

## Putative Interactions of Geckos in the Southern Mariana Islands

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**Abstract**—Recent data suggest that the introduced and native geckos, *Hemidactylus frenatus* and *Lepidodactylus lugubris*, respectively, have expanded ranges on Guam to include the entire island. Although additional information suggests that other introduced vertebrates have impacted geckos on Guam, the extirpation of the two largest species of geckos on Guam by an introduced snake greatly contributed to the local range expansion of at least one of the above species. This range expansion by *H. frenatus* may be further circumscribing local ranges of a native gecko (*Gehyra mutilata*).

### Introduction

The Mariana Islands comprise an archipelago of volcanic origin oriented north-south roughly equidistant between New Guinea and Japan. There are 15 major islands with the northernmost, Farallon de Pajaros (Uracas), located at approximately 20°N, 145°E, and the southernmost, Guam, at 13°N, 145°E. The climate of the southern Marianas is tropical with annual diurnal temperatures ranging between 22° and 31°C (Anon. 1990) and rainfall is seasonal (Anon. 1990) with most occurring between June and December.

The herpetofauna of the Mariana Islands has been characterized as depauperate (Rodda et al. 1991), consisting of 13 species of pre-western contact terrestrial reptiles and a number of recently introduced species (McCoid 1993). At this time, Cocos (Dano) Island, a reef island approximately 2 km S of Guam, possesses the most diverse reptile fauna (12 species) of any island in the Mariana archipelago. Declines in the herpetofauna of the Mariana Islands were discussed by Rodda et al. (1991), but most species formerly found on Guam still occur on Cocos Island. There are no native amphibians on the Mariana Islands.

Until recently, the gecko community of Guam consisted of six species, one of which (*Hemidactylus frenatus*) is suspected of being introduced after contact with western societies (Rodda et al. 1991, McCoid 1993). Another species, *Nactus pelagicus*, is terrestrial, saxicolous, and disappeared from Guam after 1945 (Rodda & Fritts 1992). The remaining species (*Lepidodactylus lugubris* [*sensu lato*],

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McCoid & Hensley (1991) identified two clones *vide* Ineich (1988)], *Gehyra mutilata*, *G. oceanica*, *H. frenatus*, and *Perochirus ateles*) are arboreal and have experienced, since 1945, either an increase in relative abundance (*H. frenatus* and *L. lugubris*) or a decrease/extirpation (all other species) on Guam proper (Rodda & Fritts 1992). Both *G. oceanica* and *P. ateles*, along with the remaining species on Guam, can still be found on Cocos Island.

Although factors affecting distributions of gekkonids in the southern Marianas were discussed by Rodda & Fritts (1992), few data on interactions of geckos were presented. I herein present observations and additional data on gecko interactions from several sites on Guam and Cocos Island.

#### HISTORICAL GECKO COMMUNITY

The best historical record of distribution and abundance of geckos in the southern Mariana Islands comes from Sabath (1981), who sampled geckos on Guam in 1969–70 and showed that the gecko community was not uniformly distributed in five surveyed habitats. Equivalent habitats currently found on Guam were discussed by Rodda & Fritts (1992).

No historical study comparable to Sabath (1981) exists for the other islands in the Mariana archipelago, although McCoid & Hensley (1994) suggested that *P. ateles* has never been common on any islands in the Marianas other than Guam and Cocos. Downs (1948) implied that the most common gecko encountered on Tinian in 1945 was *H. frenatus*.

#### PRESENT GECKO COMMUNITY

On Rota, Wiles et al. (1990) described the lizard community as resembling the original fauna more than any other island in the southern Marianas. Wiles et al. (1990) recorded the most sightings of *G. oceanica* on larger surface area vegetation (*Pandanus* sp. leaves and trunks of trees). They also recorded the most sightings of *G. mutilata* on tree trunks. *Lepidodactylus lugubris* was most often observed in tree foliage and on small diameter trees. *Hemidactylus frenatus* was most often observed on man-made structures. Rota harbors the densest population of *N. pelagicus* in the Marianas; this species can be encountered on rocky outcrops (Wiles et al. 1990). The single known specimen from Guam of *N. pelagicus* was collected in 1945 (Rodda & Fritts 1992) in an area with exposed limestone outcrops.

On Tinian, *G. oceanica* is now found in primary, secondary, and tangantangan forests (66% of the island) and abandoned Japanese air-raid shelters, bunkers, and caves (Wiles et al. 1989). *Gehyra mutilata* was judged to be common by Wiles et al. (1989) and occurred in several habitats. *Hemidactylus frenatus* was most commonly recorded in urban situations. *Lepidodactylus lugubris* was recorded at numerous locations including urban areas, but was judged by Wiles et al. (1989) to be less common in urban areas than *H. frenatus*.

At this time on Guam, *H. frenatus* and *L. lugubris* are abundant in all habitats, having successfully invaded forested areas where they were formerly absent (Sabath 1981). Although data are somewhat anecdotal, observations of *H. fren-*

*atus* and *L. lugubris* in urban areas suggest that *L. lugubris* is more homophilic than *H. frenatus* (pers. obs.). The former species tends to be found foraging in well-lighted areas more than the latter species and is occasionally crepuscular or diurnal in the presence of sugar-based food scraps (Sabath 1981; McCoid & Hensley 1993). Additional observations suggest that *L. lugubris* will routinely forage on lighted windows and screens (McCoid & Hensley 1991) while *H. frenatus* generally appears to select window frames and areas adjacent to windows to forage (pers. obs.). There may be some partitioning of oviposition sites in urban areas (McCoid 1994). Collections in non-urban areas of Guam indicated that both species can be equally encountered in forested areas (pers. obs.). *Gehyra mutilata* still occurs in all of Sabath's habitats, but the species is now localized and less abundant than historically recorded (Rodda & Fritts 1992). *Gehyra mutilata* now tends to form dense colonies in or on specific sites or structures and appears to be absent from intervening areas. For example, in some abandoned Japanese air-raid shelters, abandoned wooden sheds, and certain old concrete structures, only *G. mutilata* was found, while surrounding forests and habitats supported *H. frenatus* and *L. lugubris* (pers. obs.). In forests in northern Guam, the now rarely encountered *G. mutilata* may occasionally be found by kicking apart larger termite mounds (G. Rodda pers. comm.). Nocturnal surveys in these same areas ('limestone forest' of Sabath (1981)) yielded only *H. frenatus* and *L. lugubris*. In the few areas on Guam where *G. mutilata* is known to persist as a forest occupant, *G. mutilata* occupied the wide leaves of screw pines (*Pandanus* sp.) and larger trunks of papaya trees (*Carica papaya*), while smaller diameter and width vegetation were occupied by *H. frenatus* and *L. lugubris* (McCoid 1989). Although *G. oceanica* is now very rare on Guam proper and *P. ateles* has been extirpated from Guam proper (Rodda & Fritts 1992), both remain conspicuous on Cocos Island (McCoid & Hensley 1993). On Cocos Island, during the study period between 1988 and 1992, both *G. mutilata* and *L. lugubris* were rare in the developed resort area where *G. oceanica*, *P. ateles*, and *H. frenatus* were common (McCoid 1996).

#### CAUSATIVE FACTORS IN GECKO DECLINES

It is likely that the present intra-island distributions of geckos in the southern Marianas were strongly influenced by habitat damage associated with activities prior to and during WW II (Wiles et al. 1989, 1990). Tinian experienced considerable clearing for sugarcane agriculture prior to WW II (Fosberg 1960) and construction of a WW II U.S. air base occupying approximately 1/2 the island. Although Saipan also experienced considerable clearing and damages associated with WW II, habitat alterations were less extensive than Tinian (Downs 1948). Guam also experienced considerable habitat changes prior to and during WW II (Fosberg 1960). Rota, perhaps the least affected by clearing and WW II activities, remains forested on 60% of the island (Wiles et al. 1990).

The Mariana Islands have endured and now support a suite of introduced vertebrates, some of which may have affected island-wide distributions of geckos. Rodda & Fritts (1992) suggested that an introduced terrestrial shrew (*Suncus murinus*) may have been responsible for the extirpation of *N. pelagicus* on Guam.

Shrews have not yet been introduced to Rota, the only island in the Marianas where *N. pelagicus* is seemingly common. Perhaps the best documented causative agent in changes of a gecko community in the Marianas is the brown tree snake (*Boiga irregularis*). Rodda & Fritts (1992) correlated the decimation of *G. oceanica* and extirpation of *P. ateles* from Guam with the introduction and subsequent irruption of *B. irregularis*. Cocos Island, which is currently *B. irregularis*-free, supports a population of both species.

Until recently, perceived declines in native geckos caused by introduced con-familials were not supported by experimental data. Observational reports (McKeown 1978, McCoy 1980, Gibbons 1985, Jarecki & Lazell 1987, Case & Bolger 1991, Rodda et al. 1991, Zug 1991, McCoid 1993) ascribed declines in native geckos to interactions with introduced *H. frenatus*. However, in Hawai'i, Petren et al. (1993) experimentally manipulated populations of introduced *H. frenatus* and native *L. lugubris* and concluded that *L. lugubris* was behaviorally excluded by *H. frenatus*. These data strongly support Frogner (1967), who suggested that *H. frenatus* displaced *L. lugubris* from refugia and also preyed on juvenile *L. lugubris*. McCoid & Hensley (1993) augmented this portrait and suggested that predation might also play a role in interactions of *H. frenatus* and *L. lugubris* on Guam.

#### PUTATIVE GECKO INTERACTIONS

In the southern Mariana Islands, substantial differences exist between species in snoutvent lengths and masses. Former and current species on Guam, ranked from smallest to largest, are: *L. lugubris* (45.4 SVL mm maximum, 2.3 g maximum, N = 160 specimens examined in this study), *G. mutilata* (52.4 mm, 3.6 g, N = 114), *H. frenatus* (59 mm, 4.7 g, N = 295), *P. ateles* (68.4 mm, 7.6 g, N = 63), and *G. oceanica* (88.5 mm, 17.4 g, N = 24). The invasion and apparent replacement of *G. oceanica* and *P. ateles* in forest habitats on Guam by *H. frenatus* and *L. lugubris* suggest a size component in gecko community structure; the former community structure and distribution on Guam may have been influenced, to some extent, by the presence of the two larger species.

Rodda & Fritts (1992) did not wholly attribute the decline in *G. mutilata* populations to interactions with *H. frenatus* and suggested that predation by *B. irregularis* was also important. The causative agent in declines of both *G. mutilata* and *G. oceanica* has also been singularly identified as *B. irregularis* (Rodda 1992). While there can be little doubt that *B. irregularis* has negatively impacted *G. mutilata* on Guam and may be responsible for patchy distributions, additional observations from Guam suggest an important role for *H. frenatus* in maintaining, at least in certain situations, the present patchy distribution of *G. mutilata*. During 1989 and 1990, efforts were made to capture and/or mark all geckos in a house (McCoid & Hensley 1991) in eastern Guam. Captures of *G. mutilata* in or on the house, which harbored a substantial (but unestimated) population of *H. frenatus*, were usually after 2400 h or on dark backgrounds (the lower outside border of the house was painted maroon). After removal of ca. 30 adult *H. frenatus* from the house during a one-time collection event, *G. mutilata* was subsequently rou-

tinely encountered in the house after dusk. Adjacent to this house was an abandoned shed exclusively occupied by *G. mutilata* that became active at dusk (ca. 1900–2000 h). Although these observations are anecdotal, coupled with accounts of localized distributions presented above, the data suggest that the presence of *H. frenatus* may affect foraging/activity patterns of *G. mutilata* on Guam. On Java, Church & Lim (1961) found that *G. mutilata*, which co-occurred with confamilials (including *H. frenatus*), occupied darker habitats.

Although *G. oceanica* has been assumed to prey on native and introduced geckos on Guam (Rodda & Fritts 1992), the role that *G. oceanica* played in shaping gecko communities in the southern Marianas via predation remains unassessed. Distributional data suggest the presence of *G. oceanica* affects local distributions of *H. frenatus*. On many islands where *H. frenatus* has been introduced, the species remains relatively restricted to urban or disturbed situations (e.g. Solomon Islands, McCoy 1980; Fiji, Zug 1991; American Sāmoa, Schwaner 1980; Rota, Wiles et al. 1990; Tinian, Wiles et al. 1989). On these same islands, *G. oceanica* is a common non-urban/forest species. On islands where *H. frenatus* has expanded its range to include non-urban areas (Hawai'i, McKeown 1978; and Guam, Rodda & Fritts, 1992), large confamilials (e.g. *G. oceanica*) are absent. On the Hawaiian Islands (Beckon 1992) and Guam, *G. oceanica* has either never occurred or has been extirpated.

Tail damage and regeneration in lizards have been used as a measure of intra- and interspecific interactions (Pianka & Pianka 1976, Vitt et al. 1977). On Guam and Cocos Island, using tail-break frequencies, it is possible to estimate intra- and inter-specific interactions of extant geckos. Comparison of two study sites with respect to tail-break frequencies is presented in Table 1.

## Discussion

Historical data on tail-break frequencies of gekkonids in the Marianas are few; Cagle (1946) compiled tail damage rates of 126 *H. garnotii* (= *H. frenatus*, G. Rodda, pers. comm.) from WW II Tinian. He found that 33% of the males, 29% of the females, and 10% of the juveniles had regenerated tails. These break frequencies are less than recorded for both surveyed populations (Table 1). It is likely, however, that this population was at a lowered density because of WW II combat/construction activities and was collected from recently established military housing. It is also likely that these same areas did not support *G. oceanica* or *P. ateles* as neither species is found in highly disturbed areas (Wiles et al. 1989).

Although a comparative population was not sampled on Cocos Island, the tail-break frequencies of *G. mutilata* from Guam are the lowest of all species recorded in this study (Table 1). This low frequency may reflect the tendency for *G. mutilata* to physically and temporally segregate from the aggressive *H. frenatus* (see above), thereby minimizing inter-specific interactions. Intra-specific interactions may also be behaviorally mediated. Zucker (1989) reported that dominant males of the phrynosomatid *Urosaurus ornatus* exhibited a dark dorsal color phase, presumably signaling others of their social status. In a shed in eastern

Table 1. Tail break frequencies of geckos from two sites in the southern Mariana Islands. Numbers in parentheses are sample sizes. Frequencies are calculated for a single sex or size class. Juvenile class also includes immatures (determined by internal examination of each species (McCoid 1989)).

	Cocos Island	Guam
<i>L. lugubris</i>		
females	— (2)*	64.7 (196)
juveniles	— (1)*	40.6 (32)
<i>G. mutilata</i>		
males	— (0)	38.8 (36)
females	— (0)	37.7 (45)
juveniles	— (0)	27.6 (31)
<i>G. oceanica</i>		
males	50.0 (6)	— (0)
females	50.0 (4)	— (0)
juveniles	14.2 (7)	— (0)
<i>P. ateles</i>		
males	56.6 (30)	— (0)
females	47.4 (19)	— (0)
juveniles	16.6 (12)	— (0)
<i>H. frenatus</i>		
males	91.6 (24)	67.3 (52)
females	63.5 (47)	60.0 (55)
juveniles	— (3)*	53.3 (30)

\*insufficient sample size for computation

Guam that harbored only *G. mutilata* (see above), a single large male exhibited a uniformly black dorsal pattern. Other syntopic *G. mutilata* exhibited either pale gray dorsal patterns (adult males and females) or blotched gray and black (juveniles). Although these observations are anecdotal, the color phases may serve as signals to minimize aggressive encounters.

Tail-break frequencies for *L. lugubris*, *P. ateles*, and *G. oceanica* also cannot be placed in perspective as there were no measurable complementary populations. However, *L. lugubris* was recorded on Cocos Island in low numbers (Table 1) and it may be important that two of the three specimens collected were on the ground. On Guam, *L. lugubris* is rarely encountered on the ground. This may indicate that *L. lugubris* may have been relegated to a less optimal habitat on Cocos Island by larger confamilials. Wiles et al. (1990) and Sabath (1981) recorded the highest sighting rates of *L. lugubris* in habitats with the lowest sighting rates of *G. oceanica*. The relatively high tail-break frequency of *L. lugubris* in the Guam population can be explained by observations of intra-specific interactions and interactions with *H. frenatus* (McCoid & Hensley 1991, 1993).

With the exception of the three *L. lugubris* found on Cocos Island during this study, the only species that was found in both study sites was *H. frenatus*. Although *G. oceanica* and *P. ateles* were never collected together on lighted structures on Cocos Island, *H. frenatus* was commonly observed or collected syntop-

ically with both species. At the Guam site (Table 1), *H. frenatus* was collected with *L. lugubris* and, rarely, *G. mutilata*. Tail-breaks in this Guam population were most frequent in male *H. frenatus*, followed by females, and juveniles. Since non-ophidian predators of lizards (small mammals and birds) potentially affecting gecko populations had been eliminated or severely reduced on Guam (Savidge 1987, Fritts 1988, McCoid 1991) due to predation by *B. irregularis*, the tail-break frequencies are most likely primarily due to interactions with confamilials. Effects on geckos in the Guam study area by *B. irregularis* were minimized by frequent snake collections. On the Cocos Island study site, which also lacks lizard predators, *B. irregularis* is not yet established.

On Cocos Island, the same pattern in *H. frenatus* was observed, but frequency of tail-breaks in males was significantly higher ( $X^2_{\text{calc. df}=1} = 6.48$ ,  $p = 0.011$ ), suggesting that males are under more inter-specific pressure than on Guam, which lacks large confamilials. There are additional differences between these two populations of *H. frenatus*. The sex ratio of the Guam population was 1 male:1.06 females, while that of the Cocos Island population was 1 male:1.96 females. The proportion of the Guam population that were juveniles was 21.8%, but was 4.0% on Cocos Island. These data suggest that, on Cocos Island, some male *H. frenatus* are not surviving encounters with either *P. ateles* or *G. oceanica* and juvenile survivorship and recruitment is less than on Guam due to predation by these same species.

### Conclusions

*Hemidactylus frenatus* has been established in the southern Mariana Islands at least 150 years (Fitzinger 1843). Until at least 1970 on Guam (and continuing to the present on Rota and Tinian), *H. frenatus* was primarily restricted to urban/disturbed habitats. On Guam, the introduction of *B. irregularis* in the late 1940's (Rodda et al. 1992) resulted in the extirpation of *P. ateles* and decimation of *G. oceanica* by the mid-1980's (Rodda & Fritts 1992). During the time interval (ca. 20 years) between Sabath's sampling and this study, both *H. frenatus* and *L. lugubris* successfully occupied habitats where they were formerly absent. If tail-break frequencies are reflective of species interactions, then the extirpation of *P. ateles* and decimation of *G. oceanica* greatly enhanced the success of *H. frenatus* and possibly *L. lugubris* on Guam. Although *B. irregularis* may have initially negatively impacted *G. mutilata*, observations presented here indicate that *H. frenatus* is further circumscribing local distributions of *G. mutilata*. Although other factors may have also played roles in the successful expansion of *H. frenatus* on Guam (Rodda & Fritts 1992), predation by *B. irregularis* was the trigger that allowed the cascade of gecko community changes to occur. The sequence of gecko events (over the past 50 years) on Guam may be reconstructed as follows: (1) entrenchment of *H. frenatus* in urban areas, (2) extirpation of *N. pelagicus* due to predation by a shrew and possibly *B. irregularis*, (3) extirpation of *P. ateles* and *G. oceanica* due to predation by *B. irregularis*; population reductions of *G. mutilata* due to predation by *B. irregularis*, (4) range expansion of *H. frenatus* and

*L. lugubris* into non-urban areas due to release from predatory pressure by *P. ateles* and/or *G. oceanica*, and (5) increasing range restriction of *G. mutilata* by *H. frenatus*.

Petren et al. (1993) stated that *H. frenatus* may exhibit a competitive edge over *L. lugubris*. This may also be the case in *H. frenatus* over *G. mutilata* on Guam. The range expansion of *H. frenatus* on Hawai'i and Guam, where large confamilials are absent, and apparent containment to urban/disturbed habitats on other islands in the Pacific Basin, where large confamilials are present, is not surprising in light of the above data. This situation is strongly underscored by the colonization success of *H. frenatus* in the New World (an area that lacks large, arboreal, nocturnal confamilials); specimens have been recorded in 13 states of Mexico, El Salvador, Nicaragua, Guatemala, Costa Rica, Panama (unpubl. data), Texas (P. Klawinski, pers. comm.), and Florida (Meshaka et al. 1994).

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