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# A comparison of the foraging biology of two tropical gecko species in disturbed areas

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**Abstract.** The traditional foraging mode dichotomy in lizards has been one of ambush predators vs. wide ranging predators. Each mode has been associated with its own suite of other complementary characteristics, including metabolic rates, sensory capacities, as well as predator and prey species. While foraging mode within lizard families is often consistent, few studies have compared the foraging modes of sympatric members of a clade in which one species is nocturnal and the other diurnal. *Hemidactylus frenatus*, an introduced, nocturnal house gecko, and *Gonatodes albogularis*, a native, diurnal species, inhabit disturbed habitats in Costa Rica. Using traditional movement-based indices, moves per minute (MPM) and percent time spent moving (PTM), we found *H. frenatus* to move significantly less (MPM = 0.47) and spend significantly less time moving (PTM = 0.74%) than *G. albogularis* (MPM = 0.97, PTM = 3.94%) during peak activity times. One reason for this difference in activity level could be the beneficial effects of artificial lighting in attracting arthropods to *H. frenatus* foraging areas.

**Keywords.** Diet; Ecology; Gekkota; Neotropics; Reptile; Sit and wait.

**Resumen.** La dicotomía del modo de alimentación tradicional en los lagartos ha sido uno de los depredadores de la emboscada contra los depredadores de amplio espectro. Cada modo se ha asociado con su propio conjunto de otras características complementarias, incluidas las tasas metabólicas, las capacidades sensoriales, así como las especies de depredadores y presas. Mientras que el modo de búsqueda de alimento dentro de las familias de lagartos a menudo es consistente, pocos estudios han comparado los modos de alimentación de los miembros simpátricos de un clado donde una especie es nocturna y la otra diurna. *Hemidactylus frenatus*, un gecko nocturno introducido, y *Gonatodes albogularis*, una especie diurna nativa, habitan hábitats perturbados en Costa Rica. Utilizando índices basados en movimientos tradicionales, movimientos por minuto (MPM) y porcentaje de tiempo de movimiento (PTM), encontramos que *H. frenatus* se mueve significativamente menos (MPM = 0.47) y pasa significativamente menos tiempo en movimiento (PTM = 0.74%) que *G. albogularis* (MPM = 0.97, PTM = 3.94%) durante los tiempos pico de actividad. Una razón para esta diferencia en el nivel de actividad podría ser los efectos beneficiosos de la iluminación artificial para atraer a los artrópodos a las áreas de alimentación de *H. frenatus*.

## INTRODUCTION

For more than 50 years, foraging behavior, particularly in lizards, has been a research topic of interest (Miles et al., 2007). Starting in the 1960s, a dichotomy of foraging modes was realized: wide foraging and “sit-and-wait,” or ambush, foraging (Pianka, 1966; Huey and Pianka, 1981). This foraging mode paradigm, while useful for explaining behavior, remains controversial because of the continuity in foraging variation, making it uncertain whether all lizards fall under two discrete categories (Huey and Pianka, 1981; McLaughlin, 1989; Perry, 1999; Cooper, 2005). Within his five study species, Pietruška (1986) found the variation in foraging to be a continuum. Using a larger dataset, McLaughlin (1989) found evidence of bimodality. Perry (1999), however, used a larger dataset still and found no support for bimodality. Without a better paradigm, however, this study treats foraging mode dichotomously.

Dichotomous foraging modes are often understood as driving the evolution of several aspects of lizard biology (Cooper, 2005; Miles et al., 2007). Energy budgets, metabolic rates, sensory capacities, as well as predator and

prey types are amongst the suite of characters that have coevolved (Huey and Pianka, 1981). Body form tends to be more robust in ambush predators, while active foragers are much more streamlined (Vitt and Congdon, 1978). Prey, to some extent, also appears to be a function of foraging mode (Huey and Pianka, 1981). Mobile prey are eaten significantly more by ambush foragers, whereas active foragers are more likely to find and consume prey that are largely sedentary and patchily distributed, termites being a prime example (Gerritsen and Strickler, 1977; Wilson and Clark, 1977; Krebs et al., 1978; Eckhardt, 1979; Huey and Pianka, 1981). In fact, this link between prey species and foraging mode can make resolving lingering questions on foraging mode difficult, as foraging mode in gekkotans is too often classified on the sole basis of diet, without any observations into how that diet was acquired (Bauer, 2007).

There are, however, several factors causing variation in foraging. For example, some models predict a change in foraging mode as a response to food availability levels, and short-term variation within species has been observed (Norberg, 1977; Tollestrup, 1979; Toft, 1980). Ad-

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ditionally, foraging behavior can vary by sex, with either sex being more active than the other in different species (Werner et al., 2006). Whether or not an individual's tail has been lost and regenerated also has an effect, whereby lizards that have lost their tails reduce the amount of time they spend foraging (Martín and Salvador, 1997). The two factors, however, are possibly linked, with Werner et al. (2006) reporting that tail loss increases foraging activity in females of *Goniurosaurus kuroiwae kuroiwae* (Namiye, 1912) while reducing the activity of male conspecifics. Similar foraging mode connections are found between sex and lunar phase (Werner et al., 2006). Other environmental factors, such as temperature and season, are known to affect foraging behavior (Werner et al., 2006).

Whilst variation is certainly present, generally speaking, foraging behavior remains relatively consistent among families of lizards (Cooper, 1994; Perry, 1999). Exceptions to this rule occur in the clades Gekkota Cuvier, 1817, Lacertidae Oppel, 1811, and Scincidae Gray, 1825 (Cooper, 1994; Werner et al., 1997; Perry, 1999). While there is some knowledge of gekkotan foraging (i.e., a large majority studied to date have been ambush foragers), relatively few (~100) of the 1,100+ species have been subject to foraging studies, and even fewer to quantitative foraging studies (Cooper Jr., 1995; Perry, 1999; Bauer, 2007).

The best way to determine which model best describes lizard foraging and which ecological factors are associated with foraging mode is more quantitative behavioral data. In an effort to provide more information for answering these questions, we focused on two tropical geckos: the yellow-headed gecko, *Gonatodes albogularis* (Duméril and Bibron, 1836), and the introduced Asian house gecko, *Hemidactylus frenatus* (Duméril and Bibron, 1836). Very little has been published on the biology of *G. albogularis* apart from the occasional natural history note (Bello et al., 2000; Filipiak and Lewis, 2012; Moreno-Arias, 2016; Barquero, 2017). *Hemidactylus frenatus*, in contrast, is fairly well studied, and its foraging behavior was examined previously (Perry, 1999; Díaz-Pérez et al., 2012; Barquero, 2017; Brown et al., 2017; Díaz-Pérez et al., 2017). These two geckos were chosen because they co-occur in disturbed areas, are arboreal or semi-arboreal, and are of similar sizes (*G. albogularis* maximum snout–vent length [SVL] 50 mm, *H. frenatus* maximum SVL 60 mm; Krysko and Daniels, 2005). The main ecological difference between the two is time of peak activity, with *G. albogularis* being diurnal and *H. frenatus* being nocturnal (Ellingson et al., 1995; Zozaya et al., 2015).

We focused on the difference in foraging brought about by different times of peak activity. For nocturnal geckos, inhabiting disturbed areas is likely to be of benefit due to the artificial lighting that often attracts insect prey (Zozaya et al., 2015). This seems to hold true for other species, albeit in very different taxa (Heiling, 1999; González-Bernal et al., 2016). Orb-web spiders in Vienna, Austria will preferentially seek out artificially lit sites for webs, resulting in greater numbers of insects caught than those spiders whose webs were not artificially lit (Heiling, 1999). A study of cane toads (*Rhinella marina* [Linnaeus,

1758]) in Australia, an introduced species, concluded that the population of toads was denser in disturbed habitats around buildings due to higher insect densities brought about by artificial lighting (Gonzalez-Bernal et al., 2016). These toads were also found to be more sedentary than conspecifics inhabiting less disturbed areas, and this was also attributed to higher densities of insects in disturbed habitats leading to more frequent encounters between toad and prey (Gonzalez-Bernal et al., 2016). These studies, taken together, lead us to believe that nocturnal geckos in disturbed environments tend to be less active foragers than their diurnal counterparts, possibly due to the increased insect density surrounding artificial lighting.

## MATERIALS AND METHODS

### Study area

This study took place at La Selva Biological Station in Puerto Viejo de Sarapiquí, Heredia, Costa Rica (84°00'W, 10°25'N) from June to August 2013. The station encompasses a broad range of habitats, from primary and secondary tropical rainforest to abandoned plantations and cultivated arboreta. This research took place in and amongst buildings and surrounding disturbed clearings.

### Foraging indices

There are three movement-based indices by which foraging mode is measured. Moves per minute (MPM) is the number of total moves over the total minutes of observation (Pianka et al., 1979), while percent time spent moving (PTM) is the duration of total movement over duration of total time observed (Pianka et al., 1979). Finally, percent of attacks initiated while moving is defined as number of attacks initiated while in motion over total attacks (Cooper and Whiting, 1999; Cooper Jr. et al., 2001). For all indices, movement is defined as traveling more than a body length and not simply shuffling in place.

In order to quantify foraging behavior, the movement-based indices MPM and PTM were calculated. The first author observed geckos from a distance of 5–10 m for up to 10 min (average observation time: 5 min 52 s), as longer observation times artificially alter data (Werner et al., 2006). Although no specific measures were used to avoid repeated sampling of the same individual, no geckos were observed within approximately 10 m of one another. *Gonatodes albogularis* individuals were also identified as male or female, as this species, unlike *Hemidactylus frenatus*, is sexually dimorphic in coloration (Ellingson et al., 1995). Animals were strictly observed with no capture or handling of the individuals. A video camera was used to record animal movements. Later analysis used a stopwatch to record time stationary, time spent moving, and consequently, total time observed. While analyzing the video, the author tallied the number of movements made.

**Table 1.** Summary of results. *n* = number of individuals of each species; Obs. = the number of seconds individuals were observed on average; Movement = the number of seconds an individual moved on average during the observation. Moves Per Minute (MPM) and Percent Time Moving (PTM) are foraging movement indices. All values are reported as mean  $\pm$  SD. The previously reported values for *Hemidactylus frenatus* are shown in brackets (Perry, 1999).

Species	Obs. (s)	Movement (s)	MPM	PTM
<i>Gonatodes albogularis</i> ( <i>n</i> = 11)	322.1 $\pm$ 148.5	10.5 $\pm$ 8.4	0.9700 $\pm$ 0.5303	3.9436 $\pm$ 3.5070
<i>Hemidactylus frenatus</i> ( <i>n</i> = 9)	387.9 $\pm$ 184.5	2.4 $\pm$ 1.7	0.4667 $\pm$ 0.4204 [0.75 $\pm$ 0.81]	0.7422 $\pm$ 0.5322 [2.66 $\pm$ 4.01]

### Statistical analysis

Data were analyzed in R (R Core Team, 2014). Although visual inspection suggested the PTM and MPM data might be non-normally distributed, a Shapiro-Wilk test did not reject the null hypothesis that the data were normally distributed. Therefore, an independent *t*-test (parametric, but robust to violations of normality) was used to test for significances of difference between the MPM and PTM of each species. The same methods were used to test for significances of difference between male and female *Gonatodes albogularis*.

### RESULTS

An independent *t*-test ( $P = 0.013$ ) revealed significantly different PTMs between the two species. *Hemidactylus frenatus* individuals spent an average of  $0.74 \pm 0.53\%$  of their active time moving, significantly less than their diurnal counterpart *Gonatodes albogularis* at  $3.94 \pm 3.51\%$  (Table 1). Likewise, an independent *t*-test ( $P = 0.027$ ) indicated a significant difference in MPM between the two species. *Hemidactylus frenatus* individuals made, on average, fewer MPMs ( $0.47 \pm 0.42$ ) than *G. albogularis* ( $0.97 \pm 0.53$ ; Table 1). There was no statistically significant difference in PTM ( $P = 0.836$ ) and MPM ( $P = 0.108$ ) between sexes in *G. albogularis*. Males ( $n = 6$ ) had a PTM of  $3.70 \pm 2.45\%$ , while females ( $n = 5$ ) had PTM of  $3.70 \pm 2.45\%$ . Males had an MPM of  $0.73 \pm 0.58$ , while females had an MPM of  $1.26 \pm 0.53$ .

### DISCUSSION

Our results indicate that the foraging activity of *Hemidactylus frenatus* and *Gonatodes albogularis* differs significantly. Our data suggest, however, that while the PTM and MPM values differ significantly between these species, *G. albogularis* still falls in line with those species considered to be sit-and-wait foragers (Bauer, 2007). In Bauer's (2007) review of gecko foraging, 98 species of gekkotans had had their foraging mode classified, with only 15–27 being considered widely foraging and the remaining 71 ambush foragers. With the foraging mode of ~1,100 gekkotans remaining unclassified, there is still great uncertainty as to whether gekkotans exist in a continuum of foraging or in two or three discrete modes. The only way to answer this question is to continue gathering more data on more species.

Finding *Gonatodes albogularis* to be a sit-and-wait forager suggests strong phylogenetic conservatism in foraging mode as all of the other quantitatively described *Gonatodes* species examined thus far have also been sit-and-wait foragers (Vitt and Zani, 1996; Persaud et al., 2003). *Gonatodes concinnatus* (O'Shaughnessy, 1881) and *G. hasemani* (Griffin, 1917) have also been qualitatively described as sit-and-wait foragers (Van Damme and Vanhooydonck, 2001; Bauer, 2007). Still, "other species" within *Gonatodes* have been qualitatively described as widely foraging, but the methodology for such classification is unclear (Arnold, 1993). Amongst quantitatively analyzed species, *G. albogularis* did, however, have higher PTM and MPM values than what has been found previously for *G. vittatus* (Liechtenstein and Martens, 1856) ( $n = 42$ , PTM = 3.55%, MPM = 0.36), *G. humeralis* (Guichenot, 1855) ( $n = 19$ , PTM = 2.32%, MPM = 0.23), and *G. ocellatus* (Gray, 1831) ( $n = 11$ , PTM = 1.6%, MPM = 0.18; Persaud et al., 2003). This might be explained by a combination of the sample sizes of both studies, variation in habitat disturbance levels, as well as real differences in the foraging activity of these species.

That *Hemidactylus frenatus* was a less active forager than *Gonatodes albogularis* is understandable, given their preference for foraging near the artificial lights of man-made structures (Case et al., 1994). It is exactly because of their ability to live in and around human settlements that this species has been so successful, often to the point of out-competing native, nocturnal gecko species that are unable to take advantage of this resource (Case et al., 1994; Hanley et al., 1998; Brown et al., 2002; Cole et al., 2005; Zozaya et al., 2015). The authors speculate that the energy savings from reduced foraging activity may be then put towards reproductive effort, leading to increased local and global dominance.

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### REFERENCES

- Arnold E.N. 1993. Historical changes in the ecology and behaviour of Semaphore geckos (*Pristurus*, Gekkonidae) and their relatives. *Journal of Zoology* 229:353–384. DOI
- Barquero M.D. 2017. *Hemidactylus frenatus* (Common House Gecko). Diet. *Herpetological Review* 48:645.
- Bauer A.M. 2007. The foraging biology of the Gekkotans: life in the middle. Pp. 371–404, in Reilly S.M., McBrayer L.D., Miles D.B. (Eds.), *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. Cambridge University Press, Cambridge. DOI



- Bello R.E. 2000. *Anoli* sp. and *Gonatodes albogularis* (Yellow-headed gecko). Predation. *Herpetological Review* 31:239–340.
- Brown S., Lebrun R., Yamasaki J., Ishii-Thoene D. 2002. Indirect competition between a resident unisexual and an invading bisexual gecko. *Behaviour* 139:1161–1173. [DOI](#)
- Brown T.W., Mayron D.F., Clayton S.M. 2017. *Hemidactylus frenatus* (Asian House Gecko). Diet. *Herpetological Review* 48:645–646.
- Case T.J., Bolger D.T., Petren K. 1994. Invasions and competitive displacement among house geckos in the tropical Pacific. *Ecology* 75:464–477. [DOI](#)
- Cole N.C., Jones C.G., Harris S. 2005. The need for enemy-free space: the impact of an invasive gecko on island endemics. *Biological Conservation* 125:467–474. [DOI](#)
- Cooper W.E. 1994. Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. *Journal of Chemical Ecology* 20:439–487. [DOI](#)
- Cooper W.E. Jr. 1995. Prey chemical discrimination and foraging mode in gekkonoid lizards. *Herpetological Monographs* 9:120–129. [DOI](#)
- Cooper W.E. 2005. Duration of movement as a lizard foraging movement variable. *Herpetologica* 61:363–372. [DOI](#)
- Cooper W.E., Whiting M.J. 1999. Foraging modes in lacertid lizards from southern Africa. *Amphibia-Reptilia* 20:299–311. [DOI](#)
- Cooper W.E. Jr., Vitt L.J., Caldwell J.P., Fox S.F. 2001. Foraging modes of some American lizards: relationships among measurement variables and discreteness of modes. *Herpetologica* 57:65–76.
- Cuvier G. 1817. Le Règne Animal Distribué d'après son Organisation, pour servir de Base à l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie Comparée. Tome 2. Les Reptiles, les Poissons, les Mollusques et les Annélides. Déterville, Paris. [DOI](#)
- Díaz-Pérez J.A., Dávila-Suárez J.A., Alvarez-García D.M., Sampedro-Marín A.C. 2012. Dieta de *Hemidactylus frenatus* (Sauria: Gekkonidae) en un área urbana de la región Caribe Colombiana. *Acta Zoológica Mexicana* 28:613–616. [DOI](#)
- Díaz-Pérez J.A., Sampedro-Marín A.C., Ramírez-Pinilla M.P. 2017. Actividad reproductiva y dieta de *Hemidactylus frenatus* (Sauria: Gekkonidae) en el norte de Colombia. *Papéis Avulsos de Zoologia* 57:459–472. [DOI](#)
- Duméril A.M.C., Bibron G. 1836. *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*. Tome troisième. Librairie Encyclopédique de Roret, Paris. [DOI](#)
- Eckhardt R.C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. *Ecological Monographs* 49:129–149. [DOI](#)
- Ellingson J.M., Fleishman L.J., Loew E.R. 1995. Visual pigments and spectral sensitivity of the diurnal gecko *Gonatodes albogularis*. *Journal of Comparative Physiology A* 177:559–567. [DOI](#)
- Filipiak D., Lewis T. 2012. *Gonatodes albogularis* (Yellow-headed dwarf gecko) predation. *Herpetological Review* 43:485–486.
- Gerritsen J., Strickler J.R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *Journal of the Fisheries Research Board of Canada* 34:73–82. [DOI](#)
- González-Bernal E., Greenlees M.J., Brown G.P., Shine R. 2016. Toads in the backyard: why do invasive cane toads (*Rhinella marina*) prefer buildings to bushland? *Population Ecology* 58:293–308. [DOI](#)
- Gray J.E. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. *Annals of Philosophy Series* 2 10:193–217.
- Gray J.E. 1831. A synopsis of the species of the class Reptilia. Pp. 1–110, in Griffith E. et al. (Eds.). *The Animal Kingdom Arranged in Conformity With Its Organization by the Baron Cuvier With Additional Descriptions of All the Species Hitherto Named, and of Many Not Before Noticed*. Volume 9. Whittaker, Treacher and Co., London. [DOI](#)
- Griffin L.E. 1917. A list of the South American lizards of the Carnegie Museum, with descriptions of four new species. *Annals of the Carnegie Museum* 11:304–320.
- Guichenot A. 1855. Animaux nouveaux ou rares recueillis pendant l'Expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Para. Reptiles. P. Bertrand, Paris. [DOI](#)
- Hanley K.A., Petren K., Case T.J. 1998. An experimental investigation of the competitive displacement of a native gecko by an invading gecko: no role for parasites. *Oecologia* 115:196–205.
- Heiling A.M. 1999. Why do nocturnal orb-web spiders (Araneidae) search for light? *Behavioral Ecology and Sociobiology* 46:43–49. [DOI](#)
- Huey R.B., Pianka E.R. 1981. Ecological consequences of foraging mode. *Ecology* 62:991–999. [DOI](#)
- Krebs J.R., Kacelnik A., Taylor P. 1978. Test of optimal sampling by foraging great tits. *Nature* 275:27–31. [DOI](#)
- Krysko K.L., Daniels K.J. 2005. A key to the geckos (Sauria: Gekkonidae) of Florida. *Caribbean Journal of Science* 41:28–36.
- Lichtenstein H., Martens E.v. 1856. *Nomenclator Reptilium et Amphibiorum Musei Zoologici Berolinensis*. Namenverzeichnis der in der zoologischen Sammlung der Königlichen Universität zu Berlin aufgestellten Arten von Reptilien und Amphibien nach ihren Ordnungen, Familien und Gattungen. Berlin. [DOI](#)
- Linnaeus C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differential, synonymis, locis*, Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiae. [DOI](#)
- Martín J., Salvador A. 1997. Effects of tail loss on the time-budgets, movements, and spacing patterns of Iberian rock lizards, *Lacerta monticola*. *Herpetologica* 53:117–125.
- McLaughlin R.L. 1989. Search modes of birds and lizards: evidence for alternative movement patterns. *The American Naturalist* 133:654–670. [DOI](#)
- Miles D.B., Losos J.B., Irschick D.J. 2007. Morphology, performance, and foraging mode. Pp. 49–93, in Reilly S.M., McBrayer L.D., Miles D.B. (Eds.). *Lizard Ecology: The Evolutionary Consequences of Foraging Mode*. Cambridge University Press, Cambridge. [DOI](#)
- Moreno-Arias R.A. 2016. *Gonatodes albogularis* (Yellow-headed dwarf gecko). Predation. *Herpetological Review* 47:669–670.
- Namiye M. 1912. The geckos from the Okinawa Islands. *Dobutugaku Zasshi (Zoological Magazine)* 24:442–445.
- Norberg R.A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. *Journal of Animal Ecology* 46:511–529. [DOI](#)
- O'Shaughnessy A.W.E. 1881. An account of the collection of lizards made by Mr. Buckley in Ecuador, and now in the British Museum, with descriptions of the new species. *Proceedings of the Zoological Society of London* 1881:227–245.
- Oppel M. 1811. Die ordnungen, familien und gattungen der reptilien als prodrom einer naturgeschichte derselben. J. Lindauer, München. [DOI](#)
- Perry G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *The American Naturalist* 153:98–109. [DOI](#)
- Persaud D., Werner N., Werner Y.L. 2003. Foraging behaviour of three Sphaerodactylus geckos on Trinidad and Tobago (Sauria: Gekkonomorpha: Sphaerodactylini: *Gonatodes*). *Journal of Natural History* 37:1765–1777. [DOI](#)
- Pianka E.R. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47:1055–1059. [DOI](#)
- Pianka E.R., Huey R.B., Lawlor L.R. 1979. Niche segregation in desert lizards. Pp. 67–115, in Horn D.J., Stairs G.R., Mitchell R.D. (Eds.), *Analysis of Ecological Systems*. Ohio State University Press, Columbus.
- Pietruszka R.D. 1986. Search tactics of desert lizards: how polarized are they? *Animal Behaviour* 34:1742–1758. [DOI](#)
- Toft C.A. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* 45:131–141. [DOI](#)
- Tollestrup K. 1979. *The Ecology, Social Structure, and Foraging Behavior of Two Closely Related Species of Leopard Lizards, Gambelia silus and Gambelia wislizenii*. University of California Press, Berkeley.
- Van Damme R., Vanhooydonck B. 2001. Origins of interspecific variation in lizard sprint capacity. *Functional Ecology* 15:186–202. [DOI](#)
- Vitt L.J., Congdon J.D. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *The American Naturalist* 112:595–608. [DOI](#)
- Vitt L.J., Zani P.A. 1996. Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. *Canadian Journal of Zoology* 74:1313–1335. [DOI](#)
- Werner Y.L., Okada S., Ota H., Perry G., Tokunaga S. 1997. Varied and fluctuating foraging modes in nocturnal lizards of the family Gekkonidae. *Asiatic Herpetological Research* 7:153–165.
- Werner Y.L., Takahashi H., Yasukawa Y., Ota H. 2006. Factors affecting foraging behaviour, as seen in a nocturnal ground lizard, *Goniurosaurus kuroiwae*. *Journal of Natural History* 40:439–459. [DOI](#)
- Wilson D.S., Clark A.B. 1977. Above ground predator defense in the harvester termite, *Hodotermes mossambicus* (Hagen). *Journal of the Entomological Society of Southern Africa* 40:271–282.
- Zozaya S.M., Alford R.A., Schwarzkopf L. 2015. Invasive house geckos are more willing to use artificial lights than are native Geckos. *Austral Ecology* 40:982–987. [DOI](#)