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Habitat Use and Activity Patterns in the Nocturnal Gecko, *Chondrodactylus turneri*

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Abstract: Intraspecific variation in behavior is often associated with age or size class, with many animals experiencing ontogenetic differences in diet, predation risk, physiological function, and competition. The nature of intraspecific behavioral variation will depend on the environmental context and has been more thoroughly examined for diurnal species. We studied microhabitat use and activity relative to time of night and the lunar cycle for the nocturnal gecko *Chondrodactylus turneri,* in the Namib Desert. Geckos preferred larger rocks with more crevices and were clumped in their occupancy of rocks, with some rocks being occupied by as many as eight individuals. Age classes differed in their use of open areas, with juveniles being encountered more often in the open. Activity levels varied with moon phase and time, with adults and juveniles exhibiting different relationships. Our results indicate that multiple factors might be influencing intraspecific behavioral variation.

Key words: Behavior; Ecology; Lizard; Lunar cycle; Morphometrics; Namib Desert; Turner's Thick-toed Geckos

For many animals, individuals of different age classes or sexes often have different habitat requirements. Different diets, predation risks, and levels of competition can lead to intraspecific variation in habitat use and activity patterns. The response of individuals will depend on the environmental context; for example, nocturnal or saxicolous animals might have different patterns of intraspecific behavioral variation than expected for a diurnal sand dweller.

We gathered behavioral and ecological data on a nocturnal gecko that is relatively abundant in southern African desert communities to provide an initial assessment of age-based differences in habitat use and activity. Turner's Thick-toed Geckos (*Chondrodactylus turneri*) occupy rocky areas within northern regions of southern Africa (Namibia, Botswana, Zimbabwe, northeast South Africa, and southwest Mozambique; Branch 1998). Their habitat includes granite outcrops in the gravel plains of the Namib Desert (Gramentz 2005; Henschel et al. 2006), where they emerge from crevices at night to forage (Alexander and Marais 2007). The gravel plains habitat consists of a sparsely vegetated, primarily flat, sand and gravel substrate containing embedded granite and quartz stones, interspersed with granite outcrops (Henschel et al. 2003, 2006). Rocky outcrops offer diverse habitat options (Schlesinger and Shine 1994; Howard and Hailey 1999). The presence of suitable refuges in rock habitats can affect the social structure, promoting aggregations when refuges are limited (Graves and Duvall 1995; Mouton 2011; Gardner et al. 2015). When suitable refuges are clustered and aggregations result, competition for food can be minimized if prey are obtained away from refuges (Mouton 2011). Physical attributes of rocks, particularly their size and retreat structure, influence the thermoregulatory abilities of resident animals (Huey et al. 1989; Croak et al. 2008), and crevice choices during inactive periods ultimately influence physiological functioning during active periods (Ibargüengoytía et al. 2007).

The interplay between *C. turneri*'s habitat choice and activity relative to age and sex was the focus of our study. Specifically, we examined the natural history of Turner's Thick-toed Geckos relative to characteristics of rocks containing potentially habitable crevices, and addressed four broad questions: (1) Which physical features of rock outcrops are associated with rock occupancy (Schlesinger and Shine 1994)? (2) Is the distribution of geckos affected by age, sex, or rock characteristics? (3) When are *C. turneri* active? and (4) Does the timing of activity vary with the lunar cycle (Werner et al. 2006)?

Materials and Methods

We collected data from 19 December 2011 to 14 January 2012 on the gravel plains of the Namib–Naukluft National Park, Namibia (23°33′25.86″S, 15°2′23.79″E; datum = WGS84). The 4–5-ha study site, which formed a trapezoid (dimensions = 234 m, 230 m, 230 m, 180 m), was open, flat, and characterized by coarse sand interspersed with rocks and plants (e.g., Rough-leaved Bushman grass (Poaceae: *Stipagrostris gonatostachys*) and Hoodia (Asclepiadaceae: *Hoodia currorii;* Henschel et al. 2006).

During the nights of 22 December 2011–13 January 2012, we conducted systematic searches for lizards during peak activity times (2000 to 0400 h) to quantify their occurrence on either rock outcrops or on the sand between rocks. When a lizard was sighted, we marked its location, captured the lizard by hand, and recorded its original location (on a rock or on the ground between rocks). For lizards captured on rocks, we noted whether any part of the lizard's body was in a crevice. Upon capture, we uniquely marked each lizard with colored bands on the base of the tail using nontoxic paint pens, measured the snout–vent length (SVL) and tail length (a ruler, ±1 mm), and recorded evidence of tail breakage (intact, autotomized, or regenerated). We assigned lizards to age class based on the two distinct size-classes of lizard we observed, herein referred to as adult (SVL ≥70 mm) and juvenile (SVL ≤60 mm); we did not assess reproductive maturity. Hatchling *C. turneri* are present from December to March and are of the smaller size corresponding to our

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juvenile designation (~60–65 mm SVL; Branch 1998). We sexed adult subjects using a cloacal probe and measured their head length and head width using digital calipers (±0.1 mm). We measured head length from the anterior edge of the otic opening to the tip of the snout and measured head width at the widest part of the head. When we resighted a marked lizard, we recorded time of resighting and location. Lizards were considered occupants of a rock on which they were sighted during the study.

We measured rock characteristics from 27 December 2011 to 13 January 2012. To minimize potential disturbance to the lizards during night-time data collection for surveys, we measured rocks on the study site at midday. Rocks were measured if they were $\geq 0.5 \times 0.5$ m in dimension and had at least one crevice measuring 15 cm long × 5 cm deep. The crevice criteria were based on the length and width of adult *C. turneri*, approximating the space into which we postulated they could fit. On each rock, we counted the number of crevices equal to or exceeding these dimensions, and measured the rock's maximum height, length, and width (perpendicular to length). Measured rocks were numbered with paint; unmeasured rocks were left unmarked but were counted.

To determine the activity period of the lizards, we surveyed the study site by walking linear transects throughout the site starting at one of the four corners, scanning the rocks and intervening ground every 2 h from 2000 to 0400 h; each survey took 30–60 min and was separated from the next survey by ≥60 min. To minimize disturbance, lizards were sighted with red light through the use of light-emitting diode (LED) headlamps (Black Diamond Storm or Petzl Tikka). We suspended surveys focused on capturing, marking, and measuring geckos when assessing activity cycles. No captures were made during activity surveys; any visible lizard was classified as active whether observed moving, sitting still, or partially in a crevice. Activity surveys were conducted during two 3-d periods corresponding to the new moon (22–25 December 2011) and full moon (8–10 January 2012). To account for the possible role of temperature, we incorporated into our analysis the air temperature at the start of each activity survey, recorded at a Gobabeb Research and Training Centre's weather station adjacent to our study site.

Statistical analyses were completed using Minitab 16 (State College, PA) and results were considered significant at $\alpha \leq 0.05$. All values are reported as means ± 1 SE. For morphometric data, we examined sexual dimorphism in head size using analyses of covariance (ANCOVA) with sex as the independent variable and SVL as the covariate. We used chi-square tests to determine whether tail breakage varied between age groups or sexes. We applied chi-square tests to determine the use of measured and unmeasured rocks by different age classes of lizard, and linear regressions to evaluate rock characteristics associated with rock occupancy. We assessed patterns of multiple occupancy of rocks by comparing the number of individual lizards observed occupying each measured rock to expectations from a random (Poisson) distribution using a chi-square test. We assessed gecko activity patterns using General Linear Models, with the categorical variables age, moon phase, 2-h time interval, and their interactions as well as the continuous variable of temperature. We used chi-square tests to look for age and sex differences in sightings (in the open or in a crevice).

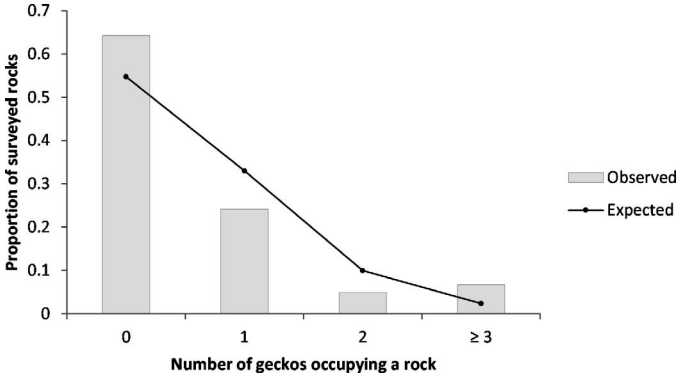

FIG. 1.—Frequency distribution of rocks measured in the gravel plains of the Namib–Naukluft National Park, Namibia, that were occupied by Turner's Thick-toed Geckos (*Chondrodactylus turneri*), relative to a random distribution (Poisson, indicated by the line). Bars indicate the proportion of measured rocks ($n = 224$) having a given level of gecko occupancy (observed mean occupancy = 0.6 geckos/rock).

RESULTS

We captured 135 *C. turneri* at the study site: 48 adults and 87 juveniles. Of the captured adults, 43.7% were male ($n = 21$) and 56.3% female ($n = 27$). Adult males and females did not differ in overall body size (SVL, $t = 0.33$, df = 45, $P = 0.75$; mass, $t = 1.20$, df = 44, $P = 0.24$), but did differ in the relative size of their heads. Adult head length was unrelated to sex ($F_{1,44} = 0.15$, $P = 0.70$), or the interaction between sex and SVL ($F_{1,44} = 0.08$, $P = 0.78$), but head width was related to the interaction between SVL and sex ($F_{1,44} = 8.45$, $P = 0.006$). Male head width increased with SVL and males had wider heads than females of the same size. Tail breakage was more common in adults than juveniles ($\chi^2 = 17.50$, df = 1, $P < 0.001$)—no juveniles had experienced tail breakage whereas 18.7% of adults had. Furthermore, tail breakage was more common in adult males than in females ($\chi^2 = 5.20$, df = 1, $P = 0.02$).

Juveniles were found in the open, and adults at least partially in crevices, more often than random expectations (initial sightings in the open = 85% for juveniles vs. 54% for adults; $\chi^2 = 10.04$, df = 1, $P = 0.002$). Adult males and females were similar in their likelihood of being encountered in the open ($\chi^2 = 1.92$, df = 1, $P = 0.17$). Geckos were clumped in their distribution on rocks: Measured rocks that had no geckos or that had at least three gecko occupants occurred more often, and rocks with one or two gecko occupants occurred less often than expected when compared with a random distribution ($\chi^2 = 32.99$, df = 2, $P < 0.0001$; Fig. 1). The occurrence of adult gecko occupants on a rock was positively correlated with the occurrence of juvenile occupants on the same rock ($r = 0.26$, $P < 0.001$). We documented 26 rocks where more than one lizard was observed. Some rocks were used by as many as six juveniles, but there were never more than three adults (one male and two females) recorded from the same rock. Juveniles and females were present on rocks known to harbor individuals of all demographic classes, but adult males were observed on multiple-occupancy rocks only when used by adult females

TABLE 1.—Pearson correlation coefficients (r) for characteristics of rocks measured in the gravel plains of the Namib–Naukluft National Park, Namibia. (NS: not significant, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $P \leq 0.001$).

	Rock height	Number of crevices	Distance to nearest rock
Number of crevices	0.67^{***}		
Distance to nearest rock	-0.12^{NS}	-0.16^{*}	
Number of *Chondrodactylus turneri*	0.52^{***}	0.51^{***}	-0.08^{NS}

and juveniles (not by other adult males). Males recorded from multiple-occupancy rocks were smaller than those recorded from single-occupancy rocks (SVL, $t = 2.25$, df = 15, $P = 0.04$). We resighted 45 lizards (33.3%) during the course of our study ($n = 25$ juveniles, 11 females, 9 males). Resightings occurred with similar frequency regardless of age class or sex ($\chi^2 = 2.35$, df = 2, $P = 0.31$).

We assessed 401 rocks on the study site: 224 met our size and crevice criteria (measured rocks = 56%), and an additional 177 did not (unmeasured rocks = 44%). Both juvenile and adult geckos occurred on measured rocks more often than random expectations ($\chi^2 = 34.46$, df = 3, $P < 0.001$). Geckos occupied 80 measured rocks (36%), with occupancy levels ranging from 1 to 8 geckos (Fig. 1). Rock height, length, and width were positively correlated with each other and number of gecko occupants; we report results for rock height because it was most strongly correlated with occupancy. Rock height and the number of crevices were positively correlated with the number of geckos recorded from a rock (Table 1). A two-variable linear regression including rock height and the number of crevices was a better predictor of gecko occupancy than any single variable (geckos = –0.503 + 0.0542 crevice number + 1.04 height; $R^2 = 0.32$, $F_{2,220} = 51.32$, $P < 0.001$).

Activity was influenced by both demographic and environmental factors. Overall activity was not directly related to any single variable (age, moon phase, time, or temperature), but was related to the interaction between variables: age × time ($F_{4,37} = 3.65$, $P = 0.013$) and moon × age × time ($F_{4,37} = 2.76$, $P = 0.04$; overall $R^2 = 55.9$; Fig. 2). The role of the environment differed between the age classes. Whereas both adults and juveniles showed a peak in activity during the night, that peak was earlier among adults; moon phase had less of an influence on adult activity (Fig. 2A). There was no relationship between residuals one step apart, indicating a lack of autocorrelation in activity data ($r = 0.02$, $P = 0.92$). There was no relationship between adult and juvenile activity levels ($r = 0.05$, $P = 0.80$).

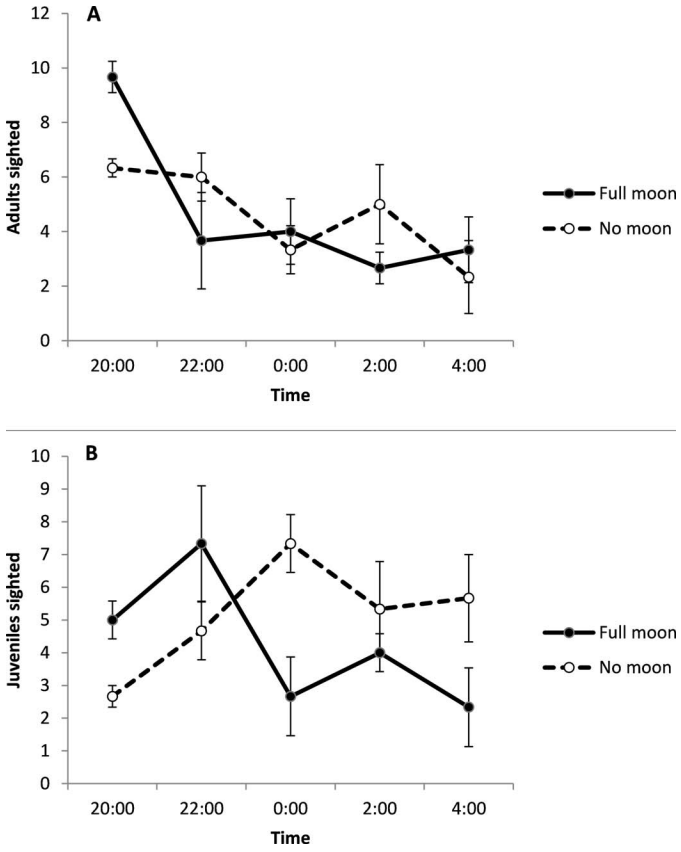

FIG. 2.—Activity of adult (A) and juvenile (B) Turner's Thick-toed Geckos (*Chondrodactylus turneri*) in Namib–Naukluft National Park, Namibia, during full- and no-moon phases. Values represent the mean number (±1 SE) of geckos encountered during three consecutive nights of surveys.

DISCUSSION

Intraspecific variation in behavior is often associated with age or size class, with many animals experiencing ontogenetic differences in diet, predation risk, physiological needs, and competition. The nature of intraspecific behavioral variation will depend on the environmental context. *Chondrodactylus turneri* tended to be clumped in their distribution on rocks, and they show intraspecific variation in habitat use. Many factors can influence habitat use including differences in foraging strategy and direct competition. Juvenile *C. turneri* were found most often in open areas, away from crevices, and often not on rocks. Although we found no direct evidence of interactions between age classes, the greater incidence of juveniles in the open at night could result from displacement to suboptimal habitat by adults (Vasconcelos et al. 2012). Larger individual lizards can dominate smaller individuals (Stamps 1977; Stamps and Tanaka 1981), with cannibalism occurring in some lizard species (Keren-Rotem et al. 2006; Pincheira-Donoso 2012; Childers and Eifler 2013). The fact that there were many creviced rocks on the study site that were not used by lizards indicates that juveniles had access to suitable rocks in the habitat. Alternatively, juvenile lizards might employ different foraging strategies than adults, which could result in different habitat-use patterns (Eifler 1995; Eifler et al. 2007). *Chondrodactylus turneri* have been primarily characterized as ambush predators (Alexander and Marais 2007), which is a strategy that might be more apt for adults. Our general impression was that juveniles were more active than adults, which would lead to this age-class being less tied to crevices than are adults that ambush prey. Higher levels of activity coupled with the possibility of a different diet might account for age-related differences in habitat use. A more detailed assessment of juvenile crevice use and foraging behavior is needed.

Our study provides indirect evidence for male–male competition operating in *C. turneri*. First, on any given rock, no more than one adult male *C. turneri* was ever recorded as an occupant, indicating avoidance of, or possible

contesting for, desirable rocks. Single males on rocks tend to be larger than those on multiple-occupancy rocks, possibly because they are better able to exclude competitors. Among lizards, head size dimorphism is typically associated with greater bite force in males (Vanhooydonck et al. 2010), which can be advantageous during intrasexual aggressive encounters (Anderson and Vitt 1990). Furthermore, evidence of tail autotomy was more frequent among adult male *C. turneri* than among adult females. Tail autotomy might have occurred not only during a failed predatory attack, but also could result from intrasexual fighting (Bateman and Fleming 2009). Male skinks (*Mabuya heathi*) experience greater frequencies of tail autotomy and, when captive, often bite at each other's tails (Vitt 1981). *Chondrodactylus bibronii,* a close-relative to *C. turneri,* provides some interesting avenues for future research—aggregations are common and are formed either by mutual conspecific attraction or by a shortage of optimal shelters, with aggregations only containing a single male (Meyer and Mouton 2007). Their aggregations might be driven by foraging that occurs away from the crevice entrance, coupled with their nocturnal, rock-dwelling lifestyle (Mouton 2011). For *C. turneri,* we saw little evidence for communal crevice use and, even at night, adults seemed to stay close to crevices. Focused observations of adult foraging, male–male interactions and crevice use are needed to identify factors influencing habitat use.

Activity patterns for *C. turneri* varied with both time and moon phase, but adults and juveniles exhibited different relationships. Notably, moon phase seemed to have a more dramatic influence on activity in juveniles than adults. At first, we suspected that perhaps the differing relationship might have been attributable to juveniles avoiding periods when adults were active, but there was no correlation between adult and juvenile activity levels. Rather, our observed differences point to the complexity of age-related responses to the physical and social environment. For juveniles, the interaction between time of night and moon phase was important, but the same interaction did not exist for adults (Fig. 2). For nocturnal animals, the amount of illumination can be an important factor affecting activity, influencing both predation risk and foraging prospects that can vary with age (Kronfeld-Schor et al. 2013). Animals might face a conflict concerning whether various lunar phases represent net opportunities or risks. There is no clear cut way to anticipate how animals will respond to differences in brightness; moonlight has been shown to both enhance and decrease activity in different species of geckos (Werner et al. 2006). Furthermore, activity could be adjusted in multiple ways to respond to changes in luminosity. The gecko *Stenodactylus doriae* exhibits decreased locomotor activity with decreased moonlight, but the number of individuals encountered might not change (Bouskila et al. 1992). Our observed variation in lizard activity is not likely to be caused by a luminosity-related ability to detect nocturnal geckos on rocks. The observed variation in activity did not consistently shift toward one sampling period and we standardized our efforts by using red LED headlamps throughout the study. Our systematic search patterns and efforts when searching the rocks should offset differences in luminosity at different times of night and during full and no moon periods. Our data come from a single moon cycle, which limits our ability to make broader inferences. To more fully understand why *C. turneri* activity varies with time and moon phase, we must understand the relationship between environmental conditions and activity of the larger community.

Our investigation into the ecology and natural history of *C. turneri* indicates that the characteristics of their rocky outcrop habitat, such as rock dimensions, are related to habitat use and activity, and that different demographic groups of the geckos use the same environment in different ways. Our study also raised many questions, particularly with regard to the dynamics between age classes and how aspects of habitat use and activity periods vary as geckos mature. Much can be gained in future work by examining predation pressures and how other species, such as sympatric, diurnal geckos, use the rock habitat.

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