

Ecology of the Common Barking Gecko (*Ptenopus garrulus*) in Southern Africa

TOBY J. HIBBITTS,^{1,2} ERIC R. PIANKA,³ RAYMOND B. HUEY,⁴ AND MARTIN J. WHITING¹

¹School of Animal, Plant, and Environmental Sciences, University of the Witwatersrand,
Private Bag 3, Wits 2050, South Africa

³Section of Integrative Biology (C0930), School of Biological Sciences, University of Texas,
Patterson Laboratories, 24th at Speedway, Austin, Texas 78712-1064, USA

⁴Department of Biology, Box 351800, University of Washington, Seattle, Washington 98185-1800, USA

ABSTRACT.—We examined museum specimens of the Common Barking Gecko (*Ptenopus garrulus*) from the Kalahari and Namib Deserts to assess sexual size dimorphism, reproductive status, and diet. Males had significantly wider heads than females of the same body size; however, *P. garrulus* showed no sexual dimorphism in any other morphological character. The smallest mature male was 36 mm snout-vent length, whereas the smallest female was 31 mm. Peak reproductive activity for both sexes was in September and October. Clutch size was fixed at one large egg (average size = 5.9×4.4 mm); all eggs were in the right ovary, but more than one clutch may be laid in a single breeding season. *Ptenopus garrulus*, when compared with other geckos, produces very large offspring and thereby invest heavily in a single offspring. We recorded 15 arthropod orders in the diet of *P. garrulus*. Termites dominated their diet both numerically and volumetrically. Males and females ate prey of similar taxa and sizes, suggesting that trophic partitioning is absent. Therefore, the evidence suggests that the evolution of head width differences is driven by male contest competition.

Basic natural history data are fundamental to understanding and developing life-history theory. In this regard, squamate reptiles have been the focus of relatively intensive ecological study because unlike many other vertebrates, they are often easily sampled and identifiable prey items are readily recovered (e.g., Pianka, 1986; Huey et al., 2001; Vitt et al., 2003). Recently, Vitt et al. (2003) synthesized the global ecology of squamates to test the influence of phylogenetic history on current patterns of community assemblages. This analysis depended in part on life-history data. Future analyses will benefit from more extensive datasets that include more taxa from geographically disparate areas and possibly, more detailed natural history data.

Morphology is tightly linked to an organism's ecology (Miles, 1994). Sexual size dimorphism (SSD) is of special interest because the size difference between males and females potentially affects many aspects of their ecology (Andersson, 1994). The three most common explanations for SSD are (1) intersexual resource partitioning (Schoener, 1967); (2) sexual selection (usually male contest competition; Trivers, 1976); and (3) fecundity selection (Hedrick and Temeles, 1989; Shine, 1989; Stamps, 1995). When SSD has an ecological basis, one sex usually has an alternative feeding strategy in which different sized prey are selected caused by size-related functional constraints (Houston and Shine, 1993). This phenomenon may arise either because of competition for resources or as a by-product of sex-related selective pressures, such as sexual selection. Sexual selection is most commonly associated with situations where the male is larger than the female. Larger male size typically results from male-

² Corresponding Author. E-mail: toby@gecko.biol.wits.ac.za

male interactions associated with competition for territories and/or access to mates (Vitt and Cooper, 1985; Olsson et al., 2002). Males may also be smaller than females in situations where the males have to search for widely scattered females and where a small-male advantage exists (e.g., horned lizards; Zamudio, 1998). Fecundity selection is the notion that larger females are capable of producing more (or larger) eggs or offspring (Fitch, 1981; Olsson et al., 2002). Basic ecological data on diet and reproduction are necessary to explain the evolution of SSD.

We studied the ecology of the Common Barking Gecko, *Ptenopus garrulus*, a small sized (max 60 mm SVL) lizard of the Kalahari and Namib Deserts of southern Africa. This species constructs burrows that are up to 38 cm deep in loose soils and usually have several branches (Haacke, 1975). Males have yellow throats and emit calls from the entrance of their burrows at dusk and dawn (Haacke, 1969). Pianka and Huey (1978) studied aspects of the ecology of several species of geckos in the southern Kalahari. They reported that *P. garrulus* had an invariant clutch size of one and that termites dominated their diet by volume. Our study had three main objectives: (1) to determine the extent of sexual size dimorphism; (2) to examine seasonal and sexual differences in diet; and (3) to examine the reproductive ecology of males and females and especially to examine offspring size relative to female size.

MATERIALS AND METHODS

We examined 150 specimens (Transvaal Museum) that had been collected in the following regions of Southern Africa: Northern Namibia, Southern Namibia, Central Botswana, Namaqualand, Kgalagadi Transfrontier Park, and Limpopo Province of South Africa. We examined an additional 490 specimens of *P. garrulus* collected in 1969 and 1970 in the Kalahari region of Botswana, Namibia, and South Africa by ERP and RBH. Diet and reproductive status from all specimens were analyzed. Methods used for these specimens are discussed in Pianka and Pianka (1976) and Pianka and Huey (1978).

Sexual Size Dimorphism.—We measured SVL (snout-vent length), tail length, head width, head depth, head length, torso length (axilla to groin), arm length (head of humerus to the end of the claw on the longest finger), humerus length, leg length (head of femur to the end of the claw on the longest toe), femur length, pes length, and fourth toe length of 150 preserved specimens (Transvaal Museum). All measurements were made to the nearest 0.01 mm using digital calipers. Characters were chosen based on studies of sexual selection and sexual dimorphism (head characters and torso length) and observations of *P. garrulus* breeding behavior (arm and leg characters). Sex of juveniles was verified by dissection. Prior to testing for sexual dimorphism, we log-transformed all variables and subjected each to an ANCOVA with log SVL as the covariate. A *t*-test for unequal variances was used on the raw SVL data. We used a reduced major axis (RMA) regression (Fairbairn, 1997) to investigate growth patterns of those characters, which were significantly different between the sexes.

Reproduction.—Growth patterns of characters were determined via dissection. Females were determined to be sexually mature when they contained oviductal eggs

or enlarged vitellogenic follicles. For gravid females, length and width of the egg was measured to the nearest 0.01 mm with digital calipers. Egg volume was estimated for each egg using the formula for a prolate spheroid (Vitt, 1991). Sexual maturity in males was determined by finding enlarged testes and convoluted epididymides. We measured the length and width of the left testis to the nearest 0.01 mm and estimated testes volume (formula for prolate spheroid). We used a Kruskal-Wallis test to determine differences in testes volume and egg length by month. Hatchlings were obtained during a field study of *P. garrulus* in 2003 and 2004 at Molopo Nature Reserve (25°50'S, 22°55'E) located in the eastern Kalahari, Northwest Province, South Africa, focusing on other aspects of their life history.

Diet.—Stomach contents were identified to order. Number and types of prey items were recorded for each individual. Measurements of length and width were made for complete prey items (to nearest 0.01 mm) and used to estimate volume (formula for prolate spheroid). We calculated correlations of prey size to SVL and head width, and prey size to head width with the effects of SVL removed. We tested for differences in diet between the sexes using Chi-square tests. We also tested for differences in prey size consumed between the sexes using ANCOVA with head width as a covariate and with a *t*-test assuming unequal variances. We used a Chi-square test to examine variation in diet by month. Dietary niche breadth was determined using Simpson's (1949) diversity index.

Foraging Mode.—A population of *P. garrulus* at Molopo Nature Reserve was studied to determine foraging mode. The substrate was sand throughout, and the vegetation was dominated by *Acacia mellifera* and *Acacia erioloba*, with very little ground cover. All focal observations were made between 1900 and 2200 h in November 2004.

Foraging mode is often determined from measurements of movements per minute (MPM) and percent time spent moving (PTM). A criterion of PTM = 10 was used by Perry (1995) to distinguish between ambush and active foraging, with ambush foragers falling below 10. We quantified foraging mode using 10-min focal observations of 11 adult *P. garrulus*. The observer sat about 4 m from the burrow using an artificial light source to view activity. Geckos appeared to act normally under these conditions. All observations were carried out on individuals that were visible at the entrance to their burrows. Any movement and prey capture attempts were recorded. Adult *P. garrulus* are solitary inhabitants of a burrow. The individuals observed were of known size and sex from an ongoing population study at the same site.

RESULTS

Sexual Size Dimorphism.—Males (mean \pm SE: 44.9 \pm 0.4) and females (45.2 \pm 0.4) did not differ significantly in SVL ($t_{628} = 0.519$, $P = 0.60$). However, males had significantly wider heads than females when controlling for SVL ($F_{133} = 8.5$, $P = 0.004$; Fig. 1). The sexes did not differ in any other morphological characters ($P > 0.05$). Head width of males grew isometrically with SVL ($r^2 = 0.89$, slope = 0.997, 95% CI = 0.807–1.071), whereas female head width grew less quickly than SVL ($r^2 = 0.87$, slope = 0.888, 95% CI = 0.807–0.970; Fig. 1).

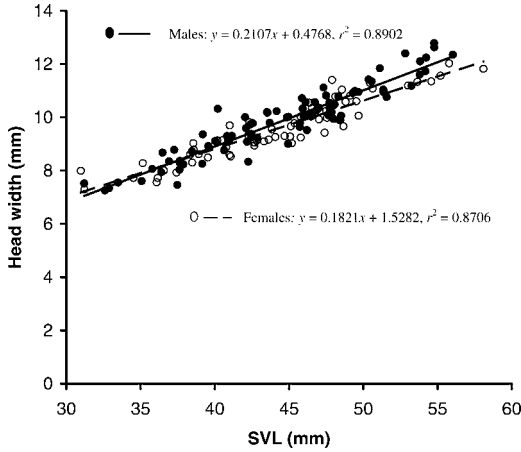


FIG. 1. Relationship between head width and snout-vent length of male and of female *Ptenopus garrulus*.

Reproduction.—Minimum size at sexual maturity for males was 36 mm SVL. Testicular volume peaked in September and October (Fig. 2), and these two months were significantly different than testicular volume in all other months ($H_{7,257} = 114.2, P < 0.001$). Minimum size at sexual maturity for females was 31 mm SVL. Egg volume was highest in September and October ($H_{7,56} = 17.6, P = 0.014$) and a similar statistical pattern to testicular volume existed, although not as strong. Eggs were present from August through April (Fig. 3). Clutch size was fixed at one; however, 8% of all females ($N = 4$) had two eggs at different stages of development suggesting that they lay a second clutch. All eggs were in the right oviduct, even when a second egg was developing.

Fifty-five *P. garrulus* less than 30 mm SVL were collected during fieldwork, with the two smallest individuals measuring 22 mm SVL. This size is also smaller than that reported for hatchlings by Haacke (1975). Minimum hatchling size was large relative to size at sexual maturity. Hatchling *P. garrulus* were also large relative to adult female size when compared to hatchling/female size in other gekkonids (Fig. 4). The regression line explained most of the variation ($r^2 = 0.95$), and *P. garrulus* was the only outlier.

Diet.—We identified 17 categories of prey (Table 1). Numerically, termites (51.1%) and ants (35.6%) dominated the diet. Volumetrically, termites were again the most important prey type (60%) followed by ants (8.9%) and beetles (8%). More gecko stomachs contained ants (46%) than any other food item, followed by termites (39%) and beetles (19%; Table 1). Eighteen percent ($N = 115$ out of 640) of all stomachs were empty and 17 geckos had eaten sloughed skins. The four most common prey types composed at least 90% of the diet in all months. Termites were most prevalent in December, composing 70% of the diet by number. Ants were eaten more commonly than termites in March and September and were most prevalent in September, making up 47% of the diet (by number) in that month. During all other months, termites were the most commonly eaten prey (Fig. 5). However, there were no significant differences between months ($\chi^2_7 = 0.15$;

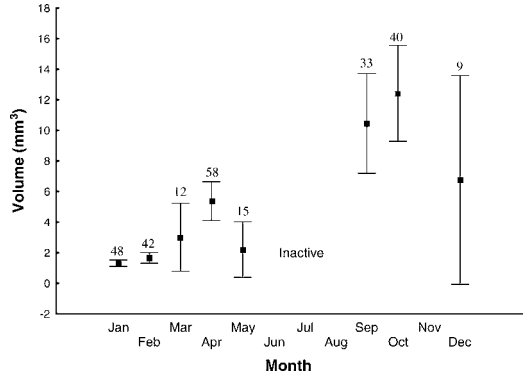


FIG. 2. Estimated testis volume by month. Mean (\pm SE) is displayed for each month. Sample size is listed above each error bar. Months with fewer than five males are excluded.

$P < 0.9$). *Ptenopus garrulus* are inactive in the winter months of June and July.

No differences existed between males and females in the numbers of the four most abundant prey groups and a group of all other prey items ($\chi^2_3 = 3.62; P < 0.5$). There was a significant correlation between prey size and SVL ($r = 0.39, P < 0.001$) and prey size and head width ($r = 0.4, P < 0.001$), but with the effects of SVL removed, there was no difference between prey size and head width ($r = 0.099, P = 0.44$). No difference between the sexes in relation to size of prey eaten was found when accounting for head width ($F_{59} = 0.287, P = 0.59$) or when not accounting for head width ($t_{170} = 0.158, P = 0.87$).

Foraging mode.—We determined MPM and PTM for six male and five female adult *P. garrulus*. All trials except one (8.6 min) were for the full 10 min: *P. garrulus* were classic ambush foragers. With the sexes pooled, adults moved infrequently (MPM = $0.4 \pm 1.9, 0-2.1$) and spent little time moving (PTM = 4.6 ± 1.9 sec, 0-16.7).

DISCUSSION

Males and females were sexually dimorphic only in relation to head width, with males having wider heads. Two major functions have been attributed to wider head width in one sex: ecological segregation in diet (Schoener, 1971; Camilleri and Shine, 1990; Shine, 1991)

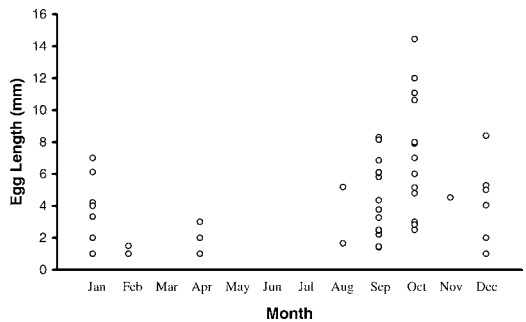


FIG. 3. Length of individual eggs in relation to month.

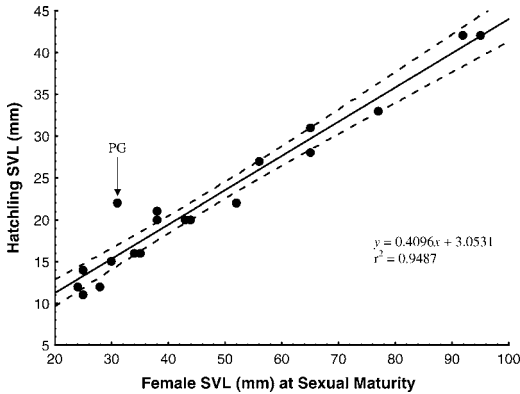


FIG. 4. Comparison of minimum hatchling size to female SVL at sexual maturity in 19 gekkonid species (Inger and Greenburg, 1966, *Cyrtodactylus malayanus*; Vitt, 1986; and references therein, *Phyllopezus pollicaris*, *Hemidactylus mabouia*, *Lygodactylus klugei*, *Gymnodactylus geckoides*, *Pseudogonatodes guianensis*, *Lygodactylus somalicus*, *Lygodactylus picturatus*, *Gonatodes concinnatus*, *Lepidodactylus lugubris*, *Hemidactylus frenatus*, *Gehyra mutilata*; Marquet et al., 1990, *Garthia gaudichaudi*; Doughty and Shine, 1995, *Phyllurus platurus*; Vitt and Zani, 1997, *Thecadactylus rapicauda*; Okada et al., 2002, *Gekko hokouensis*; Colli et al., 2003, *Gymnodactylus amarali*). Arrow marks *Ptenopus garrulus*.

and sexual selection (male contest competition; Vitt and Cooper, 1985; Saenz and Conner, 1996; Kratochvíl and Frynta, 2002; Reaney and Whiting, 2002). To determine whether head shape dimorphism is related to sexual selection, experiments must be conducted that deal with either mate choice or male-male interactions (Tokarz, 1995). However, ecological segregation in diet can be addressed by analyzing the diet of each sex. Increased head width should increase gape size allowing the sex with the wider head to eat larger prey items (Schoener, 1971; Camilleri and Shine, 1990). We found no difference in the diet of males and females. Termites and ants were the dominant prey of both sexes and the size of prey items eaten by males and females did not differ significantly. Thus, the dimorphism in head size seems unrelated to food niche segregation. The other explanation for SSD in head size in *P. garrulus* is sexual selection. Males have two traits that are likely "ornaments" for sexual selection. They vocalize from the mouth of their burrow and will defend an area within a radius of 1 m (TJH, pers. obs.); and males also have yellow throat patches, which are absent in females. We also observed frequent bite mark scars on males in the field (TJH, pers. obs.). Larger male head width is, therefore, best explained by male contest competition, though fights between males have not been witnessed.

Males attained sexual maturity at 36 mm and females at 31 mm. In gekkonids, males typically attain sexual maturity at smaller or similar sizes to females (Inger and Greenburg, 1966; Vitt and Zani, 1997; Vitt et al., 1997; Okada et al., 2002). These sizes can be reached in less than a year. The greater size of maturity for male *Ptenopus* may be caused by some form of reproductive suppression by rival males. Male *P. garrulus* have an

TABLE 1. Summary of the diet of *Ptenopus garrulus*. Total number and percent number categories include 640 specimens. Volume and percent volume categories are from 150 specimens dissected by TJH. Volumetric data for the other 490 stomachs are presented in Pianka and Huey (1978). Volumes for the 490 specimens were not combined with the other 150 specimens because different methods of volume estimation were used. Frequency is the number of stomachs containing the particular food item.

Prey Type	N	N%	Freq.	V (mm ³)	V%
Myriopoda					
Centipedes	2	0.06	2	—	—
Arachnida					
Acarina	2	0.06	2	—	—
Aranea	67	2.2	54	82.6	0.8
Solpugidae	6	0.2	6	—	—
Pseudoscorpiones	2	0.06	2	4.7	<0.1
Hexapoda					
Blattoidea	7	0.2	5	421.1	4.3
Coleoptera	191	6.2	120	788.4	8.0
Diptera	10	0.3	9	10.3	0.1
Hemiptera	60	1.9	35	709.3	7.2
Hymenoptera					
Formicinae	1100	35.6	294	875.9	8.9
Other	14	0.5	12	346.4	3.5
Isoptera	1578	51.1	247	5883.3	60.0
Neuroptera	4	0.1	2	50	0.5
Lepidoptera	8	0.3	7	316.9	3.2
Orthoptera	16	0.6	16	303.2	3.1
Thysanoptera	7	0.2	6	13	0.1
Larvae	12	0.4	12	17	0.2
Total	3086	100.0		9822.1	100.0
Niche Breadth				2.5	2.6

advertisement call, and the pitch of that call is negatively correlated with body size (TJH, pers. obs.). If a small male calls too close to a larger resident male, the smaller male might be physically challenged by the larger male and could suffer an injury. Males observed in the field frequently bore bite mark scars (TJH, pers. obs.). Small males are unlikely to secure matings in this scenario, and sexual maturity may be delayed to reduce conflict with larger males. Alternatively, males may grow at a more rapid rate than females and mature at the same age or females may choose larger males for copulations causing the evolution of later maturation.

Breeding is restricted to early summer months with peak testicular volume and largest egg size in October. Rainfall in the Kalahari can be quite erratic but hatchlings of eggs laid in October will likely emerge after significant summer rains when insect prey is expected to peak (late December to early January).

Females have an invariant clutch size of one, but four individuals had a second egg at an earlier developmental stage. Too few individuals with two eggs were found to test for a correlation between female size and number of clutches. All gekkonids have an invariant clutch size; however most produce two eggs with one egg produced in each ovary (Fitch, 1970). A growing

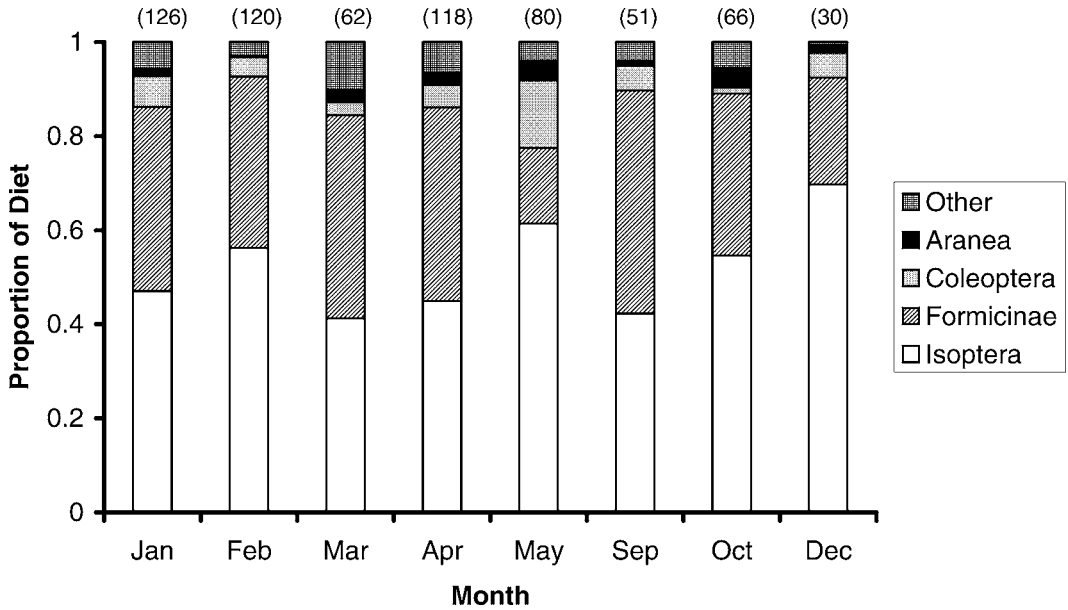


FIG. 5. Seasonal representation of the four most abundant prey types by prey number found in gut contents of *Ptenopus garrulus*. Number of guts examined is listed in parentheses.

number of species have been reported to have a clutch size of only one (see Werner, 1989, *Cyrtodactylus amictophilis*, *Tropicolotes steudneri*, and *Gehyra variegata*; Marquet et al., 1990, *Garthia gaudichaudi*; Vitt and Zani, 1997, *Thecadactylus rapicauda*). Interestingly, all *P. garrulus* eggs ($N = 56$) were in the right ovary, suggesting that the left ovary may be nonfunctional. *Thecadactylus rapicauda* is a large gecko (up to 126 mm SVL) that also lays one egg but produces eggs in both ovaries (Vitt and Zani, 1997). Most single-egg gekkonids are small (< 35 mm SVL and weigh < 1 g), which may explain why they have one egg clutches (Fitch, 1970). But adult *Ptenopus* can exceed 55 mm SVL and weigh more than 4 g, which is as large as many geckos that produce two-egg clutches. The reason for a single-egg clutch is unknown. A plausible adaptive explanation is that larger juveniles have a survival advantage; however, phylogenetic history may also be an explanation through similar juvenile size in close relatives. Hatchling *P. garrulus* are very large in relation to adult female size, and this ratio is much larger than for any other gecko reported (Fig. 4). One factor limiting egg size is the size of the pelvic aperture (Vitt, 1986; Sinervo and Licht, 1991). The hard-shelled eggs producing relatively large juveniles in *P. garrulus* suggest that an adaptation in the size of the pelvic aperture may have occurred, permitting a larger than expected egg to be laid.

Diet of *P. garrulus* consisted mainly of termites, both numerically and volumetrically. However, these lizards should not be considered termite specialists. In arid areas of southern Africa, termites are patchily distributed both spatially and temporally (Lepage and Darlington, 2000; Traniello and Leuthold, 2000). Some of the sampled geckos had eaten more than 30 *Hodotermes* termites, indicating that the resource is patchy.

Ptenopus are normally sit-and-wait foragers, waiting at the mouth of their burrow to ambush prey; confirmed by the observed low values for MPM and PTM. When termites swarm, however, *P. garrulus* come out of their burrows, even during the day, and become transient wide foragers (Huey and Pianka, 1981) and at these times they are often killed by shrikes (Huey and Pianka, 1981). *Ptenopus garrulus* may gain significant amounts of their nourishment while actively foraging during termite swarms and or termite foraging aggregations.

A broad survey of diets of many ($N \approx 200$) lizard species revealed differences among three major clades (Pianka and Vitt, 2003; Vitt et al., 2003). Iguanians tend to consume more ants than gekkotans or autarchoglossans. *Ptenopus garrulus* is unusual among gekkotans in consuming ants. Among the diets of desert geckos listed by Pianka (1986), only the diurnal Kalahari gecko *Lygodactylus capensis* consumes more ants than does *P. garrulus*.

In conclusion, we found that males become sexually mature at a larger size than females. *Ptenopus garrulus* have single egg clutches that are always produced in the right ovary. And, in relation to size, they have larger offspring than other geckos. Finally, *P. garrulus* are among a relatively small number of geckos to consume ants. These findings along with their use of a self-constructed burrow and calling behavior make the ecology of *P. garrulus* unique among other known gekkonids.

Acknowledgments.—We thank M. Burger and L. Mahlangu (Transvaal Museum) for the loan of specimens. TJH's fieldwork was funded by a National Research Foundation grant to MJW. TJH would like to thank the Northwest Parks Board for access to Molopo Nature Reserve and S. Gore for his support and

cooperation. TJH thanks D. Laurencio, L. Laurencio, and K. Hodges for assistance in the field. Also, G. Botha and I. Botha welcomed TJH into their home for the occasional meal and break from the bush, and R. Gallagher is thanked for endless patience and support. RBH and ERP thank L. Coons and T. Papenfuss for field assistance. Fieldwork in the Northwest Province was conducted under a permit to MJW and TJH and approved by the University of the Witwatersrand Animal Ethics Screening Committee (2003/29/2A). Data collection by ERP and RBH in 1969 and 1970 was supported by the National Science Foundation (Grants GB-8727, GB-31006, and BMS-47-0231), the Los Angeles County Museum of Natural History Foundation, the University of Texas Graduate School, the National Geographic Society, the Museum of Vertebrate Zoology, and the Miller Institute for Basic Research in Science. All specimens collected by ERP and RBH are deposited in the Los Angeles County Museum of Natural History. This paper was greatly improved by the editing of D. Saenz.

LITERATURE CITED

- ANDERSSON, M. 1994. *Sexual Selection*. Princeton Univ. Press, Princeton, NJ.
- CAMILLERI, C., AND R. SHINE. 1990. Sexual dimorphism and dietary divergence: differences in trophic morphology between male and female snakes. *Copeia* 1990:649–658.
- COLLI, G. R., D. O. MESQUITA, P. V. RODRIGUES, AND K. KITAYAMA. 2003. Ecology of the gecko *Gymnodactylus geckoides amarali* in a neotropical savanna. *Journal of Herpetology* 37:694–706.
- DOUGHTY, P., AND R. SHINE. 1995. Life in two dimensions: natural history of the Southern Leaf-Tailed Gecko, *Phyllurus platurus*. *Herpetologica* 51:193–201.
- FAIRBAIRN, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* 28:659–687.
- FITCH, H. S. 1970. Reproductive cycles of lizards and snakes. Univ. of Kansas Museum of Natural History Miscellaneous Publication 52, Lawrence.
- . 1981. Sexual size difference in reptiles. Univ. of Kansas Museum of Natural History Miscellaneous Publication 70:1–72.
- 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.
- HEDRICK, A. V., AND E. J. TEMELES. 1989. The evolution of sexual size dimorphism in animals: hypotheses and tests. *Trends in Ecology and Evolution* 4:136–138.
- HOUSTON, D., AND R. SHINE. 1993. Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *Journal of Animal Ecology* 62:737–748.
- HUEY, R. B., AND E. R. PIANKA. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991–999.
- HUEY, R. B., E. R. PIANKA, AND L. J. VITT. 2001. How often do lizards “run on empty”? *Ecology* 82:1–7.
- INGER, R. F., AND B. GREENBURG. 1966. Annual reproductive patterns of lizards from a Bornean rain forest. *Ecology* 47:1007–1021.
- KRATOCHVÍL, L., AND D. FRYNTA. 2002. Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). *Biological Journal of the Linnean Society* 76: 303–314.
- LEPAGE, M., AND J. P. E. C. DARLINGTON. 2000. Population dynamics of termites. In T. Abe, D. E. Bignell, and M. Higashi (eds.), *Termites: Evolution, Sociality, Symbioses, Ecology*, pp. 333–361. Kluwer Academic Publishers, Dordrecht, Netherlands.
- MARQUET, P. A., F. BOZINOVIC, R. G. MEDEL, Y. L. WERNER, AND F. M. JAKSIĆ. 1990. Ecology of *Garthia gaudichaudi*, a gecko endemic to the semiarid region of Chile. *Journal of Herpetology* 24:431–434.
- MILES, D. B. 1994. Covariation between morphology and locomotory performance in Sceloporine lizards. In L. J. Vitt and E. R. Pianka (eds.), *Lizard Ecology: Historical and Experimental Perspectives*, pp. 207–235. Princeton Univ. Press, Princeton, NJ.
- OKADA, S., M. IZAWA, AND H. OTA. 2002. Growth and reproduction of *Gekko hokouensis* (Reptilia: Squamata) on Okinawajima Island of the Ryukyu Archipelago, Japan. *Journal of Herpetology* 36:473–479.
- OLSSON, M., R. SHINE, E. WAPSTRA, B. UJVARI, AND T. MADSEN. 2002. Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* 56:1538–1542.
- PERRY, G. 1995. *The Evolutionary Ecology of Lizard Foraging: A Comparative Study*. Unpubl. Ph.D. diss., Univ. of Texas, Austin.
- PIANKA, E. R. 1986. *Ecology and Natural History of Desert Lizards*. Princeton Univ. Press, Princeton, NJ.
- PIANKA, E. R., AND R. B. HUEY. 1978. Comparative ecology, resource utilization and niche segregation among gekkonid lizards in the southern Kalahari. *Copeia* 1978:691–701.
- PIANKA, E. R., AND H. D. PIANKA. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the western Australian desert. *Copeia* 1976:125–142.
- PIANKA, E. R., AND L. J. VITT. 2003. *Lizards: Windows to the Evolution of Diversity*. Univ. of California Press, Berkeley.
- REANEY, L. T., AND M. J. WHITING. 2002. Life on a limb: ecology of the tree agama (*Acanthocercus a. atricollis*) in southern Africa. *Journal of Zoology, London* 257:439–448.
- SAENZ, D., AND R. N. CONNER. 1996. Sexual dimorphism in head size of the Mediterranean gecko, *Hemidactylus turcicus* (Sauria: Gekkonidae). *Texas Journal of Science* 48:207–212.
- SCHOENER, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155:474–477.
- . 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2:369–404.
- SHINE, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* 64:419–461.
- . 1991. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* 138:103–122.

- . 1994. Sexual size dimorphism in snakes revisited. *Copeia* 1994:326–346.
- SIMPSON, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- SINERVO, B., AND P. LICHT. 1991. Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. *Science* 252:1300–1302.
- STAMPS, J. A. 1995. Using growth-based models to study behavioral factors affecting sexual size dimorphism. *Herpetological Monographs* 9:75–87.
- TOKARZ, R. R. 1995. Mate choice in lizards: a review. *Herpetological Monographs* 9:17–40.
- TRANEILLO, J. F. A., AND R. H. LEUTHOLD. 2000. Behavior and ecology of foraging in termites. In T. Abe, D. E. Bignell, and M. Higashi (eds.), *Termites: Evolution, Sociality, Symbioses, Ecology*, pp. 141–168. Kluwer Academic Publishers, Dordrecht, Netherlands.
- TRIVERS, R. L. 1976. Sexual selection and resource accruing abilities in *Anolis garmani*. *Evolution* 30:253–269.
- VITT, L. J. 1986. Reproductive tactics of sympatric gekkonid lizards with comment on the evolutionary ecological consequences of invariant clutch size. *Copeia* 1986:773–786.
- . 1991. Ecology and life history of the scansorial arboreal lizard *Plica plica* (Iguanidae) in Amazonian Brazil. *Canadian Journal of Zoology* 69:504–511.
- VITT, L. J., AND W. E. COOPER JR. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. *Canadian Journal of Zoology* 63:995–1002.
- VITT, L. J., AND P. A. ZANI. 1997. Ecology of the nocturnal lizard *Thecadactylus rapicauda* (Sauria: Gekkonidae) in the Amazon region. *Herpetologica* 53:165–179.
- VITT, L. J., P. A. ZANI, AND A. A. MONTEIRO DE BARROS. 1997. Ecological variation among populations of the gekkonid lizard *Gonatodes humeralis* in the Amazon basin. *Copeia* 1997:32–43.
- VITT, L. J., E. R. PIANKA, W. E. COOPER JR. AND K. SCHWENK. 2003. History and the global ecology of squamate reptiles. *American Naturalist* 162: 44–60.
- WERNER, Y. L. 1989. Egg size and egg shape in near-eastern gekkonid lizards. *Israel Journal of Zoology* 35:199–213.
- ZAMUDIO, K. R. 1998. The evolution of female-based sexual size dimorphism: a population-level comparative study in horned lizards (*Phrynosoma*). *Evolution* 52:1821–1833.

Accepted: 18 May 2005.