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Sexual Dimorphism and Ecology of the Gecko, *Ptyodactylus guttatus*

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ABSTRACT.—**Geckos are generally nocturnal and show no sexual dichromatism, and males are usually smaller than females. *Ptyodactylus guttatus* is an unusual gecko. It is active by day and night and is sexually dichromatic, and males are larger than females. We studied *P. guttatus* at two sites in southern Israel. Eggs were laid between May and October at Haluqim, where we studied eggs in natural caves. At a second site, Hazeva, *P. guttatus* occur on buildings at a density of 390 ha^{-1}. This is 195 times the density that the species occurs in natural habitats. At Hazeva, adult males inhabited large home ranges, which generally overlapped with one or more smaller home ranges of females. The pattern of home-range overlap presumably reflects the opportunities for mating. A path analysis was consistent with the hypothesis that females spaced themselves to gain access to insects (which they eat) attracted to wall lights on the buildings, and that males space themselves to gain access to female mates. We did not find evidence of territoriality in this population but observed males guarding females. Large male body size may provide priority access to mates, and the distinct male dorsal pattern may have arisen because light does not constrain the use of visual signals in these unusual, largely diurnal geckos, to the same extent as it may in nocturnal geckos.**

There has been considerable interest in the degree to which environmental constraints may affect the evolution of social signals (Johnstone, 1997). The availability of light or habitat complexity and geometry may act as a constraint on visual communication and effect social behavior (Endler and Thery, 1996). These constraints may result in different traits being involved in social communication in organisms inhabiting different environments.

Diurnal organisms that live in open, light-filled habitats often have sexually dichromatic traits that play a role in visual communication (Andersson, 1994). Organisms that live in dark, forest habitats may develop brighter signals to overcome environmental constraints imposed by low light levels (Marchetti, 1993). Nocturnal organisms, or organisms in which vision is limited, may have little use for visual signals and rely more on other channels for communication (e.g., vocalization or olfaction, see Regalado, 2003b). For example, in diurnal lizards, males are often larger than females and show bright nuptial coloration. This pattern of sexual dimorphism is probably a result of sexual selection, derived from male competition for large home ranges that provide access to mates, because female choice is rare among reptiles (Olsson and Madsen, 1998). The mainly nocturnal lizards of the infraorder Gekkota (geckos and relatives) show a pattern of sexual dimorphism that contrasts with that found in diurnal lizards. Male geckos are usually smaller than females and do not differ in color from females (Zug et al., 2001). This may be caused by the constraint imposed by low light levels resulting from their nocturnal habits (Roll, 2000). If this hypothesis were true, one would expect any diurnal species of gecko to show a similar pattern of home-range behavior and sexual dimorphism to diurnal lizards in other families.

Fan-Toed Geckos (genus *Ptyodactylus*) from the Middle East and northern Africa provide some evidence for the hypothesis that nocturnality constrains selection on male lizards. Different species of *Ptyodactylus* vary in activity from nocturnal to diurnal (Frankenberg, 1978). The most diurnal species (*Ptyodactylus puiseuxii*) shows brighter coloration in males, whereas in the nocturnal species (*Ptyodactylus hasselquistii*) males are similar in coloration to females (Werner and Sivan, 1994). Although this pattern of variation in sexual dimorphism is suggestive, it is difficult to assess its real relevance in the absence of data on the ecological context in which these patterns of sexual dimorphism occur.

This paper describes the ecology and pattern of sexual dimorphism in *Ptyodactylus guttatus*, a species that shows considerable diurnal activity. Specifically, we explore the degree to which this species conforms to the patterns of behavior found in other lizard families that are primarily diurnal, as compared with other, nocturnal geckos.

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Materials and Methods

The majority of this study was done at Hazeva Research and Development Centre, located in the 'Arava Valley, 4 km west of the border between Israel and Jordan (30°46'N, 35°16'E). We studied the geckos that inhabited a group of 19 buildings arranged in a C-shape around a central courtyard. We studied the geckos at Hazeva over 12 days on three separate visits between 21 and 25 April 1999, 12 and 16 May 1999, and on 18 and 19 June 1999. The climate at Hazeva is hot and dry (Barak and Dorfman, 1978). Mean daily temperature in the hottest month (August) is 31.4°C and in the coolest month (January) is 13.8°C. The average annual rainfall at Hazeva is 71 mm. There was no precipitation during our study.

Standard searches were made at Hazeva by walking 3 m from the external wall of the buildings and recording any gecko observed. Thirty-six standard searches were made during the study. Searches were conducted at all hours of the day and were made a minimum of three hours apart. An attempt was made to capture all unmarked geckos with a noose. Upon capture each lizard was measured, marked with a painted number on the back using yellow, nontoxic acrylic paints, and released. All lizards were returned to the site of capture within 24 h, most within 3 h. Measurements taken were snout–vent length (SVL), depth of the head immediately behind the eye (HD), head length from the anterior tip of the snout to the posterior tip of the mandible (HL), maximum head width across the ear openings (HW), hind-limb length (HLL), forelimb length (FLL), fourth-toe length (TL), and mass. All linear measurements were made with plastic vernier calipers to the nearest 0.1 mm. Lizards were weighed to the nearest 0.1 g on Bonso 150 g pocket electronic scales. The number of pale and dark spots that intersected a line running paravertebrally between the axilla and groin were counted for each lizard. We took care that these counts were made under standard illumination conditions, by one person (GJ), at a fixed distance and angle to the lizard while held in the hand to reduce variables that may influence color perception. Repeated captures of some individuals showed that the counts of dark and pale spots were highly repeatable, and the pale and dark spots on individual *Ptyodactylus* remained distinct, despite minor changes in the background color of individual lizards (unpubl. data). Any damage to the tail and scars were recorded, as were the presence of oviductal eggs in females. Lizards were regarded as males if they everted hemipenes or if they had bilateral raised areas on either side of the tail base that house the hemipenes. All other lizards were regarded as female.

Population size was estimated using the Peterson index (Caughley, 1977) based on mark-recapture data from the two five-day study periods in April and May. Observed sex ratio was compared with the expected male to female ratio of one using chi-squared test. Population density was estimated from the mark-recapture estimate of population size and the ground area of the buildings at Hazeva (1200 m^2).

Adult females, α-males, and β-males (see Results) were compared for all morphological variables using one-way analysis of variance. When a significant difference was found over all three groups, Scheffe post hoc tests were used to identify where differences occurred. A discriminant function analysis was done to explore the multivariate differences between the three groups of geckos, based on the eight body measurements (Sokal and Rohlf, 1995).

The activity of geckos was recorded as the number of geckos visible on the external walls of the buildings during each standard search. The total number of geckos seen during searches was compared between four time periods (0000–0600 h, 0600–1200 h, 1200–1800 h, and 1800–2400 h) using a one-way analysis of variance. To compare activity patterns of females, α-males, and β-males, the number of individuals in each group seen during standard searches on a particular visit to Hazeva was expressed as a proportion of the number of geckos in that group known to be alive during the visit. All standard searches were then grouped into eight three-hour periods to indicate daily activity patterns. Friedman's nonparametric test was used to test the null hypothesis that geckos in the three groups were equally active. Wilcoxon's signed ranks tests were used to make pairwise comparisons of activity among females, α-males, and β-males.

Home ranges were calculated for individual geckos that had been recorded at 10 or more separate locations ($N = 16$). Marked geckos were usually easily identified from the painted numbers on their backs during standard searches. The location of all geckos was recorded to the nearest 0.5 m on a map of the study buildings. Home-range areas were measured as the minimum convex polygon (Jennrich and Turner, 1969) that encompassed all known locations for an individual gecko. Patterns of home-range overlap were calculated by counting the number of male and female geckos that had been found within the home range of the 19 geckos for which home range

was calculated. Average home-range size and home-range overlap was compared between these males and females with one-way analyses of variance. The relationship between home-range size and the number of lizards with which a home range overlapped was analyzed using linear regression. The regressions for males and females were compared using analysis of covariance.

Putative determinants of gecko density were tested using path analysis (Sokal and Rohlf, 1995). During each of the three visits to Hazeva, people inhabited different buildings. When people were living in a building, fluorescent internal and external wall lights were left on for much of the evening. Each of the 19 buildings was scored for the number of visits to Hazeva that they were inhabited (0–3), and the number of geckos that were observed at least once on each unit was counted. Lights attracted insects to the buildings in which people lived, but the fluorescent tubes did not provide an important source of heat because of the high air temperatures during the study. Thus, lights were a proximate measure of the food resources available to geckos at each building. These data were used to test whether the density of females (potential mates) or the presence of lights around the unit (insects) determined the abundance of male *P. guttatus*. The data were tested for concordance with this hypothesized set of causative relationships using a path analysis based on linear regression analysis and correlation coefficients (Sokal and Rohlf, 1995). Fisher's exact probabilities were calculated to test whether an equal number of males and females had scars on their body and broken or regrown tails.

Reproductive seasonality was determined by monitoring gecko eggs in five caves on Haluqim Ridge near Sede Boqer, Israel (30°53'N, 34°46'E) between 20 June and 7 October 1999. This site was visited every 1–6 days ($\bar{x}$ = 2.4 days between visits). During each visit to the caves any newly laid eggs were found, their location was noted and their diameter measured with vernier calipers to the nearest 0.1 mm. All old eggs were located, their color was noted, and any sign of hatching was recorded, following Werner (1986). The diameter of eggs was compared between caves and between clutches using one-way analysis of variance. Clutches were identified as two eggs that appeared during the same interval between visits and that were laid touching each other. The incubation period was calculated as the number of days between when an egg was newly found and the day on which it was found to have hatched. Means are given ±1 SD.

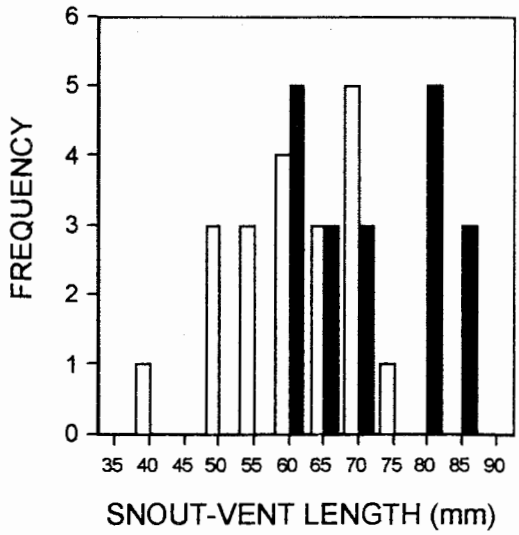


FIG. 1. Size frequency distribution of male (solid black) and female (hatched) *Ptyodactylus guttatus* at Hazeva, Israel.

RESULTS

Population Size.—A total of 479 sightings were made of geckos on the buildings at Hazeva during the 12 observation days. Thirty-nine geckos were captured and individually marked. These included 19 females and 20 males. This sex ratio was not different from unity (χ_1^2 = 0.03, P = 0.87). The individual identity of the gecko was ascertained for most (382) sightings. The remaining 97 sightings were of unmarked geckos or of marked geckos that could not be identified. Marked lizards were positively identified between one and 34 times each.

Twenty-six geckos were caught and marked during the April visit. During the May visit, 26 geckos were caught, of which 14 were recaptures that had been marked in April, yielding a Petersen population estimate of 46.8 ± 7.8 geckos living on the buildings at Hazeva during the study. This represents a density estimate of 390 sexually mature *P. guttatus* ha^{-1} of suitable habitat.

Sexual Dimorphism.—At Hazeva, there were two distinct groups of male *P. guttatus* (Fig. 1). One group had SVLs > 77 mm (α-males), whereas the other group had SVLs < 71 mm (β-males). There were significant univariate differences between α-males, β-males, and females for the eight measurements taken (Table 1). Post hoc tests showed that α-males were larger than both β-males and females for all measurements (Scheffe Ps < 0.001). Females and β-males did not differ from each other for any of the eight measurements (Scheffe Ps > 0.11).

TABLE 1. Comparison of measurements (in millimeters, except mass) between mature female, α-male, and β-male *Ptyodactylus guttatus* at Hazeva, Israel. Descriptive statistics are given as mean ± SD and minimum-maximum values.

Variable	Females (N = 19)	β-males (N = 11)	α-males (N = 8)	F-value	P
Snout–vent length	63.0 ± 4.050 53–78	66.5 ± 8.072 58–70	81.0 ± 2.582 78–86	18.51	< 0.001
Head depth	8.4 ± 0.748 7.1–10.3	8.9 ± 0.898 7.6–9.6	10.7 ± 0.435 10.1–11.4	18.81	< 0.001
Head length	17.8 ± 1.128 14.7–23.2	18.2 ± 2.180 16.0–19.4	22.3 ± 0.818 21.3–23.8	17.85	< 0.001
Head width	14.4 ± 0.973 11.7–17.0	14.7 ± 1.671 12.9–15.9	17.8 ± 0.416 17.3–18.7	16.67	< 0.001
Hind-limb length	41.8 ± 2.857 35.0–47.0	41.6 ± 3.697 37.0–47.0	48.5 ± 1.767 45.9–51.0	13.04	< 0.001
Forelimb length	28.4 ± 2.111 24.0–32.1	28.5 ± 2.442 25.0–32.0	33.9± 1.279 31.4–36.2	17.91	< 0.001
Fourth toe length	7.4 ± 0.735 6.1–9.3	7.7 ± 0.999 6.3–8.9	9.3 ± 0.943 7.3–10.0	9.84	< 0.001
Mass (g)	6.1 ± 1.660 3.3–13.5	8.4 ± 3.607 4.1–9.7	13.4 ± 1.037 12.1–15.0	14.99	< 0.001
Pale spots	5.9 ± 1.39 3–9	7.3 ± 1.36 5–9	7.7 ± 1.56 6–11	5.79	0.007
Dark spots	2.1 ± 1.62 0–6	3.1 ± 2.42 0–7	1.5 ± 1.63 0–4	1.99	0.152

Discriminant function analysis of eight measurements using α-males, β-males, and females as a priori groups (Fig. 2), resulted in correct identification of 89.2% of lizards overall. All α-males, 95% of females, and 73% of β-males were correctly grouped. The single misidentified female was incorrectly grouped with β-males. Misidentified β-males were most often (18%) incorrectly grouped with females. The first discriminant function explained 59.5% of the variance (Wilk's $\lambda = 0.25$, $P = 0.0003$), whereas the second discriminant function explained the remaining 40.5% (Wilk's $\lambda = 0.52$, $P = 0.004$). Unstandardized discriminant function coefficients and their correlations to discriminant functions are presented in Table 2. Most measurements of the head and limbs were most highly correlated with the first discriminant function, which most clearly separated males from females. Mass was most highly correlated with the second discriminant function, which most clearly separated α-males, and β-males (Fig. 2).

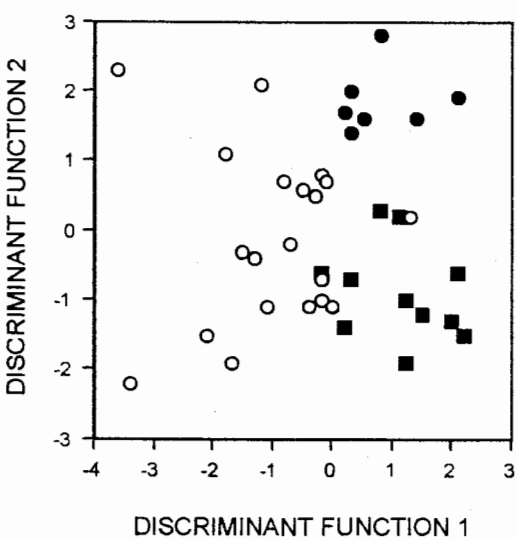


FIG. 2. Plot of discriminant function scores based on morphology for α-male (●), β-male (■), and female (○) *Ptyodactylus guttatus*.

In addition to morphometric differences, there are also differences in color pattern between females, α-males, and β-males (Table 1). α-Males had more pale spots on the dorsum than females (Scheffe $P = 0.01$), but they did not differ from β-males (Scheffe $P = 0.67$). Females and β-males also had similar numbers of pale spots on the dorsum (Scheffe $P = 0.17$).

Activity.—The total number of geckos visible on the walls of the buildings at Hazeva during each of 36 standard searches varied between two and 22. The mean number of geckos seen during a search ($x = 10 \pm 4.79$) remained constant throughout the day ($F_{3,32} = 0.28$, $P = 0.84$).

The numbers of individuals known to be present in the population that were seen during each standard search differed between α-males, β-males, and females (Freidman $\chi^2_2 = 16.0$, $P = 0.00$; Fig. 3). A greater proportion of α-males (0.13–0.66, mean = 0.41 ± 0.196) than females

TABLE 2. Unstandardized discriminant function coefficients (and pooled-within-groups correlations with discriminant functions) of eight measurements for female, α-male, and β-male *Ptyodactylus guttatus* from Hazeva, Israel.

Variable	Discriminant function I	Discriminant function II
Forelimb length	0.292(0.804)	−0.201(0.361)
Head length	0.443(0.774)	−0.292(0.444)
Head width	0.675(0.739)	−1.388(0.451)
Snout–vent length	0.055(0.731)	0.069(0.576)
Head depth	−0.035(0.727)	1.658(0.598)
Hind-limb length	0.102(0.697)	−0.210(0.269)
Fourth toe length	−0.545(0.561)	0.406(0.362)
Weight	−0.593(0.577)	0.678(0.644)
Constant	−25.680	12.730

(0.11–0.30, mean = 0.20 ± 0.063) were observed per search (Wilcoxon's signed ranks = −2.52, P = 0.01). A greater proportion of females than β-males (0.02–0.12, mean = 0.10 ± 0.033) were observed per search (Wilcoxon's signed ranks = −2.52, P = 0.01). A greater proportion of α-males than β-males were observed per search (Wilcoxon's signed ranks = −2.52, P = 0.01).

Home Range.—Male home ranges (mean = 25.1 ± 21.66 m^2, N = 9) were similar in area to female home ranges (mean = 10.6 ± 13.13 m^2, N = 7; $F_{1,15}$ = 0.94, P = 0.35). The males that were sighted at more than 10 locations, and for which a home-range area was calculated (see Materials and Methods), included eight adult α-males and one β-male.

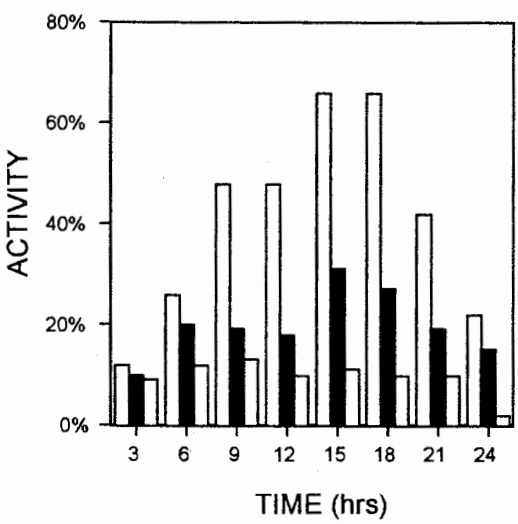


FIG. 3. Diel variation in activity of *Ptyodactylus guttatus* at Hazeva, Israel. Activity is expressed as the average percent of female (black), α-males (white), and β-males (hatched) that were observed during 36 standard searches.

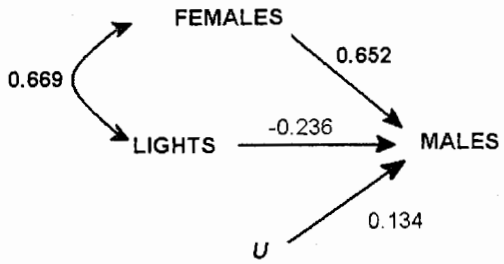


FIG. 4. Path diagram illustrating hypothetical causative relationships between density of male and female *Ptyodactylus guttatus* and frequency with which artificial lights were on in buildings at Hazeva, Israel. Significant (P < 0.05) coefficients are shown in bold.

On average 37% (± 39.9%, 0–100%) of each of these male's home ranges overlapped with that of another male. This figure is similar to the overlap between female home ranges (mean = 0.20 ± 37.5%, 0–100%; $F_{1,15}$ = 0.52, P = 0.48).

Male home ranges overlapped with 0–5 female home ranges (mean = 2.67 ± 1.66, N = 9), whereas female home ranges overlapped with 0–4 male home ranges (mean = 1.86 ± 1.22, N = 7; $F_{1,15}$ = 1.17, P = 0.30). This pattern of overlap gives an indication of the number of potential mates. The relationship between home-range area and the number of potential mates was similar for males and females (slopes: $F_{12,1}$ = 0.23, P = 0.64; intercepts: $F_{12,1}$ = 0.46, P = 0.51). The regression of combined male and female data showed a nearly significant positive relationship between the number of potential mates and home-range area (R^2 = 0.23; $F_{1,15}$ = 4.16, P = 0.06).

Determinants of Gecko Distribution.—There was a significant correlation (Pearson r = 0.67, P = 0.002) between the number of female *P. guttatus* found on each of 19 buildings at Hazeva throughout the study and the number of visits to Hazeva in which lights were left on over night. The results of the multiple regression analysis were consistent with the hypothesis that the density of females *P. guttatus* determined the density of males (unstandardized regression coefficient = 0.538, t = 2.28, P = 0.04). Conversely, the number of visits in which lights were left on over night in each flat did not appear to influence male density (unstandardized regression coefficient = −0.215, t = −0.83, P = 0.42). Eighty seven percent of the variance in male density was explained by the combined effects of female density and the number of visits lights were left on in flats. These relationships are illustrated in a path diagram (Fig. 4).

Mate Guarding.—Four pairs of adults were observed during the study. These pairs consisted of an α-male and a female that were within 0.5 m of each other. All four paired females had palpable ovarian follicles. After pairs ceased their association, three of the four females were recaptured, and they contained palpable oviductal eggs. The male of one pair called when a second male approached the pair and then chased the intruder away from the female. One pair was observed together consistently over five days. They were often observed touching. Sometimes the male placed his forelimb on the back of the female.

Scars and Tail Damage.—Males had more scars than females (Fisher's exact $P = 0.01$). Six of 19 males (32%) were scarred, whereas none of the 20 females had any scars.

The proportion of males and females with damaged or regrown tails did not differ (Fisher's exact $P = 0.11$). Eleven of 19 (57%) males showed evidence of damage to their tails. Six of 20 (30%) females showed evidence of damage to their tails.

Reproduction.—At Hazeva, nearly half (9/19) of the females contained palpable oviductal eggs during the study. Although we found no laid eggs at Hazeva, one hatchling was observed there on 18 June.

On Haluqim Ridge, 24 clutches of eggs were found in five caves. Clutches consisted of one ($N = 3$) or two ($N = 21$) eggs ($x = 1.87 \pm 0.34$). Eggs were between 11.5 mm and 14.9 mm in diameter (mean = 13.4 ± 1.04 mm, $N = 45$). The diameter of the eggs differed between the caves ($F_{4,39} = 4.64$, $P = 0.004$) and also between clutches ($F_{23,21} = 10.3$, $P = <0.001$). Eighteen clutches were laid and hatched during the study period (x incubation period = 46.9 ± 3.78 days). Only one of 45 eggs failed to hatch. Clutches of eggs hatched in July ($N = 3$), August ($N = 11$), September ($N = 9$), and October ($N = 1$). Eggs were white when first laid and turned yellow within two days. They were then yellow until four to eight days after being laid, after which they gradually turned pink and then grey.

Discussion

The pattern of sexual dimorphism and behavior shown by *P. guttatus* is reminiscent of many diurnal lizards in several respects and contrasts with the general pattern among nocturnal geckos (Zug et al., 2001). Most notably, α-males had more white spots than females, giving them the appearance of being more distinctly patterned. They also had larger bodies, larger heads, and longer limbs than females. Geckos of neither sex had exclusive use of their home range (i.e., they were not territorial), but their home range provided access to several potential mates. However, there did appear to be competition between males for access to mates. Male density was more highly correlated with the density of females than with the availability of wall lights (a proxy measure of food abundance), and males appeared to guard females around the time they ovulated. Males exhibited more scars than females, indicating a greater incidence of fights between males. In contrast to this, males of the nocturnal, sexually monochromatic Ground Gecko *Stenodactylus doriae,* which occurs on sandy areas around Hazeva, are the smaller sex and do not differ from the females in the number of bite scars inflicted by other geckos (Bouskila, 1987).

The density of *P. guttatus* on the buildings at Hazeva is remarkable, given that this site is extremely arid and shows very low productivity. This density is reminiscent of lizards from more temperate or tropical environments (Turner, 1977) and is 195 times higher than has been reported previously for this species. In the rocky habitats, where it occurs naturally, the density of *P. guttatus* varied between 0.14 ha^{-1} and 1.67 ha^{-1} (Shenbrot and Krasnov, 1997), compared with our estimate of 390 ha^{-1}. Both natural rock outcrops and artificial buildings are complex three-dimensional structures that offer greater surface area for gecko to move over than the ground area covered by this structure would suggest. Differences in the surface area of the buildings at Hazeva compared to natural rock outcrops may partially explain the density differences. The density of geckos at Hazeva may also be high because the buildings there have wall lights that attract insects from surrounding areas and provide a localized abundance of food. The buildings may also provide an abundance of shelter sites that may be used by geckos as refuges from predators and environmental extremes. The presence of humans may also reduce predation on the geckos inhabiting the buildings.

Previous observations of *Ptyodactylus* have suggested they may be territorial. Males are known to fight, and their vocalizations may have a territorial function (Werner, 1965). We found no clear evidence for territoriality among *P. guttatus* at Hazeva. The high density of the population at Hazeva may explain this apparent contradiction. Other species of gecko are territorial at low densities but form stable dominance hierarchies at high densities, as do some diurnal lizards (Stamps, 1977). Perhaps the social and spacing behavior of *P. guttatus* varies with population density also. The high densities of *P. guttatus* on the buildings at Hazeva may result in reduced territoriality at this site.

The field data presented here show that *P. guttatus* are active during all hours of the day and night. This result confirms previous laboratory studies (Frankenberg, 1978). It is noteworthy that the path analysis was consistent with the hypothesis that artificial lights influenced the density of females, which in turn influenced male density (Fig. 4). We did not expect that lights might be an important determinant of population density in a largely diurnal gecko. However, *P. guttatus* is not strictly diurnal. A large proportion of the population is also active at night (Fig. 3). Wall lights may determine the abundance of *P. guttatus* if they attract to the buildings insects that are eaten at night. Alternatively, the insects may occur at higher densities near lights during the day, having been attracted to the buildings when lights are on in the evenings. An experimental manipulation in which wall lamps are added or deleted to see whether they change the distribution and abundance of the gecko's arthropod prey and result in a change in gecko density might be an appropriate test of this hypothesis. Experimental manipulations of food resources have demonstrated that food is an important determinant of density, territory size, and access to mates in diurnal lizards (Simon, 1975; Hews, 1993).

We may have underestimated the proportion of geckos active at Hazeva. This is because only geckos on the outside walls of buildings could be seen during standard searches. Any geckos that were active on the inside walls of the buildings could not be seen. We do not think this is a problem for interpretation of the data for several reasons. First, the method was consistent during the study. So the patterns of activity should be unaffected by the absolute number of geckos present inside and outside of the buildings. Second, residents in the buildings reported seeing very few geckos inside walls of inhabited buildings. This is likely to be reliable because the geckos are conspicuous animals. Third, the number of geckos we marked during the study was within one standard error of the estimated population at the study site. This suggests that we missed very few geckos during the study and that any systematic bias in our results (caused by some geckos living exclusively on internal or external walls of the buildings) is unlikely.

Egg laying on Haluqim Ridge show a similar temporal pattern to that found for *P. guttatus* in the Judean Hills (Werner, 1986). Hazeva is hotter and at lower altitude than Haluqim Ridge (143 m below sea level vs. 500 m above sea level), which may result in different timing of reproduction. The approximate age of eggs could be told from a predictable sequence of more or less gradual color changes. The most useful and abrupt of these changes occurred when eggs turned from white to yellow within two days of being laid. This change has not been reported previously. This may have been because Werner (1986) was unable to visit egg-laying sites as frequently as we were. The incubation period at Haluqim Ridge was similar to that in the Judean Hills (Werner, 1986). Mortality of the eggs at Haluqim was lower than at most sites reported by Werner (1986). Captive female *P. guttatus* lay several clutches at the same site over the breeding season (Werner, 1972). We suspect this is also true of wild females, as was suggested by Werner (1986). The pattern of home-range overlap we found at Hazeva suggests that there is a potential for multiple paternity in very dense populations.

Ptyodactylus guttatus are known to live up to eight years, whereas another species (*P. hasselquistii*) is known to live for 12 years (Werner et al., 1993). These figures are derived from captive individuals, and survivorship is unknown in the field. However, it is clear that *Ptyodactylus* spp. are potentially long-lived animals. Even though our data were gained over a very short period of three months, they suggest that *P. guttatus* at Hazeva probably interact with each other over prolonged periods of time, both within and between breeding seasons. Such long patterns of association between individuals would select for the development of social signals in the context of mate choice and reducing the costs of repeated contests between males. *P. guttatus* produce a complex array of calls (Frankenberg, 1974), which may act as social signals, and their extensive diurnal activity may allow them to use variation in dorsal patterning as visual signal also.

The sexual dichromatism exhibited by *P. guttatus* is unusual among geckos. The few other diurnal geckos also tend to show sexual dichromatism (Cooper and Greenberg, 1992; Regalado, 2003a). Most geckos are nocturnal and sexually monochromatic (Cooper and Greenberg, 1992; Regalado, 2003b), even though they are able to distinguish colors at short range in low light conditions (Roth and Kelber, 2004). This suggests that visual signals may not be as important among most geckos as vocalizations and olfaction (Regalado, 2003a,b). In many respects, *P. guttatus* and other species of diurnal geckos resemble the patterns of social behavior and spacing found in diurnal lizards of other families. This is consistent with the hypothesis that low light levels constrain the use of coloration in social interactions in geckos.

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