

FORAGING MODE AND THE FACTORS AFFECTING FORAGING BEHAVIOR IN THE DIURNAL ARBOREAL GECKO, *PHELSUMA LATICAUDA*

JAMES W. WEHSENER

Environmental Science Policy and Management, University of California, Berkeley, California 94720 USA

Abstract. Across a given genus, lizards often exhibit a narrow range of foraging strategies. However, in geckos foraging mode can be quite variable, changing significantly from species to species despite genus homogeneity. Nocturnal geckos often exhibit more of a mixed foraging mode with both sit-and-wait and widely foraging characteristics, while most literature to-date suggest that diurnal geckos rely primarily on sit-and-wait behaviour. This study examined the foraging behaviour of an invasive diurnal gecko, *Phelsuma laticauda*, at two sites on the island of Mo'orea, French Polynesia. Initial surveys were completed at each site to measure and mark individuals before a behavioural study was completed to record movement data. Findings confirm that *P. laticauda* is a sit-and-wait predator, although at certain times of day it exhibits widely foraging characteristics. Additionally, this study identified environmental and morphological factors that influence level of diurnal gecko foraging activity. Key behavioural findings include: as the day progressed, geckos remained stationary for longer periods of time; higher temperatures correlated to higher levels of activity; and geckos were found facing down the majority of the time (a posture that prepares them for hunting). In addition to these environmental factors, tail regeneration was also seen to affect the activity of individuals, particularly in males. Overall, findings suggest that *P. laticauda* could have significant impacts on colonized ecosystems. This could potentially affect native lizards and arthropods, and possible disease introduction could affect even more organisms.

Key words: foraging mode; sit-and-wait foraging; Phelsuma laticauda; sexual diergism; diurnal gecko; tail regeneration

INTRODUCTION

All predators employ foraging strategies to pursue or capture their prey. Which strategy they utilize varies between species and is perfected through natural selection (Schoener 1971). Schoener showed that there are four aspects of feeding strategies: optimal diet, foraging group size, foraging space, and foraging period. Different environmental and temporal factors are major components of these optimal foraging periods (Schoener 1971). Consequently, we can learn much about an organism's foraging strategy by asking what these specific factors are for a given organism.

Lizards are model organisms for studying feeding strategies (Huey *et al.* 1983). There are two foraging modes (FM) found in lizards. The first is known as widely foraging (WF), where organisms are actively searching for and or chasing prey. The second is a strategy that relies on ambushing prey from a passive position, or sit-and-wait foraging (SW). All lizards fall somewhere on this spectrum between these two strategies. In general, four descriptors act as proxies for foraging behavior

in geckos (Huey and Pianka 1981, Cooper 1995, Pianka 1966, Pietruszka 1986). These descriptors are percent time moving (PTM), moves per minute (MPM), duration of a single movement in seconds (SM), and duration of a single pause in seconds (SP). These descriptors serve as proxies for foraging behavior because direct observations of geckos feeding habits are quite rare (Cooper *et al.* 1999, Cooper *et al.* 2001).

The foraging mode of most lizard species are often genus-wide and even family-wide in cases; however, it can be quite variable in gecko species (Bauer 2007). Still, Werner *et al.* (2004 and 2006) showed that most species tend to rely on one FM more than the other, even if they can utilize both. However, this mixed FM tends to remain exclusive to nocturnal geckos. It is evolutionarily beneficial for nocturnal geckos to have mixed foraging modes, since they need to be able to utilize every strategy possible to find food (Werner, *et al.* 2011, Werner, *et al.* 1997). Werner *et al.* (2006) showed that specific biotic and abiotic factors such as presence or absence of full moon, ambient temperature, tail length and regeneration, and cessation of

oviposition can influence the foraging mode of certain nocturnal terrestrial species.

In contrast with the foraging mode of nocturnal geckos, diurnality in geckos generally translates to strict sit-and-wait behavior (Werner *et al.* 2004). Seifan *et al.* (2010) conducted a study on the difference in foraging behavior of the gold dust day gecko (*Phelsuma laticauda*) in daytime versus nighttime in Kona, Hawai'i. The factors they tested included time of day, air temperature, body temperature, and substrate temperature. Although insufficient data was collected to test the effects of substrate temperature during the daytime, they found that substrate temperature had an effect on behavior during the nighttime. Therefore, it is worthwhile to accumulate further data of *P. laticauda* substrate temperatures in the daytime as well to see if it has an equal effect.

Functional sex differences (sexual diergism) in foraging behavior occurs in many lizard species; however, it is less studied in geckos. Sexual diergism is present in nocturnal terrestrial geckos (Werner *et al.* 2006) but it has not yet been found in arboreal diurnal geckos (Persaud *et al.* 2003), possibly for two reasons. The first explanation could be that their foraging behavior has been studied less. The second possibility is that terrestrial nocturnality and sexual diergism are heavily correlated, a theory that is not yet proven but gaining ground. If more studies are conducted on arboreal diurnal gecko species that result in no significant sexual diergism than this theory can be further supported (Seifan *et al.* 2010, Werner *et al.* 1997b, Werner *et al.* 2006).

Phelsuma laticauda is an invasive day gecko that has recently colonized the island of Mo'orea (Ota and Ineich 2006). There has only been one foraging mode study conducted on this species in Hawai'i (Seifan *et al.* 2010) so not much is known about its foraging behavior. In 2015 Ingrid Lund studied *P. laticauda*'s interactions with the other geckos found on the island and determined that it can exhibit aggressive behaviors towards some of the native and other invasive species. For these above reasons, it is important to study *P. laticauda*'s foraging behaviors to understand how it can affect the native ecosystem of Mo'orea, especially since it is the only diurnal gecko on the island—all the other species are nocturnal (Lund 2015).

The aim of this study is to (1) describe foraging behavior of *P. laticauda* (2) determine environmental (abiotic) factors that affect foraging behavior (3) determine morphological (biotic) factors that affect foraging behavior (4)

examine possible differences between male and female individuals. All factors were tested through the observation of wild, marked individuals of *P. laticauda* in the North and northwestern parts of the island of Mo'orea, French Polynesia. The environmental factors tested were: perch height, time of day, observation duration, direct substrate temperature, air temperature 1 meter above substrate (AT1) and air temp 5+ Meters away (AT 2). The morphological factors tested were: snout-vent length (SVL) and snout-tail length (STL), tail length, body mass, state of tail regeneration, and relative fitness (body condition index). The foraging behavior and morphology of males and females was compared to one another for possible sexual diergism or dimorphism. These factors were based off similar foraging behavior studies done on nocturnal and diurnal species (Werner *et al.* 2006 and Persaud *et al.* 2003).

METHODS

Study site

This study took place at two different field sites on the island of Mo'orea, French Polynesia. (1) The Mo'orea Sunset Beach Hotel, and (2) the Atitia Center. The hotel site had a large, dark wood office building with two decks, each with a large overhanging awning, all of which the geckos frequented. Other main areas of observation were dense plant cover in front of the decks as well as part of the property set aside for garbage, which had two large outside trash bins, a smaller bin, and a large wooden fence. The Atitia Center research site, adjacent to the UC Gump Research Station, had fewer large building structures and instead more open space. This site included a variety of coconut trees, banana plants, and other leafy plants that were used by the geckos, in addition to many small bamboo auxiliary buildings scattered around the property.

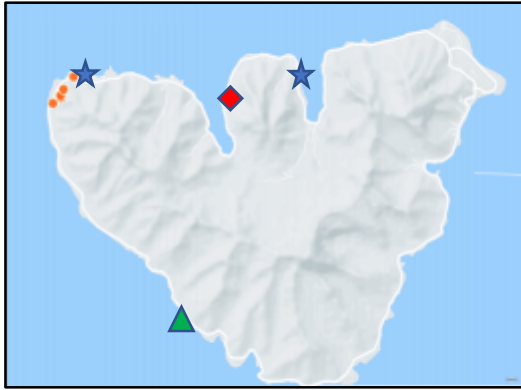


FIG. 1. Map of Mo'orea with various sites of *P. laticauda*. The blue stars are field sites from this study. The orange circles are the field sites from the Lund (2015) study. The red diamond marks the most eastern sighting of *P. laticauda* from in person interviews from Lund (2015). The green triangle is the site where *P. laticauda* was first introduced to the island.

Study organism

Phelsuma laticauda is a small invasive gecko and is one of the 52 unique day-gecko species from the *Phelsuma* genus that radiated and expanded from their native island of Madagascar (Rocha *et al.* 2009). *P. laticauda* is an invasive species, having spread to the Comoros, Hawaii (Rocha *et al.* 2007, Seifan *et al.* 2010) and French Polynesia (Ota and Ineich 2006) in recent years. It is estimated to have arrived on the island of Mo'orea within the last fifteen years (Ota and Ineich 2006). Defining morphological traits include a thick stout tail, calcium sacs on the neck (females only (Encyclopedia of Life 2018)), a vibrant green and sometimes even blue coloring, three reddish/orange tear drops located dorsally in between the hind legs, three orange bands running across the front of the snout, blue coloring around the toepads and encircling the eye, and gold yellow spots scattered from the neck to the middle of the dorsum that give it the distinguishing common name, gold dust gecko (Heygen 2004).

Data collection

The initial captures and associated measurements of geckos for this study were conducted from 8 October to 23 October between 10:00 and 16:00hrs, with some additional morphological measurements of

unmarked individuals taken after said individuals were observed. Temperatures of the substrate and 1 meter above ranged between 25.1-34.0 °C. The weather remained stable, with a few days of light rain and heavy winds. Prior to observations 76 individuals were marked and measured. Of these marked individuals 29 were observed (12 female, 17 male). In addition, 2 juveniles and 10 unmarked individuals encountered for a total of 41 observations. Due to only 2 juveniles (sex unknown), a separate category was not made for them when data was split between males and females.

The methods employed here were adapted from two recent studies (Werner *et al.* 2006 and Tal Seifan *et al.* 2010). The geckos were caught by hand, after it was determined that, due to their good eyesight, noosing would not be feasible approach. Captured geckos were then sexed, weighed (0.01g), measured (details below, mm), and marked. Measurements taken included: head length (HL), snout to vent length (SVL), and snout to tail length (STL).

Additional tail measurements were also taken, including: tail length total (TLT), original portion (TLO), and regenerated portion (TLN). The three tail lengths were measured as a percentage of SVL to rule out bias between younger, smaller individuals and older, larger individuals. Degree of regeneration was determined as such:

$$\frac{\text{(Length of regenerated portion)}}{\text{(Desired length of regenerated portion)}}$$

Desired regeneration portion was estimated by averaging the total tail lengths of the measured individuals with full intact tails, 10 individuals. This average was formatted as a percentage of SVL as the other tail measurements were. Thus, Desired length of regenerated portion:

$$\frac{\text{(Average length of intact tail)} - \text{(length of original portion)}}{\text{(Average length of intact tail)}}$$

Body condition index (BCI) was calculated in two different ways. These two methods were used from different studies to calculate this index. The first was from a study done by (Labocha *et al.* 2014) on body condition indices in *Mus Musculus* and was a simple ration of the log of body mass over the log of body length (SVL). Their study showed that there are not enough studies using all the possible body condition indices to determine which is the most accurate. Consequently, the best index can vary from species to species and even

between sexes. However, it was concluded that including zygomatic breadth and pelvic circumference along with the traditional body length and body mass can greatly increase the accuracy of all methods. Data was unavailable in my study for those additional variables so the choice was made to use the body condition index that yielded the next best results for both males and females: $(\log(\text{body mass})) / (\log(\text{body length}))$. The second index used to determine relative body condition index used residuals from an ordinary least squares regression of SVL vs. body mass, a common method within ecology (Andy J. Green 2001). Both of these methods for body condition index were used in order to acknowledge that there is not one clear way that is the best method for determining body condition. Once these two indices were calculated they were both analyzed separately by linear regression against the four foraging mode descriptors.

The males were marked on the dorsum between the front limbs and females on the dorsum between the hind legs. Marks were made using a pen, drawing a unique ID number. Sex was determined in males by the presence of preano-femoral pores and secretions from them (Glaw and Vences Miguel 1994), and in females by the presence of eggs, calcium sacs, or the absence of preano-femoral pores.

Whenever an individual was caught, the temperature of the substrate under the individual (microclimate) was measured. In addition, air temperature was measured in two ways: air temperature 1m above the substrate (microclimate 2) and ambient temperature of the habitat, measured 5+ m away. All individuals were released at the initial site of capture. These handling and tagging methods are approved under UC Berkeley institutional animal care and use protocol AUP-2018-04-11006.

Behavioral trials

Observation shifts at the study sites were recorded between 23 October to 9 November, 2018 from 10:00-17:00hrs. The behavior of *P. laticauda* was recorded on subsequent days (i.e., following the measurement and marking day), when marked geckos were encountered. At encounter, each marked individual was tracked for 30 minutes at a distance of 2-6 meters (Ikeuchi *et al.* 2005). Binoculars were used to observe behaviors and distinguish individuals when needed.

The foraging modes descriptors, percent time moving (PTM), moves per minute (MPM), duration of a single movement (SM), and duration of pausing (SP), were recorded as the behavioral data. "Movement" was determined as an instance where the entire body of an individual was translocated to a new position, including: walking, running, crawling, jumping, and jerking forward/backward. Social interactions with other conspecifics and shuffling/repositioning were noted but not recorded as foraging movement. In addition, the location, orientation (facing upward, downward, or horizontal), and elevation of the individual at first detection was recorded. The total distance traveled throughout the 30-minute observation period, final elevation, and the three temperatures (substrate, ambient 1, and ambient 2) were also taken. When unmarked individuals were encountered, they were observed following the procedures described above and, at the end of the observation period, they were captured and all the initial measurements were taken. There were several unmarked observed geckos that eluded capture at the end of the observation period and thus exact measurements and the sex were not determined for this subset of individuals, but they were subjectively placed into one of the three length categories based on the observer's determination. The same observer was used for every observation to rule out observation bias.

Statistical analyses

Statistical analyses proceeded following Werner *et al.* 2006 and (Hagey *et al.* 2010), using the same four foraging mode descriptors as (Werner *et al.* 2006): percent time moving (PTM), moves per minute (MPM), duration of a single movement (SM), and duration of a single pause (SP). Foraging mode was determined using the parameter of less than 1-2 moves per minute and less than 15% time moving = sit-and-wait; greater than 1.5-2 moves per minute and greater than 30% time moving = widely foraging (Huey and Pianka 1981, Ikeuchi *et al.* 2005).

To examine the effect of sex a t-test and Mann-Whitney U test was used. All samples were analyzed by and f-test, revealing equal variances. The normality of samples was tested by the Shapiro Wilk test. Parametric samples were tested for significance using a t-test and non-parametric samples were tested for significance using the Mann-Whitney U test.

Other factors potentially effecting foraging mode—size (SVL & STL), tail size in relation to body, state of tail regeneration, mass, elevation, time of day, direct substrate temperature, and ambient temperature—were tested by ordinary least squares linear regression analysis with an alpha value = 0.05.

RESULTS

Foraging mode

During observation periods, there was high individualistic variation; during some periods an individual did not move once, and others an individual would locomote the entire period. The averages of the four foraging descriptors are as follows: percent time moving (PTM) 7.24 ± 6.81 , moves per minute (MPM) 1.14 ± 0.92 , duration of single movement (SM) 883.44 ± 1.55 sec, and duration of single pause (SP) 125.30 ± 169.11 sec.

Environmental factors

All environmental factors were analyzed via ordinary least squares linear regression analysis with a significant alpha value of $P = 0.05 >$.

Percent time moving, moves per minute, and duration of a single movement were not significantly affected by time of day. However, duration of a single pause was positively affected by time of day ($r=0.350$, $p=0.027$) (Fig. 1).

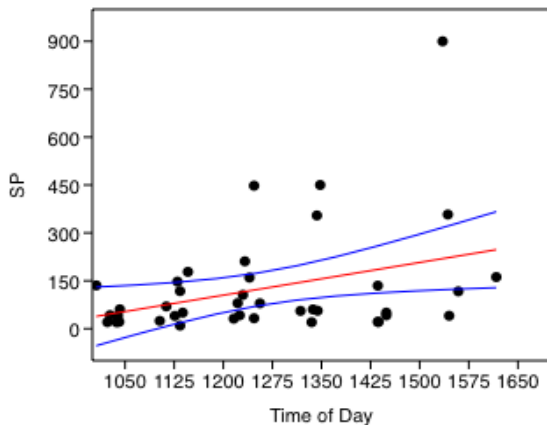


FIG. 2. Linear regression analysis of the effect of time of day on duration of a single pause (SP).

There was a positive correlation for air temperature (1 m above the substrate) and moves per minute ($r=0.332$, $p=0.036$), and a

negative correlation for duration of pausing ($p=0.030$, $r=-0.343$) (FIG. 2). Percent time moving only showed a positive trend that was not significant ($p=0.055$, $r=0.305$).

Similarly, there was a statistically significant correlation for percent time moving ($r=0.41008$, $p=0.012992$), moves per minute ($r=0.44639$, $p=0.0063532$), and duration of a single pause ($r=-0.37886$, $p=0.022691$) for air temperature taken 5+ m away from capture (AT2) (FIG. 4).

Direct substrate temperature also had a statistically significant effect on the foraging behaviors. Percent time moving and moves per minute were positively correlated ($p=0.032$, $r=0.344$; and $p=0.019$, $r=0.374$). Duration of a single pause was negatively correlated ($p=0.012$, $r=-0.400$). (FIG. 3. and 4.).

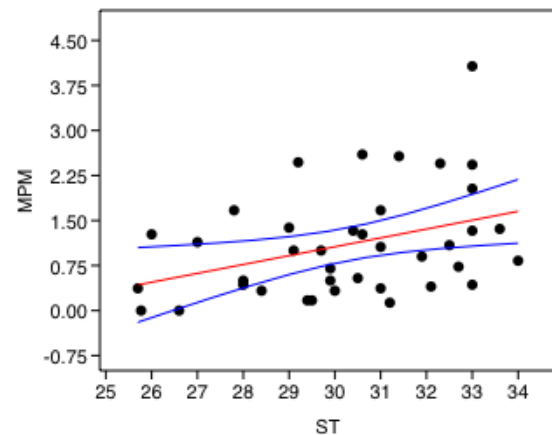


FIG. 3. Linear regression analysis of the effect of substrate temperature (ST), on moves per minute (MPM).

The data was widely distributed for the test parameter of perch height on foraging behavior and there was no significance seen for any of the four descriptors.

Morphological factors

The morphological characteristics: mass, SVL, STL, and tail length (original, regenerated, and total) were compared to the four foraging descriptors studied and analyzed via ordinary least squares linear regression analysis. All of these traits appeared to have no significant effect on the foraging behavior. However, total tail length (TLT), had a negative

trend for the duration of a single pause (SP), with $p = 0.1094$, $r = -0.29321$ (FIG. 5.)

The condition of the tail was also calculated and then the degree of regeneration was analyzed by linear regression to see the effect it had on the foraging mode descriptors. This tail

statistically insignificant, females showed the opposite correlation for single movement duration (SM; $n = 12$, $r = -0.16392$, $p = 0.6107$).

Body condition index was also tested for its possible effect on foraging mode. BCI was calculated in two unique ways. However, there

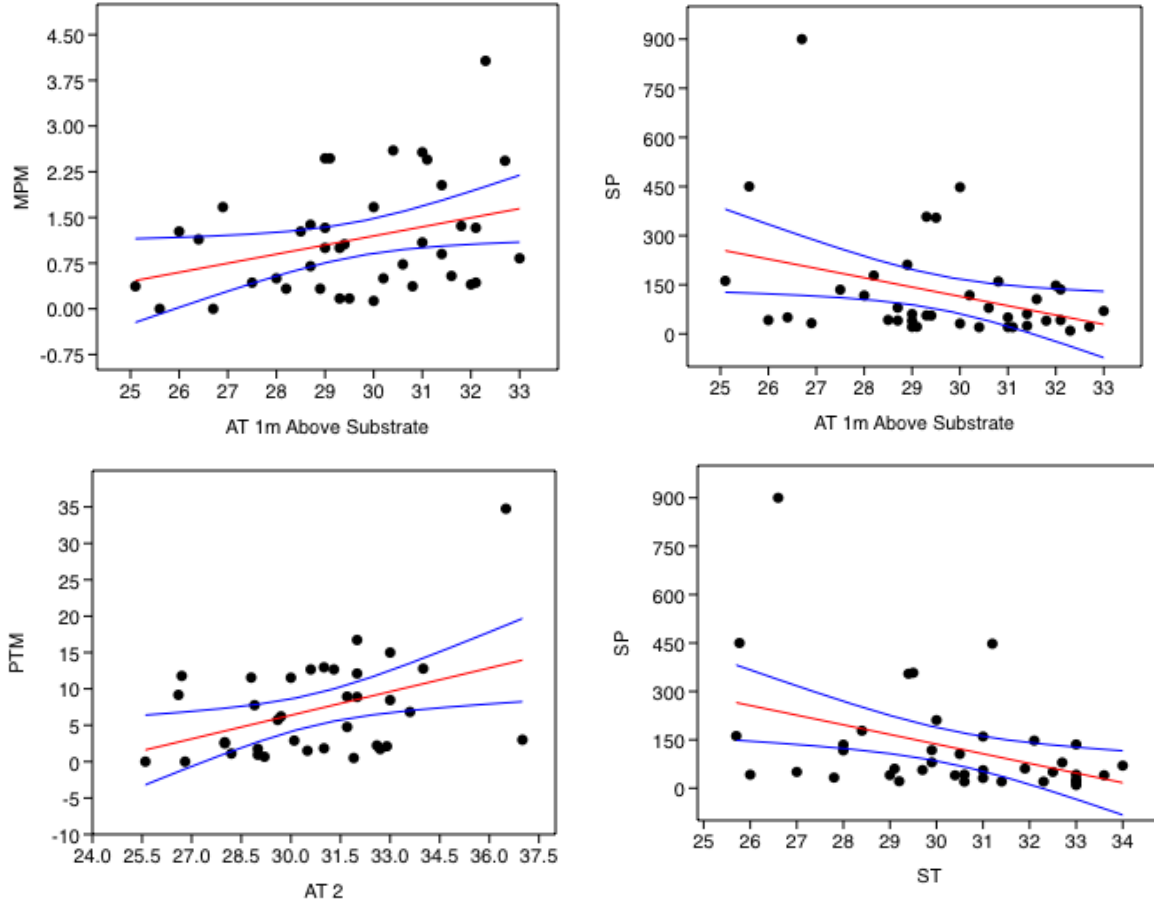


FIG. 4. From top left to right to bottom left to right: (a) Linear regression analysis of the effect of air temperature (AT) 1m above substrate on Moves per Minute (MPM). (b) Duration of a single pause (SP). (c) Linear regression analysis of the effect of air temp 5+ m away from capture (AT 2) on percent time moving (PTM). (d) Linear regression analysis of the effect of substrate temperature (ST) on duration of a single pause (SP).

condition and degree of regeneration formula was developed in (Werner *et al.* 2006) to test the effects it had on a nocturnal terrestrial gecko, *Goniurosaurus kuroiwae kuroiwae*. Data was analyzed for all observations collectively then based on sex. Holistic data showed that there was a negative correlation with pause duration; the closer and individual was to having its desired tail length, the less time it spent pausing (SP; $r = -0.35632$, $p = 0.049126$).

When segregated, the males' periods of movement were longer in duration the closer their tails were to completeness (SM; $n = 17$, $r = 0.5583$, $p = 0.019847$) (FIG. 6.). Although it was

was no significant effect seen for either of these indices

On average, the males were larger than females in SVL (53.69 vs 46.99 mm), STL (107.28 vs 91.94 mm), and mass (4.33 vs 2.98 g). These differences were all statistically significant tested by equal variances t-test. This is consistent with the hypothesis since males are often larger than females in territorial lizards (Stamps 1983). As expected from a diurnal arboreal gecko, there was no significant sexual diergism in foraging behavior. For tail length Females had a larger TLO (49.41%SVL vs 47.65%SVL). Males had a larger TLN

(48.58%SVL vs 43.24%SVL) and larger TLT (98.20%SVL vs 95.17%SVL). However, none of these tail differences were statistically significant.

Werner *et al.* (2006) pointed out another factor that needs to be examined, effect of the duration of observational periods. There is no easy way to control for this variable since long observations are needed to gain an accurate representation of foraging movement, but observational periods were sometimes inconsistent in length due to individuals escaping. However, when observation duration was tested via linear regression analysis against the four foraging descriptors, there was no significant effect.

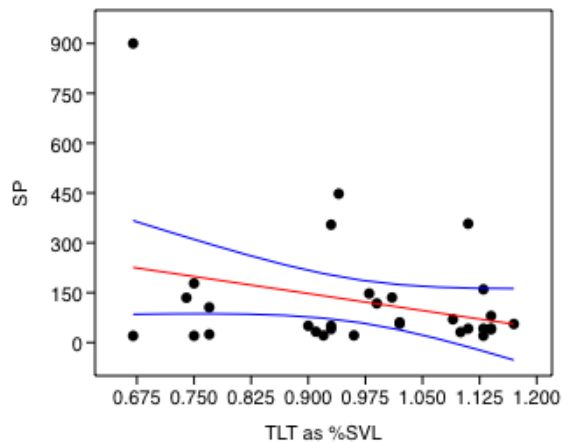


FIG. 5. Linear regression analysis of the effect of total tail length (TLT) on duration of single pause (SP).

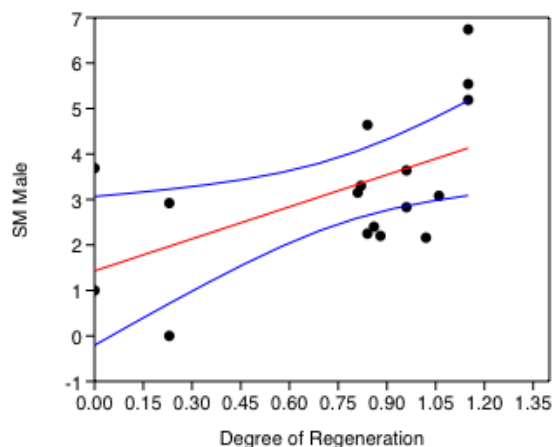


FIG. 6. Linear regression analysis of the effect of degree of tail regeneration on duration of a single movement (SM)—males only.

DISCUSSION

Foraging mode

Even though there was high individualistic variation in activity, this study showed that *P. laticauda* is in fact a sit-and-wait predator (Outliers showing this individualistic variation can be seen in FIG. 2. —FIG. 6.). This supports the classification by Seifan *et al.* (2010) of *P. laticauda*'s foraging mode on Kona, Hawai'i. This conclusion also provides further evidence to support the theory that a more flexible, mixed foraging mode as seen in many nocturnal geckos (Werner *et al.* 2004 and 2006 and 1997b), could be correlated to nocturnality itself due to the challenges of hunting in the dark (Persaud *et al.* 2003). The foraging mode of geckos can be quite varied (Bauer 2007), but all studies on diurnal geckos so far have defined them as sit-and-wait predators (Persaud *et al.* 2003 and Seifan *et al.* 2010) with more variation seen in nocturnal geckos (Werner *et al.* 1997b).

Environmental factors

Time of day did have a significant influence *P. laticauda*'s foraging mode showing that the geckos remain stationary for longer periods of time as the day progressed (see FIG. 2.). These findings were not consistent with other diurnal gecko studies. Perusad *et al.* (2003) did not find any significant correlation with time of day on three diurnal geckos of the *Gonatodes* genus, nor did Seifan *et al.* (2010) in *P. laticauda*. However, Werner *et al.* (2006) saw a significant effect of time of day on the nocturnal terrestrial gecko, *Goniurosaurus kuroiwaie kuroiwaie*. This is very interesting because nocturnal geckos often exhibit very different behaviours than diurnal geckos, as seen with in the cases of sexual diergism and mixed foraging mode. It is unknown why *P. laticuada* responds to this temporal factor in the same way as this nocturnal gecko rather than its own species found on a different island.

Air temperature 1 m above the substrate showed statistical significance on the foraging descriptors. In the range of 25-33 °C, the higher the temperature the more an individual moved and spent less time pausing during the observation period. Similar to time of day, this

TABLE 1. Compilation of all analyses run included what factor, the type of test performed, and the respective p values for the four foraging descriptors: percent time moving, moves per minute, duration of a single movement, and duration of a single pause.

Test Description	Test	P (PTM)	P(MPM)	P(SM)	P(SP)
Time of Day	Linear regression	0.087	0.089	0.107	0.027
AT 1	Linear regression	0.055	0.036	0.125	0.030
AT 2	Linear regression	0.013	0.006	0.575	0.023
ST	Linear regression	0.032	0.019	0.115	0.012
Mass	Linear regression	0.242	0.425	0.208	0.947
SVL	Linear regression	0.427	0.433	0.821	0.848
STL	Linear regression	0.409	0.367	0.787	0.475
Perch Height	Linear regression	0.740	0.482	0.391	0.560
TLO %SVL	Linear regression	0.860	0.752	0.669	0.947
TLN %SVL	Linear regression	0.915	0.775	0.919	0.215
TLT %SVL	Linear regression	0.862	0.763	0.284	0.109
Tail Regeneration	Linear regression	0.537	0.761	0.159	0.049
Regeneration (Male)	Linear regression	0.215	0.809	0.020	0.255
Regeneration (Female)	Linear regression	0.887	0.909	0.611	0.778
Body Condition Index (BCI)	Linear regression	0.277	0.406	0.346	0.977
Observation Duration	Linear regression	0.256	0.259	0.355	0.666
BCI Residuals	Linear regression	0.951	0.762	0.154	0.915
Male vs. Female	Mann Whitney U-Test/t-test	0.566 (MW)	0.899 (t-test)	0.203 (t-test)	0.947 (MW)

correlation was not seen in Siefan *et al.* (2010) nor in Persuad *et al.* (2003). Air temperature of the entire habitat range (AT 2) had a significant influence on the number of moves and movement percentage. Consequently, there was a negative correlation seen in the duration of pauses. Air temperature 2 may be the most accurate since substrate temperature at the start of the observation can be drastically different from the end of the observation as the

gecko moves across different substrates. In the same way, air temperature 1 could change more frequently than AT 2 as the gecko moves from shade into sun or vice versa. Whereas air temperature 2 includes the temperature of the the entire habitat range that an individual covers throughout the observational period and thus is less dependent on a gecko's exact location. Similar to time of day, this correlation for air temperature from any distance was not

seen in Siefan *et al.* (2010) nor in Persuad *et al.* (2003).

Substrate temperature showed a similar correlation. The hotter the substrate, the more an individual moved and spent more time moving during the period, resulting in shorter single pauses. The range of substrate temperatures taken was 25-34 °C. In the study in Hawai'i (Seifan *et al.* 2010), despite data sparsity of daytime temperatures, they found that at night an increase in temperature corresponded to decreased movement, which led to the conclusion that the same depressed effect on activity would be seen during the daytime. However, my study showed the opposite was true: increase in ambient temperature = increase in activity. Possible explanations for this shift in behavior could be that during the night it is more energetically favorable for individuals to remain in one position to maintain body temperatures, but daytime provides warmer, more favorable temperatures so the individual is free to forage.

The findings of these temperature effects are important because they all contradict the only other study done on *Phelsuma laticauda's* foraging behavior by Seifan *et al.* (2010). There are two possible reasons for this. (1) The sample size was not large enough in the 2010 study. (2) *P. laticauda's* foraging behaviour is not necessarily consistent, even within its own species, and it may uniquely affect every environment it colonizes.

It is well known that the activity of thermoregulatory animals such as reptiles is reliant upon temperature. However, this is not on an exponential scale, there is an upper threshold beyond which lizards cannot survive (Grigg and Buckley 2013) The upper range of lizard species as defined by Grigg and Buckley ranged from 33.4°C to 51°C. It is possible that during my study individuals were just below their upper critical threshold temperature. When ambient temperature and substrate temperature exceeded 33°C individuals were below the line of best fit rather than above it, possibly indicating that a temperature increase beyond 34°C would possibly lead to a decrease in activity as *P. laticauda* reaches its critical threshold temperature.

Perch height was quite irrelevant to foraging behaviour, showing no correlations. Yet, it was observed that the majority of individuals were facing downward upon initial discovery (53%), similar to a study on three diurnal geckos of the *Gonatodes* genus, which were found oriented downward 68-76%

of the time (Persuad *et al.* 2003). There are several possible explanations for this behavior. One is that it is related to prey detection and that is more efficient to look with direction of the light source (i.e. sun is above so gecko is looking down) as opposed to looking at a light source. (Persuad *et al.* 2003). Another possible explanation is that this behavior is a survival tactic, keeping an eye out for possible predators. This could be corroborated by anecdotal observations from this study, showing *P. laticauda* to be very cautious and to possess excellent vision. However, further study of the organisms that prey on *P. laticauda* is required to see if they come from below (terrestrial predators) or above (avian predators) in order to justify the latter theory.

Morphological factors

Morphological lengths of individuals were tested for possible effects on foraging behavior but no significant effects were shown after analysis. Thus, tail condition was the only morphological factor that significantly affected foraging behavior (see Table 1).

Tail condition showed significance for some of the foraging descriptors. When the data was clumped together, individuals spent less time pausing the closer they were to having their desired tail length, and similarly males moved for longer periods the closer they were to having their desired tail length. The latter can be justified by the social importance of tail completeness (Fox and Rostker 1982, Fox *et al.* 1990). Males with full tails will have a higher social status and better choice of home range and mates. Individuals with missing tails and even smaller tails may not be able to retain their own territories or be able to win over a mate (Fox and Rostker 1982, Fox *et al.* 1990). Consequently, males will spend less time moving when the tail is missing in order to conserve energy to regenerate the tail as fast as possible (Werner *et al.* 2006). This reasoning for males moving for longer durations as regeneration reached completeness is confirmed by Fox and Rostker and is consistent with what is seen by Werner *et al.* 2006. Yet, it doesn't reveal why the complementary trend of shorter pause durations would be seen when both males and females are analyzed as one dataset. One possible explanation for this is the male data was more statistically powerful due to more observed males (n = 17) than females (n = 12). Thus, when male and female data are combined the males mask the effect, of tail condition on the females. Or, maybe there is

some other underlying benefit to tail completeness which leads to both sexes pausing more often in order to commit energy to tail regeneration. When females were segregated, no significance was shown but there were trends observed. Both pause duration and duration of single movements showed a very slight negative trend as tail completeness increased. These two trends contradict one another and it is unknown why this was shown or what implications it could have. Considering that both descriptors decreasing at the same time is contradictory, the first explanation—that males possess more statistical power—is more plausible.

Body Condition Index/relative fitness had no observed influence on any of the foraging mode descriptors (see Table 1). It is possible that there is no difference between more and less fit individuals. However, it is also possible that the two methods used to calculate this relative fitness did not accurately capture the data. If zygomatic breadth and pelvic circumference were measured it might provide a more complete picture of an individual's fitness and could show a significant influence. There was not an effect of body condition on *Goniurosaurus kuroiwae kuroiwae* (Werner *et al.* 2006). This is possibly due to inaccurate body condition methods since individuals that are more fit probably are in better condition for some specific reason. So, it would make sense if less fit individuals are also less active.

Sex differences

Significant sexual size dimorphism was seen in *P. laticauda*, males being significantly larger than females. In only 30% of all gecko species males are larger than females (Ikeuchi *et al.* 2005). This is consistent with territorial geckos (Ikeuchi *et al.* 2005). Females on average autotomized their tail farther from the base resulting in larger original stumps than those of the males. The reason for this is not known. One possible explanation for this is that both sexes autotomize their tails as a predatory defense but male lizards also have been known to bite off each other tails when competing for territory and mates (Fox *et al.* 1990, Fox and Rostker 1982) Simply due to there being more potential instances for males losing a tail could result to a higher likelihood of a shorter original stump. As expected, there was no sexual foraging diergism observed, even with a sufficient sample size. This result contributes to the thought that sexual diergism, like mixed foraging mode, is only observed in nocturnal

and terrestrial geckos and is absent in diurnal scansorial geckos. (Werner *et al.* 2004 and 2006, Persuad *et al.* 2003, Seifan *et al.* 2010) The reason for this observation in only nocturnal geckos is unknown but if further research can be done on both fronts of diurnal and nocturnal geckos perhaps, we can conclude that sexual diergism is significantly correlated to nocturnality just as mixed foraging mode is.

Unidentified factors

Due to equipment malfunction and time constraints in this study, certain environmental that have been shown in other studies to affect the foraging mode were not tested. One example is light intensity (in terms of lux) which was not able to be tested because of equipment malfunction and calibration failure. This factor was shown to have a significant effect on the foraging in another diurnal gecko, *Gonatodes humeralis* (Persuad *et al.* 2003). In addition, light intensity interacts very closely with temperature both of which can affect foraging behavior (Frankenberg 1979).

Gravidity and cessation of oviposition are two other factors that are very likely to affect foraging behavior. Females will be more active to restore energy spent during gravidity (Werner *et al.* 2006). Unfortunately, not enough gravid females were observed in order to test this effect.

It is important to consider the distribution, availability, and diversity of insect populations when considering the foraging mode of insectivorous geckos as pointed out by (Seifan *et al.* 2010), yet time would not allow for this secondary survey to consider this factor. Whether an individual has eaten recently or not can affect how much they would move around in search of food (Werner *et al.* 2006). For this particular study, I did not possess the permits to pump lizard stomachs to determine the contents, so this difference in stomach condition could not be looked at. This could explain the high individualistic variation so in this study and requires further consideration in future foraging mode studies.

Lastly, it is important to recognize that certain times geckos could be moving in order to maintain thermoregulation and not to find food. There is no current method to my knowledge that could distinguish these two behaviours, and thus it remains a bias in this study as well as all reptile foraging behaviour studies.

Further Research

It was noted that the peak number of feeding attempts from observed individuals and other active individuals in close proximity occurred between 1000-1200. It is very rare to observe geckos actively eating during foraging mode studies (Werner *et al.* 2006, (Cooper *et al.* 1999, Cooper *et al.* 2001). So, *P. laticauda* could potentially be a good model organism to determine the accuracy of using PTM, MPM, SM, and SP as a proxy for foraging mode by comparing those results to attempts and success rates of geckos feeding and how much they move around during this time.

Anecdotal observations during this study showed that when individuals were being measured and handled, shortly after capture (less than 1 minute at times) they would become considerably darker than when they were being observed. This apparent color change was observed to a certain extent in every individual captured. Color change due to stress, aggression, social interactions, and environmental conditions have been observed in several other lizard and gecko species (Das *et al.* 2014, Greenberg and Crews 1990, Lewis *et al.* 2017, Vroonen *et al.* 2012) and is not heavily studied but could be common among geckos (Vroonen *et al.* 2012) Thus, it is potentially worth further consideration in *P. laticauda*.

Further research is required in the field of sexual diergism in both nocturnal and diurnal geckos. The evidence points to a correlation between nocturnality and sexual diergism but without further data on both the diurnal and nocturnal front we cannot conclude this correlation as fact (Seifan *et al.* 2010, Werner *et al.* 2006). In the lens of conservation, it is important to conduct foraging mode studies to determine how geckos, and all reptiles, are affected as global temperatures rise. This study revealed more about the foraging mode and general behavior of *P. laticauda* and the data obtained could be used to help predict the impact and ecological risks this invasive species could have on the native ecosystem and species in it (Hagey *et al.* 2010, Watari *et al.* 2008).

Conclusions

In conclusion, *P. laticauda* is a sit-and-wait predator and several environmental factors and morphological traits effect its foraging mode. Time of day showed only a correlation with the duration of pausing, increasing in duration as the day progressed. Substrate temperature and ambient temperature 1m

away and 5+m away increases the activity of *P. laticauda*. Tail loss increases the duration of pausing in both sexes, and depressed the duration of single movements in males. *P. laticauda* exhibits male-biased sexual size dimorphism; the males are longer (SVL, and snout to tail length) and heavier.

ACKNOWLEDGMENTS

I would like to thank my professors Ivo Duijnste, Cindy Looy, Stephanie Carlson, and Vincent Resh for their guidance and feedback throughout my research. I would also like to thank my graduate student instructors, James LaChance, and Renske Kirchholtes. Special thanks to graduate student instructor Clay Noss for his expertise in lizards and geckos, as well as Nannaphat Sirison, Sally Dowd, and Kylie Tuitavuki and all my other classmates for their continued support and assistance in the field.

LITERATURE CITED

- Andy J. Green. 2001. Mass/Length Residuals: Measures of Body Condition or Generators of Spurious Results? *Ecology* 82:1473-1483.
- Bauer, A. M. 2007. The foraging biology of the Gekkota: life in the middle. *Lizard Ecology* 12:371-404.
- Cooper, W. E. 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Animal Behaviour* 50:973-985.
- Cooper, W. E., L. J. Vitt, J. P. Caldwell, and S. F. Fox. 2001. Foraging Modes of Some American Lizards: Relationships among Measurement Variables and Discreteness of Modes. *Herpetologica* 57:65-76.
- Cooper, W. E., M. J. Whiting, J. H. V. Wyk, and Mouton, P. Le F. N. 1999. Movement- and attack-based indices of foraging mode and ambush foraging in some gekkonid and agamine lizards from southern Africa. *Amphibia Reptilia* 20:391-399.
- Das, M., P. C. Bhattacharjee, B. Biswa, and J. Purkayastha. 2014. Effect of light and dark phase on dorsum colour and pattern in *Hemidactylus* sp. of Assam. *Northeast Journal of Contemporary Research* 1:1-7.
- Fox, S. F., and M. A. Rostker. 1982. Social Cost of Tail Loss in *Uta stansburiana*. *Science* 218:692-693.
- Fox, S. F., N. A. Heger, and L. S. Delay. 1990. Social cost of tail loss in *Uta stansburiana*: lizard tails as status-signalling badges. *Animal Behaviour* 39:549-554.

- Frankenberg, E. 1979. Influence of light and temperature on daily activity patterns of three Israeli forms of *Ptyodactylus* (Reptilia: Gekkoninae). *Journal of Zoology* 189:21-30.
- Glaw, F., and Vences Miguel. 1994. A Field Guide to the Amphibians and Reptiles of Madagascar. Cologne, Vences & Glaw Verlag.
- Greenberg, N., and D. Crews. 1990. Endocrine and behavioral responses to aggression and social dominance in the green anole lizard, *Anolis carolinensis*. *General and Comparative Endocrinology* 77:246-255.
- Grigg, J., W., and L. Buckley B. 2013. Conservatism of lizard thermal tolerances and body temperatures across evolutionary history and geography. *Biology Letters* 9(2).
- Hagey, J. T., B. J. Losos, and J. L. Harmon. 2010. Cruise Foraging of Invasive Chameleon (*Chamaeleo jacksonii xantholophus*) In Hawai'i. *Breviora* 519:1-7.
- Heygen, V. E. 2004. The genus *Phelsuma* Gray, 1825 on the Ampasindava peninsula, Madagascar. *Phelsuma* 12:99-117
- Huey, B., Raymond, and R. Pianka Eric. 1981. Ecological Consequences of Foraging Mode. *Ecology* 62:991-999.
- Ikeuchi, I., M. Hasegawa, and A. Mori. 2005. Natural history of *Phelsuma madagascariensis kochi* from a dry forest in Madagascar. *Amphibia-Reptilia* 26:475-483.
- Labocha, M. K., H. Schutz, and J. P. Hayes. 2014. Which body condition index is best? *Oikos* 123:111-119.
- Lewis, A. C., K. J. Rankin, A. J. Pask, and D. Stuart-Fox. 2017. Stress-induced changes in color expression mediated by iridophores in a polymorphic lizard. *Ecology and Evolution* 7:8262-8272.
- Ota, H., and I. Ineich. 2006. Colonization of the Gold Dust Day Gecko, *Phelsuma laticauda* (Reptilia: Gekkonidae), in Moorea of the Society Archipelago, French Polynesia. *Current Herpetology* 25:97-99.
- Persaud, D., N. Werner, and Y. L. Werner. 2003. Foraging behaviour of three sphaerodactylin geckos on Trinidad and Tobago (Sauria: Gekkonomorpha: Sphaerodactylini:Gonatodes). *Journal of Natural History* 37:1765-1777.
- Pianka, R., Eric. 1966. Convexity, Desert Lizards, and Spatial Heterogeneity. *Ecology* 47:1055-1059.
- Pietruszka, R. D. 1986. Search tactics of desert lizards: how polarized are they? *Animal Behaviour* 34:1742-1758.
- Rocha, S., M. Vences, F. Glaw, D. Posada, and D. J. Harris. 2009. Multigene phylogeny of Malagasy day geckos of the genus *Phelsuma*. *Molecular Phylogenetics and Evolution* 52:530-537.
- Schoener T., W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics* 2:369-404.
- Seifan, T., A. Federman, W. J. Mautz, K. J. Smith, and Y. L. Werner. 2010. Nocturnal foraging in a diurnal tropical lizard (Squamata: Gekkonidae: *Phelsuma laticauda*) on Hawaii. *Journal of Tropical Ecology* 26:243-246.
- Vroonen, J., B. Vervust, D. Fulgione, V. Maselli, and R. Van Damme. 2012. Physiological colour change in the Moorish gecko, *Tarentola mauritanica* (Squamata: Gekkonidae): effects of background, light, and temperature. *Biological Journal of the Linnean Society* 107:182-191.
- Watari, Y., S. Takatsuki, and T. Miyashita. 2008. Effects of exotic mongoose (*Herpestes javanicus*) on the native fauna of Amami-Oshima Island, southern Japan, estimated by distribution patterns along the historical gradient of mongoose invasion. *Biological Invasions* 10:7-17.
- Werner, Y. L., S. Okada, H. Ota, G. Perry, and S. Tokunaga. 1997a. Varied and fluctuating foraging modes in nocturnal lizards of the family Gekkonidae. *Asiatic Herpetological Research* 7:153-165.
- Werner, Y. L., A. Bouskila, Davies, S. J. J. F., and N. Werner. 1997b. Observations and Comments on Active Foraging in Geckos. *Russian Journal of Herpetology* 4:34-39.
- Werner, Y. L., H. Takahashi, Y. Yasukawa, and H. Ota. 2006. Factors affecting foraging behaviour, as seen in a nocturnal ground lizard, *Goniurosaurus kuroiwae kuroiwae*. *Journal of Natural History* 40:439-459.
- Werner, Y. L., H. Takahashi, Y. Yasukawa, and H. Ota. 2004. The varied foraging mode of the subtropical eublepharid gecko *Goniurosaurus kuroiwae orientalis*. *Journal of Natural History* 38:119-134.