ECTOPARASITE PREFERENCE AND DISPERSAL ACROSS GEKKONID LIZARDS AFTER RECENT INVASION OF HEMIDACTYLUS FRENATUS ON AN OCEANIC ISLAND (MOOREA, FRENCH POLYNESIA)

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Abstract. The composition of gecko communities on oceanic islands provide unique opportunities to study fundamental questions in ecology, with four gecko species living and interacting in sympatry. Ectoparasite studies may provide novel theoretical support for these important community interactions. Earlier research documented the first occurrence of a parasitic mite hosting on gecko species in the Society Islands. The study was conducted shortly after the introduction of the invasive gecko, Hemidactylus frenatus. H. frenatus is observed with high parasitic mite intensities and is known to displace resident gecko diversity throughout its invaded range. This study aimed to better understand the relationship between parasitic mites and their gecko hosts, and quantify the compositional changes within the host community since the introduction of H. frenatus to Moorea. A field survey of the abundance of ectoparasites on host species was used to determine if ectoparasites were more common on H. frenatus than the resident species, or more prevalent in habitats with high densities of H. frenatus. Results suggest that ectoparasites prefer H. frenatus to the resident gecko species, and are in more abundant in areas with high H. frenatus densities. The findings from this study provide insight into the ectoparasite-host relationships within gecko communities on the island of Moorea, and provide further evidence of competitive displacement of resident gecko species by invasive *H. frenatus*.

Key words: ectoparasites; Gekkonidae; invasive species; Moorea, French Polynesia; competitive displacement; Hemidactylus frenatus, resident diversity

INTRODUCTION

Long-distance dispersal between isolated islands has been of interest to biogeographers for centuries (Wallace 1881). Lizards, birds, and bats are the terrestrial vertebrate groups that have been the most successful at long distance dispersal, and due to this have been the subject of much discussion (MacArthur and Wilson 1967). There are two basic ways that species of lizards can disperse across ocean barriers to isolated islands: naturally rafting on floating mats (Wallace 1881) or human mediated dispersal in canoes (Fisher 1997). In the Pacific Ocean, human mediated dispersal has been invoked as the main mode of transport for lizards to many islands (Beckon 1992). The Pacific Basin has experienced three separate waves of human movements and each has been implicated in the dispersal of various plants and animals across the Pacific (Case et al. 1994). Polynesians began dispersing from southern Asia over 3000 years ago, and Europeans began arriving 300 years ago and continue

today (Case et al. 1994). Lizards in the Gekkonidae family invaded the remote islands of the Pacific through human vectors with each of these movements (Reeder 2005). The gecko communities of the Pacific islands have dynamic compositions and provide opportunities to study fundamental questions in ecology, such as competitive species interactions, and microhabitat preference (Moritz et al. 1993). In locations where multiple gecko species coexist, one species usually dominates and monopolizes an ideal microhabitat and there are many factors that contribute to a species competitive advantage (Hanley et al. 1998).

Competitive displacement of one or more species by another can occur when attacks by a predator or parasite on one species increases the presence of the second species (Holt 1997). This is especially true if non-indigenous species can gain an advantage over native competitors via apparent competition (Holt 1997) mediated by their shared parasites. Introduced geckos host an array of mite parasites. These ectoparasites, in the genus

Geckobia, are known to feed on the blood of lizards and can transfer inter and intraspecifically among gecko individuals (Hanley et al. 1995). Pterygosomatid mites cause many negative effects on their gecko hosts including dehydration, lethargy, anemia, chronic debility from blood loss, and dermatitis Parasites can give an (McKeon 2004). advantage to an invading species when the invader (1) introduces a new parasite that has a greater detrimental effect on the resident species than on the invader, (2) is less susceptible to endemic parasites than the (3)resident, and/or increases susceptibility of the resident to parasites (Hanely et al. 1995). The spread of invading geckos carrying high ectoparasite loads could be a threat to the resident diversity of geckos.

Behavioral experiments on the geckos of the Pacific islands have shown that the invasive house gecko Hemidactylus frenatus displaces resident gecko species populations by means of exploitation and interference competition (Case et al. 1994). The mites present on *H. frenatus*, could allow them to be superior competitors against resident species Lepidodactylus lugubris, Gehyra oceanica, and Gehyra mutilata. The interactions between H. frenatus and the other gecko species on the islands are characterized as a form of apparent competition; as the invading species increases in abundance, the parasite prevalence increases, which leads to the decline of the more resident species (Holt 1997). In Hawaii, parasites are known to have transferred from

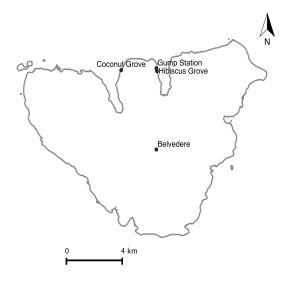


FIG. 1. Location of survey sites on Moorea, French Polynesia.

invading *H. frenatus*, to *L. lugubris* (Hanley et al. 1995). Interactions among organisms have major impacts on community structure, and it is possible that parasites contribute to considerable niche partitioning and community compositions (Chen et al. 2011).

There are at least four species of gecko on Moorea in the Society Islands: Gehyra oceanica, Gehyra mutilata, parthenogenic populations of Lepidodactylus lugubris, and the most recently introduced Hemidactylus frenatus. It is widely assumed that each species was carried by a human vector with varying introduction times. L. lugubris is assumed to be the most resident, invading during the ancient Polynesian movement, while H. frenatus is assumed to be the most recent, invading just over two decades ago (Reeder 2005, Tonione et al. 2011). H. frenatus, G. oceanica, and G. mutilata have all been recorded carrying ectoparasites, many of which are novel to areas of recent introduction (Hanley et al. 1995, McKeon 2004), such as Moorea. Earlier research by Andrew McKeon (2004) revealed that the two invading Gehyra species were infected with mites while no mites were found on the resident gecko, L. lugubris (McKeon However, he did not survey the ectoparasite loads of invading gecko species, H. frenatus, leaving open the question of whether individuals of this species transfer mites to resident species on Moorea. Across the Pacific, H. frenatus has competitively displaced L. lugubris and G. oceanica in urban and suburban settings (Case et al. 1994). Reeder (2005) found that distributions of *L*. lugubris, H. frenatus, and G. oceanica on Moorea are consistent with those found elsewhere in the Pacific. This suggests that parasitic mites are more likely to transfer between species in areas where interspecific interactions are high. The ectoparasite survey conducted McKeon (2004) revealed that L. lugubris individuals contained no mites, interspecific interactions and microhabitat preference were not taken into account.

In the present study, the four gecko species present on Moorea, French Polynesia were surveyed for ectoparasite intensities. Detailed observations made each individual's microhabitat preference and interactions with *H. frenatus*. Based on a previous study conduced by Hanley (1995), it is predicted that *H. frenatus* individuals will have the largest ectoparasite loads. I predicted that individuals of the other three species, *G. oceanica*, *G. mutilata*, and *L. lugubris* will have lower ectoparasite loads in comparison to *H.*

frenatus. The individuals caught in microhabitats where *H. frenatus* are not present should have no ectoparasites present. *H. frenatus is* predicted to be a vector for ectoparasite spread and dispersal, and individuals found in microhabitats dominated by this species will have high ectoparasite intensities.

METHODS

To quantify patterns of ectoparasite abundance on the four gekkonid species on the island, I conducted a survey of gecko individuals on Moorea, French Polynesia (17°30′S, 149°50′W) from October 15 to November 20, 2013.

Study site

Moorea, an oceanic island located in the Society Archipelagos, encompasses an area of 133km² and has varying habitats including both native and invasive vegetation. laboratory trials were conducted on the Gump Station, located on the West side of Cook's Bay with an elevation range of 20 meters. Surveys were conducted at four sites on Moorea (Fig. 1), two sites of low human disturbance, and two of high human disturbance. species dwell in high abundances in human disturbed habitats, so each site had a degree of disturbance. The Gump Station (17°29'20.12"S, 149°49'33.04"W) and coconut grove (17°29'29.72"S, 149°51'01.69"W) were classified as sites with high human disturbance, both consisting of man-made buildings varying in size and are surrounded by coastal tree species. The Belvedere (17°32′25.17″S, 149°49′36.69″W) and hibiscus grove (17°29'35.05"S, 149°49'34.14"W) were classified sites with low human as disturbance, both 10 meters away from a road. These sites were chosen due to confirmed presence and relatively high abundance of Gehyra oceanica, Gehyra mutilata, Hemidactylus frenatus, and Lepidodactylus lugubris during preliminary surveys of the island.

Study organisms

The host system used in this study was composed of four species in the family Gekkonidae, *G. oceanica*, *G. mutilata*, *H. frenatus*, and *L. lugubris*. A total of 201 specimens were caught throughout the study. Surveying was conducted between the hours of 15:00 to 23:00. In the study sites, all feasible individuals were caught using hand capture

or standard lizard noose capture. Following capture, size, age class, sex, and species was 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 for using snout-vent length species individuals measurements, surpassing a specific SVL were recorded as adults, and individuals smaller than the set length were recorded as juveniles. Enlarged femoral pores and a swollen tail base identified males and females were identified by a lack of enlarged femoral pores and swollen tail base (Zug, 1991). Some juveniles had underdeveloped sex organs and sex could not be recorded. Species identifications were determined using three visible characteristics: 1) chin shields, 2) toe lamellae and 3) tail scales (McKeown, 1978, Zug, 1991).

Ectoparasite survey

Mite prevalence and intensity was recorded for each individual caught. Mite prevalence was recorded as a presence (1) or absence (0) of mites and mite intensity was recorded as the number of mites per individual. A visual count of mites was noted, by eye, by looking at the individual gecko in great detail. Mites appeared as bright orange or red dots and were located on the limbs, head, dorsum, venter, tail, and toes of the specimens (Appendix A). Body location of mites on the individual was recorded. Mite voucher specimens were collected for identification. Upon capture, the microhabitat of each individual gecko was recorded.

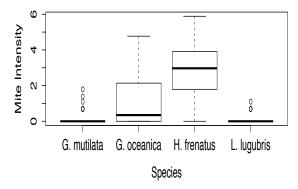


FIG. 2. Boxplots of the log of mite intensities for the four gecko species on Moorea. Ancova, (F=65.3, p<0.001).

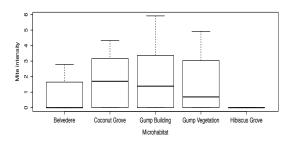


FIG. 4. Boxplots of the log of mite intensities at the four survey sites. Ancova, (F=3.9, p=0.004).

Microhabitat was described by the substrate of collection location, proximal vegetation, and closest man-made structures. Species densities were observed and recorded for each microhabitat as a count of the number of species. individuals present of each Individuals were marked with non-toxic paint and released to their exact location of capture after data was recorded. Data from the ectoparasite survey was compared to data collected from a similar study in 2004 (McKeon, 2004) to compare differences in gecko species composition.

Ectoparasite transfer trials

Forty trials were performed to test for ectoparasite transfer and attachment. To test for ectoparasite transfer between two individuals, five trials were performed in which one mite infested *H. frenatus* was placed in a 10 Liter terrarium with one *L. lugubris, G. oceanica,* or *G. mutilata* with no mite prevalence. *H. frenatus* was chosen as the infected host due to the high mite intensity observed on most individuals, all infested *H. frenatus* individuals used in the trials had a mite intensity of thirty or higher. As a control,

five trials were performed using two *H. frenatus* individuals, one infested with mites, and the other with mites removed. The two individuals were kept in the terrarium for a ten-hour period whilst species interactions were recorded. After the ten-hour trial, the individuals were again measured for mite prevalence and intensity. Spearman's Rank Correlation (McKeon, 2004) was then used to test for a correlation between initial mite intensity and mite transfer.

To test for mite attachment, twenty trials were performed where mites were directly transferred, by hand, from a H. frenatus individual, to a L. lugubris, G. oceanica, G. mutilata, or H. frenatus individual with no original mite prevalence. After direct mite transfer, the individual was kept in a terrarium for ten hours in isolate. After the ten-hour trial, the individual was checked for mite attachment. Data collected from these trials were used to support the hypothesis that all four species are viable hosts for parasitic mites. All terrariums used for trials included a water source. No individual was returned to the field with more mites than originally recorded and all work conformed to the guidelines of UC Berkeley Animal Use Protocol T042-0814.

Statistical Methods

All data was analyzed using statistical software package R (R Development Core Team 2013). Measurements of ectoparasite intensities as it relates to sex, species and habitat were tested using analysis of covariance (ANCOVA) and Tukey tests. A Pearson's chi-square test was used to test the relationship between species and habitat and species and mite placement. A Pearson's chi-square test was also used to test for a relationship between ectoparasite intensities

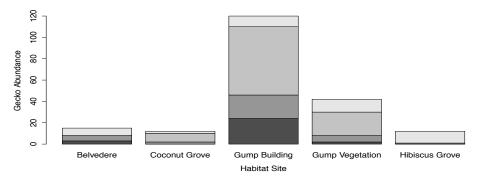


FIG. 3. Barplots of gecko species abundances at the four survey sites. The Gump Station was separated into Gump Building and Gump Vegetation. Pearson's chi-squared, ($x^2=70.94$, df=12, p<0.001).

TABLE 1. Comparison of ectoparasite survey results. (Top) Data collected from the 2004 survey (McKeon, 2004). (Bottom) Data collected from 2013 survey.

	G. oceanica	G. mutilata	L. lugubris	
Total(n)	144	14	24	
n mite prevalence	93	4	0	
% with mite prevalence	65	24	0	
Max/individual	41	5	0	
Mean mite intensity	6.9	3.3	0	
	G. oceanica	G. mutilata	L. lugubris	H. frenatus
Total(n)	36	29	42	94
n mite prevalence	18	6	4	83
% with mite prevalence	50	21	9	86
Max/individual	117	5	2	359
Mean mite intensity	8.4	0.5	0.1	36

of *G. oceanica, G. mutilata,* and *L. lugubris* and *H. frenatus* densities. A general linear model was used to determine the relationship between *H. frenatus* size and ectoparasite intensities. A linear regression analysis was run to test for a correlation between *H. frenatus* densities and *H. frenatus* ectoparasite intensities.

RESULTS

Ectoparasite survey

The ectoparasite survey revealed a significant difference in the ectoparasite intensities of the four species. The abundance of ectoparasites ranged from 1 to 359 mites per individual, and differed among species of geckos, with H. frenatus having significantly more mites (Ancova, F=65.3, p<0.001) than the other species (Fig. 2). H. frenatus individuals had mite intensities ranging from 1-359 with a mean intensity of 36 mites per individual and 83 out of the total 94 were observed with a mite prevalence. G. oceanica individuals had intensities ranging from 1 to 117 with a mean intensity of 8.4 mites per individual and 18 out of the 36 were observed with mite prevalence. G. mutilata individuals had intensities ranging from 1 to 5 with a mean of 0.5 mites per individual and 6 out of the 29 individuals caught were observed with mite prevalence. Lastly, L. lugubris individuals had mite intensities ranging from 1 to 2, with a mean mite intensity of 0.1 mite per individual and 4 out of the total 42 individuals caught were observed with mite prevalence (Table 1).

The ectoparasite survey revealed a significant difference in the distribution of the four species among the sites of varying human

disturbance. Species densities ranged from 0 to 64 individuals per habitat. Sites of high human disturbance, Coconut Grove and Gump Station, had significantly higher abundances of H. frenatus (Pearson's chisquared, $x^2=70.94$, df=12, p<0.001) than sites of low human disturbance, Belvedere and Hibiscus Grove, (Fig. 3). Ectoparasite abundances significantly differed between the four sites (Ancova, F=3.9, p=0.004, Fig 4), as well as species compositions. The sites of high human disturbance had significantly higher mite intensities than the Hibiscus grove, a site of low human disturbance, (TukeyHSD, HG-GB, p=0.005, HG-GV, p=0.034, HG-CG, p=0.05), but did not show significantly different mite intensities than the Belvedere survey site.

A Pearson's chi-squared test yielded significant trends in ectoparasite placement on the four species (Pearson's chi-squared, x^2 =46.66, df=9, p<0.001 Fig. 5). 103 total individuals were found with mite prevalence.

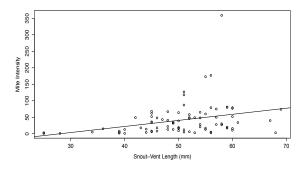


FIG. 6. Mite intensities increase with size of *H. frenatus* individuals. Linear model analysis, (*df*= 79, F=23.81, p<0.001).

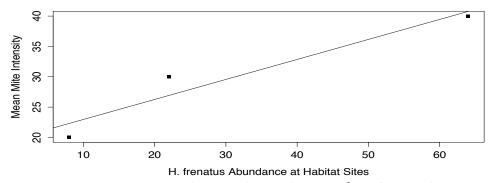


FIG. 7. Mite intensities and positively correlation with H. frenatus densities. Linear model regression analysis, (F=12, R^2 =0.84, p=0.18).

H. frenatus individuals were all found with mites on their limbs while 78% of G. oceanica individuals were found with mites on their ventral area.

For *H. frenatus* individuals, size (Snout-Vent-Length) is a significant predictor of mite intensities (Regression analysis, F=23.81, R²=0.22, p<0.001, Fig. 6). No significant trend was observed between size and mite intensity for the other three species.

Ectoparasite intensities of G. mutilata, G. oceanica, and L. lugubris are greater when they were caught on the Coconut Grove and Gump Station, habitats sites with high H. frenatus densities (Fig. 3). G. mutilata individuals from the Belvedere had a mean mite intensity of 1, compared to a mean mite intensity of 2.2 from the Gump Station (Pearson's chi-squared, x^2 =0.16, df=1, p=0.89, Table 2). G. oceanica individuals from the Belvedere and Hibiscus Grove had a mean mite intensity of 7, compared to a mean mite intensity of 27.6 from the Coconut Grove and Gump Station (Pearson's chi-squared, $x^2=2.86$, df=1, p=0.09, Table 2). Lastly, L. lugubris individuals had no mite prevalence at the Belvedere and Hibiscus Grove survey sites. L. lugubris individuals found at the Coconut Grove and Gump Station had a mean mite intensity of 1.25 (Pearson's chi-squared, $x^2=3.32$, df=1, p=0.06, Similarly, there is a positive Table 2). correlation between the mite intensities of *H*. frenatus and the abundance of H. frenatus (Regression analysis, $R^2=0.84$, Fig. 7).

Using data sampled from Moorea in 2004 as a representative of species compositions, it is clear there have been large species composition changes over the past decade (Table 1). McKeon (2004) sampled 144 *G. oceanica* individuals, compared to 36 individuals sampled in 2013. *L. lugubris*

individuals were observed with no mite prevalence in 2004, 4 individuals were observed with a mite prevalence in 2013.

Ectoparasite transfer trials

No ectoparasite transfer was observed in any of the forty trials. All ectoparasites intensities remained the same for each individual throughout the twelve-hour trial.

TABLE 2. Impact of *H. frenatus* densities on mite prevalence and intensity of the three resident species.

H. frenatus presnet	H. frenatus absent
5	3
2	1
2.2	1
H. frenatus presnet	H. frenatus absent
11	15
8	3
27.6	7
H. frenatus presnet	H. frenatus absent
4	0
20	18
1.25	0
	H. frenatus presnet 11 8 27.6 H. frenatus presnet 20

DISCUSSION

Ectoparasite Survey

There is a strong relationship between ectoparasite intensity and host species. As predicted, *H. frenatus* had an overall higher ratio of individuals with a mite prevalence, as well as higher mite intensities than *G. oceanica*, *G. mutilata*, and *L. lugubris*. This suggests that *Geckobia* mites prefer *H. frenatus* but what

traits lead to this preference are unknown and untested.

The ectoparasite survey supported the statements that all four gecko species reside in areas of high human disturbance (Reeder, 2005). For example, all four species were found in the Gump Station, a survey site categorized as a site of high human disturbance. As predicted, H. frenatus densities were highest in the sites of high human disturbance, they were the most common species found at the Gump Station and Coconut Grove sites. This provides evidence of the growth and spread of H. frenatus because all resident species were rare in comparison to *H. frenatus* densities. This data can also be interpreted to answer about the changing species questions compositions since the invasion of *H. frenatus*. H. frenatus has high densities in areas of high human disturbance but is still absent from the more remote areas, of low human disturbance. This result suggests that gecko individuals in the areas of low human disturbance are currently avoiding direct competition with *H*. frenatus. In the future, it is possible that the areas of low human disturbance will be the only areas left with resident gecko diversity present.

The mean mite intensities significantly higher at the sites of high human disturbance, and that is most likely contributed to the high abundance of H. frenatus individuals at these locations. frenatus is a common factor between the human disturbed habitats and high mite intensities. The impact of *H. frenatus* is clearly seen when looking at the mean mite intensities of the resident gecko species. The results from this study suggest that if individuals of G. oceanica, G. mutilata, and L. lugubris continue to reside in habitats with high H. frenatus densities, the mite intensities of the three species will increase. With even greater samples sizes, I predict these trends will be even more significant. It is possible that give H. frenatus ectoparasites competitive advantage over resident gecko species.

The parasite-host trends from this study contradict past parasitism studies that contribute the post invasion success of introduced species to reduced parasitism (Torchin and Mitchell, 2004). The study observes an opposite trend. *H. frenatus* is an extremely successful competitor on Moorea, yet the species is observed with the highest levels of parasitism by *Geckobia* mites. The

negative effects of the mites may not have detrimental outcomes for the host species like other parasites. The results from this study suggest that ectoparasites do not affect the spread and growth of *H. frenatus* populations.

Distinct ectoparasite trends were observed within *H. frenatus* populations throughout the For example, there is a positive study. correlation between mite intensities and size of *H. frenatus* individuals, higher intensities are observed on larger individuals. This trend could be explained by skin shedding. Mature geckos shed on average, once every 5-7 weeks, but fast growing juveniles, shed almost twice as often. Ectoparasite intensities are shed when a gecko shed their skin (McKeon, 2004). Since smaller juveniles shed more than adults, they are also shedding their mite intensities more than adults. Adult geckos are a longer lasting host for these mites, allowing for more time for mites to attach, host, and reproduce.

There is a significant relationship between host species and mite placement along the body. Mites are currently only identified to the genus level, but this ectoparasite community could be multi-species, with different species specializing on different areas of the host body.

Large species composition changes have occurred on Moorea over the past decade, since the invasion of *H. frenatus*. *G. oceanica* is becoming rare in comparison to *H. frenatus* densities, a sign of resident diversity displacement. One decade ago, no *L. lugubris* individuals were observed with mites. Just nine years later, mites have spread to resident species as *H. frenatus* populations continue to spread and displace these resident species.

Ectoparasite transfer trials

In the space and time provided for the laboratory trails, no mites successfully transferred or attached to individuals with no original mite prevalence. Within the large terrariums, no direct contact occurred between individuals suggesting that extended direct contact may be necessary for mite transfer to occur between individuals. Because geckos shed their ectoparasites when they shed their skin, it is possible that mites are transferred to a new host once they have been released from an individuals' body onto free habitat substrate, but this has yet to be tested. Because all four species were found with mite intensities in the survey, it is clear that all four species are viable hosts for parasitic mites, but the significant difference in mite intensities between the four species leads to the assumption that some species are more preferred by ectoparasites. Future research is crucial to better understand parasite-host relationship within this community.

Conclusion

In conclusion, parasites are common and important components of oceanic island ecological communities. This study highlights ectoparasite trends within a multi-species gecko community on an oceanic island. Mites were found in higher intensities on H. frenatus but why this trend exists remains uncertain. Is H. frenatus a more preferable host or do they tend to exist in habitats where mite transfer rates are higher through environmental vectors? Resident gecko species have higher mite intensities in areas where H. frenatus densities are high. This specific result has conservation implications. If H. frenatus continues to spread at such high rates, it is possible that resident diversity will continue to see an increase in mite intensities. Future studies should test if invasive H. frenatus is a dispersal vector for mites and seek to answer the question: are ectoparasites a factor that contributes to invasion success?

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LITERATURE CITED

- Beckon, W. N. 1992. The giant Pacific geckos of the genus *Gehyra*: morphological variation, distribution, and biogeorgraphy. Copeia, **1992**:443-460.
- Case, T. J., Bolger, D. T., and K. Petren. (1994). Invasions and competitive displacement among house geckos in the tropical pacific. Ecology, 75:464-477.
- Fisher, R. N. (1997). Dispersal and evolution of the pacific basin gekkonid lizards *gehyra* oceanica and *gehyra mutilata*. Evolution,

- 51(3):906-921
- Hanley, K. A., Petren, K., and T. J. Case. (1998). An experimental investigation of the competitive displacement of a native gecko by an invading gecko: No role for parasites. Oecologia, **115**:196-205.
- Hanley, K. A., Vollmer, D. M., and T. J. Case. (1995). The distribution and prevalence of helminths, coccidia and blood parasites in two competing species of gecko: Implications for apparent competition. Oecologia, **102**(2):220-229.
- Holt, R. D. (1997). Predation, apparent competition and the structure of prey communities. Theorhetical Population Biology, **12:**19-229.
- Hoskin, C. J. (2011). The invasion and potential impact of the asian house gecko (*hemidactylus frenatus*) in australia. Austral Ecology, **36**(3):240.
- Ineich, I. (1998). Distribution of terrestrial reptiles in eastern Polynesia. Atoll Research Bulletin, 318:1-75.
- MacArthur, R. H. and E. O. Wilson.1967. The theory of island biogeography. *Princeton Univ. Press*, Princeton, New Jersey, USA.
- MacNeil, C., Dick, J. T. A., Hatcher, M. J., Terry, R. S., Smith, J. E., and A. M. Dunn. (2003). Parasite-mediated predation between native and invasive amphipods. Proceedings: Biological Sciences, 270(1521):1309-1314.
- McKeon, A. P. (2004). Pterysogamtid invasion: Ectoparsite load as related to maturity across Gekkonidae lizards *Gehyra oceanica*, *Gehyra mutilata*, and *Lepidodactylus lugubris* on Mo'orea, French Polynesia. Biology and Geomorphology of Tropical Islands, **1:**107-113
- McKeown, S. 1978, Hawaiin Reptiles and Amphibians. The Oriental Publishing Co., Honolulu.
- Moritz, C., McCallum, H., Donnellan, S., and J. D. Robert. (1991). Parasite loads in parthenogenic and sexual lizards (heteronotia binoei): Supporting for the red queen hypothesis. Proceedings of the Royal Society London, **244**:145-149.
- Moritz, C., Case, T. J., Bolger, D. T., and S. Donnellan. (1993). Genetic diversity and the history of pacific island house geckos (*Hemidactylus* and *Lepidodactylus*). Biological Journal of the Linnean Society, **48:**113-133.
- R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical

- Computing, Vienna Austria. Retrieved from http://www.R-project.org/.
- Reeder, N. M. M. (2005). The effects of competition on the distributions of three gecko species on Moorea, French Polynesia. Biology and Geomorphology of Tropical Islands, 14.
- Stebbins, R. C. (2003). *A field guide to western reptiles and amphibians* (3rd ed.). New York, New York: Houghton Mifflin Company.
- Tonione, M. A., Reeder, N., and C. C. Moritz. 2011. High Genetic Diversity Despite the Potential for Stepping-Stone Colonizations in an Invasive Species of Gecko on Moorea, French Polynesia. PLOS ONE.
- Torchin, M. E, and C. E. Mitchell. 2004. Parasites, pathogens, and invasions by plants and animals. Frontiers in Ecology and the Environment, 2(4):183-190.
- Wallace, A. R. 1881. Island life or, the phenomenon and causes of insular faunas and floras. Harper and Brothers, Franklin Square, New York, USA.
- Yamashiro, S., Toda, M., and O. Hidetoshi. 2000. Clonal composition of the parthenogenetic gecko, *Lepidodactylus lugubris*, at the northernmost extremity of its range. Zoological Science, **17:**1013-1020.
- Zug, G. R. 1991. Lizards of Fiji: Natural history and systematics. Bishop Museum Press, Honolulu.

APPENDIX A

FIG. 8. Host species, *Gehyra oceanica*, with 3 mites on the upper ventral area.



FIG. 9. Dropped tail of host species, *Hemidactylus frenatus*, with a high mite intensity.

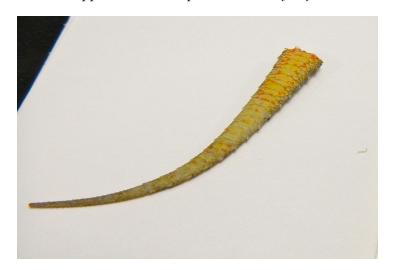


Fig. 10. Host species, *Hemidactylus frenatus*, with mite intensities on its' limbs and toes.

