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Lizards of the Thar Desert – Resource partitioning and community composition

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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.

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*, *Crotolaria 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 sindicus*, *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. sindicus* and *C. bifloris* and shrubs *Aerva* spp., *C. polygonoides*, *C. burhia* and *H. salicornium*; gravely 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*.

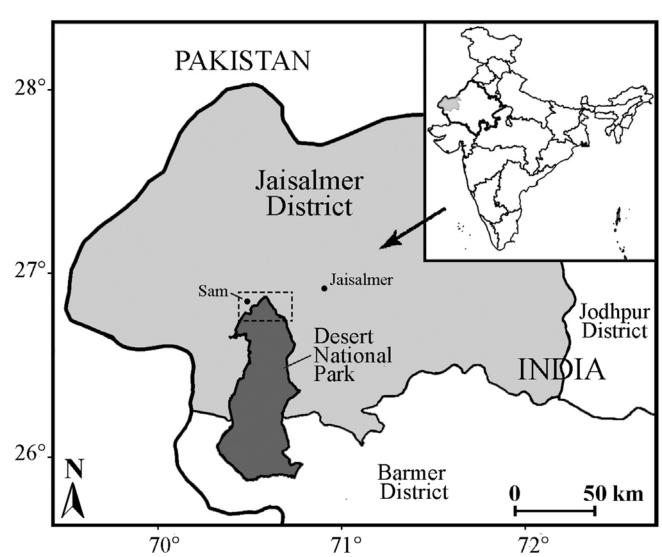

Fig. 1. Location of the study area (dashed line) in Jaisalmer District, Rajasthan, India. The small inset map shows the location of Jaisalmer District (gray highlight) within India.

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), *Bufoniceps 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 (1hr 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