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The Distributional Patterns of Reptiles and Amphibians in the Mariana Islands

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Abstract—Recent collections of reptiles and amphibians on Cocos, Guam, Aguijan, Saipan, Anatahan, Guguan, Alamagan, Agrihan, and Asuncion have produced new distribution records for the Mariana Islands. Because the islands are so isolated, all of the Marianas' reptile species are necessarily excellent dispersers. Only *Emoia slevini* is an endemic. Species richness declines from the larger southern islands to the smaller northern islands. Proximity to source areas does not appear to influence species richness, perhaps because all the islands are extremely remote. Some native species appear to have declined or disappeared as a result of the introduction of exotic snakes and lizards.

Introduction

The Mariana Islands are a line of small islands in the western Pacific Ocean. The chain extends northward approximately 800 km from Guam (13° 13′ N) to the uninhabited Farallon de Pajaros (= Uracas, 21° 30′ N). The archipelago is isolated relative to other island masses. Although its biogeographic affinities are with the Australasian area, prevailing oceanic currents would not promote waif transport of reptiles directly to the Marianas from source islands such as New Guinea. Thus, it is likely that colonizing species have spread from tiny island to tiny island rather than having rafted directly across the nearly 2,000 km separating Guam from larger islands in Australasia.

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The biogeography of island reptiles has been critically examined with reference to islands near Indonesia (Cogger et al. 1983), Papua New Guinea (Heatwole 1975), and in the Caribbean (e.g., Levins & Heatwole 1963). However, little attention has been directed to remote oceanic chains such as the Marianas. The catastrophic loss of vertebrate species associated with the introduction of the Brown Tree Snake *Boiga irregularis* on Guam (Savidge 1987, Fritts 1988), has stimulated herpetological interest in the Mariana Islands. Elsewhere we will analyze the impacts of *Boiga* on the native lizards of Guam. In this work, we report a variety of new reptile records for the Marianas, summarize what is presently known about the distribution of reptiles and amphibians in the Marianas, and compare the Mariana Islands' observed distributional patterns with those that might be expected based on generalities derived from continental islands.

Methods

During 1988 and 1989 we used standard herpetological collecting techniques to obtain reptile and amphibian specimens from various islands in the Marianas: Cocos, Guam, Rota, Aguijan, Tinian, Saipan, Anatahan, Guguan, Alamagan, Pagan, Agrihan, Asuncion, and Maug. Most specimens were captured by hand or with adhesive traps. All specimens were verified and deposited in the U.S. National Museum or the Museum of Southwestern Biology, University of New Mexico. A conscious effort was made to sample as many different habitats as possible on each island, but the sampling was not designed to quantify island-wide populations. Our intent was to quantify populations at particular sites and to verify the presence of species.

An island was considered well surveyed if a professional herpetologist had intensively collected the island at least once. For a collection to be considered intensive, it had to cover the full range of habitats present on the island, include both day and night sampling, and use at least one method other than visual censusing. The larger, more diverse islands required greater sampling effort. The four large southern islands of Guam, Rota, Tinian, and Saipan have been sampled repeatedly by many herpetologists.

Island Occurrences

The current status of island records for reptiles and amphibians in the Marianas is shown in Table 1. Twenty-four new records verified by our specimens are indicated with an "a". The previous records are based on Crombie (unpub. data), Wiles et al. (1989), and Wiles et al. (1990). The new records for *E. slevini* expand its known range from just Guam/Cocos to almost the entire Mariana chain. The other new island records are less surprising, and help solidify the distributional patterns analysed below. The nine questionable records are as follows:

1) Several *Varanus indicus* have been purposely translocated to Cocos by a Guam resident (M. McCoid, pers. comm.). In addition, two captive *Varanus* are

Table 1. Summary of known occurrences. An "x" indicates an established museum record; "a" indicates a record reported here for the first time; "?" denotes a questionable report for which a specimen has not been procured (each explained in text). Island names are listed from south to north by their first four letters; full island names are given in the Appendix. No data are available for omitted islands (e.g., Farallon de Medinilla, Uracas). Species are alphabetical within groupings.

Species	Coco	Guam	Rota	Agui	Tini	Saip	Anat	Sari	Gugu	Alam	Paga	Agri	Asun	Maug
Amphibians														
B. marinus	x	x	x		x	x					?			
L. fallax		x				?								
Turtles														
C. japonica	x	x	x		x	x								
E. imbricata		x												
T. scripta		x				?								
Snakes														
B. irregularis		x												
R. braminus		x	x		x	x	x	x		a	x	x		
Lizards (Gekkonidae)														
G. mutilata	x	x	x		x	a		x	x	a	x	a		
G. oceanica	x	x	x	x	x	x			x	a			a	
H. frenatus	a	x	x		x	x				a	x	a		
L. lugubris	x	x	x		x	x			a	a	x	x	a	
N. pelagicus		x	x		x	?								
P. ateles	x	x			x	x								

Table 1. Continued

Species	Coco	Guam	Rota	Agui	Tini	Saip	Anat	Sari	Gugu	Alam	Paga	Agri	Asun	Maug
(Iguanidae)														
A. carolinensis		x	x			x								
(Scincidae)														
C. fusca	a	x			x	x								
C. poecilopleurus	x	x	x	a	x	x	x	x	x	a		a	a	x
E. atrocostata	x		x											
E. caeruleocauda	x	x	x	a	x	x	a	x		a	x	x	a	
E. cyanura	x	?												
E. slevini	x	x	x		x					a			a	
L. noctua		a	?											
L smaragdina					x	x								
(Varanidae)														
V. indicus	?	x	x	x	x	x	x	x		?	x	?		

believed to have escaped from a resort on the island. We have seen at least two individuals, but do not know if the population is self sustaining.

2) *Emoia cyanura* was reportedly collected in the Geus River valley on Guam (Kami et al. 1974). Although the collectors retained no voucher specimens, they did identify both *E. cyanura* and *E. caeruleocauda* from the valley. Therefore, it is unlikely that the *E. cyanura* record is a misidentification of *E. caeruleocauda.* The Geus River is among the most likely sites on Guam where *E. cyanura* would occur, as the river drains into the Cocos lagoon, and *E. cyanura* is common on Cocos. Furthermore, on biogeographical grounds one would expect that any species on Cocos would have reached that tiny islet by way of its much larger neighbor, Guam. Therefore, it seems likely that *E. cyanura* once occurred on Guam even if it is now extirpated.

3) The record of *Lipinia noctua* from Rota is based on a sight record by Norm Scott of the U.S. Fish and Wildlife Service in 1985 and in a similar undocumented observation by Thomas Fritts.

4) The call of a *Litoria fallax* on Saipan was heard by Phil Glass, wildlife biologist for the Commonwealth of the Northern Mariana Islands.

5) *Trachemys scripta* have been collected on Saipan, but the record is listed with a question mark because it is not known if this population is self-sustaining. Turtles of all sizes have been seen, suggesting that the population is established.

6) A *Nactus pelagicus* was seen by Phil Glass on Saipan.

7–9) Island residents report the establishment of *Bufo marinus* on Pagan and *Varanus indicus* on Alamagan and Agrihan. Although local reports are sometimes unreliable, no other species in the area could be mistaken for these animals.

Although we have no records of *Emoia atrocostata* from Guam, its existence on both Cocos and Rota strongly suggests that it was once on Guam. The habitat occupied by *E. atrocostata* on Guam has been colonized by the introduced skink *Carlia fusca.* Thus *E. atrocostata* may have been displaced from Guam before its occurrence was documented. It is extremely wary and difficult to see in the dense coastal scrub which is its preferred habitat. Furthermore, suitable habitat for *E. atrocostata* occurs only in an extremely narrow and discontinuous strip along rocky shorelines. This species possibly still occurs at the poorly sampled southern end of Guam. A similar caveat would apply to *Cryptoblepharus poecilopleurus*, which has not been collected on Guam in recent years.

Species-Area Relationships

Before analyzing the distributional patterns revealed by Table 1, we considered the possibility that incomplete sampling might be responsible for some of the differences among islands. The theory of island biogeography (MacArthur & Wilson 1967) makes predictions about species richness that can be used to evaluate the thoroughness of collecting efforts. Two main variables have been found to influence the numbers of reptile species on islands: island area and distance from source areas. Following Heatwole (1975), we attempted to model observed species richnesses using island area in hectares, maximum height of the island in meters (a measure of habitat diversity), and reciprocal of the distance to the nearest larger island (an estimate of colonization opportunities). Like Heatwole (1975), we found that only island area contributed significantly to explaining species diversity ($R^2 = 0.875$, $P = 0.002$; all other variables $P \geqslant 0.15$). Compared to the islands Heatwole considered, habitat diversity is relatively uniform in the Marianas; and with the exception of the islands Cocos and Aguijan, all of the Marianas are at least tens of kilometers distant from another island that is substantially richer in species. This may account for the statistical insignificance of distance from source area. Because Cocos and Aguijan are anomalous in their proximity to source islands, they have been excluded from the following analysis of sampling adequacy.

The relationship between island area and species abundance of reptiles may be used to estimate undersampling of species richness in two ways. First, we compared the observed number of all terrestrial herptile species on each island with the number of species to be expected on each island based on the species-area relationship derived by Heatwole (1975) for small islands off the coast of Papua New Guinea. Second, we executed a similar analysis for the well-studied islands of the Marianas chain (Guam, Rota, Tinian, Saipan, Alamagan, Asuncion, and Guguan). From the regression of $\log_{10}$(species richness) on $\log_{10}$(island area), we computed the species richness values that would be expected for islands of the sizes corresponding to those of the less-studied islands (Anatahan, Sarigan Pagan, Agrihan, and Maug). In this second data sufficiency analysis, only native species were used. We assumed that the number of native species more likely reflects an equilibrium condition than does the total current species richness (evidence for instability due to recent species introductions is given in the next section).

A species was considered native if there were no indications of its arrival in the Marianas within historical times. Crombie & Steadman (1987) have argued that all reptiles and amphibians on very remote islands have been introduced by man, perhaps in prehistoric times. However, this is unlikely to be the case with the island endemics, and at present no way exists to determine which nonendemic species might have been introduced prehistorically. If all reptiles (except island endemics) were introduced by man, distributional patterns would not support biogeographic inferences except for subsequent extinctions influenced by island size and ecological diversity. Extinctions have undoubtedly occurred in the Marianas and our incomplete knowledge of these events obscure our understanding of the origins of several widespread species and the mode of dispersal to and among the Mariana islands.

The species-area relationship empirically determined by Heatwole (1975) for small islands off the east coast of Papua New Guinea was: species richness = $0.51(\text{island area})^{0.355}$, where area is measured in hectares. The predictions of this relationship closely match the species richnesses that have been observed in the Marianas. They also match the predictions based on the regression independently derived for the well-studied islands in the Marianas [species richness = $1.42(\text{island area})^{0.198}$; Fig. 1, Table 2]. The lower exponent in the computation for

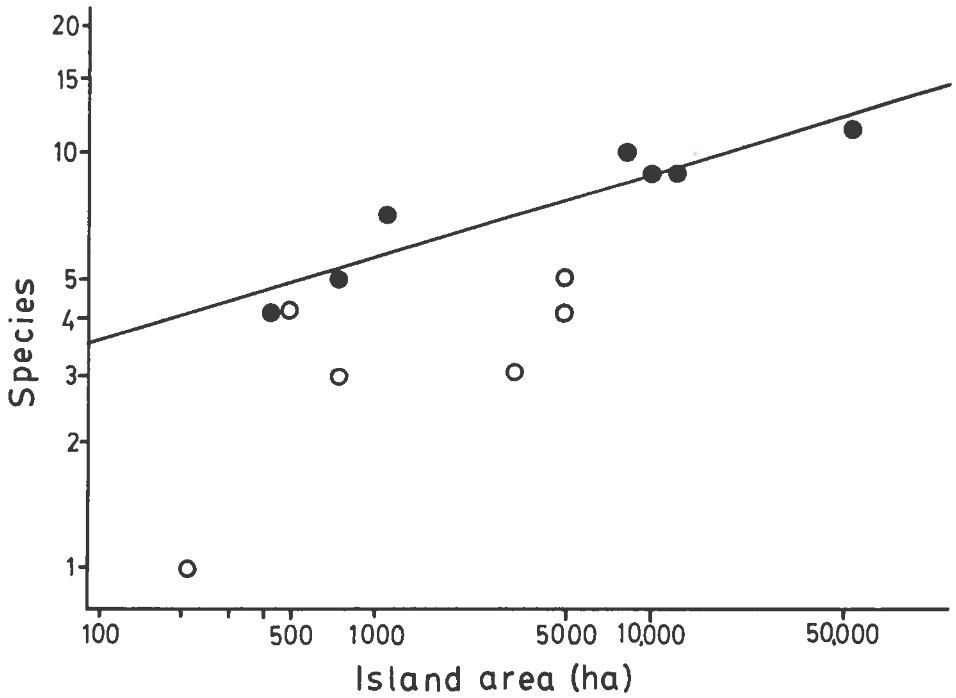

Figure 1. Relationship between island area and species richness for the native reptiles and amphibians of the Mariana Islands. Regression line is fitted to the well-studied island (solid dots). Note that the less-studied islands (open circles) fall below the regression line. See Table 2 for specific island values.

the well-studied islands of the Marianas is consistent with expectations of theory for small islands that are very distant from a source area (MacArthur & Wilson 1967). Despite the difference in exponent, the two regressions give nearly identical species richness predictions, with Guam showing the greatest discrepancy (Table 2). For Guam, Heatwole's regression predicts a number substantially greater than the number of extant native species. Perhaps Guam has always been relatively depauperate because it is the largest island in the group, so no larger nearby island could act as a source for additional species (the nearest island larger than Guam is Manus, 1,720 km to the south, a direction inappropriate for natural waif dispersal). Guam's low species richness may also indicate inadequate sampling prior to recent extinctions, or a prehistoric reduction in species due to intensive habitat alterations by man (some historians estimate a pre-Magellan population of over 100,000 people on this 54,100-ha island). Contrasting the poor fit obtained using the indigenous species, a good match exists between Heatwole's expected species number and the total number of species on Guam (i.e., including introduced species). Heatwole did not distinguish between native and introduced species as the fraction of introduced species in his study area was relatively insignificant.

Table 2. Adequacy of sampling based on island size and two regressions relating species richness to island size. Species totals are for terrestrial species only. Within categories, islands are listed from south to north.

Island	Area (ha)	Heatwole prediction	Sp. present		This study's prediction	Other native spp. likely to be found
			All	Native		
Well studied						
Guam	54,100	19.6	19	11	12.4	
Rota	8,520	10.6	14	10	8.6	
Tinian	10,180	11.2	14	9	8.9	
Saipan	12,290	12.0	17	9	9.2	
Guguan	420	3.9	4	4	4.7	
Alamagan	1,130	5.4	9	7	5.7	
Asuncion	730	4.6	5	5	5.3	
Poorly studied						
Anatahan*	3,230	7.6	4	3	7.1	*E. slevini, L. lugubris, G. oceanica, G. mutilata*
Sarigan	500	4.1	5	4	4.9	*L. lugubris*
Pagan*	4,830	8.7	7	4	7.7	*C. poecilopleurus, E. slevini, G. oceanica*
Agrihan	4,740	8.7	7	5	7.6	*G. oceanica, E. slevini*
Maug	210	3.1	1	1	4.1	*E. caeruleocauda, L. lugubris, G. oceanica*

*These islands have undergone severe recent volcanism and may not have the full complement of species that would be expected.

The right-hand column in Table 2 lists species that we judge most likely to be discovered with additional collecting on the poorly sampled islands. The number of expected additional species was based on the approximate discrepancy between the number now known and the number expected on the basis of island size. The predicted species were selected on the basis of the biogeographic and ecological generalities developed in the final section of this paper.

Interpretation of Distributional Patterns

INTRODUCED SPECIES

Amphibians do not tolerate long exposure to salt water and therefore are not normally native to oceanic islands. Two species have been introduced to the Marianas. The gigantic poisonous toad *Bufo marinus*, which has been introduced to tropical areas throughout the world, was released on Guam for garden slug control in 1937 (Anon. 1940, Eldredge 1988) and to the other large islands of the Marianas during the Japanese period. It will probably eventually spread to many of the other islands as it has done throughout the world.

Litoria fallax, a small green treefrog, was accidentally introduced to Guam from Australia in 1968 (Eldredge 1988). To date, it has not spread beyond Guam although there is the sound record for Saipan; and the frog's preferred habitat (marshes and drainage ditches) is relatively abundant on Tinian and Saipan.

Sea turtles were once common around the Marianas (Pritchard 1981), probably nesting on the limited numbers of suitable beaches. No terrestrial or aquatic turtles are native, although *Trachemys scripta*, the common turtle of the pet trade, has apparently become established on Guam and probably Saipan. With help from man, it could spread to other islands, such as Tinian, that have adequate freshwater streams or ponds.

The worm-like snake *Ramphotyphlops braminus*, transported with soil to virtually all warm areas of the world, has the widest range of any terrestrial reptile (Ernst & Barbour 1989). Some herpetologists assume that it was brought to the Marianas by the prehistoric settlers (Brown 1956). At present, however, it is impossible to distinguish the area where it originated from the numerous similar places to which humans have inadvertently transported it (McDowell 1974). Despite its cryptic habits, *R. braminus* was among the first reptiles to be collected in the Marianas (in Paris Museum by early 1840s, see Van Denburgh 1917). Being parthenogenetic (McDowell 1974, Nussbaum 1980) it could readily establish itself after a single individual floated to an island on debris set loose during typhoons. It is known from every well-studied island and probably occurs on most of the others.

The Brown Tree Snake, *Boiga irregularis*, is at present confined to Guam, where it was accidentally introduced shortly after World War II (Savidge 1987, Fritts 1988, Rodda et al. 1992). However, records of it being accidentally transported to other islands (Fritts 1987, 1988; McCoid & Stinson 1991) suggest that it will reach the other southern Marianas.

On the basis of implausibility of natural dispersal to the Marianas, *Varanus indicus* is thought to have been introduced there, as it has been throughout the Pacific (Brown 1956). It has been seen on every well-studied island of the chain and may be expected to have reached the others.

Hemidactylus frenatus, a widespread human comensal, is thought by most herpetologists to have been introduced to the Marianas, although it has been in the chain for at least 150 years. Fitzinger (1843) reported a *H. javanicus* (= *frenatus*) from the Marianas, probably Guam. This would make it among the first reptiles collected in the Marianas. On most Pacific islands where it occurs, *H. frenatus* does not occur away from houses (McCoy 1980). This limitation does not hold for the Marianas; *H. frenatus* constitutes over 90% of the gecko individuals in many forested areas of Guam (Rodda & Fritts unpub. data) and it is widespread in disturbed but vegetated sites on Tinian and Rota (Wiles et al. 1989, 1990). Because it is an aggressive colonist, it will probably spread throughout the Marianas.

The skink *Carlia fusca* was introduced to southern Marianas in the 1960s. G. Ingram (in litt.) suggests that the nominal species is a complex of many similar species. The Marianas form will probably be given a new name; for the time being we will continue to use *C. fusca*. An extremely aggressive lizard, it readily takes food from other small terrestrial, diurnal lizards. It does especially well along roadsides or in suburban lawns but will also invade other habitats, such as beach strand. *C. fusca* may have played a role in the disappearance of *Cryptoblepharus poecilopleurus, Emoia atrocostata*, and *E. slevini* from several islands. Where they coexist, *Carlia* may also affect the numbers of *E. caeruleocauda*, especially on the ground. Recently, *Carlia* has become conspicuous and widespread on Cocos; but studies on the impact of this expansion have not been completed.

The other two introduced lizards, *Anolis carolinensis* and *Lamprolepis smaragdina*, have expanded their ranges more slowly than *Carlia*. *A. carolinensis* is an arboreal, diurnal insectivore that does well around human habitations or other places where water is regularly available. It spread rapidly after its introduction to Guam in the mid-1950s (Eldredge 1988), but it is a preferred prey item for the introduced Brown Tree Snake (Smith & Fritts unpub. data). The lizard's numbers appear to have subsequently declined in areas heavily populated by the snake. On the other major islands, *Anolis* arrived more recently and is still rare away from human settlements. It apparently has not become established on Tinian. The California Academy of Sciences has a single specimen from Tinian, (Greg Mayer, pers. comm.), but none was evident on the island during recent intensive searches (see also Wiles et al. 1989). Additional inadvertent introductions to Tinian are likely, and the habitat appears similar to that occupied by *Anolis* on the other Marianas. Its dispersal to new islands in the Marianas is not impeded by competition from other lizards, as the Marianas have no native, diurnal lizards found primarily in foliage.

The large green skink *Lamprolepis smaragdina* has become established only on Saipan and Tinian. It is locally abundant on large trunks and in the open crowns of trees, especially in urban areas. Ornamental trees are a preferred habitat, but it will occupy large trees in forested areas as well. An attempt to introduce it to Mangilao, Guam in the 1960s failed (Eldredge 1988), perhaps due to predation by *Boiga. Lamprolepis* shows a strong preference for large, exposed tree trunks, a habitat not used to any great extent by native skinks (*Emoia slevini* uses such a habitat a little, and the crepuscular *Lipinia noctua* may use large tree trunks, especially those with loose bark). Food and available habitat for *Lamprolepis* exist throughout the Marianas; but on the basis of its slow spread, the species does not appear to be an aggressive colonizer.

The introduction to the Marianas of 9–11 species of reptiles and amphibians has destabilized the resident herpetological communities. Note the large proportion of population decreases and range reductions among native species listed in Table 3. The most affected island is Guam, which hosts the largest number of exotics as well as the greatest loss of native species. Given the probable continuation of human alterations to the environment, an equilibrium condition is not likely to be reestablished in the foreseeable future.

NATIVE SPECIES

Of the 11 native lizards, six have been found on almost every well-studied island: *Cryptoblepharus poecilopleurus, Emoia caeruleocauda, Emoia slevini, Lepidodactylus lugubris, Gehyra mutilata,* and *Gehyra oceanica.* With the exception of *E. slevini*, the only known Marianas endemic, all are widespread species (Table 3). *E. slevini* is also anomalous in that it apparently has become rare or disappeared from Guam, Rota, and Tinian in historic times. At present, dense populations are known only from the far northern islands Asuncion and Alamagan. It is present but not common on Cocos. This spotty pattern suggests a relictual distribution, although it may also indicate inadequate sampling prior to human-caused habitat disruption. Being endemic, it must have been present in the chain for an evolutionarily long time and may have been ecologically supplanted by more recent arrivals even before the disturbances and introductions brought by man. *E. slevini* is larger than the other native skinks. If it has or is being ecologically displaced by them, its large size would argue against a mechanism of direct behavioral interference as applies to the food thefts by the large aggressive *Carlia* in encounters with the smaller *E. caeruleocauda.* We have found *E. slevini* in clearings, around abandoned buildings, on the forest floor, and in trees. Thus, it does not appear to be a habitat specialist and would not be likely to compete intensively with any other single species. It will overlap to some extent with all of the other skinks except *E. atrocostata.* It may be vulnerable to exotic predators: *Boiga irregularis, Varanus indicus, Lamprolepis smaragdina, Rattus* sp., and the shrew *Suncus murinus.*

In contrast to *E. slevini*, the other widespread native lizards are likely to be found on nearly all islands in the Marianas. Some of the northern islands are apparently too small to support the full complement of native lizards, as suggested by the species-area relationship (Fig. 1). All five species occur from one end of the chain to the other, but may be missing on particular islands. For example,

Table 3. Biogeographic and ecological attributes of Mariana Islands reptiles and amphibians (established terrestrial species only). Order of species was chosen to emphasize relationships between ecological and distribution variables (columns), with native species appearing in the first rows.

Species	Wide sp. range	Hab. spec.	In South Mar. only	Native	Recent pop. decline or range contract.
Lipinia noctua	x	x	x	x	?
Emoia cyanura	x	x	x	x	
Emoia atrocostata	x	x	x	x	?
Nactus pelagicus	x	x	x	x	x (Guam, Tinian)
Perochirus ateles	x	x	x	x	x (Guam, Tin., Sai.)
C. poecilopleurus	x	x		x	x (Guam)
Emoia caeruleocauda	x			x	
Emoia slevini				x	x (Guam, Rota, Tin.)
Lepidodactylus lugubris	x			x	
Gehyra mutilata	x			x	x (Guam)
Gehyra oceanica	x			x	x (Guam)
Ramphotyphlops braminus	x			?	
Bufo marinus	x		?		
Litoria fallax			x		
Trachemys scripta	x		x		
Boiga irregularis	x		x		
Anolis carolinensis	x		x		
Lamprolepis smaragdina	x	x	x		
Carlia fusca	x		x		
Hemidactylus frenatus	x		x		
Varanus indicus	x				

Gehyra mutilata is missing from Asuncion and *E. caeruleocauda* does not inhabit Guguan; but all species were historically present on the four large islands. On the islands where a species is missing, a similar species appears to have expanded its niche to include the unoccupied space. For example, on Asuncion, *Gehyra oceanica* is extremely abundant and occupies the surfaces normally inhabited by its missing congener. On Guguan, *Cryptoblepharus* is the ubiquitous ground skink, a role occupied by *E. caeruleocauda* on the other islands. On islands where *Cryptoblepharus* and *E. caeruleocauda* coexist, *Cryptoblepharus* specializes on tree trunks and areas near shorelines. Guguan has extensive areas of loose sandy soil throughout the island, a feature which may be advantageous to *Cryptoblepharus.*

Although the six widespread native lizards are found on almost every island in the Marianas, the other five native lizards are all restricted to the four large southern islands and none is known to occur on all four islands: *Lipinia noctua, Emoia cyanura, Emoia atrocostata, Nactus pelagicus*, and *Perochirus ateles*. Although these five lizards are specialized in their habits compared to the six widespread species, they are not geographically restricted in their species ranges (Table 3). Most are found throughout the Pacific, although some of the distributional records may be due to erroneous identifications of morphologically similar species. *E. cyanura* has been confused with *E. impar* and the *Nactus* found in the Marianas is part of a unisexual/bisexual species complex that has not yet been fully resolved (Moritz 1987). One species that is arguably restricted in its distribution is *Perochirus ateles*, yet it is widespread in the Carolines and Marshalls and occurs on the remote Marcus Island. These species are probably well adapted for waif dispersal, and their absence from the smaller Mariana islands is probably due to extirpation associated with small island area, rather than their having never reached the northern Marianas.

The five geographically restricted species all have ecological specializations. *Lipinia* is the only diurnal, primarily arboreal species. *E. cyanura* reportedly specializes in hot, dry, open areas, especially those near the coast (McCoy 1980). It avoids the forested zones frequented by the morphologically similar but ecologically broader *E. caeruleocauda. E. atrocostata*, among the most specialized of the Mariana reptiles, is found exclusively along rocky shorelines. In the Solomons, it reportedly forages primarily in tide pools where it will seek refuge from disturbances (McCoy 1980). We have never found it inland from the salt spray zone marked by the shrub *Pemphis acidulus*. In the Marianas, *Nactus pelagicus* is a specialist for rocky habitats. The habits of *Perochirus ateles* are not well understood. In the Marianas, it has been found primarily in undisturbed forests, mostly on large tree trunks (Sabath 1981) and on buildings close to forests. Thus, despite having wide species ranges all five native lizards having limited ranges in the Marianas are ecologically specialized forms.

Unless most species arrived with humans, the paucity of reptile endemics in the Marianas suggests that most reptile populations that evolved in the isolation of these remote oceanic islands have either been supplanted by more recent arrivals or they did not attain reproductive isolation before genetically compatible individuals arrived to swamp the emerging local adaptations. This pattern contrasts strikingly with that of the Marianas' native birds. Paradoxically, the more mobile birds have shown a much greater tendency to remain isolated and speciate in the Marianas. Of the 21 breeding land birds of the Marianas, nine are endemics (Reichel & Glass 1991) and one additional species, the White-throated Ground Dove (*Gallicolumba xanthonura*), is found nowhere else but the nearby islands of Yap (Pratt et al. 1987). The ease with which introduced bird species have become established on many islands of the Marianas during the last few decades gives no indication that the resident bird species are especially resistant to ecological displacement. This analysis is not a strong test of the competitiveness hypothesis, of course; but it is consistent with the general characteristics associated with oceanic island land birds (Brockie et al. 1988). Furthermore, it encourages us to consider the other possibility: perhaps the high endemism of Marianas birds indicates that successful waif dispersal of non-migratory island land birds is rare relative to its occurrence in reptiles. Land birds, with their more developed abilities to resist unintended transport and their more limited survival time when deprived of food, may not be well suited for waif dispersal to remote islands such as the Marianas. Geckos, in contrast, can survive long periods without food. Their eggs are resistant to damage by salt spray (Brown & Alcala 1957), and they are almost totally incapable of propelling themselves back to land if they are accidentally washed to sea on debris. Diamond (1984) argued that endemism in Pacific islands should vary with distance from source areas, with only the most remote areas having sufficient isolation for speciation to occur without the genetically disruptive influence of repeated immigration. If the Marianas are in some sense more remote for birds than reptiles, this argument may help explain the differences between bird and reptile endemism in these islands.

The reptiles and amphibians of the Mariana Islands are all excellent dispersers. Proximity to source areas does not appear to influence their distribution, although size of island does. The larger, southern islands of the chain have more species and a higher proportion of ecologically specialized forms. Unfortunately, these more diverse islands have all experienced declines in their native herpetofaunas associated with the introduction of exotic species.

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APPENDIX

Specimen numbers (all USNM) for new island records, and full names of islands.

New island records
R. braminus: 287196 (Alam)
G. mutilata: 301893 (Saip), 287051-8 (Alam), 287029-33 (Agri)
G. oceanica: 287059-68 (Alam), 287197-215 (Asun)
H. frenatus: 287069 (Alam), 287034 (Agri)
L. lugub: 287235-6 (Gugu), 287070-94 (Alam), 287216-8 (Asun)
C. fusca: 284622 (Coco)
C. poecilopleurus: 301890 (Agui), 287242 (Alam), 287237 (Agri), 287238-41 (Asun)
E. caeruleocauda: 301916-25 (Agui), 301928-33 (Anat), 287095-174 (Alam), 287219-26 (Asun)
E. slevini. 287175-95 (Alam), 287227 (Asun)
L. noctua. not cat. (Guam)

Island names (from south to north): Cocos, Guam, Rota, Aguijan, Tinian, Saipan, Anatahan, Sarigan, Guguan, Alamagan, Pagan, Agrihan, Asuncion, Maug.