitioning

Species richness was generally low with few species occupying a given habitat, and abundances of most species differed considerably (Table 4.2). Overall spatial overlap at the plot level was low (Table 4.9). For most species pairs that showed low to moderate spatial overlap, finer level spatial separation was by differential spatial use of the same areas – through use of different microhabitat categories and positioning at different distances to vegetation.

Additional segregation by body size (Table 2.1), foraging mode, and food were not considered.

#### 5.6.1 Microhabitat category and distance to vegetation

Microhabitat categories are a synthesis of species-specific thermal ecology and foraging mode, to a lesser extent display and sexual behaviour. Distance to vegetation is a slightly different expression of similar species-specific traits. Both these parameters may also be specific to the habitat or microhabitat type under consideration. Even when the availability of a given microhabitat is higher, each species is likely to have a different response to these constraints.

#### 5.6.3 Thermal and temporal relations

Though time is often considered the least important resource dimension for reptiles (Toft 1985), it is known to be important in reducing interspecific conflict, and exploitation competition (Pianka 1986). Time of activity is related to the thermoregulatory behaviour of the species. When expressed as hours since sunrise it is a useful proxy for both air and soil temperature (Fig. 5.1), and closely reflects the thermal constraints for each species. Though air temperature is important, substrate temperatures are probably more important in winter as substrate temperatures do become fairly high on clear days (>40°C), though air temperatures are uniformly low. *Acanthodactylus* were often seen with their bodies pressed against the sand while basking in winter. In summer on the other hand, substrate temperature may often be the limiting factor for lizard activity as temperatures are routinely above 50° C within three hours of sunrise. Winter activity too was depressed when the sand became very warm in the later afternoon. Thermal dancing was observed in *Acanthodactylus*, *Bufoniceps* and *Ophisops*.

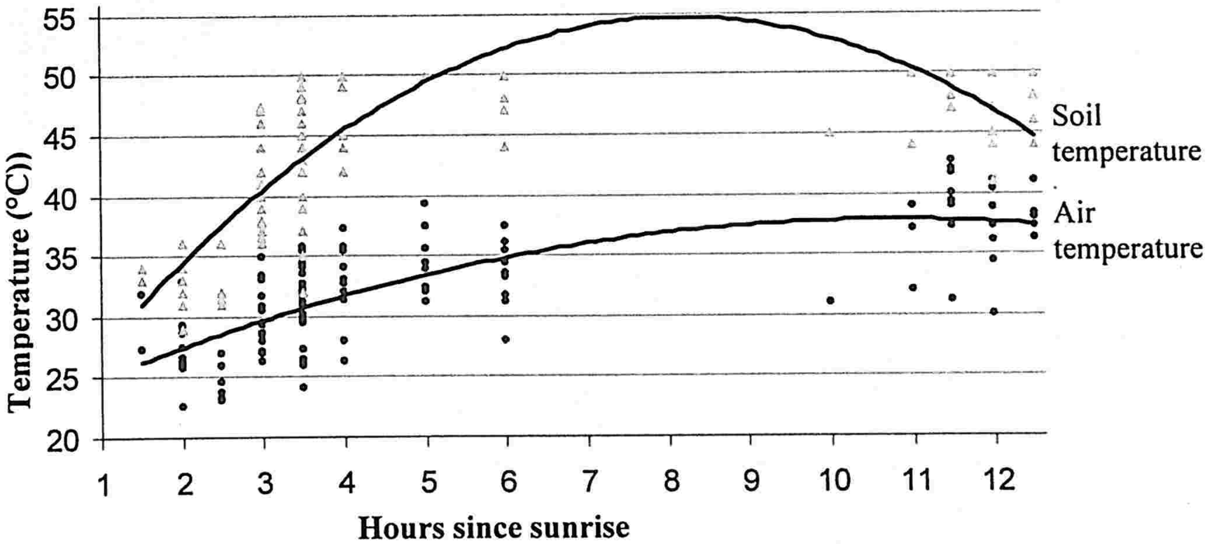


**Figure 5.1** Plot of air and soil temperatures versus hours since sunrise. Soil temperatures above 50° C were not recorded, and were noted as 50° C. Polynomial curves (second order) are fitted onto the points. Data not recorded between hours 6 to 10.

**5.7 Multivariate niche analyses**

CCA constrains the ordination based on the species matrix. The resultant classification of habitats differs from the simple scatter on PCA axes 1 and 2 (Fig. 4.5). Here, rocky hills plots separate, with a few grassland plots approaching similarity; barren dunes separate, but the major difference is that grassland and stabilized dunes plots cluster together (Fig. 5.2). This reflects the broad similarity in species composition of these two habitats. The direct gradient ordination thus differs considerably from the constrained, indirect ordination.

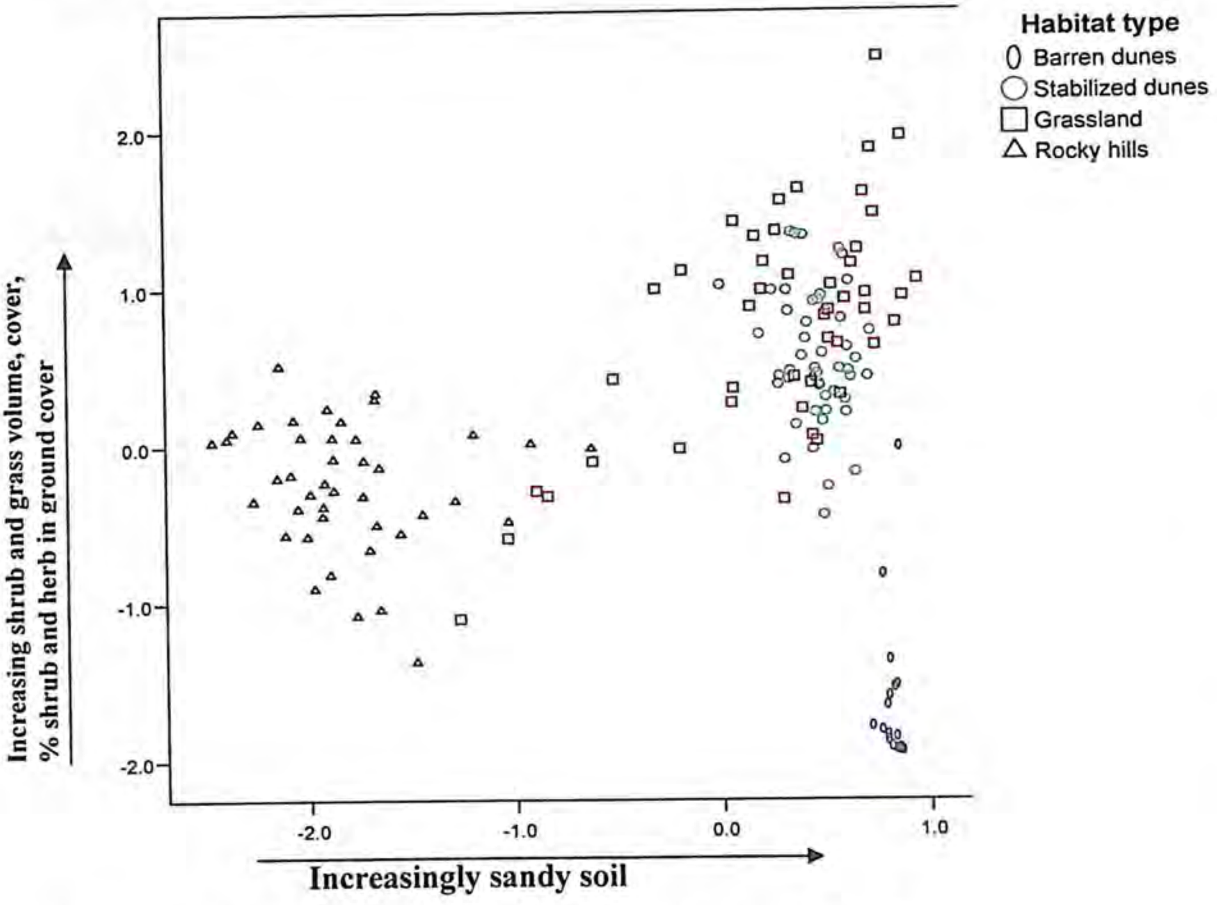


**Figure 5.2** Scatter of sample plots against canonical axes 1 and 2.

### 5.7.1 Broad niche patterns

Consistent with other studies on niche relations of desert lizard communities, the main factor separating species is soil texture (Barbault and Maury 1981; Shenbrot *et al.* 1991; Rogovin *et al.* 2000). This variation has been termed the between habitat variation as it reflects the main gradients that exist between habitats (Rogovin *et al.* 2000). The second axis is related to vegetation structure, and includes aspects of shelter as well as productivity of the plots, contributing both between and within habitat variation.

The niches of species as depicted in this study reflect the range of conditions each species can occupy, in the space of the considered habitat variables. This is an approximation in a few dimensions (the number of environmental variables contributing to axes 1 and 2) of Hutchinson's concept of the niche (1957) as an "n-dimensional hypervolume". While this is informative, the overall shape of a species niche will also have a relationship with relative abundance in different areas, assuming abundance is an adequate measure of habitat suitability (Brown 1984; but see Van Horne 1982 for a discussion on the inadequacy of abundance as a measure of habitat suitability).

### 5.7.2 Species specific niche metrics

Niche breadth reflects the tolerance of a species to varying environmental conditions, and is a reflection of whether the species is a generalist or specialist in tolerance to environmental conditions. Niche breadths of some ecologically generalist species (*Crossobamon, Ophiomorus, Trapelus*) were correspondingly high, while the niche breadth of species restricted to a particular habitat were low (Table 4.15). Niche position reflects the relative position of resources (here habitat) utilized by a species when compared to the entire community (Gaston and Lawton 1990). Clearly this will be affected by the nature of sampling, and an important factor to consider in the use of a constrained ordination such as CCA, is that sampling was in proportion to the availability of habitat in the area studied. If sampling was biased toward one habitat, the space constructed in order to approximate a species niche will change in configuration. The habitat, and species occupying that habitat, will be placed at the centre of the canonical space. Assuming a habitat is over-represented in sampling, species that inhabit this habitat will also be over-represented, and consequently the occupancy will also be higher. This is likely to automatically give rise to a negative correlation between niche position and occupancy as a statistical artifact. Broadly speaking, the rocky areas are marginal to the community space as a whole, as more sandy habitats were sampled, though this reflects the proportion of these resources in the study area (sandy habitats dominate).

*Bufoniceps* has the highest niche position, followed by *Tropiocolotes*. So at the local scale the habitats that these two species occupy are marginal. This is interesting when the overall geographic ranges are considered, *Bufoniceps* is endemic to the Thar, *Tropiocolotes persicus euphorbiacola* is endemic to the Thar and Sindh. However, *Crossobamon orientalis* has a low niche position and high niche breadth, though this species is also endemic to the Thar and Sindh. The other species with high niche positions are rocky area species (specialists), *H. persicus*, *C. scaber*, and *O. jerdoni*. While the first two are at the eastern limit of their geographic range, *O. jerdoni* is widely distributed in northern India (Table 2.1). Thus no generalizations can be made in relation to overall geographic range and niche position or breadth. Distribution for this assemblage at regional scales is likely to be governed by micro-ecological factors, while broad geographic distribution may be governed by macroclimatic and historical factors (Brandle and Brandl 2001).

Gaston *et al.* (1997) propose eight mechanisms that could possibly explain positive abundance-range size relationships. The mechanisms which may apply in this case include range position, resource breadth, and resource availability. Range position implies that species at the edge of their geographical ranges have lower abundances and occupy smaller proportion of the study area. Of the eight species used to correlate occupancy and abundance, one is a Thar endemic (*Bufoniceps*) two are Thar-Sindh endemics (*C. orientalis, T. persicus*), one is well within the limits of its range (*Ophisops jerdoni*), and the remaining four species are widely distributed species at the eastern limit of their global distribution (*A. cantoris, C. scaber, H. persicus, T. agilis*). Resource breadth and availability can both be influenced by sampling. What is 'available' is reflected by what is sampled, and is often not representative of the study area or landscape. Resource breadth is a measure less affected by sampling, as it is an inherent part of a species' ecology. Resource breadth may be affected when habitats used by a species are not sampled. Gregory and Gaston (2000) report similar findings for British birds with no correlation between niche breadth and range size, though they did find correlations at a broader spatial scale.

### 5.7.3 Associations of niche metrics with abundance, occupancy and body size

***Distribution abundance***

The distribution abundance theory states that occupancy of a species is positively related to abundance (Brown 1984). Both measures of abundance used here (average and overall) were both strongly positively correlated with occupancy ($p$=0.05 average abundance; $p$<0.01 overall abundance). Niche breadth and abundance are often thought to be positively correlated (Vandermeer 1972; Brown 1984). Niche breadth and abundance were negatively correlated for Seagle and McCracken (1986) and positively for Brown (1984), however the scales at which these relationships are examined is not the same (Seagle and McCracken 1986). Abundance patterns may be reflected by availability of microhabitat rather than the variability or range of microhabitats used (resource breadth vs. resource availability hypothesis, Gaston *et al.* 1997)

Though niche metrics were moderately correlated (nonsignificantly) with both occupancy and overall abundance, the correlation with average abundance was weak (Table 4.16). This indicates species that use atypical habitats and are specialized (e.g. *Bufoniceps*, *Ophisops*) may be locally abundant; or that some widely distributed species may have low abundances (e.g. *Trapelus agilis*). Many other studies on various taxa have failed to find a relationship between abundance and niche breadth (e.g. birds, Brandle and Brandl 2001; slugs, Seagle and McCracken 1986; lizards, Shenbrot *et al.* 1991; rodents, Shenbrot 1992). The magnitude of correlation for occupancy and niche position does however point to trends expected from theory (Gaston *et al.* 1997).

*Niche breadth and position*

A strong negative correlation between niche breadth and position implies that species whose habitat is atypical (high niche position) will also tend to use a narrow subset of environmental conditions (e.g. Dueser and Shugart 1979; Krasnov and Shenbrot 1996). However, empirical data does not often confirm this relationship (e.g. nonsignificant negative correlations- Shenbrot 1991; weak correlations- Gregory and Gaston 2001). The strong, significant negative correlation between niche breadth and position found in this study indicates species with high niche position are fairly specialized in the range of conditions they occupy. More extensive sampling of habitats, in proportion to their occurrence in the area, with larger sample sizes is necessary to confirm the trends observed here.

***Body size correlations***

The strong correlation between body size and niche breadth is indicative of a separation between large bodied generalist species and smaller specialists (Loder *et al.* 1998). Even though body size was taken from literature, and represents maximum body size reported and not the average body size observed in the study area, any biases are likely to be similar across species. This correlation indicates larger species tend to occur in the centre of resource space, or have habitat in highest availability. Niche breadth and body size have the opposite relationship, with larger species tending to more tolerant to environmental conditions and smaller species tending to be specialists. An alternate explanation is that larger species may force smaller species to occupy marginal habitats; but this seems unlikely based on the strong relationships between species with high niche position and narrow niche breadths have with their habitats.

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## APPENDIX 1

**Checklist of reptiles observed in the study area**

**Lizards:**

| | Common name | Local name |
|---|---|---|
| **Family: Agamidae** | | |
| *Bufoniceps laungwalansis* (Sharma, 1978) | Laungwala Toad-headed Agama | Girgit/ Chipkali |
| *Calotes versicolor* (Daudin, 1802) | Garden Lizard | Kirda (with spines) |
| *Trapelus agilis* (Olivier 1807) | Brilliant Agama | Kirda (color changing) |
| *Uromastyx hardwickii* Gray, 1827 | Indian Spiny-tailed Lizard | Saanda |
| **Family: Gekkonidae** | | |
| *Crossobamon orientalis* (Blanford,1876) | Sindh Sand Gecko | Bhatu |
| *Cyrtopodion scaber* (Heyden, 1827) | Warty Rock Gecko | Bhatu |
| *Hemidactylus flaviviridis* Ruppell, 1835 | Northern House Gecko | Chipkali |
| *Hemidactylus persicus* Anderson, 1872 | Persian Gecko | Chipkali |
| *Tropiocolotes persicus euphorbiacola* | Sindh Dwarf Gecko | - |
| **Family: Scincidae** | | |
| *Ophiomorus raithmai* Anderson & Leviton, 1966 | Indian Sandfish | Doodh-Gilheri |
| **Family: Lacertidae** | | |
| *Acanthodactylus cantoris* Gunther, 1864 | Indian Fringe-toed Lizard | Kiradi |
| *Ophisops jerdoni* Blyth, 1853 | Snake-eyed Lacerta | Kiradi |
| ***Family: Varanidae*** | | |
| *Varanus bengalensis* (Daudin, 1802) | Indian Monitor | Gho |
| *Varanus griseus* (Daudin, 1803) | Desert Monitor | Chandan Gho |

**Snakes:**

| | Common Name | Local Name |
|---|---|---|
| **Family: Boidae** | | |
| *Eryx johnii* (Russell 1801) | Red Sand Boa | Boghi |
| **Family: Colubridae** | | |
| *Lytorhynchus paradoxus* (Gunther 1834) | Sindh Awl-headed Snake | - |
| *Oligodon taeniolatus* (Jerdon 1853) | Streaked Kukri | - |
| *Platyceps (Coluber) ventromaculatus* (Gray 1834) | Glossy-bellied Racer | Lundee/ Ghorava |
| *Psammophis schokari* (Forskal 1775) | Afro-Asian Sandsnake | Sig |
| *Spalerosophis arenarius* (Boulenger 1875) | Red-spotted Diadem | Ghorava |
| **Family: Viperidae** | | |
| *Echis carinatus sochureki* (Schneider 1801) | Saw-scaled Viper | Baandee |