

RESOURCE PARTITIONING AND FOOD PREFERENCE OF THREE GEKKONID SPECIES ON THE ISLAND OF MOOREA, FRENCH POLYNESIA

LEA H. PEARLMAN

Department of Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. The continuous invasion of species on oceanic islands creates constantly changing environments with evolving species interactions. The composition of gecko communities on oceanic islands provides a unique opportunity to study important ecological questions regarding species interactions, with multiple species living and interacting in sympatry. Previous research studies have observed the distribution and behavioral interactions with regards to aggression and territoriality of gecko species in the Society Islands, including observations of the recent invader, *Hemidactylus frenatus* after. Studies have shown *H. frenatus* displacing resident gecko diversity throughout its invaded range, thus indicating the composition of gecko communities may be changing in order to adapt. Studying dietary behaviors may provide answers to how these geckos are surviving and distributing throughout their environment. This study aimed to better understand the gekkonid communities on the island of Moorea by comparing their diet and foraging success. An observational study of feeding behavior was used to evaluate the difference in prey types consumed by the species of geckos. In addition, an experimental study evaluated prey identification techniques. Results suggest that the three different species of geckos demonstrate different dietary preferences and that geckos are using techniques other than olfactory identification to choose prey. The findings from this study provide insight into the interspecies relationships within gecko communities on the island of Moorea, and provide further evidence that diet could be reflecting or causing a shift in the distribution of gecko species.

Key words: *dietary preference; Gekkonidae; invasive species; Moorea, French Polynesia; competitive interactions; habitat distribution*

INTRODUCTION

Invasive species can cause major shifts in habitat distribution and resource partitioning among native species. Invasive species have the ability to rapidly adapt to new environments in addition to displacing native species through competition. Competitive exclusion has been an increasing problem throughout the world (Mooney and Cleland 2001). The effects of invasion are even more extreme on an island, as resources are limited and habitats are greatly altered by invasive species. When an invasive arrives, it tends to act as a generalist and monopolizes habitats and food sources that were previously dominated by native species (Oboyski 2014). In the Pacific Basin, there have been three separate waves of human migration that have contributed to the distribution of plants and animals (Case et al 1994). The introduction of new species has led to competitive displacement and, in some cases, extinction of native insects, plants, and animals (Mooney

and Cleland 2001).

Lizards in the Gekkonidae family arrived on Moorea with all three human movements, in addition to the possibility of arriving on their own (Fisher 1997, Reeder 2005). The four species of geckos on Moorea are: *Gehyra oceanica*, *Gehyra mutilata*, *Lepidodactylus lugubris*, and *Hemidactylus frenatus*. All of these species have arrived at different times and through different means of transportation. *Gehyra oceanica* is thought to have the ability to migrate throughout the Pacific on its own, suggesting the possibility of a natural arrival on Moorea in addition to arriving as commensals (Fisher 1997). Other species such as *L. lugubris* and *H. frenatus* arrived later as human commensals and have caused changes in the distribution of the native gekkonid species in recent years (Moritz et al. 1991). The gecko communities of the Pacific islands provide the opportunity to study important ecological questions about competitive species interactions and habitat preference (Moritz et al. 1993).

As multiple species of geckos share the same habitat and resources, it is possible that competition for food has lead to displacement of native gecko species (Klawinski et al. 1994). Alternatively, various species could demonstrate different dietary preferences due to insect preference, thus suggesting that the cause of displacement in the native geckos is due to the pursuit of certain insect types (Klawinski et al. 1994). Determining whether native and invasive geckos target the same types of insects gives insight as to whether the native species have adapted to the change in resources caused by displacement, or how the species differ in terms of prey preference.

Study of the dietary preference of the Gekkonidae species is needed for an understanding of how, and if, the geckos are demonstrating food preference. It not entirely understood whether geckos are choosing their prey. If there is choice, clarification on how choices are made is necessary (Cooper 1998). It has been observed that geckos do not eat the insects known as the false blister beetles on the island of Moorea (Oboyski, 2014). Two types of false blister beetles from the Oedemeridae family are found on the island. The false blister beetles produce the chemical cantharidin, the same chemical found in Spanish fly that causes the blistering of human skin. In other studies, cantharidin has been proved to act as an antifeedant (Carrel et al. 1986). Previous studies have not identified why geckos avoid the false blister beetles, but it is possible that the geckos are avoiding the cantharidin chemical itself using olfactory cues. The false blister beetle acts as a model to test whether geckos are using olfactory cues to demonstrate dietary preference.

This study consisted of a mark and recapture component to establish the population size of *H. frenatus*, *L. lugubris*, and *G. oceanica* on the UC Berkeley Gump Field Station. A dietary study then evaluated the foraging success and dietary presence of each species. The study observed the consumption of insects from the order Isoptera (termites), Lepidoptera (moths and butterflies), Diptera (flies), and Coleoptera (beetles). Such analysis was designed to give insight as to whether the recently established *H. frenatus* is a better forager than *G. oceanica* and *L. lugubris*. The observational study also helps to understand whether the species differ in dietary preference and how this could be either affected by or altering the distribution gekkonid species. A final experimental study will evaluate whether olfactory cues are the

primary source of prey identification using the false blister beetle as a model.

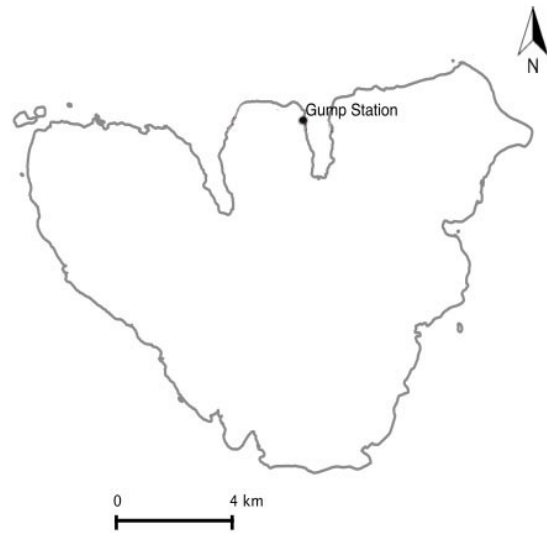


FIG. 1 Location of study site on Moorea, French Polynesia.

The goal of this study is to provide a comprehensive understanding of resource partitioning and habitat distribution among Moorean gekkonid species. The study strives to establish differences in dietary preference by evaluating population densities, foraging success, prey choice, and prey recognition techniques. I hypothesized that the native gecko species, *G. oceanica*, will demonstrate the lowest population abundance within the given study site and will be the least successful forager. In addition, I hypothesized that there will be a difference among the species with regards to dietary preference of insects, and that all gecko species will use olfactory cues in order to distinguish prey.

MATERIALS AND METHODS

To quantify dietary preference of gekkonid species, I conducted both surveys and experimental studies of gecko individuals on the island of Moorea, French Polynesia from October 14 to November 20, 2014.

Study site

Moorea, an island in the Society Archipelagos, has been colonized by humans and demonstrates a variety of different manmade structures throughout the island. Gecko species are found in abundance in areas of high human disturbance. All observations were conducted on the buildings found on the

Gump Station, located on the West side of Cook's Bay (17°29'20.12"S, 149°49'33.04"W). Geckos were observed on the external surfaces of the dorm and laboratory buildings between the hours of 17:00 and 23:00. All laboratory trials were conducted on the station as well.

Study organism

The system used in this study was composed of three species in the family Gekkonidae, *G. oceanica*, *L. lugubris*, and *H. frenatus*. All species arrived at different times, with the most recent introduction being that of *H. frenatus*. All individuals were captured using hand capture methods, at which time the size, age class, sex, and species were recorded. Size was recorded as a measure of snout-vent-length (SVL) in millimeters, which was measured from the anterior tip of the individual to the opening of the cloaca along the middle of the ventral surface of the body (Stebbins 2003). Age class was determined by SVL, individuals with an SVL greater than 4cm were considered adults. Males were identified by the presence of enlarged femoral pores and a swollen tail base. Some juvenile individuals with underdeveloped sex organs were not classified by sex (Zug 1991).

Population estimate

In order to estimate the population size of *G. oceanica*, *L. lugubris*, and *H. frenatus*, a mark and recapture study was performed on the Gump Station. Sampling was limited to the walls of the dorm building. During the sampling sessions, individuals of each species were captured, marked, and released. Marking was done with a drop of non-toxic paint on the dorsal side of the individual following the animal care and use permit. Age class, sex, SVL, and species were recorded for each individual after capture. The number of recaptured individuals was recorded as well.

The study was designed to meet the assumptions of a closed population mark-recapture model with more than two capture sessions. There were two assumptions for the desired model; 1) there is no birth, death, or emigration during the study, 2) marks are not lost (Letting and Armstrong 2003). Six sampling sessions occurred on the nights of Oct. 24, Oct. 28, Nov. 1, Nov. 4, Nov. 7, and Nov. 10. On the first night, geckos were captured until five individuals of each species were found. The remaining sessions consisted of capturing as many individuals as possible

in a three hour time period. All captures were done by hand.

Calculations of population estimates were made using the Schnabel index (Kingsolver 2006, Brown n.d.):

$$N = \frac{\sum_{i=1}^m M_i C_i}{\sum_{i=1}^m R_i}$$

where N = population size estimate, M_i = total number of previously marked animals at time i, C_i = the number caught at time i, and R_i = the number of marked animals at time i.

Dietary observation

The foraging success and prey preference of individual geckos was analyzed separately for each species using observational studies. Individuals of each species, including those of varying sizes and age classes, were found and observed on the external walls of the dorm. Using a headlamp for lighting when necessary, each individual was watched with the naked eye for 30 minutes and each feeding attempt, successful prey capture, and type of prey consumed was recorded along with any interactions with other gecko individuals during the time of observation. All observations where the individual was not successfully tracked for the entire 30-minute period were excluded from analyses. Prey insects were identified and classified by order.

The average number of insects of each order consumed by an individual gecko was used for comparison of dietary preference among the different species. Such an average was achieved by averaging the total amount of an insect type consumed by one gekkonid species with respect to the total number of individual geckos observed for that species.

Prey identification experiment

Beyond the feeding observations, experimental trials were performed in order to gain an understanding of feeding behavior and the mechanism of prey identification of gekkonid species. One gecko individual was placed in a terrarium and was allotted a two-hour adjustment period before observation. After adjustment, insects were added and

gecko behavior was observed for two hours. The terrarium was lit at one end in order to localize the congregation of insects. As a control, seven trials were conducted with individuals of varying gekkonid species. Anywhere from four to six un-altered insects were added in addition to at least one false blister beetle of each kind. The remaining seven trials followed the same methods, but the insects presented were contaminated with the scent of the blister beetles. The geckos were then monitored and the number of attempts and captures were recorded along with the type of prey consumed. Any attempts made on insects on the external surface of the terrarium were recorded.

In order to transfer the scent of the false blister beetle to the other insects, the beetles were caught and then smashed in a vial. Live insects were then immediately added to the vial of smashed blister beetles and forced to either come in direct contact with the beetles or were manually brushed with a smashed beetle. Insects from the orders Isoptera, Lepidoptera, Diptera, and Coleoptera were presented to the geckos in captivity after being inoculated with crushed up false blister beetles. In addition, at least one live false blister beetles of each kind was added. After two hours of observation, the species, weight, SVL, sex, and age class were recorded. The study was conducted with the intention of understanding whether geckos use olfactory cues to decipher preferable prey options. Each individual was re-released as close to the site of capture as possible. All terrariums used for trials included a water source and a structure for shelter. All work conformed to the guidelines of the UC Berkeley Animal Use Protocol.

Statistical methods

Data was analyzed using the statistical software package R. A Chi-Square test was used to compare the insect consumption of the three species of geckos. The affect of species and size on foraging success was compared using the ratio of captures to attempts and analyzed using Ancova, an analysis of covariance. The experimental study was analyzed using ANOVA in order to demonstrate the significance of olfactory discrimination with regards to prey choice.

RESULTS

Population estimate

The mark and recapture study proved that *G. oceanica* demonstrates the smallest population of the three gekkonid species evaluated in this study. Using the Schnabel index, the estimated population size of *G. oceanica* was 56.5. *Hemidactylus frenatus* demonstrated the next smallest population of 75.6, followed by *L. lugubris* with an estimate of 79.8. Only five *G. mutilata* individuals were found, therefore the population was not studied in any part of this project.

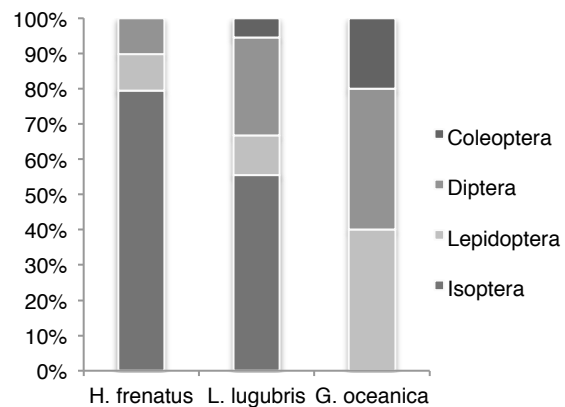


FIG. 2. Bar plots of prey, grouped by order, demonstrating the diet composition of each gekkonid species. Chi-squared, ($\chi^2=17.3368$, $p=0.008122$).

Dietary observation

Dietary analysis provided information on foraging success and prey preference of three different gekkonid species. A significant difference among the dietary preference of gekkonid species was found using a Chi-Squared test ($\chi^2=17.3368$, $p=0.008122$, Figure 2). *Hemidactylus frenatus* had a diet that consisted of an average of 2.8 Isoptera, 0.36 Diptera, 0.36 Lepidoptera, and 0 Coleoptera per individual. *Lepidodactylus lugubris* had a diet that consisted of an average of 0.9 Isoptera, 0.45 Diptera, 0.18 Lepidoptera, and 0.09 Coleoptera per individual. *Gehyra oceanica* had a diet that consisted of an average of 0 Isoptera, 0.22 Diptera, 0.22 Lepidoptera, and 0.11 Coleoptera per individual (see Table 1). Throughout the feeding observations, the geckos were not observed getting closer than 1cm to a false blister beetle and no attempts to consume a false blister beetle were made.

Hemidactylus frenatus presented with an overall higher number of feedings than the other two species. Using the ratio of captures to attempts, no indication was found that suggests species or size affect the foraging success of geckos. An analysis of covariance was used to compare the relationship between species, SVL, and foraging ratio (Ancova, $p=0.0559$).

Prey identification experiment

In the seven experimental trials evaluating the prey identification technique of geckos, two of the geckos were observed foraging. In both foraging instances, the geckos ate insects presented with the scent of false blister beetle. One gecko ate two contaminated black flies of the order Diptera, and the other ate a contaminated termite of the order Isoptera. In the seven control trials, three instances of

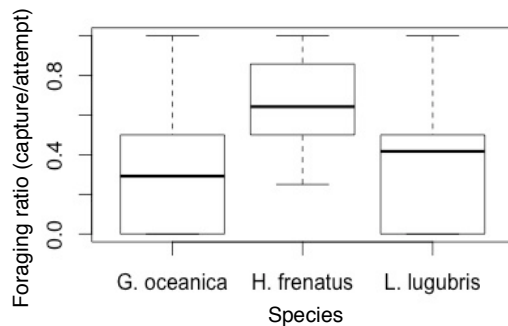


FIG. 3. Boxplots of foraging ratio of gekkonid species. Ancova, ($F=0.353$, $p=0.559$)

foraging occurred and feeding was apparent during each foraging event. The control trials demonstrated the consumption of one insect from each of the orders Isoptera, Diptera, and Lepidoptera. There was no significant difference between the consumption of scented and non-scented insects (ANOVA, $p=0.611$). No attempts were made on a false blister beetle in any trial. Observations during the trials showed multiple instances where the gecko attempted to consume insects on the outside of the terrarium.

DISCUSSION

Population estimate

In order to successfully perform the mark and recapture study, a few conditions and assumptions were met. First, the study was modeled for a closed population, meaning

that births, deaths, emigration, and immigration were limited during the time of study. Closure of the study can be assumed due to the short time period of two and a half weeks (Lettink and Armstrong 2003). The second condition, that marks are not lost, can be considered met due to the frequency of molting. Molting occurs every 4-5 weeks, which allows for the assumption that the majority of individuals would retain their skin through the duration of the study (Stebbins, 2003). The recommended minimum of five sampling sessions was satisfied with six nights of sampling (Otis et al. 1978).

There is a noticeable difference between the population size of *G. oceanica* and the other gekkonid species. As expected, *G. oceanica* presented with the smallest population estimation. It has been observed that *G. oceanica* and *L. lugubris* have been disturbed by the recent invasive of *H. frenatus* (Tonione et al. 2011). In this case, the competitive interactions between the species could be causing the displacement of *G. oceanica*. Though the population estimate of *L. lugubris* was the largest, it is not significantly different than *H. frenatus*, suggesting the displacement of *G. oceanica* could be due to the interactions with *L. lugubris* as well.

A previous Moorea class study showed that *H. frenatus* are found exclusively on and around man-made structures, where *L. lugubris* and *G. oceanica* were found in a variety of environments at different elevations (Reeder, 2005). Reeder also found that *G. oceanica* and *L. lugubris* were responsive to the presence of each other, but not to *H. frenatus*. The study suggests that the small population estimate of *G. oceanica* could be attributed to the presence of the other two species in the same habitat.

It is also possible that the difference in distribution is the result of a difference in habitat preference. Geckos could be choosing their habitats based off of food availability, competition, predation, type of available shelter, temperature, and humidity along with other factors (Schlesinger Shine, R. 2004). A difference in habitat preference could cause a shift in the population size of gekkonid species present on the dorm of the Gump station. Overall, more studies are necessary to determine the causes of distribution differences among the different gekkonid species, but the results show that *G. oceanica* has the smallest population of the three species observed.

Dietary observation

The observational study demonstrated a strong correlation between the species of gecko and the type of insect consumed. Insect availability could have a large impact on the diet of geckos. The population study showed a difference in microhabitat distribution with a geographic separation of territory establishment between the different species of geckos. Each habitat, and the territories within it, could support a different selection of insects available for consumption. This type of habitat difference could contribute to the difference in diet of the gekkonid species.

A flux in the amount of insects present in each microhabitat could also contribute to the difference in diet of the geckos. Termite blooms throughout the duration of the study provided an interesting opportunity for observation of dietary behavior. On three different occasions, the termite bloom provided access to hundreds of termites. The termites would congregate around the light sources, thus providing a gecko found nearest a light source the best opportunity for termite consumption. It was observed that *H. frenatus* and *L. lugubris* had established a higher concentration of territories around the light sources than *G. oceanica*. Such territory establishment could mean that *G. oceanica* are not able to establish the territories around the light sources, or they prefer territories elsewhere.

Though *H. frenatus* presented with an overall larger number of feedings, there was no significant finding suggesting that one species was more successful at catching insects than another. Such indication shows that all species, when given the opportunity, have the same likelihood of capturing an insect when foraging attempts are made. The difference in the total number of captures could be related to the fruitfulness of an individual's territory and habitat. There was a period of about two weeks during the study when less insects were found all over the dorm due to the use of insecticide on the Gump Station Facilities. The use of insecticides could have skewed the results of the study and should be considered when conducting similar studies in the future.

Throughout the observational study, not one false blister beetle was consumed. Approaches were observed, but no gecko was seen within 1cm of the beetle. The avoidance of the blister beetle is likely due to the production of cantharidin, which has been a known antifeedant in other dietary studies (Carrel et al. 1986).

Prey identification experiment

The prey identification trials do not provide evidence to support the hypothesis that geckos use olfactory cues to decipher between prey. The results show no distinction between the consumption of scented and non-scented insects, therefore it can be concluded that the geckos are using a non-olfactory method of identifying prey. It is possible that multiple types of prey identification methods are used, but it is clear that scent is not the only one. Observations of feeding attempts made on insects on the outside of the terrarium suggest that the geckos could be using visual cues to distinguish between desirable and undesirable prey. In order to establish the use of visual identification, further studies are necessary. In general, a larger amount of trials would greatly enhance the results of the study. The small amount of trials could be limiting the results, as not every gecko was observed foraging.

Conclusion

In conclusion, the dietary preference and foraging behavior observed in this study demonstrate the complexities of interspecies interactions of multi-species gecko communities on an oceanic island. With the smallest population estimate, *G. oceanica* demonstrated a significantly different diet than both *L. lugubris* and *H. frenatus*. Why the geckos demonstrate different prey consumptions and how this relates to distribution remains uncertain. Is a gecko choosing its habitats based on the insect selection that inhabits it or is a gecko's diet altered by its ability to establish "preferable" territories? The findings of the study show that geckos are deciphering between prey due

TABLE 1. Comparison of average number of insects from each order per individual gecko.

Species	Isoptera	Lepidoptera	Diptera	Coleoptera
<i>H. frenatus</i>	2.82	0.36	0.36	0.00
<i>L. lugubris</i>	0.91	0.18	0.45	0.09
<i>G. oceanica</i>	0.00	0.22	0.22	0.11

to the avoidance of the false blister beetle. In the dietary analysis, experimental trials proved that geckos use prey identification techniques other than olfactory cues in order to decipher between prey. Together, these results prove that the different gekkonid species demonstrate insect preference and are identifying unwanted prey with techniques other than olfactory recognition. Future studies should test if the dispersal patterns of geckos are caused by dietary preference and seek to answer the question: are native species adjusting dietary habits in order to adapt to the presence of invasive species?

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APPENDIX A

TABLE 2. Identification key for four gekkonid species found on Moorea.

Species	Coloration	Markings	Distinct Body Identifications	Characteristics
<i>G. oceanica</i> (pacific gecko)	White/ yellow ventral coloration, mottled brown and pale brown	Orange stripe across hind toes, broad pale brown bands on tail	Wide/ oval toe pads, tail tapered steadily from the base Adult male – large heads with robust masticator muscles and thick jowls	Skin peels easily, SVL up to 18 cm
<i>G. mutilata</i> (four-clawed gecko)	Purple/ pink gray skin	Dark toe pads, evenly spaced tubercles along the tail		Delicate skin
<i>L. lugubris</i> (mourning gecko)	Pale coloration	Distinct chevron pattern that extends from tip of prehensile tail to nape of the neck	Shiny eyes with gold flakes	Parthenogenetic, smooth skin, SVL ~ 45 mm
<i>H. frenatus</i>	Light/ translucent color	‘V’ shaped markings at top of spine, blunt tail tubercles	Reduced digit in the 3-4 position of front foot and 4-5 of hind foot	

FIG. 4. *Hemidactylus frenatus*



FIG. 5. *Lepidodactylus lugubris*



FIG. 6. *Gehyra oceanica*

