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Disentangling Morphological and Environmental Drivers of Foraging Activity in an Invasive Diurnal Gecko, *Phelsuma laticauda*

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ABSTRACT.—In recent years, substantial variation in foraging behavior has been documented in lizards, including within and between closely related species. However, the exceptionally variable Gekkota still suffers from low sampling effort and historical averaging of foraging mode values across taxonomic levels. Herein, we address the gap in foraging modes of geckos by parsing out environmental and morphological sources of variation in foraging mode within the diurnal arboreal gecko, *Phelsuma laticauda*. Foraging behavior was examined at two sites on the island of Mo'orea, French Polynesia. In fall 2018, we made observations for a maximum duration of 30 min on 31 individual geckos. We found that *P. laticauda* exhibits a sit-and-wait strategy and that its foraging behavior is influenced by several ecological and morphological correlates: sex, body size, temperature, and date of observation. Notably, we found a trend for more active foraging by females than by males, challenging the notion that only nocturnal geckos exhibit sexual foraging diergism. The amount of time spent pausing and the maximum single movement exhibited a negative relationship with the body size of an individual. At higher temperatures, the amount of head movements, likely pertaining to locating prey, increased. Several foraging metrics varied with date of observation. Our results emphasize the need to consider multiple ecological correlates when studying foraging behavior as well as the importance of measuring multiple behavioral metrics beyond the standard percent time moving and moves per minute.

The acquisition of energy through locating food, or foraging, is central for all organisms' vital activities: growth, development, mate attraction, predator avoidance, and reproduction (Rosenberg and Cooper, 1990). Studying life-history traits, such as foraging, can illuminate much about the ecological and evolutionary role an organism plays in its environment (Schoener, 1971; Rosenberg and Cooper, 1990). All predators use foraging strategies to pursue and capture prey (Lewis and Price, 1975; Huey and Pianka, 1981). Foraging strategies vary among species and environments and are shaped through natural selection (MacArthur and Pianka, 1966; Pianka, 1966; Reilly et al., 2007). As a result, an organism's foraging strategy can indicate its evolutionary lineage and possible evolutionary constraints on behavior (Reilly et al., 2007).

Foraging modes (FMs; distinct foraging strategies) are conceptualized as a spectrum, from active foraging (AF) to sit-and-wait (SW) foraging. Predators with SW strategies use ambush tactics, an energetically favorable strategy that involves attacking prey from a stationary position (Pianka, 1966). AF predators search for small and grouped prey items while on the move, a more energetically demanding strategy (Pianka, 1966). The concept of a FM spectrum is useful in a practical sense to quantitatively assess behaviors and is helpful when comparing one species to another or individuals within a species or population. In addition, it can illuminate broad evolutionary patterns and ecological roles within a study system (Reilly et al., 2007). However, strict adherence to a foraging dichotomy, rather than a continuous spectrum, has historically led to the issue of averaging FM values across entire genera and even families based on phylogenetic relationships (Reilly et al., 2007). Although entire lizard families can be constrained to a specific FM, there are many exceptions (Reilly et al., 2007). Averaging FM values may mask important variation present among or within species (Bolnick et al., 2003). Indeed, many unique exceptions to the dichotomy have been found, including mixed FMs (Balent and Andreadis, 1998; Werner et al., 2006; Tunney and Steingrímsson, 2012), cruise foraging (Butler, 2005), sit-and-pursue foraging (Schmitz and Suttle, 2001; Barkae et al., 2010), and saltatory foraging (although saltatory foraging has been used to describe two different variations [Eifler and Eifler, 1999; Cooper et al., 2005]). All mixed strategies can be described as "intermediate modes" along a continuum between the extremes.

Detailed studies integrating life-history strategies, adaptive morphology, physiology, and evolution have made lizards the model organism for understanding FM and optimal foraging theory (Huey and Pianka, 1981; Reilly et al., 2007). Morphology and physiology of an individual lizard, phylogenetic constraints of the species, phenology, and environmental factors (both large and small scale) can all influence its FM. Yet many FM studies only consider one or two potential sources of variation (Werner et al., 2006). The studies of Werner et al. (2004, 2006) on *Goniurosaurus* geckos were some of the first to consider multiple variables that could influence FM, finding that sex, tail loss, temperature, seasonality, and lunar phase all contribute to variation. Because FM is so biologically important, it is essential to understand how it may vary with multiple ecological contexts, even if at first glance a system appears to fit into the classic dichotomy. Detailed information on foraging could be particularly useful for studying how invasive species forage in novel environments and how they impact invaded ecosystems (Fritts and Rodda, 1998; Phillips et al., 2003; Watari et al., 2008).

Gecko FM is relatively understudied, resulting in particular oversimplification and low taxonomic resolution for this group (Regal, 1978; Werner et al., 1997a; Perry, 1999; Reilly et al., 2007). In fact, for some time all of Gekkota was considered SW foragers (Regal, 1978). However, more recent studies show that gecko foraging is quite variable (Werner et al., 1997b; Bauer, 2007). Many gecko species exhibit AF modes as well as mixed intermediate modes (Werner et al., 2006). Werner et al. (2004, 2006) showed that most species tend to rely on one FM more than the other FM, but often can use both. Interestingly, this mixed FM is thought to be exclusive to nocturnal geckos. Diurnal geckos that have been studied to date exhibit only SW tactics. Furthermore, sex-based differences in foraging (sexual diergism) have not yet been documented in diurnal geckos. This

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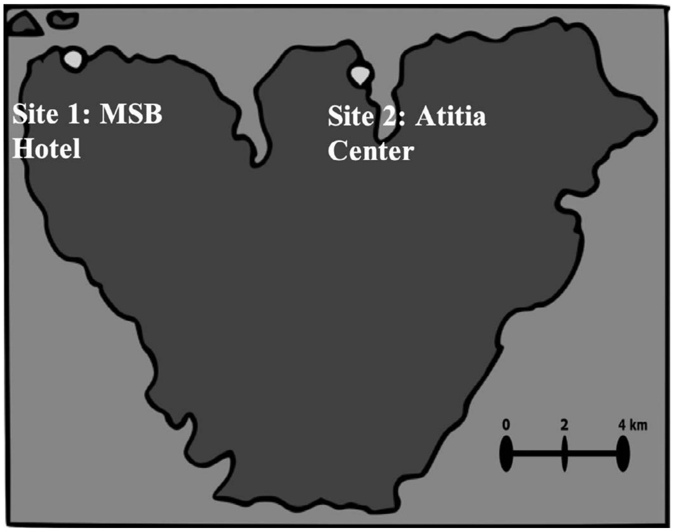


FIG. 1. Map of the Island of Mo'orea, with the two study sites depicted by circles on the map.

correlation of a specific foraging strategy with diel activity in geckos is a distinction not seen in other lizard clades (Werner et al., 2006), yet diurnal gecko foraging data are particularly lacking, so the prevalence of this pattern is unknown (but see Werner et al., 1997b, 2006; Persaud et al., 2003; Seifan et al., 2010).

Herein, we address the gap in our knowledge of FMs within the Gekkota by studying a diurnal arboreal gecko, *Phelsuma laticauda*. *Phelsuma laticauda* is a widely established invasive species introduced to the Comoros, the Mascarenes, the Seychelles, French Polynesia, the Hawaiian Islands, Florida, Pennsylvania, Texas, and California (McKeown, 1996; Ota and Ineich, 2006; Cole, 2007; Rocha et al., 2007, 2009; Kraus, 2009; Krysko et al., 2011; iNaturalist 2021). Although little is known about the biology of *P. laticauda*, researchers have found that it is much more abundant in human-disturbed edge habitats in their native range (Humphrey and Ward, 2018). It is estimated to have arrived on the island of Mo'orea within the past 15 yr (Ota and Ineich, 2006). We quantified and parsed sources of variation in FM within this species, specifically addressing what 1) FM *P. laticauda* exhibits on Mo'orea and 2) environmental and morphological factors contribute to variation in foraging behavior.

MATERIALS AND METHODS

Study Organism.—*Phelsuma laticauda* is a medium-sized gecko (58 mm snout–vent length [SVL]; Henkel and Schmidt, 2000). One of 46 day gecko species from the *Phelsuma* genus, *P. laticauda* is native to the island of Madagascar (Rocha et al., 2010).

Study Site.—Our study was conducted at two localities on the island of Mo'orea, French Polynesia, 14.5 km apart from one another: 1) the Mo'orea Sunset Beach Hotel and 2) the Atitia Cultural Center (Fig. 1). The hotel site is characterized by artificial substrates and modifications: wooden buildings and fences, planter beds, large mechanical equipment, and garbage bins. The Atitia Cultural Center, adjacent to University of California (UC) Berkeley Richard B. Gump South Pacific Research Station, has fewer large building structures (only small bamboo auxiliary buildings scattered around the property) and includes a greater variety of natural foliage—coconut trees, banana plants, and other leafy plants—used by geckos.

Data Collection.—Initial capture, marking of individuals, and acquisition of morphological measurements of geckos was conducted from 8 October to 23 October 2018 between 1000 and 1600 h, at the end of the dry season in French Polynesia. We marked males with a unique ID on the dorsum between the front limbs and females on the dorsum between the hind legs. Seventy-six geckos were initially caught and uniquely marked.

The foraging behavior of *P. laticauda* was recorded whenever individuals were encountered in the field. All observations of foraging were made by the same observer (JWW), with data recorded by a field assistant. Observations were made between 23 October and 9 November 2018 between 1000 and 1700 h. When a marked gecko was encountered, that individual was tracked for a maximum of 30 min (or until out of view) at a distance of 2–6 m (Ikeuchi et al., 2005). Presence of conspecifics was noted to properly contextualize behavior. When unmarked individuals were encountered, they were observed by following the procedures described above. At the end of the observation period, they were captured and all the initial morphological measurements were obtained. There were several unmarked geckos that we observed but that eluded capture at the end of the observation period. Unmarked individuals ($n = 6$) were excluded from analyses of morphology, but we included them for analyses of environmental factors.

In general, the metrics of percent time moving (PTM) and moves per minute (MPM) serve as proxies for quantifying foraging behavior in lizards (Pianka, 1966; Huey and Pianka, 1981; Pietruszka, 1986; Cooper, 1995). But some studies also consider average duration of movements (SM.Avg) and average duration of pauses (SP.Avg) as well (Werner et al., 2004, 2006; Cooper, 2005; Halperin et al., 2018). Indeed, Halperin et al. (2018) proposed that the average move–average stop plane is a more useful index than the MPM-PTM plane, especially when exploring ecological and evolutionary correlates of foraging behavior. The MPM metric suffers from inherent inaccuracy, is constrained by minimal move and stop durations (which can lead to similarly low values for SW foragers and AFs), and is interdependent with PTM. Therefore, we decided to measure both MPM-PTM metrics and average move–average stop metrics. Behavioral data included the FM descriptors PTM, MPM, SM.Avg, SP.Avg, and the maximum single movement (SM.Max). "Movement" was determined as an instance where the entire body of an individual was translocated to a new position, including: walking, running, crawling, and jerking forward/backward (Fig. 2). In addition, attacks on prey (AOP), body repositions per minute (RPM), head raises per minute (HRPM), tail waves (TW), and jumps per minute (JPM) were all recorded (Fig. 2).

Environmental data included substrate type (natural or artificial), substrate temperature under the individual, initial body orientation (facing upward, downward, or horizontal), initial elevation (in meters), time of day, observation date, observation duration (in seconds), and study site. Temperatures of the substrate ranged between 25.1 and 34.0°C. Morphological data included sex, SVL (in millimeters), body condition index (BCI), and percent original tail (TLO). The BCI was estimated using the standard method of residuals from an ordinary least-squares regression of SVL on body mass (in grams) and was calculated as follows: [log(body mass)]/[log(body length)] (Green, 2001; Labocha et al., 2014). Our TLO measurement is

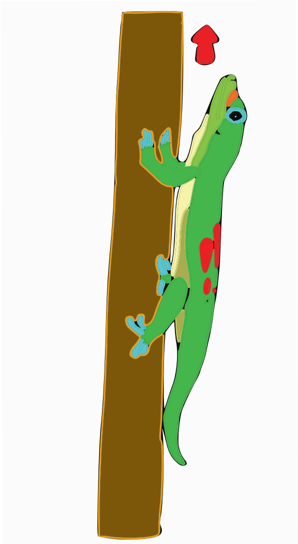
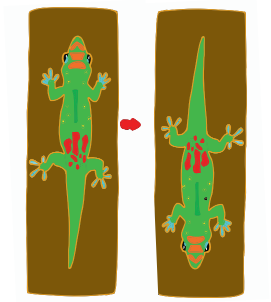
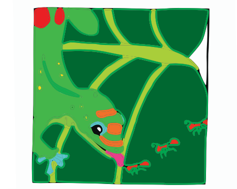
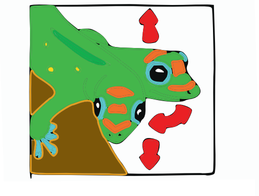
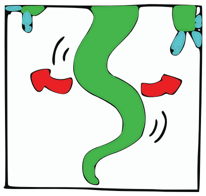
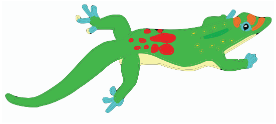
PTM	Percent Time Moving	Percentage of the observation period spent moving (walking, running, crawling etc.)	
MPM	Moves Per Minute	Number of distinct movements made per minute during an observation period	
SM.Avg	Average Duration of Single Movement	Average duration of distinct movements made during observation period—measured in seconds	
SP.Avg	Average Duration of Single Pause	Average duration of distinct pauses between movements made during observation period—measured in seconds	
SM.Max	Max Duration of Single Movement	Single movement in an observation period that was the longest in duration—measured in seconds	
RPM	Repositions Per Minute	Any time a gecko changed its body orientation (i.e. vertical to horizontal) or moved without actually translocating its position	
AOP	Attacks On Prey	Number of times gecko attacked prey items (both successful and unsuccessful attempts)	
HRPM	Head Raises Per Minute	Number of head movements, turns, and raises made per minute during observation period	
TW	Tail Waves	Number of times a gecko waved or wagged tail	
JPM	Jumps Per Minute	Number of jumps made per minute during observation period	

FIG. 2. Description of behavioral metrics and abbreviations.

TABLE 1. Summary statistics for behavioral metrics.

Response variable	Mean	SD	Range (minimum–maximum)
PTM (%)	6.53	5.21	0.00–17.12
MPM	1.03	0.63	0.00–2.43
SM.Avg (s)	3.50	1.36	0.00–5.93
SP.Avg (s)	126.05	226.77	20.15–900.00
SM.Max (s)	11.81	8.09	0.00–33.00
AOP	0.32	0.48	0.00–1.00
RPM	0.23	0.22	0.00–0.96
HRPM	0.59	0.44	0.00–1.73
TW	0.22	0.43	0.00–1.00
JPM	0.08	0.10	0.00–0.43

the percentage of tail length that is not regrowth (similar to tail length of original part in Werner et al. [2006]).

Statistical Analyses.—We explored the influence of environmental (substrate type, substrate temperature, initial body orientation, initial elevation, time, date, observation duration, and study site) and morphological (sex, SVL, BCI, and TLO) characteristics on gecko foraging behavior with generalized additive models (GAMs). We trimmed our dataset to ensure that we only used one observation per individual—only the first observation was used for marked individuals, and unmarked individuals were only included if we could guarantee their independence. Outliers in behavioral response variables were identified using boxplots and the quartile method and removed if deemed high outliers (Zuur et al., 2007; Benhadi-Marín, 2018). In total 31 individuals were analyzed (11 females, 13 males, 1 unknown sex, and 6 unmarked individuals [all of which were adults]). We used principal-component analysis and pairwise plots to identify confounding explanatory variables to simplify model selection. Not all of the environmental and morphological variables measured were ultimately used in the analysis, and the full list of what was measured can be found in the Supplementary Data (Appendix 1). Data exploration also revealed that many relationships were not necessarily linear and best modeled with a flexible approach such as GAMs (Zuur et al., 2007).

We analyzed each behavioral variable separately by testing the effect of individually adding explanatory variables to a base GAM by using R 4.0.3 (R Core Team, 2020) and the mgcv package version 1.8 (Wood, 2017). Behavioral variables varied in their distributions, with Gaussian (SM.Avg), Poisson (SM.Max, RPM), gamma (SP.Avg, MPM, HRPM, JPM), and binomial (PTM, TW, AOP) distributions used (Zuur et al., 2009). An offset term was used for repositions to control for length of observation (RPM; Zuur et al., 2009). Initial data exploration revealed that gecko behavior often varied with observation date and time of day, so these variables were included in a base model. Additional explanatory variables were then added one at a time to test for an effect by using the anova.gam function in mgcv. All significant terms were then included in an additional model, and an effect was again assessed and insignificant terms dropped until only significant terms remained. A smoothing function of $k = 3$ was initially used for every term in all models to conserve degrees of freedom. We increased k if the k index fell below 1, assessed with the gam.check function and following best practices for GAMs (Wood, 2017). Significant explanatory variables were plotted against response variables to assess the directionality, if any, of the significance (Wood, 2017). Significance of smoothing terms was assessed visually by ensuring a horizontal line could not pass through the confidence interval (SE) in scatterplots (Zuur et al., 2007).

RESULTS

There was substantial interindividual variation: during some periods, an individual did not move once, and in others an individual would locomote the entire period. Average (±SD) PTM was 6.53 ± 5.23% and MPM was 1.03 ± 0.63 (Table 1), falling within the range of SW predators and concurring with findings of other studies (Reilly et al., 2007; Seifan et al., 2010).

We also found that analyzing multiple components of FM produced relatively distinct results (Table 2). Most measures of foraging behavior, including PTM and MPM, did not vary with any of the morphological or environmental variables measured (Table 2). However, a few factors do appear to contribute to variation in foraging behaviors. The SM.Avg was shorter for males than females (2.82 ± 1.39 vs. 4.08 ± 1.16; $F_{1,29} = 6.982$, $P = 0.006$; Fig. 3), with an intermediate value for individuals of unknown sex (3.83 ± 1.16). SM.Max varied with date ($\chi^2_{10,3.3} = 54.38$, $P < 0.001$) and decreased with SVL ($\chi^2_{1.9,3.3} = 24.73$, $P < 0.001$; Fig. 4). As substrate temperature increased, the frequency of HRPM increased ($F_{1,27} = 9.03$, $P = 0.006$; Fig. 5). Finally, the

TABLE 2. Results of GAMs with explanatory variables that were included in final models. Environmental explanatory variables: date, time of day (time), and substrate temperature (ST); morphological explanatory variables: sex, SVL, and BCI. Bold font indicates that the relationships passed visual inspection (e.g., the relationship between the smoothing term and the response variable was significant and directional). Variables that had no significant correlations in the models are not shown (i.e., MPM, number of AOP, number of TW, JPM, substrate type, study site, observation duration, initial orientation, initial elevation, and TLO). Sample sizes for the final models are included in the row headers. Morphological data were not collected for six individuals, so models that include morphological data had reduced sample sizes. Outliers were also identified and removed independently for each behavioral metric. Repositions (RPM) were not recorded in the beginning of the study, resulting in a further reduced sample size for this metric.

	Date	Time	ST	SEX	SVL	BCI
PTM ($n = 30$)		$\chi^2_{1,28} = 4.09$, $P = 0.043$				
SM.Avg ($n = 31$)				**$F_{1,29} = 6.98$, $P = 0.006$**		
SP.Avg ($n = 21$)	**$F_{10,2.7} = 44.3$, $P = 0.007$**				$F_{7.3,2.7} = 25.35$, $P = 0.013$	
SM.Max ($n = 18$)	$\chi^2_{10,3.3} = 54.38$, $P < 0.001$	$\chi^2_{1.8,3.3} = 22.98$, $P < 0.001$			$\chi^2_{1.9,3.3} = 24.73$, $P < 0.001$	
RPM ($n = 18$)	$\chi^2_{10,10} = 30.47$, $P = 0.001$					$\chi^2_{1,10} = 10.8$, $P = 0.001$
HRPM ($n = 28$)			**$F_{1,27} = 9.03$, $P = 0.006$**			

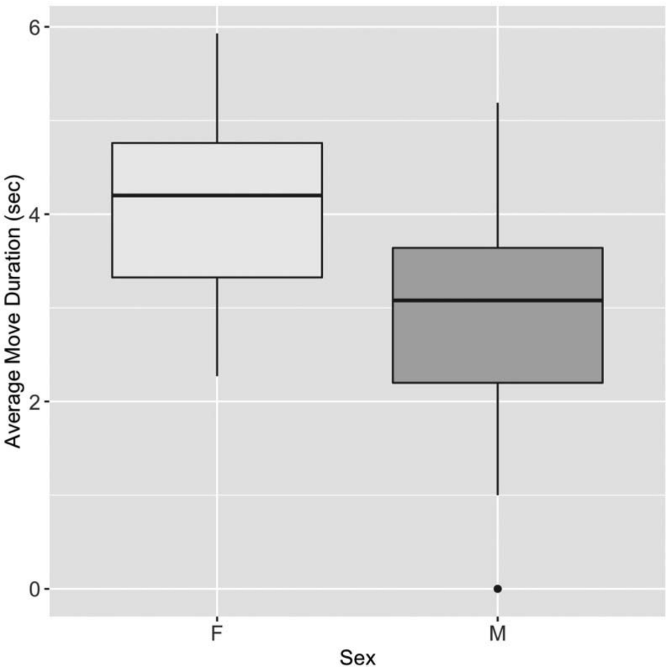


FIG. 3. Relationship between sex and SM.Avg. Whiskers extend no further than ±1.5× interquartile range, with data beyond that plotted individually.

SP.Avg varied depending on the date of observation ($F_{10,2.7} = 44.3$, $P = 0.007$).

DISCUSSION

We found that *P. laticauda* is a SW predator on the island of Mo'orea (Fig. 6A). Our classification concurs with that of Seifan et al. (2010), who observed *P. laticauda*'s FM on Kona, Hawaii. However, *P. laticauda* exhibits more interindividual variation on Mo'orea than it does on Hawaii (Seifan et al., 2010). Although the FM of geckos in general can be quite varied, all studies on diurnal geckos so far have defined them as SW predators (Persaud et al., 2003; Bauer, 2007; Seifan et al., 2010). Diurnal geckos have not been documented to be able to use more than one FM, suggesting that a more flexible mixed FM could be correlated to nocturnality itself because of the challenges of hunting in the dark (Werner et al., 1997b, 2004, 2006; Persaud et al., 2003). Another explanation for shifts in nocturnal activity is a release from predation or competition (or both), facilitating an expansion of AF at night (Schoener, 1974; Hoare et al., 2007; Pike et al., 2010; Gamble et al., 2015).

The majority of geckos studied worldwide either have a PTM $< 5\%$ or PTM $> 10\%$ (Werner et al., 1997b, 2004; Cooper et al., 1999; Werner and Chou, 2002; Persaud et al., 2003). Only one species is currently known to exceed a PTM of 30% (*Coleonyx variegatus*: 33.2%; Kingsbury, 1989), the original cutoff determined for AF predators by Huey and Pianka (1981), yet several geckos have been labeled as AF predators (Werner et al., 2004, 2006). Because there is so much variation in lizard FM, Werner et al. (2006) proposed that it is not reasonable from a biological standpoint to use a single PTM spectrum for all lizards to define them as SW, AF, or intermediate. Rather, the foraging spectrum should be viewed as fluctuating, with a different spectrum and representative values depending on the group/species being studied (Werner et al., 2006). By these taxonomically narrowed standards, *P. laticauda* is more active than most SW geckos, perhaps leaning toward a more intermediate mode (Fig. 6B), along with *Teratoscincus scincus* (Seligmann et al., 2007).

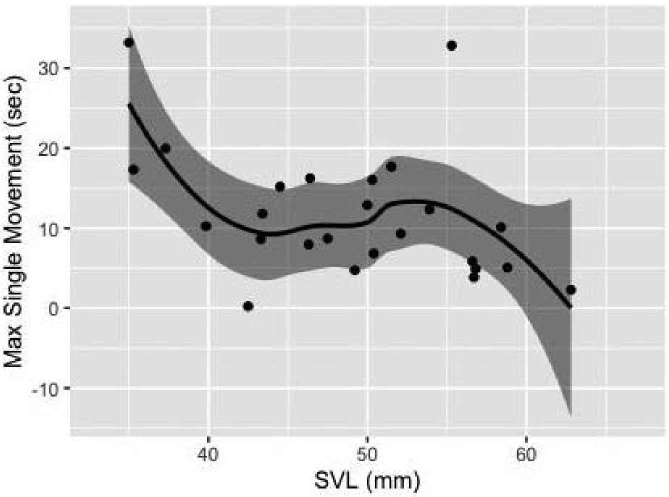


FIG. 4. Relationship between body size (SVL) and SM.Max. Shading represents the standard error.

We found that *P. laticauda* foraging behavior (both PTM and MPM) was relatively resistant to perturbations in morphology and the environment, with the caveat that we likely lacked the power to detect more subtle relationships. Despite this apparent resistance to change in PTM and MPM and low power, we have found several factors that are responsible for influencing variation in other FM metrics. Most of these factors correlate with average move and average pause duration rather than with PTM or MPM, supporting the proposition of Halperin et al. (2018) that average moves/pauses are a better index when studying ecological and evolutionary correlates of foraging behavior.

Sex Differences.—We found that females have a longer SM.Avg than males (Fig. 3). The findings of several other studies are in accordance with our findings. For example, Werner et al. (2006) found females of the nocturnal gecko species *Goniurosaurus kuroiwae* were more active than males. There have also been similar findings in many anole species, which are territorial, diurnal, SW predators with male-biased sexual size dimorphism similar to *P. laticauda*: the relatively large males reportedly moved around considerably less than the smaller females (Andrews and Asato, 1977; Parmelee and Guyer, 1995; Perry, 1996). Thus, it has been proposed that females need to eat more because they likely require a higher energy intake because of the costs of reproduction (Andrews and Asato, 1977; Parmelee and Guyer, 1995; Perry, 1996). Female *P. laticauda* may be increasing their energy reserves before reproduction, which, if similar to Hawaiian populations, would occur directly after our study period (Goldberg and Kraus, 2011). This finding is notable because sexual diergism has not been documented before in diurnal geckos. Although there was only a statistically significant difference seen in one metric—SM.Avg—on average, PTM, MPM, SM.Max, AOP, and JPM were all greater in females, whereas average pause duration was shorter in females, indicating that females are likely more active than males (see Supplementary Data, Appendix 2).

Body Size.—Smaller (via SVL) individuals tend to have a longer SM.Max (Fig. 4). For territorial SW lizards, body size or SVL directly correlates to age class, and smaller individuals are also younger. When intraspecific interactions occurred between *P.*

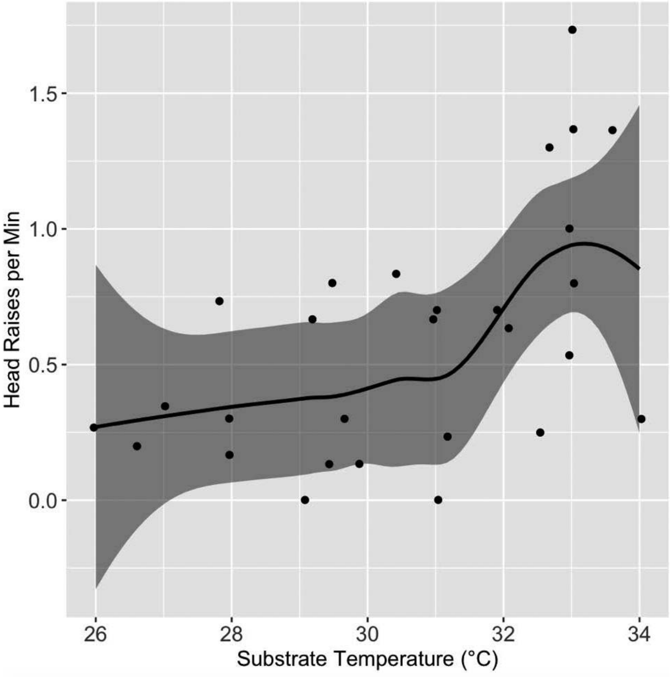


FIG. 5. Relationship between substrate temperature and HRPM.

laticauda individuals of different sizes, we noted that the larger of the two geckos would often chase away the smaller gecko. Movements made during these intraspecific encounters were discarded from foraging data, but potentially provide support that these younger adults are more vulnerable to intraspecific interactions than larger, aggressive conspecifics (e.g., *Phelsuma* are also known to be very territorial and cannibalize younger adults; Cole and Harris, 2011). If they are in fact more vulnerable, smaller individuals may forage more actively when they are near larger individuals to reduce the chances of a confrontation (Stamps, 1983; Nilsson, 2006). Therefore, this longer burst of a single movement could be reflective of a smaller gecko moving away from an older, aggressive individual's territory. There was also a negative correlation between SVL and SP.Avg. The SW *Sceloporus* lizards are also known to differ in activity based on age (Huey et al., 1990): younger adults are faster sprinters, yet have lower stamina than older adults. It is possible that the same holds true for *P. laticauda*, in which case larger individuals have shorter rests between movements because of their greater stamina.

Temperature.—HRPM tends to increase as temperature increases (Fig. 5). High temperatures are very closely tied to arthropod prey activity that consequently can affect foraging activity of geckos and other lizards, which primarily prey on arthropods (Dunham, 1978; Petren et al., 1993; Petren and Case, 1998; Aowphol et al., 2006). Iguanids (such as *Tropidurus torquatus*) have been observed to flight follow prey, lifting and turning their heads as insects fly by, and often repositioning or making short movements toward where prey landed (Ehrlich and Ehrlich, 1982). Temperature also affects predator–prey interactions through its effect on organismal velocity, thus increasing the overall encounter rate of predators and prey (Dell et al., 2014). Consequently, for the case of *P. laticauda*, head movements may have to do with searching for and locating prey items; thus, if more prey are around from increased temperature, there would be more head movement. AOP was not statistically significant, but showed a positive trend with temperature. AOP also had a positive relationship with HRPM. Both of these trends potentially provide secondary support that head raises are correlated with insect abundance and prey following. However, more work is needed to test these hypotheses.

Observation Date.—The date on which observations took place had an effect on several foraging behaviors, including SM.Max, RPM, and SP.Avg, with some values considerably higher than others, depending on the day. The observed day-to-day differences in lizard activity can be dependent on several conditions: seasonality, lunar phase, condition of gravidity, weather conditions, presence of predators, or prey abundance (Werner et al., 2006; Fenner et al., 2012; Broeckhoven and Mouton, 2015; Sales and Freire, 2015). For this study, we cannot propose any of these explanations because of either the length of the study or the absence of necessary data. Future studies of FM, for any taxa, should strive to collect data of the same individuals across multiple days and seasons.

Other Trends.—Werner et al. (2004, 2006) stressed that the correlation of SVL and mass should reflect the nutritional condition of an organism and should effect FM. We found a trend for a positive relationship between *P. laticauda* BCI and RPM, but it remains unclear what this finding might mean. Perhaps individuals with a higher BCI (i.e., healthier individuals) simply can afford to move around more because they have more energy to spare than less healthy individuals. Differences between natural and artificial substrates were not significant, but there was a trend that PTM and MPM were higher on artificial substrate than on natural vegetation. *Phelsuma laticauda* excels in human-disturbed habitats, even in its native range (Humphrey and Ward, 2018), which could explain this trend and point to why this species has become such a widespread invader. Lastly, PTM and SM.Max show a negative relationship with time of day. However, there is a second peak in activity in the late afternoon, weakly resembling the bimodal distribution of activity that is characteristic of most diurnal lizards in warmer climates or summer periods of cooler climates (Tinkle, 1967; Busack, 1976; Braña, 1991).

Intraindividual Variation.—We observed the foraging behavior of five individuals across multiple days (Table 3). Although these repeated observations lacked the power for inclusion in our models, a qualitative analysis reveals some notable patterns and discrepancies. One individual, Atitia32A, observed 10 d apart, succinctly illustrates the influence of the date of observation. Atitia32A was observed in the late afternoon immediately after it stopped raining, with a PTM and an MPM of 0, whereas Atitia32B was observed under peak activity times and fair weather conditions, with a PTM of 12.67% and an MPM of 2.6. Another individual was observed three separate times, and two of the observations began at virtually the same time under identical temperatures and yielded nearly identical behavioral measures (MSB33A and MSB33C). This consistency, 5 d apart, shows that individuals of this species likely remain consistent in their foraging activities given similar environmental conditions. For an individual that was actively attacking prey (MSB18A), its head MPM were twice as frequent as when it was observed not in the presence of prey (MSB18B). The doubling in head movement activity supports our previous conclusion that high amounts of head movement under high temperatures likely have to do with the presence of prey (Fig. 5).

Future Directions.—Comparing our work with that of Seifan et al. (2010) in Hawaii shows that even within the same species, nocturnal and diurnal foraging can be drastically different. This fact further emphasizes the problem with averaging FM values without acknowledging potential variation within a species

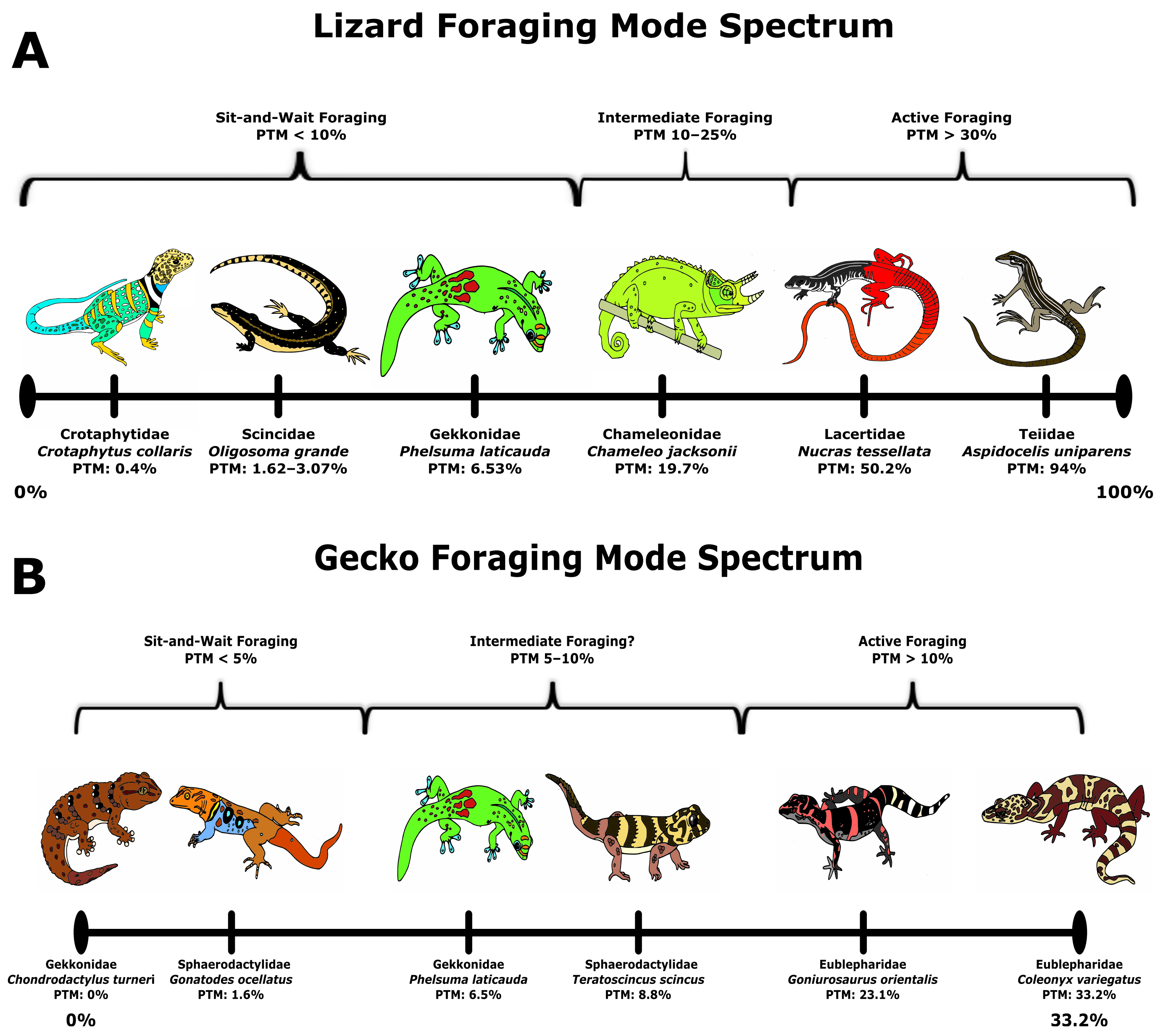


FIG. 6. (A) Position of *Phelsuma laticauda* on lizard FM spectrum as determined by PTM. Based on the cutoffs determined by Huey and Pianka (1981), with PTM < 10% = SW forager and PTM > 30% = AF, *P. laticauda* is a classic SW forager along with *Crotaphytus collaris* and *Oligosoma grande* (Eifler and Eifler, 1999; Cooper et al., 2001). FMs with PTM 10–25% represent intermediate FMs, such as the "cruise foraging" of *Chameleo jacksonii* (Hagey et al., 2010). Many lacertids and teiids, such as *Nucras tessellata* and *Aspidocelis uniparens*, lie on the upper end of the spectrum (Huey and Pianka, 1981; Cooper et al., 2001). (B) Position of *P. laticauda* on gecko FM spectrum as determined by PTM. Most SW geckos have a PTM < 5%, such as *Chondrodactylus turneri* and *Gonatodes ocellatus* (Persuad et al., 2003; Cooper, 2007). The majority of other geckos have a PTM > 10% (many of which have been classified as AF even though none come close to the extremely high PTMs of many AF lizards outside of the Gekkota infraorder), such as *Goniurosaurus orientalis* and *Coleonyx variegatus* (Kingsbury, 1989; Werner et al., 2004). Within geckos, *P. laticauda* is a more active SW forager, verging on the intermediate values of species such as *Teratoscincus scincus* (Seligmann et al., 2007).

(Bolnick et al., 2003). In addition, the knowledge that *P. laticauda* behaves differently in different environments could have conservation implications in locations where it has invaded. Our study was conducted in *P. laticauda*'s invasive range and most of the previous work on this species has been outside its native range as well. Thus, it would be interesting to not only assess behavioral variation among invasion sites, but also between invaded and native habitats where natural predators and competitors have coevolved with *P. laticauda* (Cure et al., 2012; Pickholtz et al., 2018). The *P. laticauda* populations on Mo'orea exhibit more interindividual variation in their FMs than those populations studied in Hawaii. On Mo'orea, *P. laticauda* lacks any closely related competitors and presumably has little to no competition while foraging diurnally. However, on Hawaii two other day geckos coexist with *P. laticauda* (McKeown, 1996; Kraus, 2009). The markers of ecological release are possibly different between Hawaii and Mo'orea and warrant further consideration (Wolfe, 2002; Herrmann et al., 2020). As mentioned, broader taxonomic representation in gecko studies is sorely needed, including the need for both nocturnal and diurnal gecko studies to determine the possible correlation with sexual diergism. Future studies should strive to measure multiple behavioral metrics in addition to PTM and MPM because these additional metrics can capture unique variation that would

TABLE 3. Individual lizards observed across multiple different dates. ID no. indicates the unique individual identifier and locality: MSB = Mo'orea Sunset Beach Hotel; Atitia = Atitia Cultural Center. The final letter of the ID no. distinguishes the observations: A = first observation, B = second observation, C = third observation.

ID no.	Date	Time	PTM (%)	MPM	SM.Avg	SP.Avg	SM.Max	RPM	HRPM	TW	JPM	AOP
MSB18A	4.11.18	1103	16.72	2.03	4.93	24.57	18	0.30	0.8	0	0.03	1
MSB18B	9.11.18	1230	4.76	0.54	5.29	105.86	13	0.15	0.35	0	0	0
MSB25A	24.10.18	1335	17.12	2.45	4.2	20.33	12	0.00	0	0	0	0
MSB25B	30.10.18	1146	1.11	0.33	2	178	3	0.07	0.2	0	0.03	0
MSB33A	30.10.18	1039	11.53	1.33	5.19	39.81	33	0.27	0.83	1	0	0
MSB33B	2.11.18	1222	7.76	0.7	6.74	80.05	10	0.07	0.44	0	0	0
MSB33C	4.11.18	1027	11.55	1.27	5.54	42.39	12	0.09	0.82	0	0.05	0
Atitia28A	27.10.18	1240	2.22	0.37	3.64	160	12	0.00	0.67	0	0.07	0
Atitia28B	5.11.18	1023	12.11	2.57	2.83	20.55	27	0.23	0.87	1	0.2	1
Atitia32A	29.10.18	1535	0	0	0	900	0.27	4	0.2	0	0	0
Atitia32B	8.11.18	1037	12.67	2.6	2.92	20.15	0.43	13	1.17	1	0.03	1

otherwise be masked, as shown by our study. More FM studies that look at multiple potential explanatory variables are also needed because many studies, even those that examine "classic examples" of extreme AF/SW (such as *Aspidoscelis* and *Crotaphytus*), often only consider one or two variables (Eifler and Eifler, 1998; Husak and Ackland, 2003; Higginson and Ruxton, 2015; Sales and Freire, 2015). Finally, we propose that researchers should compare interindividual and interpopulation variation in foraging behavior (Bolnick et al., 2003).

Conclusions.—*Phelsuma laticauda* exhibits a SW strategy on the island of Mo'orea, yet exhibits more interindividual variation on Mo'orea than it does on Hawaii (Seifan et al., 2010). Females foraged more actively than males (at least, as reflected by the average duration of movements), challenging the notion that only nocturnal geckos exhibit sexual foraging diergism. Smaller, younger individuals make longer SM.Max than larger individuals, whereas larger, older adults tend to pause less between movements. Temperature increases foraging behavior, particularly head movements related to locating prey. In our study, date of observation greatly influences several behavioral variables. Although we did not have the data to determine what specific factors are responsible, we stress the importance of measuring factors that change from day to day for future work and of measuring behavior across days (Frankenberg, 1978; Werner et al., 2006). Studies examining foraging behavior can reveal the ecological and evolutionary role an organism plays in its environment, thereby providing useful information for studying species interactions, population dynamics, and species diversity, areas of ever-increasing importance in the face of ongoing global climate change (Shochat, 2004; Harmon and Barton, 2013; Thorne et al., 2015; Kokubun et al., 2018). Therefore, additional studies on foraging behavior, for any taxa, are warranted as invasive species continue to spread and as environments become increasingly effected by climate change.

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Supplementary Data

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