Annu. Rev. Ecol. Syst. 1998. 29:113–40

THE ROLE OF INTRODUCED SPECIES IN THE DEGRADATION OF ISLAND ECOSYSTEMS:
A Case History of Guam[1]

Thomas H. Fritts
US Geological Survey, Patuxent Wildlife Research Center, National Museum of Natural History, MRC 111, Washington, DC 20560;
e-mail: Thomas_Fritts@usgs.gov

Gordon H. Rodda
US Geological Survey, Patuxent Wildlife Research Center, Fort Collins, Colorado 80525-3400; e-mail: gordon_rodda@compuserve.com

KEY WORDS: Guam Island, *Boiga irregularis*, brown treesnake, extinction

ABSTRACT

The accidental introduction of the brown treesnake (*Boiga irregularis*) on Guam around 1950 induced a cascade of extirpations that may be unprecedented among historical extinction events in taxonomic scope and severity. Birds, bats, and reptiles were affected, and by 1990 most forested areas on Guam retained only three native vertebrates, all of which were small lizards. Of the hypotheses to account for the severity of this extinction event, we find some support for the importance of lack of coevolution between introduced predator and prey, availability of alternate prey, extraordinary predatory capabilities of the snake, and vulnerabilities of the Guam ecosystem. In addition, there were important interactions among these factors, especially the presence of introduced prey (possessing coevolutionary experience) that were thus able to maintain their populations and provide alternate prey to the introduced predator while it was driving the native prey species to extinction. This complex of vulnerabilities is common on oceanic islands.

---

[1] The US government has the right to retain a nonexclusive, royalty-free license in and to any copyright covering this paper.

INTRODUCTION

Guam, the largest island of Micronesia [54,100 hectares (ha)], has a remarkable ecological history. In the latter half of the 20th century, Guam lost virtually all its native bird species (36, 62, 73, 81). By early 1998, only three of Guam's 13 native forest bird populations retained even a slender hold on survival (Table 1). The largest population of the Micronesian starling (*Aplonis opaca*) was restricted to an urban area and numbered about 50 birds; the cave-roosting island swiftlet (*Aerodramus vanikorensis bartschi*) occupied only a single site, where it numbered in the low hundreds; and the most endangered population (94, 98) was that of the Marianas crow (*Corvus kubaryi*), which had one known pair and fewer than 20 individuals (C Aguon, personal communication).

Less well known is the loss of other vertebrate taxa. Of three native mammal species, the Mariana fruit bat (*Pteropus mariannus* subsp. *mariannus*) survives, but its long-term prospects are very much in doubt, with failure of recruitment extending more than a decade and residual adults now numbering just over 100 individuals (G Wiles, personal communication).

All other native vertebrates in the forests of Guam are reptiles. Of the 10 to 12 native species, six survive somewhere on the island, but only three lizards are found throughout: a native blue-tailed skink (*Emoia caeruleocauda*), a native mourning gecko (*Lepidodactylus lugubris*), and a prehistoric introduction or native (61) house gecko (*Hemidactylus frenatus*).

While other recent extinction events have involved greater numbers of species (32), we are unaware of any that have involved such a diversity of major vertebrate taxa and have had an impact on such a large percentage of the indigenous species. True to Western tradition, the villain is believed to be a serpent, a previously obscure nocturnal arboreal colubrid from Australasia, the brown treesnake (*Boiga irregularis*). We review the Guam biodiversity crisis with the objective of answering three questions: To what extent were the extirpations due to the introduction of the snake? What ecological features led to so extreme an outcome? What is projected to happen to the snake population and the ecosystem in the absence of most native prey species?

EVALUATION OF ECOLOGICAL IMPACTS

Evaluating the influence of an added species involves not only determining the effect of the species, but also considering other potential causes of the same outcome. In the case of Guam, for example, the introduction of the snake was followed shortly by independent introductions of the musk shrew (*Suncus murinus*), an arboreal lizard—the green anole (*Anolis carolinensis*), a bird—the black drongo (*Dicrurus macrocercus*), and a terrestrial lizard—the

Table 1 Status of native terrestrial vertebrates breeding on the island of Guam in 1998

Vertebrate	Surviving species	Exterminated by brown treesnake (*Boiga irregularis*)
Birds		
Pelagic	0 of 4	3
Brown booby *Sula leucogaster* (breeding stopped before snake)		
Fairy tern *Gygis alba* (breeding ended—snake)		
Brown noddy *Anous stolidus* (breeding ended—snake)		
White-tailed tropic bird *Phaethon lepturus* (breeding ended—snake)		
Near-shore	1 of 1	0
Pacific reef heron *Egretta sacra* (present)		
Wetland/grassland	2 of 4	0?
Common moorhen *Gallinula chloropus* subsp. *guami* (Endangered—habitat loss)		
Yellow bittern *Ixobrychus sinensis* (present)		
Marianas mallard *Anas platyrhynchos* subsp. *oustaleti* (extirpated—habitat loss)		
White-browed crake *Poliolimnas cinereus* (extirpated—not snake)		
Forest	3 of 13	9?
Island swiftlet *Aerodramus vanikorensis* subsp. *bartschi* (one colony surviving)		
Marianas crow *Corvus kubaryi* (< 20 individuals—snake)		
Marianas starling *Aplonis opaca* (remnant populations in urban areas—snake)		
Bridled white-eye *Zosterops conspicillata* subsp. *conspicillata* (extirpated—snake)		
Guam flycatcher *Myiagra freycineti* (extinct—snake)		
Guam rail *Rallus owstoni* (extirpated—snake; captive)		
Mariana fruit-dove *Ptilinopus roseicapilla* (extirpated—snake)		
Micronesian honeyeater *Myzomela rubratra* (extirpated—snake)		
Micronesian kingfisher *Halcyon cinnamomina* subsp. *cinnamomina* (extirpated—snake; captive)		

(*Continued*)

Table 1 (*Continued*)

Vertebrate	Surviving species	Exterminated by brown treesnake (*Boiga irregularis*)
Micronesian megapode *Megapodius laperouse* subsp. *laperouse* (extirpated—not snake)		
Nightingale reed-warbler *Acrocephalus luscinia* subsp. *luscinia* (extirpated—snake?)		
Rufous fantail *Rhipidura rufifrons* (extirpated—snake)		
White-throated ground-dove *Gallicolumba xanthonura* (extirpated—snake)		
Mammals	1 of 3	?
Mariana fruit bat *Pteropus m.* subsp. *mariannus* (one colony—snake)		
Little Mariana fruit bat *Pteropus tokudae* (extinct—loss not attributable)		
Sheath-tailed bat *Emballonura semicaudata* (extirpated—loss not attributable)		
Reptiles	6 of 10–12	3–5
Blue-tailed skink *Emoia caeruleocauda* (present)		
House gecko *Hemidactylus frenatus* (present)		
Mourning gecko *Lepidodactylus lugubris* (present)		
Moth skink *Lipinia noctua* (localized)		
Pelagic gecko *Nactus pelagicus* (localized)		
Brahminy blind snake *Ramphotyphlops braminus* (not definitely native—present)		
Snake-eyed skink *Cryptoblepharus poecilopleurus* (extirpated—snake?)		
Azure-tailed skink *Emoia cyanura* (no recent records—shrew?)		
Blue-tailed copper-striped skink *Emoia impar* (no recent records—shrew?)		
Mariana skink *Emoia slevini* (extirpated—snake? shrew?)		
Spotted-belly gecko *Perochirus ateles* (extirpated—snake)		
Tide-pool skink *Emoia atrocostata* (no definite records)		

curious skink (*Carlia* cf *fusca*). In addition, it is necessary to consider ecological alterations brought on by other changes in the ecosystem, for example, deforestation. Fortunately for biodiversity conservation, but unfortunately for ecological understanding, species introductions cannot be replicated. In most cases they cannot even be tested directly with introductions into or exclusions from naturalistic enclosures. We are forced to rely on the plausibility of competing scenarios. We evaluated proposed scenarios for the effects of introduced species on Guam in light of nine inquiries:

1. Is the scenario consistent with what is known about ecological interactions in similar ecosystems? For example, have other island ecosystems been found more vulnerable to loss of primary forest or introductions of generalist predators where there were none before?

2. Is the proposed ecological interaction plausible on trophic grounds? Was the putative prey found in the diet of the putative predator? Did all members of the same prey guild show similar declines?

3. Did the putative prey attract the putative predator in substantial numbers in naturalistic field trials? For example, if brown treesnakes are alleged to decimate bird nests, are snakes drawn to traps baited with bird eggs?

4. Is the proposed scenario plausible on numerical grounds? For example, were shrews numerous enough to have been responsible for the observed decline in the pelagic gecko, *Nactus pelagicus*, given the shrew's normal diet?

5. Is the recorded expansion of the predator population temporally and geographically consistent with the observed declines in putative prey? This comparison must take into account the longevity of the species if the hypothesized predator is believed to interrupt reproduction but not harm adults.

6. Is the size distribution of proposed prey consistent with predatory capabilities of the proposed predator? In the Guam example, species losses in the 1980s affected only those species with adult sizes in the range 4–125 g. Was this consistent with the known dietary habits of the proposed predator?

7. Are proposed predator and prey syntopic? For example, the decline of the pelagic gecko, a terrestrial species, occurred at a time when brown treesnakes were not known to forage terrestrially. We infer that the snake was not a probable cause of the gecko's decline.

8. Did observed losses also occur in localities from which the putative predator was absent? For example, the scenario that brown treesnakes were responsible for the demise of Guam's population of pelagic geckos is greatly

weakened by evidence that the gecko concurrently disappeared from the islands of Saipan and Tinian but not Rota (all three of which lack the snake). However, the hypothesis that shrews were involved is supported by this test (i.e. shrews colonized Guam, Saipan, and Tinian but not Rota).

9. Did experimental removal of the putative predator result in a population rebound by the proposed prey species? This type of data is available only for the interaction between the snake and several lizards (6) but positive results constitute strong evidence. Interpretation of negative evidence is limited by the possibility that the experimental removal was carried out for too short a period (60) or was otherwise unnatural.

Among the alternate hypotheses that we considered for each proposed species interaction were those involving habitat deterioration (24, 66), environmental contaminants (34, 79), introductions of disease organisms (80, 82), alternate predator effects (5), direct human exploitation (96, 97), and competition (17).

To evaluate ecological interactions, it is desirable to have periodic measures of abundance for the constituent species. For birds, a number of published and unpublished records exist that give relative abundance (e.g. annual reports of Guam's Division of Aquatic and Wildlife Resources), as well as several estimates of absolute abundance (16, 25, 26, 64). Some absolute population densities for introduced small mammals also exist, especially after World War II (2, 4, 5, 35). In recent years, there have been more-or-less complete counts of the one surviving bat colony on Guam (98).

Replicable population estimates are generally lacking for reptiles. We partially filled this void by intensively sampling representative plots (10 × 10 m) of forest land (70). We separated the canopy of each plot from adjoining vegetation, and we blocked ground-level movement of lizards by erecting a small fence of greased aluminum flashing. These barriers were installed during the lizards' inactive period. We then removed all vegetation in small pieces and counted the number of each lizard species trapped within an isolated plot. The average number of lizard individuals captured per plot on Guam was 130, indicating that a reasonable sample was obtained. These counts have demonstrated that the biomass of reptiles in Guam forests exceeds that of all other vertebrate taxa. Reptiles provide a significant food resource to both native (Micronesian kingfisher, *Halcyon cinnamomina* subsp. *cinnamomina*) and introduced (snake) predators. By comparing lizard densities among habitat-stratified plots possessing and lacking the snake (6), and between islands possessing the snake (Guam) and lacking the snake (Saipan), and integrating this information with published counts of lizards (31, 47, 48, 68, 69, 77, 99, 101), we can roughly estimate the probable lizard densities that occurred on Guam prior and subsequent to the arrival of the snake.

Our analysis focuses on Guam's primary natural terrestrial habitat—forest. Species that have never occurred in significant portions of Guam forests are omitted (e.g. brown noddies, *Anous stolidus*, which once roosted in isolated colonies but did not occur throughout the forest), as are feral and introduced species that did not play a significant role in the vertebrate food web of most localities: sambar deer (*Cervus mariannus*), Asiatic water buffalo (*Bubalus bubalis*), feral pig (*Sus scrofa*), feral dog (*Canis familiaris*), feral cat (*Felis catus*), marine toads (*Bufo marinus*), eastern dwarf tree frog (*Litoria fallax*), feral chicken (*Gallus gallus*), black francolin (*Francolinus francolinus*), blue-breasted quail (*Coturnix chinensis*), pigeon (*Columba livia*), Eurasian tree sparrow (*Passer montanus*), and chestnut mannikin (*Lonchura malacca*).

A SHORT ECOLOGICAL HISTORY OF GUAM'S FOREST VERTEBRATES

Prehistoric Extirpations

It is likely that Guam experienced the same pattern of anthropogenic extinctions suffered by other Pacific islands (21, 85, 87). Research on Rota (61, 86), the island nearest Guam, as well as the islands just north of Rota (61, 88), indicates that a significant portion of the native fauna disappeared about the time of human colonization (ca. 1500 BC). For example, Rota lost 13 of 22 (59%) avian species, including one shearwater, one tern, one duck, one megapode, three rails, two pigeons, one parrot, one swift, one monarch flycatcher, and one parrotfinch. Reptile and mammal losses are less well documented but probably include at least one large gecko (61). Thus the historical fauna of Guam includes only part of the native fauna.

Humans not only caused extinctions, they added species, especially mammals and lizards. In addition to the usual assortment of domestic livestock (dogs, pigs), prehistoric humans were probably responsible for the establishment of Asian black rats (*Rattus tanezumi*), mutilating geckos (*Gehyra mutilata*), oceanic geckos (*Gehyra oceanica*), and possibly monitors. The exotic geckos may have induced population declines in the native geckos but are not known to have eliminated any native species.

Historic Losses

From the time of Magellan (ca. 1520) until the 20th century, few additional species were lost, and the species additions (deer, Philippine turtle-dove *Streptopelia bitorquaata*, Polynesian rat *Rattus exulans*, house mouse *Mus domesticus*) were relatively inconsequential for the vertebrate food webs discussed below. The Micronesian megapode (*Megapodius laperouse*), which was not common on Guam during the historical period (probably related to a shortage of suitable soils for oviposition) and was subject to fairly intense human exploitation (3, 93), may have survived into the 20th century. It is difficult to know what role it would have played in the food web had its numbers not been so limited by human predation. The turtle-dove was also widely hunted, but it persisted and today is a food source for brown treesnakes (11, 12).

Recent Perturbations

The modern era in Guam began with the American Navy's effort to wrest control of the island from the Japanese during World War II. The Guam assault was part of a coordinated invasion of the Marianas. The conquest of Saipan took longer than American planners had anticipated, causing the preinvasion bombardment of Guam to be extended for several weeks (51). As a result, about 80% of the island's structures were destroyed. No one seems to have quantified the damage to the island's natural habitats.

During the subsequent wartime buildup for the planned invasion of Japan, Guam's civilian population of 21,838 was augmented by more than 200,000 soldiers (54). Quarters, warehouses, and airfields were built largely on previously undeveloped land. This buildup was further expanded in some localities for the Korean War (early 1950s) and later (1960s, 1970s) cold-war activities. After the 1950s, many of the clearings reverted to forest, although much of the regrowth was tangantangan (*Leucaena leucocephala*), an introduced leguminous tree (15, 27).

Heavy but unrecorded doses of DDT and allied pesticides were broadcast on the island for several decades after the war (1). The aggregate impacts of the postwar habitat destruction and pesticide contamination are not easy to discern, because the levels of use were not recorded and populations of the possibly affected species were not monitored. Nonetheless, no species disappeared from the forests of Guam at that time (24). The insectivorous nightingale reed-warbler (*Acrocephalus luscinia* subsp. *luscinia*) disappeared from central Guam around 1968, possibly as a delayed result of pesticide contamination but more likely as a result of a combination of brown treesnake predation and wetland habitat destruction (37). Several other insectivorous bird species were judged to be inexplicably rare in the 1960s, perhaps as a result of bioamplification of contaminants or snake predation. The insectivorous sheath-tailed bat (*Emballonura semicaudata*) was lost in the mid 1970s (41), possibly as a result of pesticide contamination. However, the bat's numbers were so poorly documented that inferences about the date or cause of its extirpation can neither be supported nor refuted. In addition, several poorly documented lizard species disappeared at an undetermined time in the postwar period, possibly because of pesticide contamination or habitat loss. However, none are known to have required pristine habitat, and when pesticide residues were first sampled in Guam wildlife in the 1980s, lizards were not found to harbor high levels (34).

THE IRRUPTION OF THE SNAKE Brown treesnakes probably arrived on Guam shortly after World War II as an unintended consequence of the salvage of derelict war materials from the New Guinea area (74). In particular, the huge American naval base at Manus (an island in the Admiralty Group, north of Madang, Papua New Guinea) was used as a staging point for vehicles, aircraft, and other supplies that had been sitting in the jungle since the battles. Undoubtedly, some of the items had snakes in them when they were transported from surrounding areas to Manus and from Manus to Guam.

Snake colonization was first evident in the southern part of Guam nearest Apra Harbor (74, 81). Spread was not well documented, but it was relatively slow in comparison to that of the other postwar irruptions of vertebrates on Guam (below). In contrast to the shrew irruption, there is evidence for only one locus of snake colonization, the harbor area and adjoining naval supply depots.

Quantification of snake abundances did not begin until 1985. In the early 1980s, Savidge (81) polled local residents throughout Guam to determine the date on which they first became aware of the snake. Residents at the far northern part of the island (35 km from the harbor) were not aware of the snakes until the 1980s. The dates Savidge compiled for local awareness of the snake should probably be viewed as when the snake became relatively abundant. For example, although Savidge found that residents of Ritidian Point at the northern tip of the island became aware of the snake around 1982, a visiting herpetologist captured a snake there in 1968. Thus, the snake had reached all parts of Guam by about 1970, but the crest of the irruption moved away from the port as a concentric spreading wave. This slow buildup is consistent with the relatively low vagility and modest fecundity of the species (77).

The buildup of snakes in the southern part of the Guam in the 1950s and 1960s was concurrent with disappearance of other vertebrates in southern Guam. There are no data for lizards, but residents were well aware of the disappearance of noisy birds and edible fruit bats. Bird and bat surveys by Guam's Division of Aquatic and Wildlife Resources were discontinued in the 1970s, as there were no more native endotherms to count. The three species that persisted longest were the Mariana fruit bat, Guam rail (*Rallus owstoni*), and island swiftlet (25, 37). The long-lived rail and bat persisted for about a decade beyond the dates when small birds disappeared from a locality. The swiftlet persists.

Island swiftlets differ from the other two species by roosting in caves. They are capable of echolocation and rarely, if ever, perch except in the roost cave (3). During the 1960s and 1970s, when the other bird and bat species were being extirpated from southern Guam, the swiftlet was disappearing from caves throughout Guam, except for the single roost that remains (91). In this cave, the birds perch and raise young in saliva-mud nests glued to the ceiling. Snakes forage at the entrance to and along the walls of the cave (G Wiles, personal communication; J Morton, personal communication) and are capable of gripping and bridging among ceiling stalactites in swiftlet caves elsewhere on the island (since abandoned by the birds), but snakes do not seem capable of scaling the smooth ceiling of the surviving roost cave. Brown treesnakes can accurately strike prey in total darkness (38), and a snake that had reached a cup nest in total darkness would seem to have no problem detecting immobile prey by olfaction or vomerolfaction alone. Thus, the snake could harm swiftlet populations but only those living in caves in which it could scale the walls.

The pattern of range contraction of island swiftlets on Guam was geographically the opposite of that of the other birds: Swiftlets vanished first from the northern part of the island. This has led some observers to search for a unique cause of endangerment for this bird. Swiftlets persisted in northern Guam until about 1980, however (37), a time when snakes were well established there, probably exceeding 50/ha by 1980 (74). Thus, the snake population was already about an order of magnitude higher than that recorded for other relatively large snake species away from water or dens (55, 77).

Brown treesnake population enumeration began in 1985, at which time the density was about 100 snakes/ha at a site on the northern end of the island (28, 74). Subsequent estimates have all been lower, suggesting that the peak of the irruption in northern Guam occurred around 1985. From 1985 to 1990, the snake population declined in northern Guam and exhibited signs of food stress (very high mortality among adult females, little recruitment, high proportion of emaciated individuals, and other signs). In the period 1992–1996, the condition of adult snakes improved and prey abundances rebounded from the extraordinary lows around 1989.

THE IRRUPTION OF THE MUSK SHREW The musk shrew (*Suncus murinus*) irruption occurred much more quickly than did that of the snake. The shrew was first detected in Guam at several sites around Apra Harbor in 1953 (57). The introduction is assumed to have been accidental; a likely source is the Philippines (5, 57). For the first year of the Guam colonization, the shrew was found only near the harbor, but by the end of the second year the shrew was found over most of the northern three quarters of the island (57). Shrew populations covered the entire island by 1958, including remote forested areas that are not the preferred habitat of this species (4). Mammalogists have speculated that unintentional vehicular transport must have spread the shrew (4, 57). It does not seem likely that the shrew was able to naturally expand its population over the 35-km expanse it occupied in one year. Furthermore, if it was capable of expanding so rapidly, one would have expected it to have first colonized the southern end of the island, which was closer to the point of introduction. It is possible that the south experienced undocumented colonizations. It is also possible that the shrew had greater difficulty colonizing those parts of the island, such as the south, that were well populated with brown treesnakes. In contrast, shrews reaching the northern end of the island would not have been subject to snake predation in 1955. Although both species entered Guam via the port, the snake was the first colonist of the port and southern areas of the island, whereas the shrew was the first colonist of the northern end of Guam.

Shrew trap lines on Guam in 1962–1964 had capture rates of around 15%, about 129% of the comparable value for 1958 (5). Capture rates fell from 1960 to 1981 to 1994 (K King, C Grue, C Fecko, unpublished information). In most forested areas of northern Guam the shrew is now too rare to detect. The peak of the irruption probably occurred before 1981, and the decline of shrews extended over more than a decade. Data are insufficient to determine the year of the crest of the shrew population irruption, but anecdotes of its abundance in the early 1960s have not been matched in recent years on Guam.

In contrast to Guam, where shrew populations rose and fell sharply, the nearby and, until recently, snake-free island of Saipan has maintained high shrew populations since its colonization in 1962. A 1997 mark-recapture study of shrews indicated a density of about 55/ha (95% CL 51–71; S Vogt, unpublished information). Barbehenn (5) estimated that shrews on Guam in 1962 (near the time of the crest of their irruption) numbered about 15.5/ha. If catch rates are proportional to abundance, the current shrew density in appropriate habitat on Guam would be about 0.6/ha.

Barbehenn (5) suggested that shrews were responsible for an order of magnitude decline in house mice (*Mus domesticus*) on Guam from 1958 to 1969 and that shrews might be impacting terrestrial lizards, of which he saw none on Guam "during hundreds of hours tending trap lines in the fields during 1962 to 1964." In 1998, this statement seems incredible, for both native and introduced skinks are present in surprising numbers in suburban areas as well as disturbed and undisturbed forests. For example, in snake-free and shrew-free plots of tangantangan forest on Guam, we found an average density of 13,200 skinks/ha, a density that declines in the presence of either snakes (to 8850/ha on Guam) or shrews (to 2200/ha on Saipan). The paucity of skinks throughout Saipan (70) is consistent with an adverse effect of introduced shrews on terrestrial lizards.

Two of Guam's terrestrial lizards have disappeared since the introduction of the shrew: the pelagic gecko (*Nactus pelagicus*) and the Mariana skink (*Emoia slevini*). There is no unequivocal evidence that the shrew affected the Mariana skink (48) but the pattern of extirpations of the gecko is consistent with shrew involvement. For example, the gecko is relatively common on Rota (shrews absent), but is gone from (in the case of Tinian and Saipan) or highly localized in (in the case of Guam) the shrew-occupied parts of its historical range in the southern Mariana Islands. The situation on Guam is complex because of the highly localized present distribution of the gecko (69). On Guam, the gecko occurs in relatively undisturbed forest in several portions of the island but is widespread only in southern forests (69). The area occupied by geckos in the southern portion of the island was first colonized by the snake, whereas the area of the island first colonized by the shrew is generally devoid of pelagic geckos. Furthermore, the surviving populations of pelagic geckos on Guam exhibit an unexpectedly high level of arboreality, which would be consistent with behavior that prevents predation by terrestrial predators.

THE IRRUPTION OF THE GREEN ANOLE The green anole (*Anolis carolinensis*) was purposely released on Guam around 1955 by a citizen who judged it beneficial for insect control (23). The chronology of the spread of this diurnal arboreal lizard is not known, but it increased in density and spread over much of the island over the next 20 years (50). After that time, however, its abundance waned and it became rare in most nonurban areas (76). Both its rarity in nonurban areas and its primary effect on Guam's ecology were illustrated by sampling conducted by B Smith and T Fritts in 1985. They collected snakes and lizards (snake prey) in the Northwest Field area of northern Guam to determine if the snakes were preying on lizards in the same relative proportions that the lizards were discovered by herpetologists. Over half (52%) of 91 lizards preyed upon by the 168 snakes collected were anoles, whereas only 4.3% of the 494 lizards collected by herpetologists were anoles, even though anoles are conspicuous to humans. These data suggest that anoles are unusually vulnerable to snake predation. Anoles have not been found on Northwest Field since 1985, presumably reflecting a population decline in the lizard brought on by extremely effective snake predation.

The discrepancy between utilization and apparent availability of Guam anoles is mirrored by the exceptional ability of brown treesnakes to find agamid lizards in Australia (84) at night. In both cases the prey are taken at night. Brown treesnakes cruise slowly through the twig ends of foliage at night; thus, they are able to discover and capture lizards while the lizards sleep on the ends of branches. Guam's native lizards do not sleep in such locations. Thus, one potentially major effect of the anole's introduction to Guam was that it provided a prey item that was uniquely suited to the snake's manner of foraging. Because of its rarity and unique niche, it is unlikely that the anole currently has a direct impact on the welfare of Guam's native lizards.

THE IRRUPTION OF THE BLACK DRONGO The black drongo (*Dicrurus macrocercus*) was translocated from Taiwan to Rota for insect control shortly before World War II (37). It is believed to have colonized northern Guam through overwater dispersal from Rota in the 1950s (R Ryder, personal communication) or

1960s (37, 43). By 1967, it was reported to be the fourth most common bird in Guam roadside counts (R Ryder, personal communication). It had reached the southern end of the island by 1970, when it was judged common in central Guam (40). By 1981, it was fourth in population density, having about one sixth the abundance of the Micronesian starling (25). In the mid-1980s, drongo counts along roadsides began a steep decline, especially in northern Guam (according to annual reports of Guam's Division of Aquatic and Wildlife Resources).

Drongos are strongly territorial, aggressive birds that are believed to displace smaller birds that might otherwise nest within their territories. Although this has been proposed to account for declines in species of smaller birds, the only attempt to document a demographic impact failed to show an effect (43). Because drongo abundances on Guam have declined since these experiments, it is likely that present effects are relatively small.

THE IRRUPTION OF THE CURIOUS SKINK In vertebrate biomass, the most significant of the postwar irruptions was that of the curious skink (*Carlia* cf *fusca*). The cause and origin of this colonization is unknown, as is the exact species (45). The early years of the irruption are undocumented, although it appears to have first colonized central Guam (23).

The skink arrived on Guam in the midst of the shrew irruption, which probably limited the skink's initial population growth and spread. [Unfortunately, the only surviving evidence is of relative abundance of this skink in comparison to the native skinks (31, 68).] Those data show that the curious skink rapidly expanded its populations and soon came to dominate collections of skinks (31, 74) from Guam (75%), Tinian (>90%), and Saipan (>95%). The growing dominance of *Carlia* in collections might have meant that the introduced skink was displacing the native skinks, but that inference is only partially supported by direct assessments of abundance. *Carlia* were not as dominant as is suggested by the museum collections. Because most herpetological collections are made along roadsides, in habitats that are highly disturbed, it is probable that skinks in disturbed habitats are overrepresented in museum collections. Curious skinks may also be more readily detected because they are bold and inquisitive. Our total removal samples indicate that it constitutes only a small fraction of the skink fauna in native forest (8.3%) and highly disturbed ravine forest (10.2%). Even in highly disturbed tangantangan forest it barely constitutes a majority (55%). Therefore, it seems likely that the rise of the curious skink from 0% to about 75% of skink collections in the interval 1960 to 1990 represents primarily the increasing dominance of curious skinks in disturbed habitats. Severe typhoons, which were unusually frequent in Guam in the 1990s, may have increased the amount of disturbed habitat; thus the irruption of the curious skink may not yet have crested.

By the 1990s, the curious skink constituted the primary prey item for most brown treesnakes (75). The smallest snakes are relatively arboreal in their habits and consume substantial numbers of geckos along with skinks; intermediate-sized snakes eat almost exclusively *Carlia*; and the largest snakes shift to a diet including endotherms, especially rats, but also including skinks. Therefore, the skinks make a major contribution to sustaining populations of the introduced snake.

The Consequences of Five Irruptions

To illustrate trophic interactions, we prepared food webs for northern Guam in 1945 (Figure 1), 1965 (Figure 2), and 1995 (Figure 3). We obtained mean masses of each species from our collections or from the literature (35, 37, 41, 56) and multiplied these by estimated absolute population densities to obtain crude estimates of biomass density for each species.

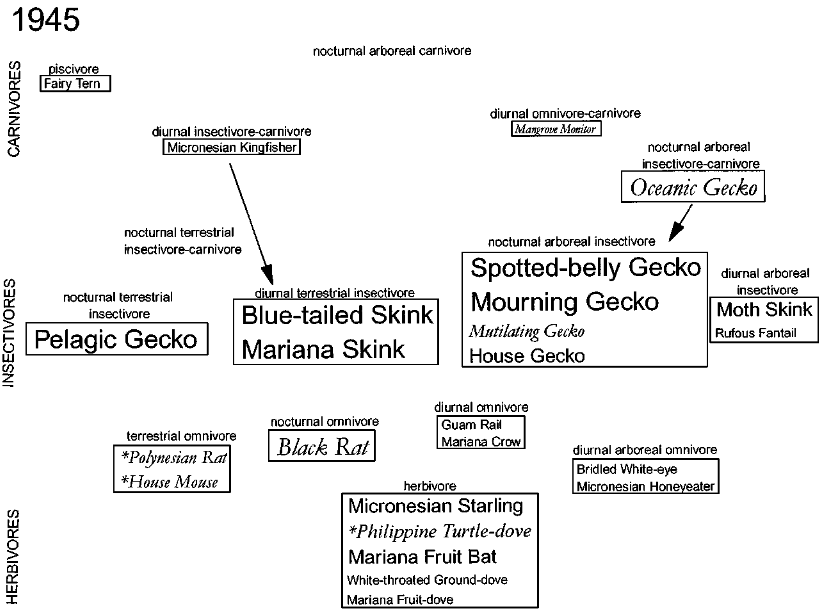

Figure 1 Typical vertebrate food web for northern Guam in 1945. *Italic*, introduced species; *asterisks*, historic introductions; *type size*, relative biomass abundance by order of magnitude from 0.01 to >10 kg/hectare (ha). Biomass densities were grouped by order of magnitude into four classes (0.01–0.099 kg/ha; 0.1–0.99 kg/ha; 1.0–9.9 kg/ha; and >10 kg/ha). Species represented by <0.01 kg/ha were considered trophically insignificant and were omitted from the figures. The figures show major trophic interactions within the vertebrates, and the niche box labels indicate the major trophic interactions between vertebrate and nonvertebrate species (Figures 1–3). See text and Table 1 for additional information.

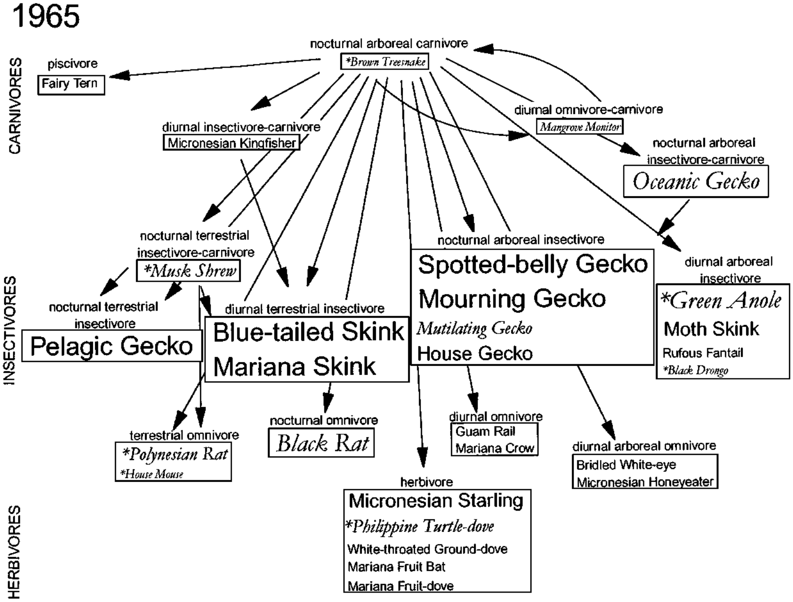

Figure 2 Typical vertebrate food web for northern Guam in 1965. *Italic*, introduced species; *asterisks*, historic introductions; *type size*, relative biomass abundance by order of magnitude from 0.01 to >10 kg/hectare (ha). Biomass densities were grouped by order of magnitude into four classes (0.01–0.099 kg/ha; 0.1–0.99 kg/ha; 1.0–9.9 kg/ha; and >10 kg/ha). Species represented by <0.01 kg/ha were considered trophically insignificant and were omitted from the figures. The figures show major trophic interactions within the vertebrates, and the niche box labels indicate the major trophic interactions between vertebrate and nonvertebrate species (Figures 1–3). See text and Table 1 for additional information.

The vertebrate forest food web on Guam today bears little resemblance to that prior to the postwar introductions (Figures 1–3). The most striking change from 1945 to 1995 is the reorganization of the food web from one in which virtually all components were native (indicated by plain typeface) and wherein vertebrates fed on nonvertebrates (plants and invertebrates) to one in which almost all major components are introduced vertebrates (italic font) that prey on other introduced species.

In 1945 (Figure 1), carnivory (consumption of vertebrates) was limited to kingfishers eating skinks and very large geckos occasionally eating smaller geckos. Mangrove monitors consumed eggs and small vertebrates opportunistically, but this interaction does not seem to have been demographically significant for the prey species. Thus, the soon-to-be-filled niches of nocturnal arboreal carnivore and nocturnal terrestrial insectivore-carnivore were vacant in 1945. It is not clear if the monitor is a native species, a prehistoric introduction,

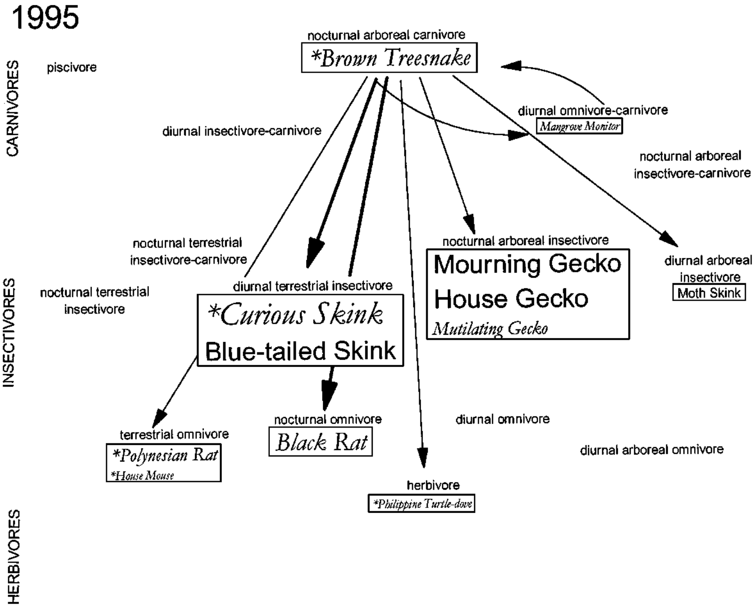

Figure 3 Typical vertebrate food web for northern Guam in 1995. *Italic*, introduced species; *asterisks*, historic introductions; *type size*, relative biomass abundance by order of magnitude from 0.01 to >10 kg/hectare (ha). Biomass densities were grouped by order of magnitude into four classes (0.01–0.099 kg/ha; 0.1–0.99 kg/ha; 1.0–9.9 kg/ha; and >10 kg/ha). Species represented by <0.01 kg/ha were considered trophically insignificant and were omitted from the figures. The figures show major trophic interactions within the vertebrates, and the niche box labels indicate the major trophic interactions between vertebrate and nonvertebrate species (Figures 1–3). See text and Table 1 for additional information.

or a recent introduction [which it is on more northern islands, although data from Guam are unresolved (G Pregill, personal communication)]. In addition to the monitor, there were only six consequential introduced species in northern Guam forests in 1945: three rodents, one game bird (Philippine turtle-dove), and two geckos. The native species dominated the food web, including twelve birds, three bats, and seven lizards.

By 1965 (Figure 2), the number of native species had not changed, but the addition of several predators, especially the shrew and the snake, had radically altered the number of predatory links within the vertebrate community (Figure 2). This increase in carnivory did not initially result in a great diminution in the abundances of the prey species. In part this was because the predators had not reached their peak abundance, and in part it was due to their eating each other. For example, the shrew diminished the abundances of several terrestrial lizards, but the snake was not only eating the shrew (thereby relieving pressure on the lizards), it was also reducing lizard predation by eating kingfishers. Thus energy utilization was shifted up the food chain, but the energetic consequence of this consumption was diffused among several trophic levels and among many prey species. A few key prey species, many of them introduced, help sustain rapid growth in predator populations. This phenomenon was greatly reinforced by the irruption of the curious skink in the 1970s and 1980s.

In the mid-1980s, however, pressure by introduced predators overwhelmed many of the native endotherms, putting additional pressure on the surviving prey species. By 1995 (Figure 3), native vertebrate prey species were so diminished that the food web was becoming comparatively top-heavy and holey: piscivores, nocturnal terrestrial insectivores, diurnal insectivore-carnivores, nocturnal arboreal insectivore-carnivores, and diurnal arboreal omnivores were entirely missing (Figure 3). Several additional niches were unfilled over most of northern Guam because the surviving species were localized and rare: nocturnal terrestrial insectivore-carnivores, diurnal omnivores, herbivores, and diurnal arboreal insectivores. With the exception of blue-tailed skinks, the vertebrate forest food web consisted of snakes preying on introduced rats, introduced skinks, and introduced geckos (the house gecko may be a prehistoric introduction).

NONVERTEBRATE IMPACTS Whatever the cause of this radical rearrangement of the food web, it seems likely that repercussions will be felt outside the vertebrate community. Although there may have been some compensatory increases in insectivory by the surviving vertebrate and invertebrate insectivores, one mammalian and many avian insectivores were lost, presumably increasing insect abundances at some cost to crop production. Newly introduced insects may also find it easier to colonize Guam. Pollination and seed dispersal services of native birds to native plants were also lost (18, 53). Subjectively, Guam seems to have a much higher density of web-building spiders than nearby islands; this is consistent with experiments in the West Indies on the importance of predation and competition between spiders and lizards on islands (19, 83) but has not been investigated on Guam. Spiders that place conspicuous filaments (stabilimenta) in their webs, presumably to avoid bird damage to their webs, do so less often on Guam than on nearby islands that have forest birds (39).

As a result of the loss of avian and mammalian herbivores on Guam, one would expect to see some reduction in herbivory, especially frugivory, which may be only partially offset by compensatory increases by invertebrate frugivores. Invertebrate frugivory can be a substantial economic burden on agriculture, so it is perhaps surprising that this phenomenon has not been investigated on Guam. The impact on native plant species of reduced vertebrate herbivory is harder to judge, and to our knowledge no one has attempted to separate the effects of this from the concurrent impacts of introduced ungulates (especially pig and deer) that we do not consider here.

TO WHAT EXTENT ARE FACTORS OTHER THAN INTRODUCED SPECIES RESPONSIBLE?

Of the factors that have been suggested as contributing to the Guam biodiversity crisis (introduced predators, habitat loss, contaminants, introduced diseases, competition from introduced species, and direct human exploitation), only introduced predators and habitat loss are believed to be generally important. Pesticide contamination may have played a role in depressing insectivore populations prior to about 1970, but it has not been linked to the loss of any species (34, 79), and pesticide contamination should have waned in importance prior to the bulk of extinctions in the 1980s. Significant problems with introduced diseases have not been discovered (80, 82). Competition between native and introduced lizards (9, 10) and birds (43) has been discounted but will be difficult to dismiss unequivocally. Direct human exploitation has been a concern primarily for the Marianas fruit bat (97), but this species continued to decline for a decade after elimination of direct exploitation pressure. Furthermore, the early bat losses in southern Guam (56) are so strikingly similar to those observed concurrently among birds that they seem likely to have been due to snake predation, which would have been more frequent but less obvious to human observers.

The role played by habitat loss is more subtle because of the strong interaction between the effects of introduced predators and habitat loss (i.e. the introduced species thrive in disturbed habitats), and the long evolutionary history native vertebrates in the Marianas have with catastrophic habitat disturbance following typhoons. Because the average time between typhoons on Guam is shorter than the interval needed to restore primary forest after a typhoon, few or no native species are rigidly dependent on old growth (24). Still, the issue is complex enough to warrant explicit analysis.

Are any of the native vertebrates restricted to old native forest? Habits are unknown for a few species (e.g. little Mariana fruit bat, *Pteropus tokudae*), but the others were known to occur in disturbed habitats on either Guam or a comparable nearby island. The spotted-belly gecko (*Perochirus ateles*) may now be restricted to native forest on Saipan, perhaps owing to competition with recently introduced geckos. On Cocos Island, however, this gecko is frequently seen on buildings, a highly disturbed habitat (47). The remaining species are well documented to occur in both native forest and disturbed habitats, although they may reach higher densities in native forest (13, 14). A few species, such as the Micronesian honeyeater (*Myzomela rubrata*), do better in disturbed habitats (16).

Could postwar species losses on Guam have occurred as a result of habitat destruction? This seems improbable. No species were lost as a result of habitats having been impacted by the war. During the following period of habitat regrowth, nearly every species contracted in distribution and most were ultimately extirpated. Three caveats are appropriate: (*a*) The lack of importance of forest habitat deterioration does not apply to wetland species, which suffered severe and potentially extinction-causing loss of habitat in the postwar period (89, 92); (*b*) The presence of so much disturbed habitat facilitated the irruptions of all five of the postwar introductions (63); (*c*) Guam's rapidly expanding human population is now converting swaths of former forest into suburban landscapes, which will place a severe constraint on future species restoration. Nonetheless, we have not seen compelling evidence that the loss of any of Guam's forest vertebrates was primarily attributable to habitat degradation.

Considering all nine criteria for appraising the impacts of an introduced species, we believe that the brown treesnake was responsible for the extirpation or decline of virtually all of the native forest birds (Table 1). This excludes the wetland birds but includes sea birds such as fairy terns (*Gygis alba*) that nested in forested areas. Pesticides and habitat deterioration may have played a role in population declines, especially in the immediate postwar period, but outright extirpation is consistent only with the high predatory impact of the snake. The record for mammals is much less clear, but the current demographic strains being experienced by the Mariana fruit bat do seem to be a result of snake predation. Insufficient information exists to evaluate the causes of the extirpation of the other two bats.

The situation for lizards is more complex. The musk shrew irruption probably greatly diminished the pelagic gecko and may have impacted the Mariana skink. It may have played a role in the elimination of several poorly known skinks from southern Guam not discussed in this paper (the tide-pool skink *Emoia atrocostata*, the azure-tailed skink *Emoia cyanura*, and the blue-tailed copper-striped skink *Emoia impar*). *Boiga irregularis* was probably a key player in, if not the sole cause of, the reduction or extirpation of the snake-eyed skink (*Cryptoblepharus poecilopleurus*, which is restricted to southern Guam and is too poorly known for comprehensive evaluation), the spotted-belly gecko, and the introduced mutilating gecko and oceanic gecko. The oceanic gecko probably reduced population densities of the spotted-belly gecko before the brown treesnake arrived (61).

WHY SUCH AN EXTREME EFFECT?

Four explanations have been suggested to account for the unusual number and taxonomic breadth of extinctions on Guam. The first is that the resident species, having evolved in an essentially predator-free environment (Figure 1), lacked the predator defenses that would have spared mainland species from extirpation (42, 81). Based on comparison with mainland areas that have experienced introductions of snakes, and on differences between Guam's native and introduced prey species in vulnerability to snake predation, this argument is supported (73). No introduced species is known to have been extirpated during the postwar extinctions; in contrast, almost all of the native species either declined to near the limit of population viability or were lost.

With one exception, however, predator defenses of Guam species have not been tested. Campbell (6) compared the defensive behaviors of two Guam geckos, the house gecko (probably a prehistoric introduction) and the mourning gecko (native). The native species rarely (37%) fled from the scene of a simulated predator approach, whereas the introduced species routinely (76%) avoided the sites of nighttimes disturbances ($P < 0.001$ by Fisher test). This is an example of the well-known phenomenon of island tameness (62).

Pimm (58, 59) and others (46, 75) emphasized the trophic role of less vulnerable prey species. They argued that the abundance of prey species that were capable of sustaining brown treesnake predation (primarily introduced species) increased the abundance of the snake to a level at which the native prey species, taken opportunistically, could not persist. In this regard it is noteworthy that the various introduced species that irrupted in the postwar period (Figures 2 and 3) thrived, and in some cases increased their abundance, in the face of heavy predation by the brown treesnake. Had the introduced species not been present, it seems probable that the snake could not have attained nearly as high a density as it did. Indeed, had the snake been limited to feeding on native species, it would have had virtually nothing to eat in 1985 in northern Guam. Instead the snake reached maximum densities of around 100/ha.

The brown treesnake possesses certain characteristics that make it a particularly attractive candidate for disrupting island ecosystems. It is nocturnal, a generalist feeder, and an exceptional climber (29). Generalist predators are known to be especially problematic (22, 58). Nocturnal predators exploit the inability of most passerines to fly safely after dark. And the exceptional climbing skills of this snake give it access to virtually all refugia and nest sites except for the swiftlet nests glued to the ceilings of smooth-walled caves. Ebenhard (22) tied arboreality to greater impacts of introduced species, especially on islands.

The snake also possesses certain characteristics that limit its impact on the native fauna (90). For example, it is a relatively slow reproducer and has a longer generation time than most of the endangered species; thus it should not greatly overshoot the carrying capacity of the prey. This particular snake does possess certain attributes that make extinctions of island prey more likely (nocturnality, arboreality), but these attributes are not unique among snakes (73). At least 20 species within the genus *Boiga* share the problem-causing attributes (33), as do many other nocturnal arboreal snakes. On balance, it is difficult to ascribe the Guam crisis solely to the attributes of the invader snake.

A fourth hypothesis is that Guam has a uniquely vulnerable ecology. Being an oceanic island, Guam has a moderate climate, one that would not preclude the colonization of most invading species (73). It is also likely to have high densities of lizard prey. Our review of studies on lizard assemblage density strongly supports the generality of MacArthur's "excess density compensation" for island lizards (44), as tentatively indicated for islands in the Gulf of California by Case (8). For example, among 15 relatively simple assemblages (10 or fewer lizard and frog species) on oceanic islands, the mean biomass density of lizard assemblages averaged 16.30 kg/ha, whereas the comparable value for 23 tropical mainland locations was only 0.63 kg/ha. It is not clear, however, that oceanic islands generally have high biomasses of avian or mammalian prey (20, 44, 49), and in any event, neither of these attributes is unique to the island of Guam [Guam originally had a lower density of birds than comparable mainland areas (81)]. Moderate climates and excess density compensation should apply equally to all tropical oceanic islands.

In summary, the lack of coevolution between predator and prey was probably a major contributing factor to the severity of the Guam biodiversity crisis. In addition, the brown treesnake would not have reached such high densities if it had not had at its disposal a large and resilient prey base of introduced species. The introduced species did better in disturbed habitats; thus the native species suffered both from habitat loss and greater pressure from exotic predators in the disturbed habitat. Furthermore, the snake and the Guam environment were well suited to introduced species problems, but neither the snake nor the environment was unique; these problems could arise with any number of predators on any number of ecosystems in which coevolutionary experience between predator and prey is lacking.

WHAT WILL HAPPEN NOW?

Having heard that the native vertebrates of Guam are largely extirpated, many nonbiologists assume that the snake will run out of food. Our indications are that the food supply in northern Guam was more plentiful in 1995—well after the crest of the irruption—than it was in 1990 (closer in time to the crest), and we estimate that snake populations now averaging about 3 kg/ha can be easily supported by the remaining prey, even though important prey types are now limited to introduced species (Figure 3). We estimate that only seven prey species retain biomass densities of greater than 0.1 kg/ha. Both significant endotherm prey species in forested areas of northern Guam are introduced rats: the Polynesian rat (ca. 0.2 kg/ha) and black rat (ca. 3 kg/ha). In addition, geckos abound: the mutilating gecko (ca. 0.5 kg/ha), the house gecko (ca. 2.5 kg/ha), and the mourning gecko (ca. 2.5 kg/ha, but this species may be too small a prey for any but the youngest snakes). Finally, and most abundantly, there are leaf-litter skinks: the blue-tailed skink (ca. 6 kg/ha) and the vital curious skink (ca. 16 kg/ha). The adequate predator:prey ratio of 10:1 does not tell the whole story, of course. The recruitment rate of prey species is much greater than is that of the snake. Thus, there is no reason to predict that present snake populations cannot be sustained indefinitely on introduced prey. Furthermore, the pace of new species introductions has been accelerating over recent decades and it is probable that new food items will become available for the snake.

A new problem confronting the brown treesnake is that the food items upon which it now depends are primarily diurnal, terrestrial species of skinks that sleep in relatively sheltered locations during the night (M McCoid, personal communication). The curious skink becomes active at first light, which may increase its contact with the historically nocturnal brown treesnake (45). This may account for at least part of the greater representation of the curious skink in brown treesnake diets, in comparison to the later-arising blue-tailed skink. Whichever skink is taken, however, requires the snake to forage during the day on the ground. Perhaps this is the reason that brown treesnakes on Guam became significantly more diurnal and more terrestrial in the late 1980s when native endothermic prey vanished. While the growing diurnality of the snake has not been quantitatively verified except by the pattern of electrical power outages shown in Figure 4, anecdotal measures of activity (e.g. time when snakes are seen being caught in traps) are consistent with a profound change since the early 1980s. Snakes do not appear to be very active during the early afternoon (when skinks are also relatively quiescent), but total daytime activity approaches 50% of all movements.

In addition, significant ground-level activity was not observed in brown treesnakes on Guam prior to 1988 but is now the modal condition observed in some localities, especially of snakes large enough to depend on skink prey (65). It is difficult to know if other snake species would have had the behavioral flexibility shown by the brown treesnake to change in a few years from nocturnal arboreality to habits including diurnal terrestriality, but this foraging flexibility undoubtedly contributed to the severity of the impact the snake had on Guam wildlife.

Although skinks and geckos are abundant, they are small. Thus, the dietary shift of adult snakes from native endotherms (1980) to lizards (1990) resulted in a shift from food appropriate for adult snakes to food for juveniles. One would expect this to transform survivorship curves from high adult/low juvenile survivorship to low adult/high juvenile survivorship. Although age-stratified survivorship in brown treesnakes has not been measured, we have observed

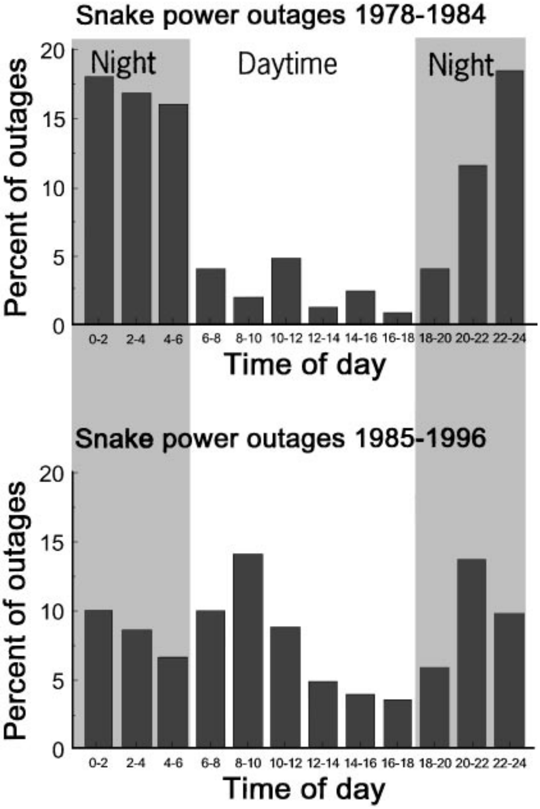

Figure 4 Change in diurnality of snake activity as measured by time of snake-induced power outages (1978–1996). Outages are attributed to a snake if an electrocuted snake was found at the site of the fault. Outages along lines not operated 24 h/day are omitted.

dramatic shifts in size distributions (71). Most notably, the percentage of the detected population that is mature has dropped from about 60% in the snake's native range, to 48% on Guam in the early 1980s, to about 25% on Guam since 1986 (77). The Guam values are surprisingly low for a snake with such a small clutch size (3–12 eggs). During 1985–1995, clutch sizes of brown treesnakes on Guam averaged about five, for which a typical snake would have a mature fraction of about 80% (55). There are problems with undersampling juvenile brown treesnakes, but this undersampling should produce a conservative error in this comparison with other snake species (67). Thus, although the brown treesnake has been able to maintain high population densities on Guam following the extirpation of native prey, it has done so at the cost of high adult mortality, probably caused by a shortage of large prey.

An additional potential source of change for the Guam population is human management. At the present time, management activities are local, influencing only the abundance and size distribution of snakes in the vicinity of port, airport, and cargo-handling facilities. However, future development of biological control agents or broadcast toxicants could result in population depletion islandwide (7). In addition, the technology for fencing snakes out of high priority wildlife management sites is maturing (72), and may soon be in place to eliminate or greatly reduce snake densities over significant areas of Guam forests.

Until islandwide snake control is operational, Guam will continue to be a source of propagules for accidental transport to other islands (28). Based on the climatic tolerances of the snake, the risk of colonization would be highest for tropical islands, but would include any locally mesic location that does not undergo a hard freeze (7). Based on the amount of commerce conducted through Guam ports, the areas of highest risk are Micronesian islands and Hawaii, followed by US West Coast ports and all US Gulf Coast locations with military facilities (30). The Caribbean possessions of the United States also receive goods, particularly military supplies and emergency equipment transferred to assist in hurricane recovery efforts. Based on the ecological interactions observed on Guam, risk factors for recipient locations include prey that lack coevolutionary experience with comparable predators, abundant vulnerable prey, and prey that share habitats with relatively invulnerable prey (e.g. species possessing coevolutionary experience with nocturnal arboreal snakes).

Taken together, these risk factors point to the Mariana, Hawaiian, and Caroline islands as being most at risk. The Mariana and Caroline islands are so similar to Guam that a brown treesnake colonization of those islands may be expected to play out in a manner very similar to that observed on Guam (albeit on a time scale commensurate with the size of the island). Hawaii is less predictable because its biotic community differs from Guam's in several major ways. First, there are introduced species for which there is no analog in the Marianas, such as mongoose (52). Mongoose now depress lizard populations on Hawaii, but would provide a high-value prey for large snakes. If their populations were to decline appreciably in the face of a brown treesnake infestation, the mongoose decline might release previously depressed populations of ground lizards and thereby provide juvenile snakes with an additional rich food source. Second, Hawaii is unique in that the native endotherms have already been eliminated from most low elevation sites by diseases and introduced species (95). The replacement of the native avifauna by several exceedingly abundant exotic birds (e.g. zebra doves, *Geopelia striata*) may accelerate snake population buildup.

Thus the pace and impacts of colonization are less predictable. The rate of colony expansion may be sufficiently slow to permit effective control actions to be implemented. Initial efforts to control an apparent colonization of Saipan have not yielded hoped-for successes, however. Additional research on the control of the brown treesnake may bring new tools to this very urgent task.

ACKNOWLEDGMENTS

We thank the US Departments of Defense and Interior for supporting this work. A host of volunteers and technicians helped us carry out the field work; we appreciate the labors of all. Earl Campbell was a major source of information and inspiration for much of our work. Kathy Dean-Bradley and Linda Wolfe provided indispensable computational and administrative assistance. We thank C Aguon, C Grue, K King, MJ McCoid, J Morton, G Pregill, R Ryder, S Vogt, and G Wiles for graciously sharing unpublished findings. Earl Campbell, Kathy Dean-Bradley, Gad Perry, and Renée Rondeau suggested improvements to the manuscript.

Literature Cited

1. Baker RH. 1946. Some effects of the war on the wildlife of Micronesia. *Trans. N. Am. Wildl. Conf.* 11:207–13
2. Baker RH. 1946. A study of rodent populations on Guam, Mariana Islands. *Ecol. Monogr.* 16:393–408
3. Baker RH. 1951. The avifauna of Micronesia, its origin, evolution, and distribution. *Univ. Kans. Publ. Mus. Nat. Hist.* 3:1–359
4. Barbehenn KR. 1962. The house shrew on Guam. In *Pacific Island Rat Ecology*, ed. TI Storer, pp. 247–56. Honolulu: Bull. Bishop Mus. 225
5. Barbehenn KR. 1974. Recent invasions of Micronesia by small mammals. *Micronesica* 10:41–50
6. Campbell EW III. 1996. *The effect of brown tree snake* (Boiga irregularis) *predation on the island of Guam's extant lizard assemblages*. PhD thesis. Ohio State Univ., Columbus, OH. 83 pp.
7. Campbell EW III, Rodda GH, Fritts TH, Bruggers RL. 1998. An integrated management plan for the brown treesnake (*Boiga irregularis*) on Pacific islands. See Ref. 78, In press
8. Case TJ. 1975. Species numbers, density compensation and colonizing ability of lizards on islands in the Gulf of California. *Ecology* 56:3–18
9. Case TJ, Bolger DT. 1991. The role of introduced species in shaping the distribution and abundance of island reptiles. *Evol. Ecol.* 5:272–90
10. Case TJ, Bolger DT, Richman AD. 1992. Reptilian extinctions: the last ten thousand years. In *Conservation Biology: the Theory and Practice of Nature Conservation Preservation and Management*, ed. P Fiedler, S Jain, pp. 91–125. New York: Chapman & Hall
11. Conry PJ. 1987. Ecology of the Philippine turtle-dove on Guam. *Guam Div. Aquat. Wildl. Res. Tech. Rep. 6*. 69 pp.
12. Conry PJ. 1988. High nest predation by brown tree snakes on Guam. *Condor* 90: 478–82
13. Craig RJ. 1990. Foraging behavior and microhabitat use of two species of white-eyes (*Zosteropidae*) on Saipan, Micronesia. *Auk* 107:500–5
14. Craig RJ. 1992. Territoriality, habitat use and ecological distinctness of an endangered Pacific Island reed-warbler. *J. Field Ornithol.* 63:436–44

15. Craig RJ. 1994. Regeneration of native Mariana Island forest in disturbed habitats. *Micronesica* 26:97–106
16. Craig RJ. 1996. Seasonal population surveys and natural history of a Micronesian bird community. *Wilson Bull.* 108:246–67
17. Craig RJ, Taisacan E. 1994. Notes on the ecology and population decline of the Rota bridled white-eye. *Wilson Bull.* 106:165–69
18. Denton GRW, Muniappan R, Marutani M. 1991. The distribution and biological control of *Lantana camara* in Micronesia. *Micronesica Suppl.* 3:71–81
19. Dial R, Roughgarden J. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* 76:1821–34
20. Diamond JM. 1970. Ecological consequences of island colonization by southwest Pacific birds. II. The effect of species diversity on total population density. *Proc. Natl. Acad. Sci. USA* 67:1715–21
21. Dye T, Steadman DW. 1990. Polynesian ancestors and their animal world. *Am. Sci.* 78:207–15
22. Ebenhard T. 1988. Introduced birds and mammals and their ecological effects. *Swed. Wildl. Res. Vilrevy* 13:1–107
23. Eldredge LG. 1988. Case studies of the impacts of introduced animal species on renewable resources in the U.S.-affiliated Pacific islands. In *OTA Commissioned Papers, Integrated Renewable Resource Management for U.S. Insular Areas ("Islands Study" 1987),* Vol. 1, ed. CK Imamura, E Towle, pp. A.26–46. Washington, DC: US Cong. Off. Technol. Assess.
24. Engbring J, Pratt HD. 1985. Endangered birds in Micronesia: their history, status, and future prospects. In *Bird Conservation*, ed. SA Temple, pp. 71–105. Madison: Univ. Wis. Press
25. Engbring J, Ramsey FL. 1984. Distribution and abundance of the forest birds of Guam: results of a 1981 survey. *US Fish Wildl. Serv., FWS/OBS-84/20.* 54 pp.
26. Engbring J, Ramsey FL, Wildman VJ. 1986. *Micronesian forest bird survey, 1982. Saipan, Tinian, Aguiguan, and Rota*. Honolulu: Rep. US Fish Wildl. Serv.
27. Fosberg FR. 1960. The vegetation of Micronesia. *Bull. Am. Mus. Nat. Hist.* 119:1–75
28. Fritts TH. 1988. The brown tree snake, *Boiga irregularis*, a threat to Pacific Islands. *Biol. Rep.* 88(31). Washington, DC: US Fish Wildl. Serv. 36 pp.
29. Fritts TH, Chiszar D. 1998. Snakes on electrical transmission lines: patterns, causes, and strategies for reducing electrical outages due to snakes. See Ref. 78, In press
30. Fritts TH, McCoid MJ, Gomez DM. 1998. Dispersal of snakes to extralimital islands: incidents of the brown treesnake, *Boiga irregularis,* dispersing to islands in ships and aircraft. See Ref. 78, In press
31. Fritts TH, Rodda GH. 1995. Invasions of the brown tree snake. In *Our Living Resources: a Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems,* ed. E LaRoe, G Farris, C Puckett, P Doran, M Mac, pp. 454–56. Washington, DC: US Natl. Biol. Serv.
32. Goldschmidt T, Witte F, Wanink J. 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Conserv. Biol.* 7:686–700
33. Greene HW. 1989. Ecological, evolutionary, and conservation implications of feeding biology in Old World cat snakes, genus *Boiga* (*Colubridae*). *Proc. Calif. Acad. Sci. Ser. 4* 46:193–207
34. Grue CE. 1985. Pesticides and the decline of Guam's native birds. *Nature* 316:301
35. Jackson WB. 1967. Productivity in high and low islands with special emphasis to rodent populations. *Micronesica* 3:5–15
36. Jaffe M. 1994. *And No Birds Sing*. New York: Simon and Schuster. 283 pp.
37. Jenkins JM. 1983. The native forest birds of Guam. *Am. Ornith. Union Ornithol. Monogr. 31.* 61 pp.
38. Kardong KV, Smith PR. 1991. The role of sensory receptors in the predatory behavior of the brown tree snake, *Boiga irregularis* (*Squamata: Colubridae*). *J. Herpetol.* 25:229–31
39. Kerr AM. 1993. Low frequency of stabilimenta in orb webs of *Argiope appensa* (*Araneae: Araneidae*) from Guam: an indirect effect of an introduced avian predator? *Pac. Sci.* 47:328–37
40. Kobayashi K. 1970. Observation of the birds of the Mariana Islands. *Tori* 20(88):24–29
41. Lemke TO. 1986. Distribution and status of the Sheath-tailed Bat (*Emballonura semicaudata*) in the Mariana Islands. *J. Mammal.* 67:745–46
42. Loope LL, Mueller-Dombois D. 1989. Characteristics of invaded islands, with special reference to Hawaii. In *Biological Invasions: a Global Perspective,* ed. JA Drake, HA Mooney, F diCastri, RH

Groves, FJ Kruger, et al, pp. 257–80. Chichester, UK: Wiley

43. Maben AF. 1982. *The feeding ecology of the black drongo* Dicrurus macrocercus *on Guam*. MS thesis. Calif. State Univ., Long Beach. 87 pp.
44. MacArthur RH, Diamond JM, Karr JR. 1972. Density compensation in island faunas. *Ecology* 53:330–42
45. McCoid MJ. 1997. *Interactions of* Carlia *cf.* fusca (Scincidae) *with the herpetofauna of Guam*. MS thesis. Texas A&M, Kingsville, Tex. 98 pp.
46. McCoid MJ. 1998. Established exotic reptiles and amphibians of the Mariana Islands. See Ref. 78, In press
47. McCoid MJ, Hensley RA. 1994. Distribution and abundance of *Perochirus ateles* (*Gekkonidae*) in the Mariana Islands. *Herpetol. Rev.* 25:97–98
48. McCoid MJ, Rodda GH, Fritts TH. 1995. Distribution and abundance of *Emoia slevini* (*Scincidae*) in the Mariana Islands. *Herpetol. Rev.* 26:70–72
49. Moller H, Craig JL. 1987. The population ecology of *Rattus exulans* on Tiritiri Matangi Island, and a model of comparative population dynamics in New Zealand. *N. Z. J. Zool.* 14:305–28
50. Moore PH. 1977. An ecological survey of pristine terrestrial communities on Guam. In *Guam Coastal Manag. Prog. Tech. Rep.*, Vol. 1, ed. D Bonvouloir, P McMakin, pp. 1–45. Agana, Guam: Govt. Guam Bur. Plan.
51. Morison SE. 1953. *New Guinea and the Marianas, March 1944–Aug. 1944*. Boston: Little, Brown. 420 pp.
52. Moulton MP, Pimm SL. 1986. Species introduction to Hawaii. In *Ecology of Biological Invasions of North America and Hawaii*, ed. HA Mooney, JA Drake, pp. 231–49. New York: Springer-Verlag
53. Muniappan R. 1988. Biological control of the weed, *Lantana camara* in Guam. *J. Pl. Prot. Trop.* 5:99–101
54. Palomo T. 1984. *An Island in Agony*. Guam: Bank of Guam. 261 pp.
55. Parker WS, Plummer MV. 1987. Population ecology. In *Snakes: Ecology and Evolutionary Biology*, ed. RA Siegel, JT Collins, SS Novak, pp. 253–301. New York: Macmillan
56. Perez GSA. 1972. Observations of Guam bats. *Micronesica* 8:141–49
57. Peterson GD Jr. 1956. *Suncus murinus*, a recent introduction to Guam. *J. Mammal.* 37:278–79
58. Pimm SL. 1987. Determining the effects of introduced species. *Trends Ecol. Evol.* 2:106–8
59. Pimm SL. 1987. The snake that ate Guam. *Trends Ecol. Evol.* 2:293–95
60. Pimm SL. 1992. *The Balance of Nature: Ecological Issues in the Conservation of Species and Communities*. Chicago: Univ. Chicago Press. 434 pp.
61. Pregill GK. 1998. Squamate reptiles from prehistoric sites in the Mariana Islands, Micronesia. *Copeia* 1998:64–75
62. Quammen D. 1996. *The Song of the Dodo*. New York: Scribner's
63. Ramakrishnan PS, Vitousek PM. 1989. Ecosystem-level processes and the consequences of biological invasions. In *Biological Invasions: a Global Perspective*, ed. JA Drake, HA Mooney, F diCastri, RH Groves, FJ Kruger, et al, pp. 281–300. Chichester, UK: Wiley
64. Ramsey FL, Harrod LA. 1995. *Results from avian surveys of Rota and Tinian Islands, Northern Marianas, 1982 and 1994*. Honolulu: Rep. US Fish Wildl. Serv.
65. Rodda GH. 1992. Foraging behaviour of the brown tree snake, *Boiga irregularis*. *Herpetol. J.* 2:110–14
66. Rodda GH, Campbell EW III, Derrickson SR. 1998. Avian conservation research needs in the Mariana Islands, western Pacific Ocean. In *Avian Conservation: Research and Management*, ed. J Marzluff, R Sallabanks. Washington, DC: Island Press
67. Rodda GH, Fritts TH. 1992. Sampling techniques for an arboreal snake, *Boiga irregularis*. *Micronesica* 25:23–40
68. Rodda GH, Fritts TH. 1992. The impact of the introduction of the brown tree snake, *Boiga irregularis,* on Guam's lizards. *J. Herpetol.* 26:166–74
69. Rodda GH, Fritts TH. 1996. *Reptiles and Amphibians: Faunal Survey for the Ordnance Annex, Naval Activities, Guam*. Honolulu: US Fish Wildl. Serv.
70. Rodda GH, Fritts TH. 1997. *Absolute population densities of Saipan lizards*. Saipan, Mariana Islands: Rep. Div. Fish Wildl.
71. Rodda GH, Fritts TH. 1997. *Modeling of brown tree snake size distributions highlights sampling problems and high adult mortality*. Presented at Annu. Meet. Am. Soc. Ichthyol. Herpetol., 77th, Seattle, p. 254. Seattle: Am. Soc. Ichthyol. Herpetol.
72. Rodda GH, Fritts TH, Campbell EW III. 1998. The feasibility of controlling the brown treesnake in small plots. See Ref. 78, In press
73. Rodda GH, Fritts TH, Chiszar D. 1997. The disappearance of Guam's wildlife;

new insights for herpetology, evolutionary ecology, and conservation. *BioScience* 47:565–74

74. Rodda GH, Fritts TH, Conry PJ. 1992. Origin and population growth of the brown tree snake, *Boiga irregularis*, on Guam. *Pac. Sci.* 46:46–57
75. Rodda GH, Fritts TH, McCoid MJ, Campbell EW III. 1998. An overview of the biology of the brown treesnake, *Boiga irregularis*, a costly introduced pest on Pacific islands. See Ref. 78, In press
76. Rodda GH, Fritts TH, Reichel JD. 1991. The distributional patterns of reptiles and amphibians in the Mariana Islands. *Micronesica* 24:195–210
77. Rodda GH, McCoid MJ, Fritts TH, Campbell EW III. 1998. Population trends and limiting factors in *Boiga irregularis*. See Ref. 78, In press
78. Rodda GH, Sawai Y, Chiszar D, Tanaka H, eds. 1998. *Problem Snake Management: Habu and Brown Treesnake Examples*. Ithaca, NY: Cornell Univ. Press. In press
79. Savidge JA. 1985. Pesticides and the decline of Guam's native birds. *Nature* 316:301
80. Savidge JA. 1986. *The role of disease and predation in the decline of Guam's avifauna*. PhD thesis. Univ. Ill., Champaign-Urbana. 79 pp.
81. Savidge JA. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68:660–68
82. Savidge JA, Sileo L, Siegfried LM. 1992. Was disease involved in the decimation of Guam's avifauna? *J. Wildl. Dis.* 28:206–14
83. Schoener TW, Spiller DA. 1987. Effects of lizards on spider populations: manipulative reconstruction of a natural experiment. *Science* 236:949–52
84. Shine R. 1991. Strangers in a strange land: ecology of Australian colubrid snakes. *Copeia* 1991, pp. 120–31
85. Steadman DW. 1989. Extinction of birds in eastern Polynesia: a review of the record and comparison with other Pacific island groups. *J. Archaeol. Sci.* 16:177–205
86. Steadman DW. 1992. Extinct and extirpated birds from Rota, Mariana Islands. *Micronesica* 25:71–84
87. Steadman DW. 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. *Science* 267: 1123–31
88. Steadman DW. 1995. *Determining the Natural Distribution of Resident Birds in the Mariana Islands*, phase 1. *Prelim. Rep. (22 Apr. 1995) Results Field Work Conduct. Jun.–Jul. 1994*, US Fish Wildl. Serv., Honolulu, Hawaii
89. Stinson DW, Ritter MW, Reichel JD. 1991. The Mariana common moorhen: decline of an island endemic. *Condor* 93: 38–43
90. Townsend CR. 1991. Exotic species management and the need for a theory of invasion ecology. *N. Z. J. Ecol.* 15:1–3
91. US Fish and Wildlife Service. 1992. *Recovery Plan for the Mariana Islands Population of the Vanikoro Swiftlet*, Aerodramus vanikorensis bartschi. Portland, OR: US Fish Wildl. Serv. 49 pp.
92. US Fish and Wildlife Service. 1992. *Recovery Plan for the Mariana Common Moorhen (Gallinule)*, Gallinula chloropus guami. Portland, OR: US Fish Wildl. Serv. 55 pp.
93. US Fish and Wildlife Service. 1997. *Technical/Agency Draft Recovery Plan for the Micronesian Megapode*. Portland, OR: US Fish Wildl. Serv. 73 pp.
94. US National Research Council. 1997. *The Scientific Bases for Preservation of the Mariana Crow*. Washington, DC: Natl. Acad. Press. 91 pp.
95. van Riper C III, van Riper SG, Goff ML, Laird M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56: 327–44
96. Wheeler ME. 1979. The Marianas fruit bat: management history, current status and future plans. *Cal.-Nev. Wildl. Trans. 1979*, pp. 149–65
97. Wiles GJ. 1987. The status of fruit bats on Guam. *Pac. Sci.* 41:148–57
98. Wiles GJ, Aguon CF, Davis GW, Grout DJ. 1995. The status and distribution of endangered animals and plants in northern Guam. *Micronesica* 28:31–49
99. Wiles GJ, Amerson AB Jr, Beck RE Jr. 1989. Notes on the herpetofauna of Tinian, Mariana Islands. *Micronesica* 22: 107–18
100. Wiles GJ, Guerrero JP. 1996. Relative abundance of lizards and marine toads of Saipan, Mariana Islands. *Pac. Sci.* 50: 274–84
101. Wiles GJ, Rodda GH, Fritts TH, Taisacan EM. 1990. Abundance and habitat use of reptiles on Rota, Mariana Islands. *Micronesica* 23:153–66