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Shouting the odds: vocalization signals status in a lizard

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Abstract Many species possess multiple sexually dimorphic traits, which incorporate different sensory modalities (e.g., acoustic, olfactory and visual), although their relative roles in sexual selection and in determining reproductive success are still poorly understood for most taxa. We assessed the role of multiple male traits, including one acoustic (dominant call frequency) and one visual (yellow throat patch) trait, in residency advertisement, contest behavior, and breeding success in barking geckos (*Ptenopus garrulus garrulus*). We show that male barking geckos maintain largely exclusive home ranges, with a trend for larger males to maintain larger home ranges. We also show that larger males have a lower dominant calling frequency. When aggressive behavior was elicited in the field using a recorded call of average frequency, resident males with low frequency calls were more likely to respond aggressively and charge the speaker compared to males with high frequency calls. However, body size and small relative throat patch size, rather than call frequency, were the best predictors of overall aggressiveness. Body size was also the best predictor of whether males bred. We suggest that call frequency in this crepuscular species constitutes an effective long-range signal of body size, used by males for remote rival assessment and to advertise home range boundaries in low-light environments.

Keywords Lizard · Acoustic communication · Multiple signals · Sensory modalities · Home range size · Male contests · Breeding success

Introduction

Most sexually dimorphic species possess multiple dimorphic traits, which may incorporate different sensory modalities, such as acoustics, olfaction, and vision. These traits may be the target of different selective mechanisms (e.g., female choice and male–male competition). Alternatively, they may function in the same context (mate choice or competition) but may encode information on different aspects of individual quality (multiple messages) or convey similar information with some error (backup signals; Møller and Pomiankowski 1993; Johnstone 1996). This is particularly true of traits that incorporate different modalities as each may be suited to different environmental conditions (Maynard Smith and Harper 2003). For example, in complex environments, acoustic signals may be more effective over longer ranges, whereas at short distances, visual and/or olfactory cues may be more important. While multiple traits have received recent attention in studies of sexual selection, few studies have examined the relative roles of signals that exploit different sensory modalities, especially in the context of male–male competition and territory defense (but see Hebets and Papaj 2005; Partan et al. 2005; Elias et al. 2006).

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In male contests, body size is often a reliable indicator of fighting ability or resource holding potential (Parker 1974), and male secondary sexual traits may function to convey information on body size. Such signals of male size facilitate accurate opponent assessment, potentially allowing contests to be settled more quickly through conventional displays rather than through more costly physical combat (Maynard Smith and Parker 1976; Huntingford et al. 2000). In addition to functioning directly in male–male contests, sexually dimorphic traits may be used as signals to advertise home range or territorial boundaries to rivals. Both home range size (space used during daily activity; Rose 1982) and territory size (area actively defended; Stamps and Krishnan 1998) may be linked to mating success or at least access to mates (Stamps 1983; Hews 1993; Smith 1995). In complex environments or in environments with low-light conditions, rather than visual signals, long-range signals such as acoustics may be more likely to evolve to effectively signal residency (Ord et al. 2002). To date, however, no evidence exists that auditory cues are important for the maintenance of territorial boundaries or in determining reproductive success in reptiles.

In lizards, male reproductive success has historically been attributed to success in male–male competition and/or mate guarding (Cooper and Vitt 1993; Censky 1995; Salvador and Veiga 2001); however, more recent studies suggest that female choice (pre- and postcopulatory) may also be important (Martín and López 2000; López et al. 2002; Kwiatkowski and Sullivan 2002; Olsson et al. 1996, 2003; but see LeBas and Marshall 2001; Olsson 2001). It is therefore necessary to determine whether traits associated with male contest behavior and defense of space are also associated with breeding success.

In this paper, we assess the role of body size and two sexually dimorphic traits that may act as potential signals of male competitive ability: male vocalization and throat color, in the common barking gecko (*Ptenopus garrulus garrulus*). Specifically, we examined the role these traits play in male defense of space, contest behavior, and breeding success. The barking gecko is a crepuscular species that potentially makes use of both an acoustic (loud clicking call) and a visual (yellow throat patch) signal, but the function of these traits is not known. Only males have yellow throats and vocalize; furthermore, males have wider heads, but are similar to females in body length (Hibbitts et al. 2005). Sexual dimorphism and their calling behavior have traditionally been used as evidence of their territoriality, although territorial behavior of males has never been quantified. We quantified male spatial patterns and examined the relationships between male home range size, body size, and sexually dimorphic traits (throat patch and dominant call frequency). We then used a recorded vocalization to elicit male contest behavior and tested whether the behavioral response of receivers was associated with their body size or sexually dimorphic traits. Finally, we tested whether body size or sexually dimorphic traits were associated with breeding success.

Materials and methods

Study species and area

Barking geckos are small (max 60 mm snout-to-vent length; SVL) lizards of the Kalahari and Namib Deserts of southern Africa. Barking geckos construct burrows that are up to 38 cm deep in loose soils, and these usually have several branches (Haacke 1975). Males call from the entrance of their burrows at dusk and dawn (Haacke 1969). When females are ready to mate, they approach and enter the burrow of a calling male (Hibbitts 2006). Copulations last approximately 10–15 min, after which, both male and female geckos remain in the burrow for a brief period (approximately 30 min) before the male moves a short distance (approximately 1 m) and begins construction of a new burrow (Hibbitts 2006). Females lay their egg in the male's former burrow, although there is no indication that males excavate burrows specifically for egg laying as copulation occurs before a female investigates the male's burrow (Hibbitts 2006). Mating occurs from September through to March; however, peak breeding is during September and October (Hibbitts et al. 2005).

We studied barking geckos at the Molopo Nature Reserve (25°50′S, 22°55′E) in the Kalahari Desert, Northwest Province, South Africa. Our study area was a 1.11 ha plot. The vegetation of the plot was dominated by *Acacia mellifera* interspersed with *A. erioloba* and *Boscia albitrunca*. There was very little ground cover, which facilitated location of gecko burrows and making behavioral observations. The site was divided into 10 m square 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. The study area was monitored daily from 9 September to 18 November 2004. We marked each burrow with a labeled 30 cm dowel stick. 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.

Male traits

Geckos were caught while surface active near their burrows or by luring them out with small insects. Each gecko was toe-clipped for permanent identification and a number was drawn on the head with an ultra fine point Sharpie® permanent marker for easy temporary identification. The following data were recorded for each gecko: SVL, mass, head width (HW), head depth (HD), throat patch size (if male), and burrow number. We measured SVL (hereafter referred to as body size) to the nearest mm using a plastic ruler and mass to the nearest 0.01 g with a digital balance. The HW and HD were measured to the nearest 0.01 mm with digital calipers. Condition was determined by regressing mass by SVL and taking the residuals as an estimate of body condition. We used the software Simple PCI® to calculate throat patch size and total throat area from a scanned image of the venter of male geckos. The throat patch consists of a bright yellow area in the center of the throat surrounded by a white margin. The rest of the venter is white. Scans were obtained using a Canon canoscan N1220U flat bed scanner. From this, we determined the proportion of the entire throat that each patch assumed. Proportions were arc-sine transformed in all analyses. Geckos were released the following day in the burrow from which they were captured.

We recorded 74 calling male barking geckos using a Nagra IV-s analog tape recorder and a Nakamichi CP-4 super directional shotgun microphone. The microphone was mounted on a tripod and directed at the gecko at a distance of 1 m. Six call groups (average five clicks per group; Fig. 1) were recorded for each gecko. The recordings were digitized at a sampling rate of 48 kHz (16 bits) and analyzed using Cool Edit Pro version 1.2a (Syntrillium Software, Phoenix, AZ). An average dominant call frequency was determined for each gecko by finding the dominant frequency of each individual "click." We tested whether body size, condition or head dimensions predicted throat patch size and dominant call frequency using linear regressions.

Male spacing patterns

We determined burrow location by estimating the distance from the nearest corner marker in the 10 m square. The estimated burrow locations were entered onto the site base map in ArcMap 8.0. We printed the study area map and estimated home range size manually on graph paper, using the minimum convex polygon method (Rose 1982). We modified this method to account for a 1-m radius around each burrow location, which is the approximate size of the territory that barking geckos will actively defend around their burrows (Polakow 1997; personal observation). A 1-m radius circle was drawn around each burrow occupied, and a tangential line was drawn connecting the circles into a polygon with rounded vertices. The barking geckos may use the same burrow for more than a year or for shorter than 1 week (personal observation). Burrows are also used as sit-and-wait foraging lookouts (Hibbitts et al. 2005); therefore, home range estimations are not based on sightings but on burrow locations occupied. We only included males observed on at least 10 days. We tested whether body size, call frequency, and/or throat patch size

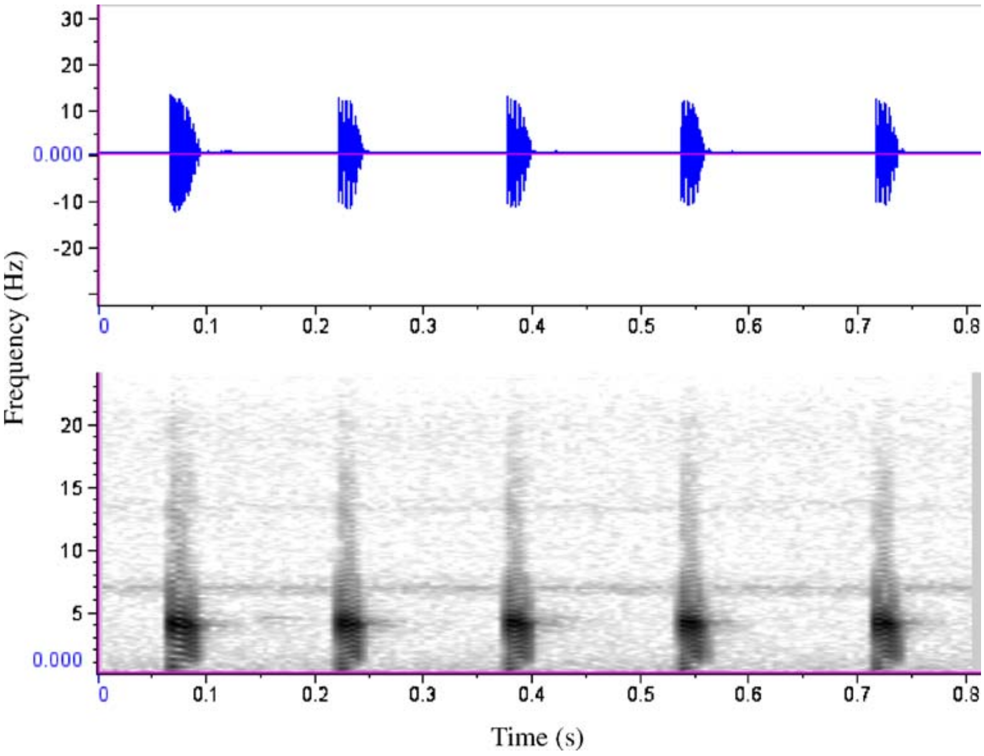

Fig. 1 Oscillogram (*top*) and sonogram (*bottom*) displaying a typical five-click call of a barking gecko (*darker shading* in the sonogram corresponds to the dominant frequency of each click)

are associated with home range size using Pearson correlations. We also calculated the number of other male home ranges overlapped by each male and percent overlap of each male's home range by other male home ranges (Abell 1998).

Male contest behavior

We used a recorded average male call to elicit behavioral responses from resident males. To obtain an average call for these playback experiments, we recorded six call groups, which on average consist of five "clicks" (Haacke 1969), from each of 20 barking geckos before the study. We determined the dominant frequency of each "click" within each call group and averaged the frequency of each click to get the dominant call frequency of an individual barking gecko. The call used for all playback experiments was 4,366 Hz.

For each actively calling barking gecko located in the study plot, we recorded its call and conducted a playback experiment to assess its response to a calling intruder. Playback experiments (n=58) were conducted on the same or following day that we located them, between 30 and 90 min after sunset. We played recordings on a Diamond DX121 CD player with the display lights covered. The CD player was positioned 1 m from the gecko burrow and set to continuously play the playback call at 70 dB at the burrow (Polakow 1997). Sound pressure level was determined using a Brüel and Kjaer 2235 precision level sound meter. The trial was recorded from a distance of about 2.5 m with a Sony DCR TRV27E digital video camera with the super nightshot function. Trials were terminated when the gecko approached the speaker to within 10 cm or after 10 min. We then captured the gecko either by hand or by digging it out of its burrow and took the same measurements listed above. None of the geckos dug out of their burrows were from the main study plot. The geckos were released the following evening at the point of capture.

The following behaviors were recorded for each gecko: orientation to playback call, call-back, charge CD player, tail wag, and retreat into burrow. We tested for a relationship between the three most commonly observed behavioral responses (retreat, call-back, charge) and body size, dominant call frequency, and relative throat patch size using a multiple logistic regression (0 = did not exhibit relevant behavior, 1 = exhibited relevant behavior). We also ranked aggressiveness of different behavioral responses on a scale of 0 to 5 as follows: 0, retreat into burrow or no response; 1, orient to playback call; 2, call back to playback call; 3, call back and charge CD player; 4, charge CD player and tail wag and 5, charge CD player. We viewed "charge" as the most aggressive behavior, as an immediate charge without associated calling or tail wagging indicated no attempt to avoid physical combat with the intruder through signaling. Tail wagging was the movement of the tail from side to side at a slow rate. Because geckos tail-wagged after partial charges, we ranked charge and tail wag at a lower rank than charge. We used a multiple regression with stepwise model selection to examine what variables best explained aggressiveness. The criterion for retaining a variable in the model was $P<0.1$. Aggressiveness rank was treated as a continuous dependent variable and body size, body condition, dominant call frequency, and relative throat patch size as independent variables. All means are reported ±1SE.

Breeding success

The unique breeding behavior of this species allowed us to indirectly determine the number of copulations per male and the percentage of males that bred in the study population during the field season. The criteria we used to determine whether a male had bred were: 1) the male moved to a new burrow 1 to 2 m from his former burrow after a visit from a female; 2) a female occupied his former burrow. We determined a male to not have bred when he remained in the same burrow for the entire study season and during which he was not observed to be visited by a female. Eighteen of the 49 males were not used in the analysis because evidence for breeding was inconclusive. We performed multiple logistic regression using bred (0 = did not breed, 1 = bred) as the dependent variable and body size, HW, HD, call frequency, and relative throat patch size as the independent variables.

Results

Male traits

Call frequency for 74 different males ranged between 3,708 and 5,207 Hz (mean=4,284±31.8 Hz; Fig. 2). Body size was negatively associated with dominant call frequency and explained a significant amount of variation in dominant call frequency (R^2=0.50, $F_{1,73}$=69.8, P<0.001; Fig. 3). There was a positive relationship between body size and relative throat patch size, but body size explained very little of the variation in relative throat patch size (R^2=0.06, $F_{1,121}$= 7.13, P<0.009). Body condition also explained very little of the variation in relative throat patch size (R^2=0.001, $F_{1,121}$=0.17, P=0.68) and dominant call frequency (R^2= 0.02, $F_{1,73}$=1.29, P=0.26).

Male spacing patterns

Mean male home range size of 51 individuals sighted on at least 10 days was 10.4±1.5 m^2 (range, 3.1–53.0). Home

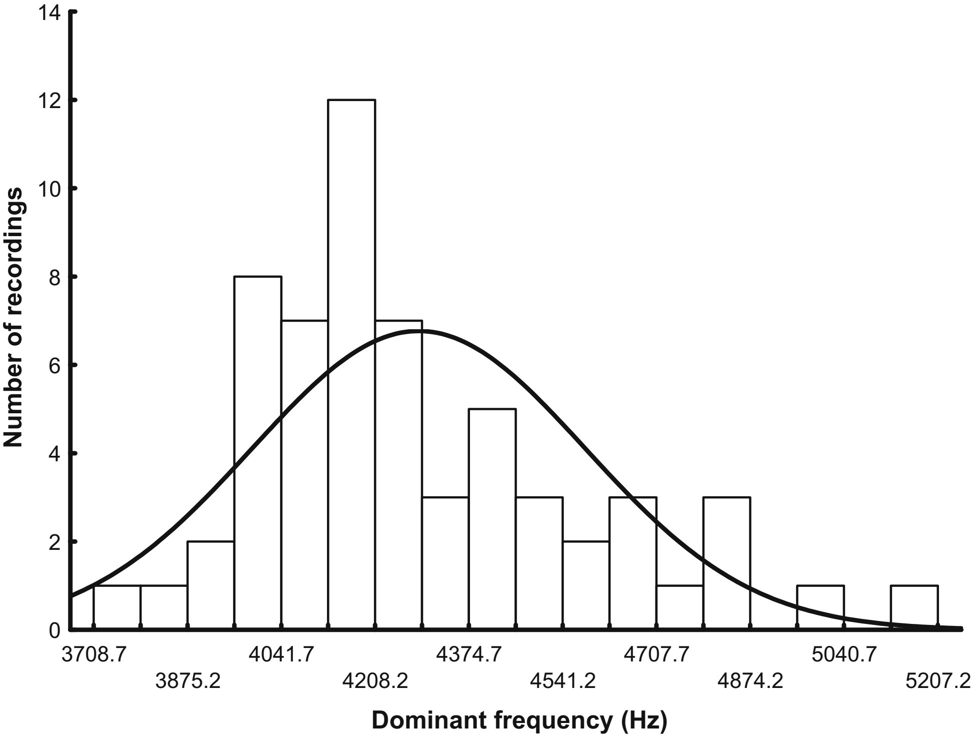

Fig. 2 Distribution of dominant frequencies of 74 barking gecko calls

range size was positively correlated with body size such that males of larger size tend to have larger home ranges (r=0.31, P=0.02, n=51), although this relationship becomes nonsignificant with Bonferroni adjustment of significance levels (P=0.0167 for three independent tests). Home range size was not associated with relative throat patch area (r=0.15, P=0.32, n=49) or dominant call frequency (r=−0.24, P=0.20, n=31). Males rarely overlapped spatially with other males (mean number overlapped=0.12±0.04, n=51), and this overlap constituted a small total area per individual (mean percent overlap=3.8± 1.7 m^2, n=51). There were three observed instances of male spatial overlap, and in each case, the male had shifted its area of activity in response to the presence of a new rival male.

Male contest behavior

During playback trials, geckos that retreated into their burrows were smaller than those that did not retreat (Table 1). No traits related to calling back were significant. Finally, geckos that charged the speaker (playback) had significantly lower dominant call frequencies and smaller relative throat patches than those that did not charge (Table 1). Overall aggressiveness rank was positively associated with body size and negatively associated with relative throat patch area, suggesting that more aggressive geckos are larger with relatively smaller yellow throat patches (Table 2).

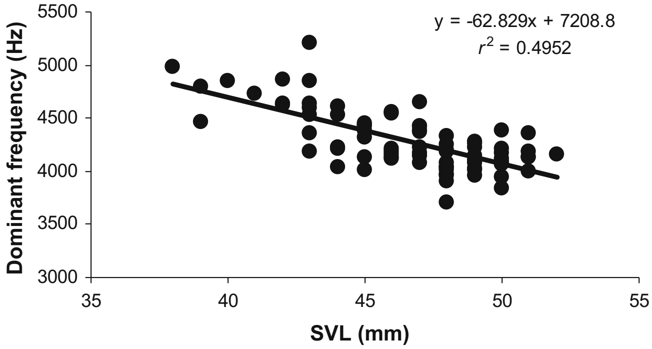

Fig. 3 Significantly negative relationship between body size (SVL) and dominant call frequency in barking geckos

Table 1 Multiple logistic regressions comparing retreat (A), call back (B), and charge (C) behavior with body size (SVL), body condition, call frequency, and relative throat patch size (TPS)

	Estimate	SE	Wald	P value
A				
SVL	−0.2831	0.126	5.094	0.024
B				
Body condition	−3.0744	1.613	3.633	0.057
C				
Call frequency	−0.0115	0.004	7.688	0.006
TPS	−0.4602	0.197	5.442	0.020

Table 2 Multiple regression model in which aggressiveness rank is explained by variance in body size (SVL), call frequency, and relative throat patch size (TPS)

	Estimate	SE	*F*	*P* value
Call frequency	−0.00147	0.00087	2.86	0.098
SVL	0.20211	0.07852	6.63	0.014
TPS	−0.10682	0.05032	4.51	0.040

The R^2 of this model is 0.43

Male breeding success

We found evidence that 20 (41%) of the 49 adult males observed in the study area bred a total of 31 times (1.55 copulations per adult who bred). Only six (30%) of the 20 males that bred, bred more than once. Additionally, 12 males did not copulate during the same time period.

The only trait significantly related to breeding success was body size (multiple logistic regression, Coefficient= 0.78±0.32; Wald χ^2=5.96; P=0.015).

Discussion

Male barking geckos are territorial, as indicated by the almost complete lack of overlap in space among males, their active avoidance of overlap by shifting burrows, and their aggressive reaction to the call of a rival during playback experiments. Given that males are nocturnal and live in an open environment, vocal signals are likely to be particularly effective at a distance. Dominant call frequency was negatively correlated with body size, which in turn was positively associated with breeding success. That larger males have calls of lower dominant frequency and are more likely to breed suggests that the vocalization is an honest signal whose production is constrained by size. The marginal trend for larger males to have larger home ranges is consistent with this view. Although body size was not associated with relative throat patch size, the most aggressive males that rushed the speaker during playback trials had smaller relative throat patch size and lower dominant call frequency. This suggests that the throat patch may play a role in close-range encounters, but that possibly, other patch factors such as spectral reflectance may be more important than simply the area of yellow on the throat.

Our results suggest that barking geckos make decisions on whether to challenge an intruder based on the frequency of his call, which conveys information on body size. Resident males that retreated into their burrows when presented with a recording of a calling intruder were significantly smaller than the expected size of the ‘playback’ male. Body size was also the most important indicator of overall aggressiveness. Larger geckos with small relative throat patches displayed more aggressive behaviors when presented with a calling intruder. Together, these results suggest that in barking geckos, call frequency signals body size, which is an important indicator of fighting ability in many lizard species (Trivers 1976; Stamps 1977; Tokarz 1985; Vitt and Cooper 1985; Olsson 1992). Body size also may predict home range size, but our data on this point are inconclusive.

The overriding importance of body size was confirmed by our finding that body size was the only significant male trait predicting whether males successfully bred. Size has also been reported to correlate with reproductive success in other lizard species (Trivers 1976; Ruby 1981; Anderson and Vitt 1990; Cooper and Vitt 1993; Censky 1995; Salvador and Veiga 2001). In most of these cases, male reproductive success has been inferred from success in male–male competition. Nevertheless, female choice cannot be ruled out as a mechanism for sexual selection in barking geckos. In the field, we observed females approach males from distances of greater than 3 m (likely much greater) under low light conditions, and probably out of sight of the calling male (TJH personal observation), suggesting that females may assess males based on their advertisement call. In addition, in the peak breeding season, up to 50 males call from within 1 ha (TJH personal observation), providing an opportunity for females to simultaneously evaluate multiple males. It is common for signals to serve dual functions (in male competition and mate choice), and this is the case for the majority of secondary sexual traits studied to date (Berglund et al. 1996). We chose to use whether a male bred as our definition of breeding success; however, within the group of males that bred, there was variation between the numbers of copulations per male. Body size is important for determining which individuals breed, but other factors such as color may predict variation in breeding success among males that successfully bred (Zucker and Murray 1996; Barki et al. 1997; Leiser et al. 2004).

The mechanism explaining why large individuals produce lower frequency calls, and thus, the maintenance of signal honesty in barking geckos is unknown. In most amphibians, larynx size primarily determines call pitch; therefore, larger individuals produce lower frequency calls (Gerhardt and Huber 2002). If the larynx scales allometrically in barking geckos as in amphibians, the same principle is likely to apply. In this situation, calling may be viewed as an ‘index’ that constitutes an honest signal because only large males are physically capable of producing calls with low dominant frequency. However, protracted calling over the breeding season is also likely to be energetically demanding as in other acoustically signaling species (Pough et al. 1992; McCauley et al. 2000; Gerhardt and Huber 2002).

Relative throat patch area predicted both the likelihood that a gecko would charge the speaker and overall aggressiveness. The relationship was in the opposite direction to that predicted: males with smaller relative throat patch sizes were more likely to charge and were more aggressive. We propose two possible explanations for this result. Relative throat patch area could be correlated with other signal properties such as the spectral qualities of the yellow patch, or expression of the yellow patch may be negatively associated with testosterone, which is documented to increase aggression in male lizards (Civantos 2000) and constrain the expression of secondary sexual traits in some taxa (Cox and John-Alder 2005; Rubolini et al. 2006).

Overall, our results suggest that barking geckos use calls as a long range signal of body size and aggressiveness in an environment in which visibility is reduced due to poor light conditions. As male barking geckos spend the majority of their time within their burrows, which are used for both shelter and foraging activity (Haacke 1975; Hibbitts et al. 2005), calling likely allows maintenance of exclusive space without the predation risk associated with territorial patrolling or flashing of conspicuous visual signals (Candolin and Voigt 2001; Díaz-Uriarte 2001). To our knowledge, there have been no published reports of a lizard using an auditory cue to advertise territory ownership and aggressiveness. Many other gecko species produce calls (e.g., Marcellini 1974, 1978; Werner et al. 1978; Frankenberg 1982; Manley 1990; Tang et al. 2001; Regalado 2003), although the functions of their calls are not known. However, an increase in calling behavior in *Gekko gecko* has been shown to coincide with an increase in androgen levels and gonadal mass (Tang et al. 2001). A likely adaptive hypothesis is that calling behavior has evolved in nocturnal geckos to advertise territories and body size over a long distance, taking the place of visual displays in diurnal lizard species.

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