

Lizards of the Thar Desert – Resource partitioning and community composition



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ARTICLE INFO

Article history:

Received 21 December 2012

Received in revised form

17 February 2015

Accepted 2 March 2015

Available online 10 March 2015

Keywords:

Desert lizard community

Visual encounter survey

Spatial overlap

Daily activity

India

ABSTRACT

How similar species co-exist in nature is a fundamental question in community ecology. Resource partitioning has been studied in desert lizard communities across four continents, but data from South Asia is lacking. We used area-constrained visual encounter surveys to study community composition and spatial and temporal resource partitioning in a lizard community during summer in the Thar Desert, western India, addressing an important biogeographic gap in knowledge. Twelve one-hectare grids divided into 25 m × 25 m plots were placed across four habitats – barren dunes, stabilized dunes, grassland, and rocky hills. We recorded 1039 sightings of 12 species during 84 sampling sessions. Lizard abundance decreased in the order stabilized dunes > grassland > barren dunes > rocky hills; richness was in roughly the opposite order. Resource partitioning was examined for the seven commonest species. Overall spatial overlap was low (<0.6) between species pairs. Overlap was higher within habitats, but species showed finer separation through use of different microhabitat categories and specific spatial resources, as well as by positioning at different distances to vegetation. Diurnal species were also separated by peak time of activity. Space appears to be an important resource dimension facilitating co-existence in this desert lizard community.

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1. Introduction

How do similar species co-exist in nature? Answering this fundamental question involves studying how species in a community partition multivariate niche space (Schoener, 1974). The three major niche dimensions across which resource partitioning has been studied are space, food and time (Pianka, 1973; Schoener, 1974). Space is among the most important resource dimensions that is partitioned in lizards (Pianka, 1973, 1986; Schoener, 1974; Toft, 1985; Vitt et al., 2000; Luiselli, 2007a). Species that are broadly sympatric in a region may or may not co-occur within specific habitats; and species that do co-occur within habitats often partition microhabitat resources, restricting further overlap (Pianka, 1973, 1986; Toft, 1985). Time of activity is closely linked to the thermoregulatory and foraging behavior of a species, and exposes lizards to differing food resources, in addition to reducing interspecific encounters (Pianka, 1986). Though differentiation

along the trophic niche has been long investigated, a recent meta-analysis using null models demonstrated that most lizard communities do not partition the trophic niche (Luiselli, 2007b). Thus, spatial and temporal segregation appear to be important in allowing the co-existence of sympatric lizards.

Desert lizard communities have proved to be a useful natural system to answer a range of questions in community ecology, with studies spanning four continents (e.g. Pianka, 1986; Shenbrot et al., 1991; Rogovin et al., 2000). The reasons these communities have been extensively studied include that desert lizards are habitat specific, diverse, relatively abundant, and easily detectable (Pianka, 1986; Toft, 1985); resources are likely to be limiting in deserts; and that the desert provides a simple system in which to explore ecological questions and hypotheses (Pianka, 1986; Kotler and Brown, 1988).

The lizard community of the Thar Desert in Western India and adjacent Pakistan is poorly studied, with previous work limited to checklists, and even basic information on community composition lacking. In order to address this biogeographic gap in knowledge, we examined spatial and temporal resource partitioning in the lizard community of the Thar Desert, Jaisalmer District, Rajasthan, India. Besides collecting data on community composition, we asked

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the following questions in order to understand how these lizards co-exist:

- (1) Which species overlap broadly at the habitat level?
- (2) What is the degree of spatial overlap within habitats? Is the observed spatial overlap significantly less or more than expected from null model analysis?
- (3) Do species that show spatial overlap within habitats separate at a finer scale?
- (4) Do the diurnal species partition the temporal niche?

2. Materials and methods

2.1. Study area

The study was conducted around Sam village (26.8725° N, 70.5056° E), which lies in the Thar Desert, close to the northern boundary of the Desert National Park, in Jaisalmer District, Rajasthan, India (Fig. 1). The area lies between 190 and 290 m asl and the climate is dry and continental. Rainfall is irregular, with annual average rainfall in Jaisalmer District 164 mm (Gupta, 1986). Average minimum and maximum temperatures are 7.9 °C and 23.6 °C in January, to 25.8 °C and 41.6 °C in May (Meena, 2000), daily temperature variation averaged 15.3 °C during the study.

We recognized four habitat types, broadly representative of the landforms of the Thar Desert (Prakash, 1962) – barren dunes (BD), stabilized dunes (SD), grassland (GG), and rocky hills (RH). Barren dunes are characterized by loose, sandy soil (>95% sand) and very low total vegetation cover (<2%), mainly of the grass *Stipagrostis plumosa* and scattered herbaceous growth of *Indigofera cordifolia* and *Cyperus arenarius*. Edges and interdunal areas are often vegetated with the grass *Panicum turgidum* and shrubs *Aerva* spp., *Calligonum polygonoides*, *Crotalaria burhia*, *Fagonia cretica*, and *Haloxylon salicornium*. *Calatropis procera*, *Capparis decidua* and *Leptadeina pyrotechnica* may occasionally be found along the edges of dune-fields. The shifting sand dunes around Sam can be classified according to shape and size into barchans and other minor sand streaks (2–6 m high), barchanoids (8–10 m) and mega-barchanoids (15–40 m; Kar, 1989). The dune-fields are generally

small, a few kilometers long and less than a kilometer wide. Stabilized dunes are gently undulating and have sandy soil (>95% sand) and low total vegetation cover (7–11%). Shrub and grass volume is highest in this habitat, with dominant species including the grasses *Lasiurus indicus*, *Cenchrus bifloris*, and *P. turgidum* and the shrubs *Aerva* spp., *C. polygonoides*, *C. burhia*, *H. salicornium*, *I. cordifolia*. Trees are few and scattered, the main species *C. decidua*. Grasslands are flat areas with gravel (up to 30% gravel) or sandy soil (up to 95% sand) and moderate vegetation cover (31–50%), dominated by grass. Sandy areas have the grasses *L. indicus* and *C. bifloris* and shrubs *Aerva* spp., *C. polygonoides*, *C. burhia* and *H. salicornium*; gravelly areas the grasses *Dactyloctenium aristatum*, *Dactyloctenium scindicum*, and the shrubs *I. cordifolia*, *F. cretica*. This habitat also has trees, mainly *C. decidua* and occasional *Zizyphus nummularia*. Rocky hills, also known as rocky and gravelly pediments (Kar, 1989), rise up to 290 m and have rocky soil (11–100% pebbles) and low vegetation cover (9–23%) with very low grass cover. This is the only habitat with relief as well as relatively many trees. 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 *D. scindicum*. Dominant shrubs are *Aerva* spp., *F. cretica*, and *Grewia tenax* (in dwarf form). Trees include *Acacia senegal*, *C. decidua*, and *Salvadora oleoides*.

2.2. Lizard species

The lizard community of the area includes 14 species (Sharma, 2002; Agarwal et al., 2009). This paper deals with the seven most abundant species (with at least 15 sightings each), *Acanthodactylus cantoris* (Indian fringe-toed lizard), *Bufo niceps laungwalaensis* (Laungwala toad-headed agama), *Crossobamon orientalis* (Sindh sand gecko), *Cyrtopodion scabrum* (keeled rock gecko), *Hemidactylus* sp., *Ophisops jerdoni* (snake-eyed lacerta), and *Trapelus agilis* (brilliant agama).

2.3. Sampling methodology

Lizards were surveyed on 12 one-hectare grids in early summer (March–April 2007), a time of high lizard activity. We used stratified sampling, with three grids in each habitat type placed to capture broad gradients in habitat structure, vegetation composition and cover (visually assessed). Grids were subdivided into 16 plots of 25 m × 25 m, which formed basic sampling units for both habitat variables and lizards, modified from Shenbrot and Krasnov (1997). The grids were sampled for lizards in the form of an area constrained visual encounter survey (Doan, 2003). These visual encounter surveys were carried out by the same two observers who were trained in spotting and identifying the species in the area, and consisted of a set of 10, non-overlapping 100 m × 10 m belt transects back and forth across the grid, with the 25 m × 25 m plot ID noted for all sighted lizards. We chose an area-constrained total count over time-constrained methods as structural complexity varied in different habitats, and we required a sampling method that was consistent across habitats – this would serve as a least count of lizard abundance. Each grid was sampled on two days, with three to five days break. There were four daily sampling sessions, during each of which an entire grid was sampled once: early morning (T1) with start time 8:00 h to 8:40 h (1 hr 30 min to 2 h after sunrise), late morning (T2), 09:30 h to 10:10 h (between 2 h 45 min to 3 h 30 min after sunrise), evening (T3), 17:00 to 17:15 (two hrs before sunset), night (T4), 20:00 to 20:25 (about one hr after sunset). T1, T2, and T4 were repeated on the second day of sampling; T3 had few sightings and was not repeated. The average time taken in a sampling session across a one-hectare grid was

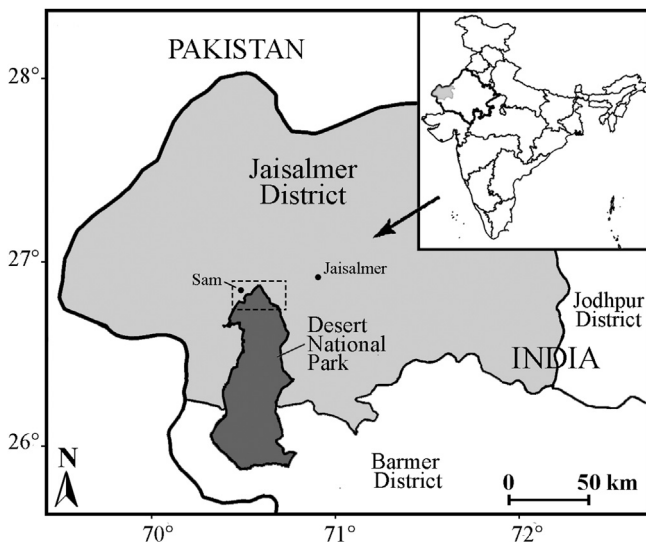


Fig. 1. Location of the study area (dashed line) in Jaisalmer District, Rajasthan, India. The small inset map shows the location of Jaisalmer District (gray highlight) within India.

69.4 ± 19.1 min (mean ± SD).

Wind and sky conditions were recorded at the start of each sampling session; ambient air temperature (in shade, ~1 m height) was recorded at half hour intervals using a digital thermometer. Species, time of sighting, 25 m × 25 m plot ID, and substrate, were recorded for all lizard sightings. We also noted presence of the fossorial, psammophilous *Ophiomorus raithmai* from its distinctive tracks on sand for additional information on species richness of habitats, as this secretive species would not be easily located in visual surveys. In BD, slope and dune position (crest, slope, edge or interdune) were noted for all lizard sightings; and rock size category (large rocks, >0.5 m; rubble, <0.5 m; sheet rock; soil) was recorded in RH. For undisturbed lizards we also recorded microhabitat category (Table 1), visually estimated distance to and type of closest vegetation (categories: <0.25 m, 0.25 m–1 m, 1 m–3 m, >3 m; shrub or grass), as well as orientation for rupicolous species. These reflect species-specific traits including thermal ecology and foraging mode, and to a lesser extent display and sexual behavior (Pianka, 1986). All lizards that were spotted were defined as active, except for *B. laungwalaensis* that were spotted buried in the sand (this species leaves a distinct impression on the sand surface when it buries itself, and is often not completely buried).

2.4. Data analysis

Abundance was determined for each grid from the sampling session with the maximum sightings for each species. This represents a lower bound of actual densities (Shenbrot and Krasnov, 1997; McNair, 2003). To standardize sampling effort for comparisons of spatial overlap, we used the sampling session for each grid that had the maximum sightings for each species. These were averaged for the two days of sampling. For calculating time overlap in diurnal species, the number of sightings in T1 and T2 were halved to be comparable with T3.

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

Spatial and temporal niche overlap was calculated with abundance data based on Pianka's (1973) measure in the program EcoSim700 (Version 7.72; Gotelli and Entsminger, 2008) and compared

with a null model to test if patterns were non-random. EcoSim was run with 30,000 iterations, and equiprobable resource states. We used algorithms RA2 and RA3 because, as well as intuitively corresponding to ecologically meaningful null models with which to compare real data, these are most reliable in detecting non-random overlap patterns (Willenmier and Pianka, 1990; Luiselli, 2007b, 2008). RA2 relaxes niche breadth but retains zero states, while RA3 retains niche breadth and reshuffles zeroes, retaining the degree of specialization for the species but allowing possible use of other available states. We analyzed spatial overlap between species-pairs of the community at two scales, first across all habitats and 192 plots, and then within specific habitats. We set 'hard zeroes', which correspond to resource states a species cannot occupy, and that are not reshuffled in the randomization process. We used this for species restricted to a particular habitat type or types, with hard zeroes in plots of the other habitat types. Chi² tests ($P < 0.05$) were used to test for differences between species with respect to specific microhabitat resources (e.g. microhabitat categories in Table 1, distance to closest vegetation, substrate) or peak times of activity. In cases where sample size did not permit chi square tests, simple percentages were used for qualitative comparisons. A Mann–Whitney U-test was used to examine differences in the temperature at which species were active. Spearman's rank correlation was used to determine whether repeat sampling sessions were similar, by pooling repeats of sampling sessions across species for all sampling sessions where at least one of the seven species was sighted. Similarly, a Wilcoxon sign rank test was used to test if differences between repeats were not significantly different from zero. Statistical analyses were conducted using SPSS (Version 14.0; SPSS Inc., Chicago, Illinois) and Excel 2007 (Microsoft®, Redmond, Washington, USA).

3. Results

3.1. Species richness and abundance

We recorded 1039 sightings of 12 species across a total of 84 sampling sessions. Table 2 summarizes species composition and abundance across habitats. *T. agilis* and *Crossobamon orientalis* were recorded from all four habitats, although *Crossobamon orientalis* was strictly associated with sand deposits. *A. cantoris* was found in the three sandy habitats (BD, SD, GG), while *B. laungwalaensis* was restricted to the barren dunes. *Uromastix hardwickii* was only found in GG; *C. scabrum*, *O. jerdoni*, *Microgecko persicus euphorbiicola*, *Hemidactylus flaviviridis* and *Hemidactylus* sp. were restricted to RH. *O. raithmai* was sighted only in BD, but tracks were observed in sandy tracts across all habitats.

RH had the lowest abundance with 19.3 lizards/ha but the highest total species richness with 9 species, while SD had the highest abundance and lowest species richness with 59.3 lizards/ha and only 3 species (Table 2). BD had 5 species with 20.3 lizards/ha and GG had 4 species with 31.3 lizards/ha (Table 2).

3.2. Comparisons across habitats

3.2.1. Spatial overlap

Spatial overlap at the level of the 25 m × 25 m plots across all habitats (Table 3) was moderate only for *Acanthodactylus*–*Crossobamon* (0.57), *Acanthodactylus*–*Trapelus* (0.46), *Crossobamon*–*Trapelus* (0.39), *Cyrtopodion*–*Hemidactylus* (0.33), *Cyrtopodion*–*Ophisops* (0.40), and high for *Crossobamon*–*Hemidactylus* (0.79). The observed niche overlap was non-significant (RA2: $P_{(obs<exp)} = 0.20$; RA3: $P_{(obs<exp)} = 0.55$).

Table 1

Microhabitat categories and their definitions, used in classifying undisturbed lizards. Modified from Pianka (1986).

Sr. No.	Microhabitat category	Definition
Diurnal		
1	Fossorial	Buried individuals
2	Open sun	Lizards in open sun
3	High sun	Lizards in the sun, perched above 100 cm
4	Low sun	Lizards in the sun, perched below 100 cm
5	Shrub	Lizards within a shrub
6	Shrub shade	Lizards using shrub shade (but not within shrub)
7	Grass	Lizards within grass
7	Grass shade	Lizards using grass shade (but not within grass)
9	Rock shade	Lizards using rock shade
10	Rodent burrow	Lizards in rodent burrows
Nocturnal		
11	Fossorial	Buried individuals
12	Terrestrial	On the ground
13	Rupicolous	On rocks

Table 2

Abundance (ind/ha) and species richness of lizards across habitats. Mean abundance is presented with the range in parentheses. For species richness, the range is presented and in parentheses is richness including *Ophiomorus raithmai* presence from tracks. BD, barren dunes; SD, stabilized dunes; GG, grassland; RH, rocky hills, Av, average across all habitats.

Family	Species	Habitat type				Av
		BD	SD	GG	RH	
AGAMIDAE	<i>Bufo laungwalaensis</i>	10.0 (8–12)	0	0	0	2.5
	<i>Calotes versicolor</i>	0	0	0	1.0 (1)	0.3
	<i>Trapelus agilis</i>	1.7 (0–4)	6.7 (3–9)	3.3 (0–9)	1.3 (1–2)	3.3
	<i>Uromastyx hardwickii</i>	0	0	0.7 (0–1)	0	0.2
GEKKONIDAE	<i>Crossobamon orientalis</i>	3.7 (0–10)	21.3 (18–23)	6.7 (1–14)	0.7 (0–2)	8.1
	<i>Cyrtopodion scaber</i>	0	0	0	4.0 (0–10)	1.0
	<i>Hemidactylus flaviviridis</i>	0	0	0	0.3 (0–1)	0.1
	<i>Hemidactylus</i> sp.	0	0	0	4.0 (0–10)	1.0
	<i>Tropicolotes persicus</i>	0	0	0	2.0 (0–5)	0.5
LACERTIDAE	<i>Acanthodactylus cantoris</i>	4.3 (0–12)	31.3 (21–50)	20.7 (16–28)	0	14.1
	<i>Ophisops jerdoni</i>	0	0	0	6.0 (3–8)	1.5
SCINCIDAE	<i>Ophiomorus raithmai</i>	1.0 (0–2)	0	0	0	0.5
	Mean abundance	20.3 (10–40)	59.3 (44–82)	31.3 (25–39)	19.3 (10–31)	32.9 (10–82)
	Species richness	1–5	3 (4)	3–4 (5)	3–8 (9)	12

Table 3

Overall spatial overlap (Pianka's measure) between species pairs across and within habitats. Species pairs with overlap values below 0.20 are not presented. AC – *Acanthodactylus cantoris*, BL – *Bufo laungwalaensis*, CO – *Crossobamon orientalis*, CS – *Cyrtopodion scaber*, HP – *Hemidactylus* sp., OJ – *Ophisops jerdoni*, TA – *Trapelus agilis*; ALL – all habitats, BD – barren dunes, SD – stabilized dunes, GG – grassland, RH – rocky hills.

Habitats				
Sand	ALL	BD	SD	GG
AC–BL	0.08	0.35	0	0
AC–CO	0.57	0.65	0.64	0.35
AC–TA	0.46	0.30	0.57	0.34
BL–CO	0.07	0.28	0	0
CO–TA	0.39	0.46	0.42	0.37
Rock	ALL	RH	–	–
CO–HP	0.07	0.79	–	–
CS–HP	0.33	0.33	–	–
CS–OJ	0.40	0.40	–	–
CS–TA	0.06	0.26	–	–
HP–OJ	0.24	0.24	–	–
OJ–TA	0.06	0.27	–	–

3.2.2. Fine-scale spatial separation: microhabitat and distance to vegetation

Acanthodactylus was most often seen in the open sun (53%, $n = 216$). The highest proportion of *Bufo* were recorded inactive, buried (48%, $n = 86$), while 93% of active *Bufo* were seen in the open sun ($n = 44$). *Trapelus* was associated with shrubs, either in or on shrubs (shrub and high sun categories combined; 57%, $n = 68$). *Ophisops* was closely associated with rocks and 50% of 30 sightings were in rock shade. Of six sightings of *Calotes*, five were on vegetation above 1.5 m high.

Acanthodactylus, *Bufo*, *Crossobamon* and *Trapelus* show significantly different spatial use across habitats when measured as distance to closest vegetation ($\chi^2 = 304.35$, $df = 9$, $P \leq 0.001$). *Bufo* was found further than 3 m from vegetation more than expected, *Crossobamon* within 3 m, *Acanthodactylus* 1 m, and *Trapelus* within 25 cm. Distance to closest vegetation was not considered for *Ophisops* because the rocky habitat has low vegetation cover and is structurally distinct from the other habitats, cover is usually among crevices.

Among nocturnal species only *Crossobamon* was abundant, with all sightings on the ground (nocturnal terrestrial; $n = 167$). On both occasions when *Ophiomorus* was located, the animals were buried just beneath the sand surface (nocturnal fossorial). This species is

almost entirely fossorial, though occasionally coming above ground (pers. obs.). All sightings of *Cyrtopodion*, *Hemidactylus* sp., *H. flaviviridis*, and *Microgecko* were associated with rocks (nocturnal rupicolous). *H. flaviviridis* was oriented vertically, *C. scaber* and *Hemidactylus* sp. used horizontal and vertical rock faces while *Microgecko* used only horizontal sheet rock or rubble.

3.3. Habitat-specific comparisons

3.3.1. Barren dunes

Within BD, spatial overlap was highest between *Acanthodactylus*, *Trapelus* and *Crossobamon* (Table 3), and was significantly higher than expected using RA3 (RA2: $P_{\text{obs} < \text{exp}} = 0.45$; RA3: $P_{\text{obs} < \text{exp}} = 0.99$), indicating that species within this habitat show non-random aggregation. *Bufo* had low overlap with other species (0.15–0.35), and had different spatial use of the dunes in two aspects, dune position (Fig. 2) and distance to closest vegetation. *Bufo* is the only species that used all parts of the barren dunes habitat, while other species were restricted largely to vegetated interdunal areas and edges (Fig. 2). This is reflected in distance from vegetation, with 56% of *Bufo* sightings ($n = 86$) more than 5 m away from the closest vegetation, and only 15% within 1 m from vegetation. On the other hand 77% of *Acanthodactylus* sightings ($n = 13$) and 63% of *Crossobamon* sightings ($n = 19$) were within 1 m of vegetation.

3.3.2. Stabilized dunes

This habitat had only three species, each at its highest

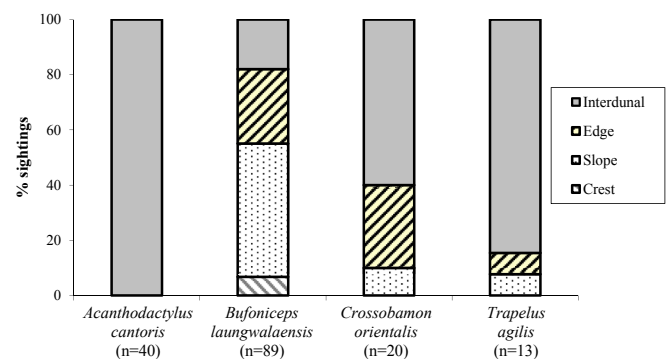


Fig. 2. Spatial use of the barren dunes habitat by four species.

abundance in this habitat (Table 2), with moderate to high non-significant (RA2: $P_{(\text{obs}<\text{exp})} = 0.44$; RA3: $P_{(\text{obs}<\text{exp})} = 0.60$) spatial overlap (Table 3). Substrate and physical structure are constant within this habitat, so the only way in which species can separate is based on microhabitat categories and distance to vegetation. A χ^2 test comparing distance to closest vegetation across these species was significant ($\chi^2 = 16.07$, $df = 4$, $P \leq 0.01$), indicating that *Trapelus* was found disproportionately often within 0.25 m of vegetation (89% of sightings in this habitat; $n = 28$), *Acanthodactylus* from 0.25 m to 1 m (39.7%, $n = 116$), *Crossobamon* from 0.25 m to 3 m (48.8%, $n = 82$). With regard to microhabitat category, 52.5% of *Acanthodactylus* sightings ($n = 139$) were in open sun, 22.3% in shrubs and, 19.4% in shade of vegetation. *Trapelus* ($n = 25$) had 40.0% of sightings in shrubs and a further 32% sightings on shrubs (low and high sun).

3.3.3. Grassland

Acanthodactylus, *Crossobamon* and *Trapelus* showed moderate spatial overlap within GG (Table 3) which was not significantly different from random (RA2: $P_{(\text{obs}<\text{exp})} = 0.85$; RA3: $P_{(\text{obs}<\text{exp})} = 0.80$). These species are 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 ($\chi^2 = 71.28$, $df = 2$, $P \leq 0.001$). *Acanthodactylus*, *Crossobamon* and *Trapelus* showed significantly different spatial use in relation to distance from vegetation ($\chi^2 = 11.15$, $df = 2$, $P \leq 0.01$). The <0.25 m distance to vegetation category had 83.0% of *Acanthodactylus* sightings ($n = 88$), 54.2% of *Crossobamon* sightings ($n = 24$), and 88.5% of *Trapelus* sightings ($n = 26$). *Acanthodactylus* and *Trapelus* are further separated by microhabitat category – with the majority of *Acanthodactylus* sightings close to grass and *Trapelus* sightings close to shrubs. 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 shrubs (low and high sun), and remaining sightings were divided between shrubs and grass (19.3% each), and open sun (15%).

3.3.4. Rocky hills

The rocky hills were characterized by high species richness and low abundance of all lizards (Table 2). Spatial overlap varied considerably between species pairs (Table 3), but was not significantly different than expected by chance (RA2: $P_{(\text{obs}<\text{exp})} = 0.59$; RA3: $P_{(\text{obs}<\text{exp})} = 0.79$). The highest overlap was between *Crossobamon*-*Hemidactylus* (0.79), followed by *Cyrtopodion*-*Ophisops* (0.40) and *Cyrtopodion*-*Hemidactylus* (0.33). *Crossobamon* was restricted to sand deposits ($n = 4$) while *Hemidactylus* sp. was found only on rocks ($n = 15$). *Cyrtopodion* ($n = 16$) and *Ophisops* ($n = 65$) were separated by rock size ($\chi^2 = 8.01$, $df = 2$, $P \leq 0.02$). *Cyrtopodion* was found more on large rocks (35.7%), sheet (42.9%), and less on rubble (21.4%); while *Ophisops* was found more among rubble (57.8%), less on sheet rock (31.3%) and large rocks (10.9%). *Cyrtopodion* and *Hemidactylus* sp. show similar microhabitat use, both associated with rocks and largely oriented horizontally (*Cyrtopodion*, 66.7% horizontal; *Hemidactylus* sp., 60.0%).

3.4. Temporal and thermal patterns of activity

Nocturnal lizards were represented by five species of geckos and a skink. Sandy habitats had only two nocturnal species, *Ophiomorus* and *Crossobamon*; and the rocky hills had four additional species, *C. scabrum*, *H. flaviviridis*, *Hemidactylus* sp. and *M. persicus*. As there was a limited sampling period at night, comparisons cannot be made between nocturnal species.

Diurnal species had distinct trends in activity (Fig. 3), with

Acanthodactylus the first to emerge with maximal activity between 2 ½ to 4 h after sunrise, followed by *Bufoinceps* with maximal activity from 3 ½ to 4 ½ h after sunrise. *Trapelus* showed maximal activity 11 ½ h after sunrise (about an hour before sunset), with indistinct peaks in mid to late morning (3–4 h after sunrise). *Ophisops* was similar, peaking 12 h after sunrise, with high activity 2 ½–3 ½ h after sunrise as well. No sampling was carried out between 5 and 11 h after sunrise, a time with limited lizard activity due to high air and substrate temperatures.

Pooled for all habitats, activity across sampling sessions was significantly different for the diurnal species ($\chi^2 = 53.46$, $df = 6$, $P \leq 0.001$; Table 4). *Acanthodactylus* had higher activity in T1, *Bufoinceps* in T2; while both *Ophisops* and *Trapelus* had highest activity in T3. Activity in T1 was lower for *Bufoinceps*, *Ophisops*, and *Trapelus*; in T2 lower for *Ophisops* and about proportional for *Acanthodactylus* and *Trapelus*; and in T3 lower for *Acanthodactylus* and *Bufoinceps*.

The air temperatures at which peak activity was recorded and average air temperatures at which species were active varied. *Acanthodactylus* showed peaks at lower temperatures than the other species (mode = 27.5 °C and 32.0 °C, mean = 31.5 °C \pm 4.3 °C, $N = 302$), followed by *Bufoinceps* (mode = 34.0 °C, mean = 31.9 °C \pm 3.5 °C, $N = 29$), while *Ophisops* (mode = 41.5 °C, mean = 35.9 °C \pm 5.0 °C, $N = 43$) and *Trapelus* (mode = 41.5 °C, mean = 36.0 °C \pm 5.3 °C, $N = 69$) showed peaks in activity at very high air temperatures. *Acanthodactylus* and *Bufoinceps* were each active at significantly different air temperatures from *Ophisops* and *Trapelus* (U-test, $P < 0.001$); though *Acanthodactylus* - *Bufoinceps*, and *Ophisops* - *Trapelus* were not significantly different (U-test, $P > 0.5$).

3.5. Sampling methodology

We found area constrained visual encounter surveys to be effective and consistent, this method has been used at a similar scale to sample lizards in a variety of habitats with success (e.g. Shenbrot and Krasnov, 1997; McNair, 2003; Doan, 2003). Based on species accumulation curves, all species were captured at less than 50% of total sampling effort. Repeats pooled across species and sampling sessions ($n = 51$) were similar (Spearman's rank correlation = 0.82, $P < 0.01$), and the differences between repeats were not significantly different from zero ($H_0 = 0$; t-test of difference between repeats, $Z = -0.996$, $P = 0.39$).

4. Discussion

Arid environments are characterized by low productivity and limited resources. It follows that an arid zone community consisting of similar species is likely to exhibit resource partitioning to some degree in order to coexist (Schoener, 1974; Pianka, 1986). This study, the first on resource partitioning in the Thar Desert, demonstrates that space is important in resource partitioning in this community, with spatial separation at different scales between all lizard species. Space and microhabitat have been previously shown to be important in structuring desert lizard communities in many independently evolved desert systems (Pianka, 1973, 1986; Barbault and Maury, 1981; Vitt et al., 1981; Toft, 1985; Shenbrot et al., 1991; Shenbrot and Krasnov, 1997; Rogovin et al., 2000). This study was carried out in relatively undisturbed areas, and it is unclear how habitat alteration will affect community composition and resource partitioning (Pelegriin et al., 2013), though abundances of single species were clearly lower in altered habitats (Agarwal, unpubl. data).

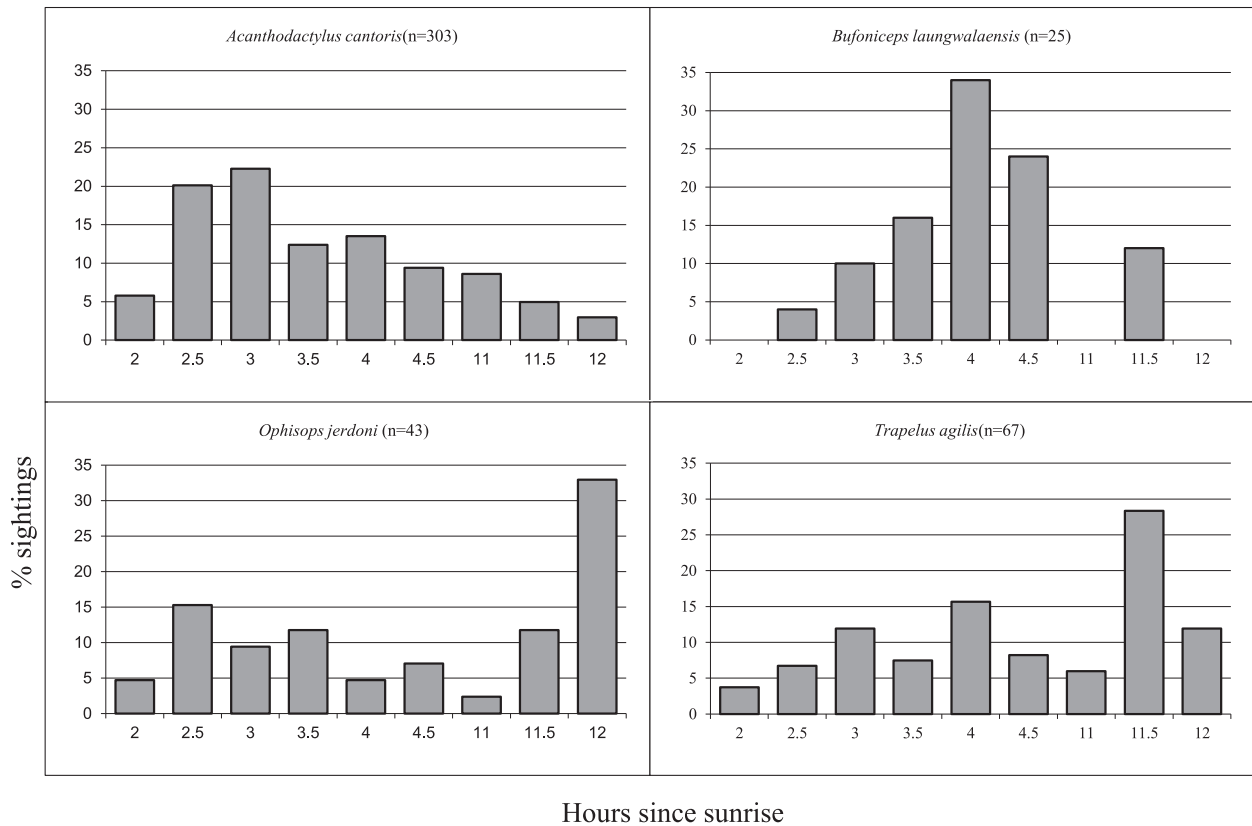


Fig. 3. Frequency distribution of percent lizard activity through the day. No sampling was carried out between 5 and 11 h after sunrise. Sampling effort is equal across time categories.

Table 4

Percentage activity of each species across sampling sessions. T1, start time 8:00 h to 8:40 h (1 h 30 min to 2 h after sunrise); T2, 09:30 h to 10:10 h (2 hrs 45 min to 3 hrs 30 min after sunrise); T3, 17:00 to 17:15 (two hrs before sunset). Sampling effort standardized across sampling sessions (refer Section 2.4).

Sampling session	<i>Acanthodactylus cantoris</i> (n = 303)	<i>Bufoniceps laungwalaensis</i> (n = 43)	<i>Ophisops jerdoni</i> (n = 43)	<i>Trapelus agilis</i> (n = 68)
T1	50.3	24.0	30.2	23.5
T2	33.2	64.0	23.3	30.9
T3	16.5	12.0	46.5	45.6

4.1. The Thar Desert lizard community

The lizard community in the Thar is relatively depauperate, with only *B. laungwalaensis* considered endemic and just two genera that have more than a single species (species: genus ratio 1.2). This may be because the Thar is a relatively young desert, with all the true desert species at the eastern limits of their range. Many species are distributed in the same habitats and some co-occur within habitats as well, but all species in this community are spatially separated by fine scale spatial partitioning as well as by peak times of activity (for diurnal species). Additionally, foraging mode, which in lizards is largely phylogenetically determined, may separate species that use similar areas based on the type of food items eaten (Pianka, 1986). Thus, widely foraging species such as the lacertids *Acanthodactylus* and *Ophisops*, and the scincid *Ophiomorus* (foraging mode based on personal observations), are likely to eat slow moving or clumped prey, while the sit and wait foragers such as the agamids *Bufoniceps* and *Trapelus*, and all the gekkonids likely

feed on more active prey (Huey and Pianka, 1981; Pianka, 1986).

4.2. Comparisons with other desert lizard communities

Overall lizard abundance observed in this study is lower than the Bukhara Desert (Shenbrot et al., 1991) and Australian Deserts (Morton and James, 1988); similar to the Gobi Desert (Rogovin et al., 2000); and higher than Israel (Shenbrot and Krasnov, 1997), the Chihuahua (Shenbrot et al., 1991), and North American Deserts (Pianka, 1967). Including *Varanus bengalensis* and *Varanus griseus* from opportunistic sightings, species richness in our study (14 species) is lower than the Australian Deserts (18–40, Pianka, 1986); similar to Israel (14, Shenbrot and Krasnov, 1997), the Bukhara and Chihuahua (17, 15, Shenbrot et al., 1991), and Kalahari (12–18, Pianka, 1971); and higher than the high latitude Gobi (4, Rogovin et al., 2000) and North American Deserts (4–10, Pianka, 1967).

Major differences in biogeographic history, elevation, rainfall, and latitude between these deserts, as well as the geographic extent of the studies can confound comparisons. However, one consistent patterns emerges from across different systems – that substrate is the main habitat variable structuring desert lizard communities (Pianka, 1986; Shenbrot et al., 1991; Shenbrot and Krasnov 1997; Barbault and Maury, 1981; Doughty et al., 2011). Highest values of abundance were in sandy habitats, and the lowest in rocky habitats, similar to deserts in Israel, the Bukhara and Chihuahua. Species richness was lowest in sandy habitats and highest in the rocky habitat, similar to Israel (Shenbrot and Krasnov, 1997). Rocky habitats have greater diversity of microhabitats (rock sizes and types, different areas of slopes, drainages, sandy tracts) and considerable horizontal and vertical heterogeneity, which may explain the consistently higher richness (Stevens and Tello, 2011).

Additionally, the lizard community in the rocky habitat included a mix of sclerophilous species, some widely distributed species, as well as a few psammophilous species associated with sand deposits. Sandy habitats may have low richness as they lack a vertical component altogether and are spatially homogenous. Another reason may be the overall geographic position of the sandy areas of the Thar, forming the easternmost limit of sandy deserts in the northern horse latitudes, and the fact that the Thar is a relatively young desert (Singhvi and Kar, 2004).

Acknowledgments

This work was carried out as part of the M.Sc. program at the Wildlife Institute of India. We thank the PCCF, Rajasthan, R. N. Mehrotra and the Deputy Director, DNP, R. Jugtawat for permission to conduct fieldwork. Tarun, the Khichi family, Hajara Ram and Jamal Khan were invaluable during fieldwork. H. C. Bohra helped in Jodhpur. IA thanks two anonymous reviewers, P. Bal, A. Captain, N D'Silva, V. B. Giri, K. Isvaran, RA and SA for comments.

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