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Spatial Distribution and Activity Patterns in African Barking Geckos: Implications for Mating System and Reproduction

Toby J. Hibbitts,[1,3] William E. Cooper Jr.,[2] and Martin J. Whiting[1,4,5]

[1]*School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits 2050, South Africa*
[2]*Department of Biology, Indiana University–Purdue University, Fort Wayne, Indiana 46805 USA*
[4]*Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia*

Abstract.—**We studied spatial clustering and activity patterns in the common Barking Gecko (*Ptenopus garrulus garrulus*) over the course of a breeding season in southern Africa. Only some populations exhibited significant clustering (two of six plots), suggesting that social and spatial organization varies according to factors such as population density and habitat. Clustering at our largest site was not influenced by soil temperature or prey availability, although burrow placement was significantly associated with vegetation coverage. We also examined the timing of the reproductive cycle by testing whether Barking Geckos exhibit protandry (male-first emergence). More males than females were active early in the breeding season and male territories were established before female emergence. Peak activity for 235 Barking Geckos at our primary study site was in late October, although males were significantly more active early in the season, consistent with the protandry model. The Barking Gecko mating system is most consistent with an iteroparous, harem polygynandry with an activity cycle that exhibits protandry. Our study highlights the importance of replicated spatial sampling for studies examining clustering and density effects on reproduction and mating systems.**

The temporal and spatial distribution of females in relation to key resources profoundly affects male mating tactics and, ultimately, the mating system (Emlen and Oring, 1977; Shuster and Wade, 2003). Males that are able to monopolize clumped resources, such as refuges or food, are likely to experience higher reproductive success by virtue of their perceived quality or simply by default. For example, in the lizard *Uta palmeri*, female distribution is driven by food availability. Reproductive success was best explained by a male's dominance and the quality of the territory that he controlled rather than by any intrinsic traits that the female might select (Hews, 1990). Alternatively, in systems where females have a strong mating preference, males may be the resource that females seek. This scenario can give rise to a polygynous mating system such as a lek, where females choose among males based on indicator traits (Höglund and Alatalo, 1995).

In many species, males compete for key resources prior to the arrival of females or before they become receptive. This "male-first emergence" (protandry; Wirklund and Fagerström, 1977) sets the stage for competition over territories and may have a significant effect on a male's reproductive success. Fitness benefits to protandry for females are that most breeding males are present and females have the opportunity of evaluating several males simultaneously (Crews, 1975). Males benefit by increasing their fitness when they emerge earlier (selection for early males; Olsson and Madsen, 1996; Olsson et al., 1999; Jenssen et al., 2001). Conversely, females that delay emergence may have a better choice among high-quality males that have already established territories (selection for delayed females; Jenssen et al., 2001). Within each sex there is still likely to be variation in spring (breeding season) emergence time. Jenssen et al. (2001) list five key hypotheses, and a series of assumptions (not listed here), that need to be met in order to satisfy protandry: 1) male-first arrival at breeding area; 2) males establish territories before the arrival of females; 3) testicular recrudescence before female arrival; 4) testosterone increases as males first arrive and again as breeding begins; and 5) larger males develop protandry-based benefits before smaller males.

In some instances males may appear to be active earlier in the breeding season due to reasons other than protandry. For example, males may be clustered on the landscape and sampling in that area could falsely indicate male activity before female activity, as is the case with breeding aggregations of frogs. Males form choruses under certain conditions, and sampling in frog choruses will be biased towards males. However, females may be active in other habitats, in similar numbers as males. Therefore, accounting for potential spatial disparity in the sexes facilitates an understanding of patterns of reproductive behavior and mating systems.

Barking Geckos (*Ptenopus garrulus garrulus*) are small lizards (maximum snout–vent length [SVL]: 60 mm) found in the Namib and Kalahari deserts of southern Africa. Males vocalize from the entrance to their burrow and larger males have a lower-frequency call that is correlated with aggressiveness (Hibbitts et al., 2007). Barking Geckos live individually in burrows (Haacke, 1975) that are opened when active and remain closed when inactive. Also, individual geckos will use the same burrow from a week to several months (T. J. Hibbitts, pers. obs.), facilitating individual identification. These characteristics allow both the measurement of daily activity of individual geckos and their spatial organization in the landscape. We examined the role of resources (prey, vegetation cover, temperature) and sex in spatial organization and asked whether the observed patterns were consistent with protandry. Specifically, we tested a key feature of protandry: whether or not males emerge before females to establish territories. We then examined the protandry model in light of previous work that addresses some of the remaining predictors of protandry (Hibbitts et al., 2005, 2007).

Materials and Methods

Study Animal.—Barking Geckos are crepuscular and construct burrows that are up to 38 cm deep in loose soils, with at least one

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[3] Present address: Texas Cooperative Wildlife Collection, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258 USA

[5] Corresponding Author. Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia. E-mail: martin.whiting@mq.edu.au

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escape tunnel ending just below the surface (Haacke, 1975). Burrows are occupied by only one Barking Gecko. Males have wider heads than females of the same body size (Hibbitts et al., 2005). Unlike females, they have a yellow throat patch and they emit calls from the mouth of their burrow at dusk and dawn on warm nights between September and April (early spring–late summer; Haacke, 1969). This vocalization consists of a loud clicking call (average five clicks) that signals body size and advertises territory ownership (Hibbitts et al., 2007). Larger males with lower-frequency calls have higher reproductive success (for details on reproductive success, see Hibbitts et al., 2007).

Study Area.—We studied Barking Geckos (*P. g. garrulus*) at the Molopo Nature Reserve (MNR; 25°50′S, 22°55′E) in the Kalahari Desert, Northwest Province, South Africa during September–November 2004 and on Farm Bergvallei (Bergvallei; 19°37′S, 14°40′E) 20 km west of Kamanjab in north-eastern Namibia during October 1994. The vegetation at MNR was dominated by *Acacia mellifera* with *Acacia erioloba* and *Boscia albitrunca* interspersed. Sparse ground cover facilitated locating gecko burrows and making behavioral observations. At Bergvallei, the ground was sandy and largely devoid of vegetation except for a camelthorn tree (*A. erioloba*). To examine spatial clustering we used five, 50-m^2 plots (four at MNR and one at Bergvallei). To examine the role of resources (prey, vegetation cover, temperature) on spatial clustering and activity cycles in the context of protandry (male-first emergence), we intensively sampled a single large, 1.11 ha (11,100 m^2) plot in MNR (MNR1, details below). The site was divided into 10-m^2 sections. We recorded the latitude and longitude of the corners of the site, and every 10 m along each side, using a Garmin GPS 76. Latitude and longitude points were entered into ArcMap 8.0 for visual representation of the plot.

Spatial Patterns.—In addition to MNR1, we chose four plots at MNR and one plot at Bergvallei specifically to test for spatial aggregation in the landscape. The plots at MNR were chosen mainly for accessibility; however, these sites were always >1 km from each other and the exact locations were randomized (1–10 km from MNR1), although they were all within 100 m of a road. The vegetation community at MNR is considered Kalahari thornveld, which is relatively homogenous in soil type and elevation. There was some variability in the abundance of woody and herbaceous vegetation but the dominant plant species were the same at each plot. At MNR, we used a 60-m tape measure (nearest cm) and compass to section off 50-m^2 plots which we divided into 25 10-m^2 sections. We searched for and flagged gecko burrows at each plot during the hour before sunset for 3 days. At Bergvallei, we measured a 50-m^2 plot and mapped all gecko burrows using a tape measure and compass. On the same day we excavated all the burrows to verify that they contained geckos and to collect most of these animals for a lab-based study. The four 50-m^2 plots at MNR and the plot at Bergvallei were monitored only for gecko spatial patterns, while at MNR1 we also quantified vegetation coverage, temperature, and prey abundance over a period of 69 days.

We used Sadieshell version 1.22 to determine the "distance to regularity" (D) for each plot. D is the cumulative distance that burrows would have to be moved to make a regular (uniform) distribution of burrows on the landscape. D observed is then compared with corresponding values from random permutations (D random) of the counts among the sample units. A formal randomization test is performed by calculating what proportion of the random permutations are larger than, or as large as, D observed to determine a P-value (Perry, 1995).

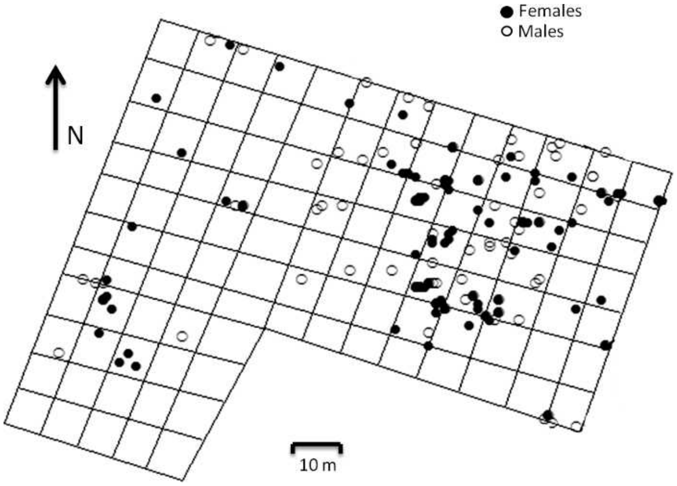

FIG. 1. Representation of locations of Barking Geckos during the breeding season (2004) at MNR1. Females are represented by closed circles and males by open circles. Soil temperature and insect abundance was recorded at 30 quadrat corners evenly spaced across MNR1.

Temporal Patterns.—We monitored adult male and female spatial patterns on MNR1 at four different times (30 September, 10 October, 20 October, and 10 November, 2004) during the breeding season to analyze clustering and if clustering changed through time. We only considered adult male Barking Geckos that were 36 mm SVL or greater and females that were at least 31 mm SVL because this is the minimum size at which they are sexually mature (Hibbitts et al., 2005). We used data from gecko activity monitoring (see below) to examine male spatial patterns on each of the dates listed above. Sadieshell (ver. 1.22) was used to determine if there was significant clustering.

Resources.—At MNR1, we characterized vegetation coverage by estimating ground cover and foliage projection cover (amount of the section with cover directly overhead) to the nearest 5% for each section. We used the vegetation estimates to determine the extent to which Barking Geckos used 10-m quadrats with a high percentage of ground cover or foliage projection cover. Regression analysis established the relationship between the number of burrows in a quadrat and the percentage of ground cover or foliage projection cover.

For MNR1, we also used a paired design to determine if Barking Geckos were constructing burrows at sites with vegetation characteristics that were different from random. First, we chose a burrow and measured the distances to grass and woody vegetation as well as ground cover and foliage projection cover within a 1-m^2 quadrat centered on the burrow. Next, we walked 10 m in a random direction from the burrow location and measured the same vegetation characteristics (nonsite "burrow" MNR1 was monitored daily from 9 September to 18 November 2004 to measure both male and female gecko activity during the breeding season. We marked each burrow with a labeled 30-cm dowel. Geckos closed their burrows during the day and opened them about 1 h before sunset if they were active. The activity at each burrow was monitored every night. We specifically avoided finding geckos by their call to avoid biasing our data towards males. Geckos were caught while surface-active near their burrow or by luring them out with small insects. Each gecko was toe-clipped for permanent identification and a number was drawn on the head using xylene-free paint pens for easy visual identification. The sex and age class (juvenile–adult) was determined for each

TABLE 1. Clustering statistic for five, 50-m^2 sampling plots at MNR (plot numbers 1–4) and Bergvallei. Distance to regularity (*D* is the required distance to evenly distribute the observed number of burrows) observed for the four plots. *D* random is the average of all random permutations of the observed number of burrows.

Plot number	*N* (geckos)	*D*	*D* random	*P*
1	34	18.6	22.35	0.95
2	39	19.12	21.57	0.78
3	31	31.51	18.84	0.01[a]
4	62	25.9	26.9	0.51
Bergvallei	53	27.38	24.01	0.18

[a] Indicates significant clustering.

gecko based on minimum size at sexual maturity (Hibbitts et al., 2005). Geckos were held overnight in cloth bags and were released the following day in the burrow from which they were captured. We used a two-factor ANOVA with sex and reproductive period (early, middle, late breeding season) as the factors to test for differences in activity between sex and period. Reproductive periods were equally split from the duration of our 69-day study period (8 September–16 November 2004) and were 23 days long.

RESULTS

Spatial Clustering.—We observed clustering at only one of the five 50-m^2 plots (Table 1) and at MNR1 on all four dates analyzed (Table 2, Fig. 1); however, the locations of the male clusters at MNR1 did not change over time. At MNR1, we observed a maximum of three male Barking Geckos within a 10-m^2 quadrat. A similar number of male Barking Geckos were observed on 30 September, 10 October, and 25 October (0.40, 0.36, 0.38 per quadrat, respectively); however, fewer males were active on 10 November (0.23 per quadrat). In November, many males became inactive, remaining in their burrows with the entrance closed.

Male and female burrows at MNR1 were located significantly closer to grasses ($t_{49} = -2.74$, $P = 0.009$) and woody vegetation ($t_{49} = -3.66$, $P < 0.001$) than would be expected by chance; however, burrows were not located in areas that had a higher percent of ground cover ($t_{49} = 0.88$, $P = 0.38$) or foliage projection cover ($t_{49} = 1.77$, $P = 0.08$) than expected by chance. The distribution of Barking Gecko burrows was not explained by temperature ($r^2 = 0.03$, $F_{29} = 0.78$, $P = 0.38$) or prey abundance ($r^2 = 0.009$ $F_{29} = 0.24$, $P = 0.63$).

TABLE 2. Clustering statistics for 4 days (30 September, 10 October, 25 October, and 10 November 2004) at MNR1. Distance to regularity (*D* is the required distance to evenly distribute the observed number of burrows) observed on the 4 days. *D* random is the average of all random permutations of the observed number of burrows. All values were significant.

Date	*N* (geckos)	*D*	*D* random	*P*
Males				
30 September	44	114.35	54.51	0.002
10 October	40	88.69	51.41	0.003
25 October	42	109.89	54.63	0.002
10 November	32	81.50	49.06	0.005
Females				
30 September	19	50.75	33.33	0.016
10 October	11	30.15	27.80	0.267
25 October	44	103.75	57.38	0.002
10 November	20	73.45	39.29	0.001

TABLE 3. A two-factor ANOVA of differences in male and female activity patterns between reproductive periods for Barking Geckos at MNR1. Period one is from 15 September to 6 October, period two from 7 October to 26 October, and period three from 27 October to 16 November 2004. Males were more active than the females during the two sampling periods in October, but not during November, when activity was similar.

Effect	SS	df	*F*	*P*
Intercept	185,437.5	1	2,889.1	<0.0001
Sex	632.9	1	9.9	0.002
Period	2,195.76	2	17.1	<0.0001
Sex*Period	977.5	2	7.6	0.0008

Activity.—Peak activity for 235 individual Barking Geckos at MNR1 was in late October. Activity patterns of adult males and females were significantly different, as was overall activity when split into three 20-day periods (Table 3, Fig. 2). Males were more active in the first two periods, and male and female activity was similar in the last period (Table 4, Fig. 2). Higher male activity could occur if males become active earlier and remain active for longer than females. In this scenario, by simply examining daily gecko activity, more males may appear to be active earlier in the season. However, many females were active during earlier periods but for shorter periods of time (making less females active on the same day). Therefore, we plotted accumulation curves of male and female captures to show that more individual males were active early in the breeding season than were females (Fig. 3). The first 7 days of activity data, which coincided with the steep part of the male accumulation curve, were excluded because we were still adding large numbers of active geckos.

DISCUSSION

We found clustering on only one of the five 50-m^2 plots during the breeding season while we found very strong clustering on the 1.1-ha study area (MNR1). There are two possible explanations for this discrepancy: 50-m^2 plots are too small to detect clustering, or clustering is driven by factors that might vary spatially such as population density or some aspect of habitat structure or resource availability. We think that 50 m^2 is a sufficient scale to detect clustering because we caught relatively high numbers of geckos on these plots (N = 31–62)

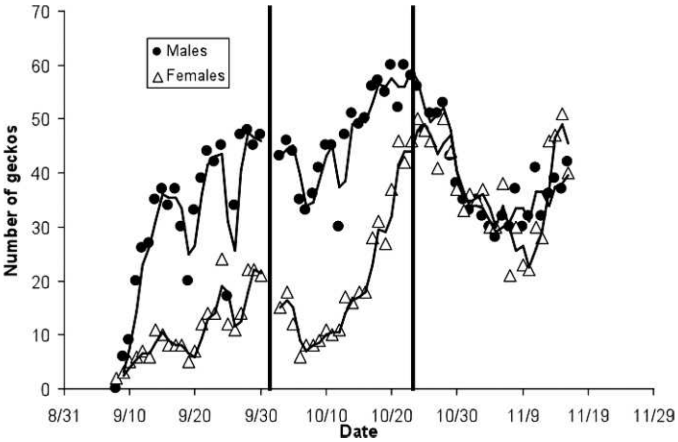

FIG. 2. Number of male and female Barking Geckos active per 24-h period during the breeding season (2004) at MNR1 based on nightly census of open burrows. Vertical lines divide activity periods (see text).

TABLE 4. Tukey's HSD post hoc test showing significant differences (*P*-values) in activity between periods and sexes at MNR1. Average number of geckos active per sex–period in parentheses (see also Fig. 2).

	Female 1	Female 2	Female 3	Male 1	Male 2	Male 3
Sex/Period	(30.1)	(40.2)	(39.9)	(38.4)	(49.0)	(36.5)
F 1		0.002[a]	0.002[a]	0.018[a]	0.0001[a]	0.119
F 2			0.999	0.978	0.009[a]	0.673
F 3				0.991	0.005[a]	0.746
M 1					0.0008[a]	0.975
M 2						0.0001[a]

[a] Indicates significant clustering.

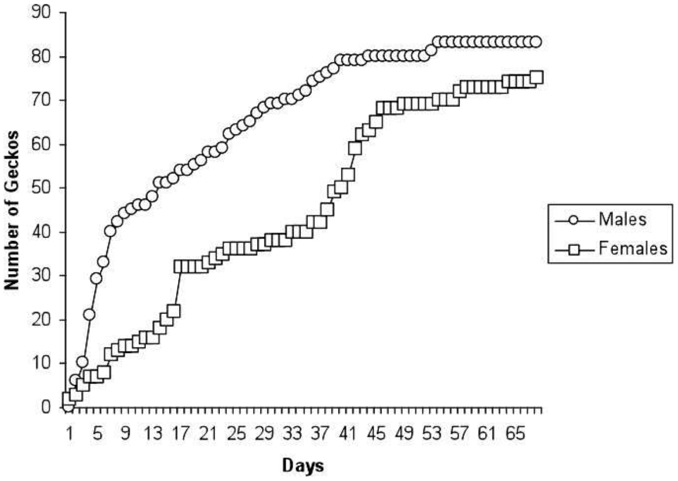

FIG. 3. Accumulation of new male and female Barking Gecko captures at MNR1. Males were captured earlier in the breeding season than were females, confirming greater male activity.

and because the only 50-m^2 plot that showed significant clustering had the fewest geckos ($N = 31$).

Clustering at MNR1 was relatively consistent for the duration of the breeding season. When we examined clustering in relation to resources, we found no effect for soil temperature or prey availability, which were relatively uniform throughout the site. However, gecko burrows were significantly closer to grass clumps and woody vegetation than expected by chance, although geckos were no more abundant in areas with a higher percentage of ground cover. This result confirms the importance of plant structure as a habitat component for geckos but also suggests a threshold at which vegetation density may be too high to be of benefit to geckos. Dense vegetation may impact geckos negatively if it degrades acoustic signals or harbors a higher densities of predators. Burrows that are near vegetation may be afforded some protection from disturbance, particularly in areas where ungulates are active. The Kalahari typically supports a variety of ungulates, all of which could inflict damage on gecko burrows through trampling. Burrows in the open may also be more susceptible to disturbance from strong winds.

Our results highlight the dynamic nature of spatial and social organization. They also underscore the importance of replicated sampling of spatial organization across the landscape. If we had only sampled MNR1, we would probably consider clustering to be a consistent feature of the social organization of burrowing geckos. Plasticity in social organization, mating system, and reproductive strategy has been repeatedly documented in a range of taxa in relation to resources and population density (Shuster and Wade, 2003), and this could be the case with Barking Geckos, too. When Barking Geckos aggregate, females have the opportunity to choose from multiple males calling from their burrow entrances, similar to an anuran amphibian chorus.

Clustering may also increase the opportunity for reproduction for some individuals. Smaller males can increase their fitness when their territories are located near large males ("hotshot" lek model; T. J. Hibbitts, unpubl. data). This suggests that smaller males may be acting as satellites, establishing territories near large males to intercept females moving towards the large male. When populations are not aggregated, it is likely that density is sufficiently high to allow females to locate calling males without high search costs.

Shuster and Wade (2003) provide a comprehensive review of mating systems using a wide range of criteria dealing with various mechanisms of sexual selection, resource use, parental care, and the temporal and spatial distribution of mates. Several lines of evidence suggest that the mating system of Barking Geckos is a form of polygyny. First, males have larger heads than do females and this is unrelated to diet (Hibbitts et al., 2005). Because males live in largely exclusive home ranges and defend their territories from rivals (Hibbitts et al., 2007), head size is likely under selection as a consequence of male contest competition, a feature of polygynous systems in which males attempt to exclude rivals from copulating with females (but see Cox et al., 2003). Also, males may copulate with multiple females, and vice versa (polygynandry), in the same breeding season (Hibbitts et al., 2007; T. J. Hibbitts, pers. obs.). Following copulation, the male leaves the burrow to the female, where she remains to lay her eggs. According to Shuster and Wade's (2003) criteria, Barking Geckos conform to an iteroparous, harem polygynandry mating system because iteroparous females are attracted to a male calling from a burrow; mating then occurs in the burrow and the female then uses the burrow as a nest site. This mating system also allows for matings between females and satellite males, although we were unable to detect satellite behavior. While assigning populations to a particular mating system may help us better understand mating system diversity and evolution, we also need to recognize the ability of animals to adjust reproductive tactics in the face of changing social and environmental conditions (Lott, 1984).

In terms of the timing of reproduction, Barking Geckos showed characteristics consistent with protandry. The key feature of protandry is sex differences in the timing of gonadal recrudescence, which results in male-first emergence. Males were more active than females in the early and middle of the breeding season, with most males active before most females. Another key assumption of protandry is that males establish territories before female emergence. We found most males were calling from their burrows (which serve as the core of their territories) when the females emerged from winter dormancy. Under protandry, testicular recrudescence is expected to be complete before female emergence. Male peak testicular size is in September and October (Hibbitts et al., 2005) and likely coincides with male emergence from winter dormancy. Therefore, males are likely primed and ready to breed when females emerge. Finally, larger males develop protandry-based benefits before smaller males (sensu Jenssen et al., 2001). Large male Barking Geckos have higher fitness than the small males and also have larger home ranges (Hibbitts et al., 2007). This suggests either that large males have established better territories due to early emergence, that large males out-compete smaller males, or that females prefer to breed with large males (or some combination of the three).

In summary, gecko clustering is spatially variable and may be affected by vegetation density. Barking Geckos conformed to a protandrous model of reproduction in which males emerge from winter first and display (vocally) from territories. Future studies of Barking Geckos that manipulate the spatial and temporal distribution of both resources and mates would greatly facilitate our understanding of territory establishment, the timing of reproduction, and the mating system.

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LITERATURE CITED

Cox, R. M., S. L. Skelly, and H. B. John-Alder. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. Evolution 57:1653–1669.

Crews, D. 1975. Psychobiology of reptilian reproduction. Science 189: 1059–1065.

Emlen, S., and L. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

Haacke, W. D. 1969. The call of the Barking Geckos. Scientific Papers of the Namib Desert Research Station 46:83–93.

———. 1975. The burrowing geckos of Southern Africa, 1 (Reptilia: Gekkonidae). Annals of the Transvaal Museum 29:198–243.

Hews, D. K. 1990. Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri*. Evolution 44:1956–1966.

Hibbitts, T. J., E. R. Pianka, R. B. Huey, and M. J. Whiting. 2005. Ecology of the common Barking Gecko (*Ptenopus garrulus*) in southern Africa. Journal of Herpetology 39:509–515.

Hibbitts, T. J., M. J. Whiting, and D. M. Stuart-Fox. 2007. Shouting the odds: vocalization signals status in a lizard. Behavioral Ecology and Sociobiology 61:1169–1176.

Höglund, J., and R. V. Alatalo. 1995. Leks. Monographs in Behavior and Ecology. Princeton University Press, Princeton, New Jersey.

Jenssen, T. A., M. B. Lovern, and J. D. Congdon. 2001. Field-testing the protandry-based mating system for the lizard, *Anolis carolinensis*: does the model organism have the right model? Behavioral Ecology and Sociobiology 50:162–172.

Lott, D. F. 1984. Intraspecific variation in the social systems of wild vertebrates. Behaviour 88:266–325.

M'Closkey, R. T., R. J. Deslippe, C. P. Szpak, and K. A. Baia. 1990. Tree Lizard distribution and mating system: the influence of habitat and food resources. Canadian Journal of Zoology 68:2083–2089.

Olsson, M. T., and T. Madsen. 1996. Cost of mating with infertile males selects for late emergence in female Sand Lizards. Copeia 1996:462–464.

Olsson, M. T., T. Birkhead, and R. Shine. 1999. Can relaxed time constraints on sperm production eliminate protandry in an ectotherm? Biological Journal of the Linnean Society 66:159–170.

Perry, J. N. 1995. Spatial analysis by distance indices. Journal of Animal Ecology 64:303–314.

Shuster, S. M., and M. J. Wade. 2003. Mating Systems and Strategies. Princeton University Press, New Jersey.

Wirklund, C., and T. Fagerström. 1977. Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. Oecologia 31:153–158.

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