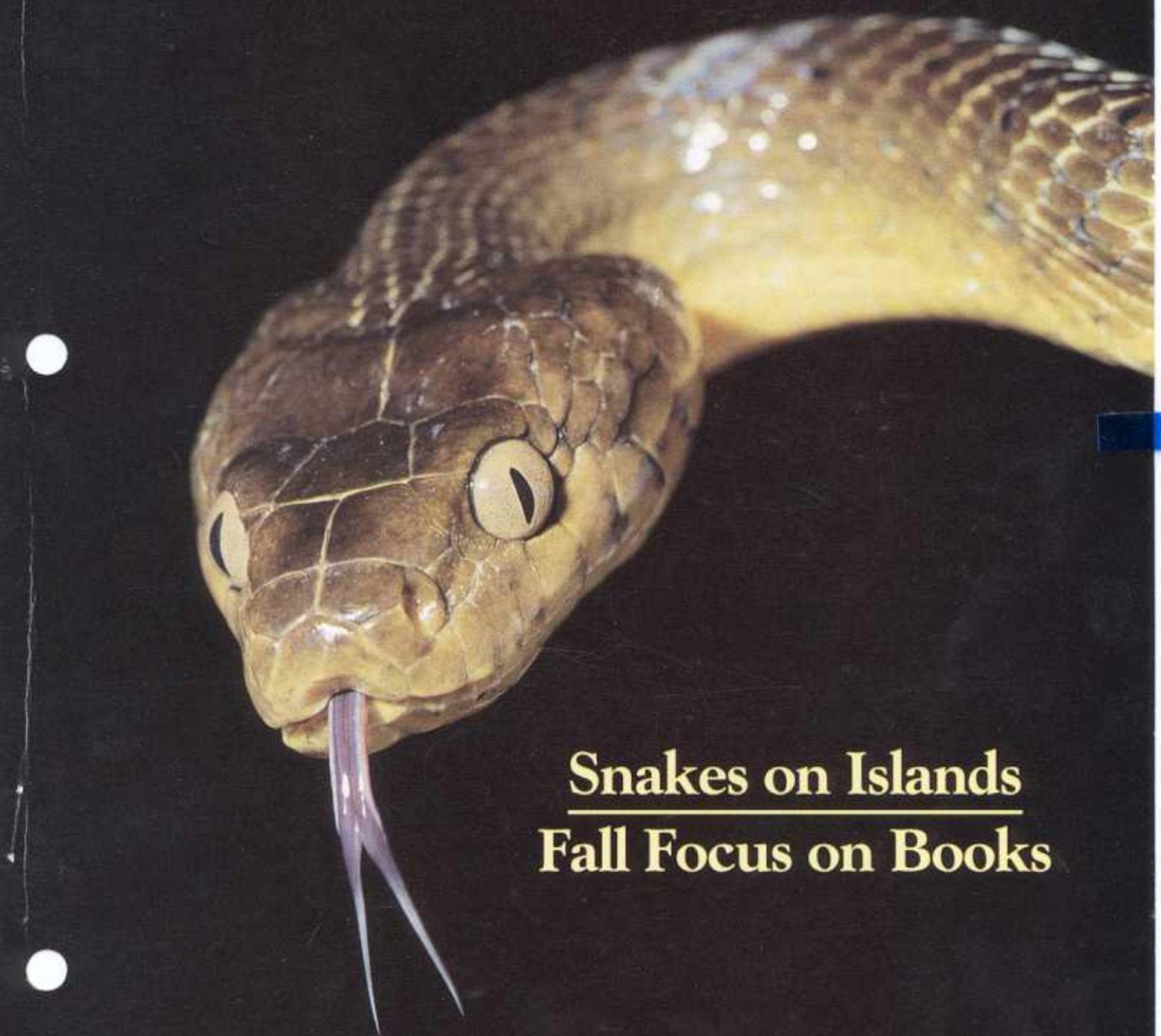
October 1997

BioScience

American Institute of Biological Sciences

Vol. 47 No. 9



Snakes on Islands

Fall Focus on Books

The Disappearance of Guam's Wildlife

New insights for herpetology, evolutionary ecology, and conservation

Gordon H. Rodda, Thomas H. Fritts, and David Chiszar

Guam is an American island near the middle of Micronesia, an archipelago of "micro" islands in the middle of the western Pacific Ocean. The largest island of Micronesia, Guam covers only 541 km^2. It is shaped like an elongated peanut, 4 km across the narrow waist and 45 km long. The closest larger island is Manus, which is 1740 km to the south, across the equator and north of New Guinea. Few species are found on small, remote islands such as Guam. To reach a land mass with levels of biodiversity comparable to what is found on continents, one must travel over 2000 km south to New Guinea, west to the Philippines, or north to Japan (Figure 1). Neither water currents nor wind brings animals from those directions, so Guam's native vertebrates are limited to those species that can fly (e.g., birds and bats), or whose eggs can ride for many weeks on small clumps of floating vegetation (e.g., small lizards). Large nonvolant vertebrates and even small delicate flyers, such as mosquitoes, fail to make the journey without human assistance. Indeed, Micronesia was free of flies and mosquitoes until Spanish conquistadors brought these insects to Guam (Carano and Sanchez 1964).

The Guam experience showed ecologists that snakes can attain densities that are sufficient to suppress prey populations

It is difficult to know how many species of animals were found on Guam before the arrival of humans, but from archeological excavations on the nearby island of Rota, scientists know that the original human colonists—or the domestic animals that the colonists brought with them—extirpated many species thousands of years ago. On Rota, as on Hawaii, approximately half of the native birds were exterminated by prehistoric humans (Steadman 1995); presumably, Guam lost a similar number. But following that spate of prehistoric extinctions, the native wildlife community remained relatively stable until the 1960s. Surprisingly, the island's fauna was little disrupted by the savage fighting of World War II (Engbring and Pratt 1985), which subjected Guam to naval bombardment so severe that some forests were leveled by artillery fire and more than 80% of the island's structures were destroyed (Morison 1953). After the war, the island was extensively reseeded with an exotic legume, *Leucaena leucocephala*, which permanently replaced native trees over vast areas (Craig 1994). As far as is known, no native bird species or other vertebrates were lost as a result of this ecological upheaval (Baker 1946). The ecological effects of the war may have been somewhat analogous to the typhoons that naturally strike Guam every few years. In 1992, for example, Guam was hit by six typhoons, three of which were "super-typhoons" with sustained winds in excess of 240 km/h. The fierce storms of the western Pacific denude forests and thereby select for species that can tolerate severe natural habitat modifications.

Major changes in Guam's vertebrate fauna became evident in the 1960s, when wildlife authorities noticed that birds were entirely absent from the southern one-third of the island and that the boundary of birdlessness seemed to be creeping steadily northward. By the end of the 1970s, birds were missing from the southern two-thirds of the island (Engbring 1983, Jenkins 1983). By 1985, most of the bird species were either isolated in small pockets at the northern tip of the island or were completely gone (Figure 2).

What was killing the birds? Two theories generated particular interest. One was that pesticides, which had been used in large amounts after World War II to control mosquitoes,

Gordon H. Rodda is a zoologist, and Thomas H. Fritts is chief of the Biological Survey Program, at the Patuxent Wildlife Research Center, Biological Resources Division, United States Geological Survey, National Museum of Natural History, Washington, DC 20560. They study tropical reptiles and the effects of species translocations. David Chiszar is a professor in the Department of Psychology, University of Colorado, Boulder, CO 80309-0345. His interests revolve around the behavior of reptiles, especially the feeding adaptations of snakes. © 1997 American Institute of Biological Sciences.

Figure 1. Guam is the largest of the more than 2100 tiny islands of Micronesia (most are too small to be seen in this view). Lying north of the equator near the middle of the western Pacific Ocean, Guam is roughly equidistant (over 2000 km) from Japan, the Philippines, and New Guinea.

had poisoned the birds, as DDT had done to some birds in mainland North America. The second, and leading, hypothesis was that an introduced bird disease, such as had ravaged the birds of Hawaii (van Riper et al. 1986, Warner 1968), had spread catastrophically through the bird populations, perhaps carried by the introduced mosquitoes. An avian pathologist, Julie Savidge, was hired by Guam's Division of Aquatic and Wildlife Resources to find the disease that was killing the birds of Guam. In collaboration with other pathologists and pesticide specialists, she scoured the forests and birds of Guam for evidence of this disease, but she came up empty-handed (Grue 1985, Savidge 1987, Savidge et al. 1992). She concluded instead that the accidentally introduced brown tree snake, *Boiga irregularis*, was responsible for the loss of the birds (Figure 3).

Figure 2. These fairy terns are among the 12 bird species (both land and sea birds) that have disappeared from Guam in the wake of the introduction of the brown tree snake.

The snake turned out to be responsible for not only the extinctions of the birds, but also the decimation of the island's lizards (Figure 4; Rodda and Fritts 1992b), mammals (Wiles 1987), and domestic animals (Fritts and McCoid 1991). When Savidge reported her discovery at a meeting of the American Ornithologists' Union in 1983, she met with skepticism from some members of the audience. Marshall (1985) noted that "Few could believe that a mere snake was that efficient a predator and could build up the numbers commensurate with such devastation" (p. 260). One commentator responded to Savidge's conclusion by devoting a column to promoting the pesticide hypothesis (Diamond 1984).

The fact that Savidge's conclusion was initially rejected but is now widely accepted, reflects the growth of ecology. How do we know that the snake caused the extirpations? Six lines of evidence point to the brown tree snake as the primary cause of Guam's avifauna extinctions (Savidge 1987): the geographic pattern of bird losses mirrored the simultaneous population expansion of the snake (that is, the snake spread northward across Guam on approximately the same schedule as bird distributions retreated to Guam's north end); the snake is an efficient predator of the species that declined; there is little or no evidence for alternate causes of declines, such as pesticides, habitat destruction, diseases, or environmental contaminants; all bird species were affected, including both native and introduced species (thus, the natives did not retreat in response to expansion of introduced species); the brown tree snake is unexpectedly common on Guam; and no comparable bird extirpations were observed on similar nearby islands that lacked the snake.

For many of the skeptics, the evidence that the brown tree snake is unexpectedly common on Guam was the clincher. Counting snakes is tough. They are notoriously difficult to spot (Rodda 1993), and the brown tree snake is particularly hard to find because it is nocturnal and arboreal. It moves slowly through the foliage at night, looking and often acting like a drab vine. Few visitors to Guam ever see a snake. However, our mark–

recapture and trapping studies suggest that the snake achieved peak densities on Guam of approximately 100/ha (Rodda et al. 1992a). By contrast, large snakes away from water or dens have maximum densities of 1–10/ha (Parker and Plummer 1987), and such snakes rarely attain densities in excess of a few individuals per hectare. For example, bullsnakes (*Pituophis melanoleucus*; Parker and Brown 1980), rat snakes (*Elaphe obsoleta*; Stickel et al. 1980), and rattlesnakes (*Crotalus horridus*; Fitch 1982) all have densities of less than 1/ha. Small snakes, such as subterranean worm-eating snakes, can reach very high densities (e.g., *Carphophis amoenus*, worm snake, has been recorded at densities of up to 729/ha; Clark 1970), but at 0.3 m, this snake is much smaller than the brown tree snake, whose maximum total length is approximately 3.1 m. Small aquatic snakes, such as *Regina alleni*, the striped crayfish snake, whose maximum length is 0.6 m, can reach densities of 1290/ha (Godley 1980), but only in small water bodies. Snakes also reach high concentrations around dens, but on a tropical island, such as Guam, no wintering behavior is seen. Thus, in relation to the densities expected of a comparable snake, the peak densities of brown tree snakes on Guam were unprecedented.

Figure 3. The brown tree snake (*Boiga irregularis*) is native to New Guinea and nearby areas; it was accidentally introduced to Guam after World War II, with catastrophic results for native wildlife.

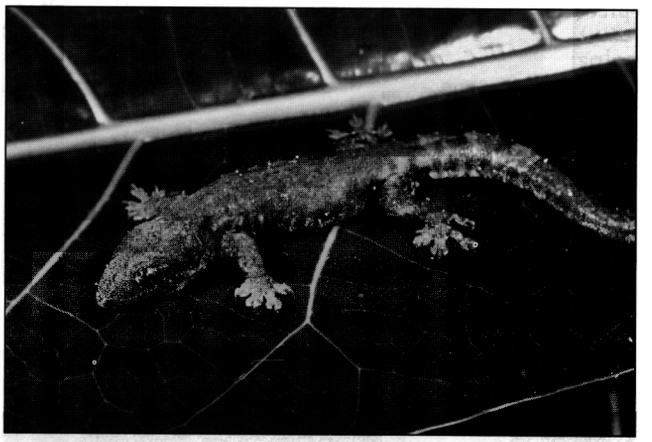


Figure 4. The spotted-belly gecko (*Perochirus ateles*) is found only in Micronesia and on Japan's tiny Marcus Island (Minami-Tori-shima). It has disappeared from Guam, where it was common in forests before the arrival of the brown tree snake.

The density of this predator was also excessive in relation to the density of the prey. Prey densities on Guam prior to the arrival of the snake were not known with any accuracy, but an estimate of the upper limit for numbers of bird individuals can be calculated by adding the maximum densities known for each of the species (Engbring and Ramsey 1984). This calculation makes the unrealistic assumption that all species might have been at their maximum density in the same place, but even so, the aggregate total bird density is only approximately 26/ha. Thus, at the crest of the initial snake population irruption, the predator would have outnumbered potential avian prey by approximately 4:1, and the peak avian biomass of approximately 0.8 kg/ha would have been only 15%–25% of the peak predator biomass, a precarious predator-to-prey ratio. For comparison, a garter snake predator–prey system in Ohio was found to have a peak biomass ratio of 1:67, much lower than the 1:4 ratio that is theoretically sustainable (Reichenbach and Dalrymple 1986). With the even higher 4:1 predator–prey ratio found temporarily in Guam, it is not surprising that such predation pressure caused bird abundances to plummet. The Guam experience showed ecologists that snakes can attain densities that are sufficient to suppress prey populations.

By October 1996, only 3 of Guam's 12 native forest bird species still survived in the wild. Of these, the Mariana crow, *Corvus kubaryi*, whose population is declining rapidly, appears doomed (the 1996 count was five individuals); the island swiftlet, *Aerodramus vanikorensis*, is relatively safe (several hundred individuals are in one unstable colony); and the Micronesian starling, *Aplonis opaca*, is precarious (one probably viable population of 50–100 individuals is in one urban area). It is, perhaps, telling that in Guam a metapopulation of several hundred birds is considered "safe." Unlike Hawaii, where low-elevation forests are densely populated with non-native bird species, most forests of Guam are now empty of avian life. The silence is conspicuous even to a casual observer (Jaffe 1994).

Although Guam's bird extirpations have received the most attention, many other species are important components of the brown tree snake's diet. Juvenile snakes eat lizards primarily, and adult snakes eagerly ingest small mammals (Greene 1989, Savidge 1988, Shine 1991). Although the disappearance of silent nocturnal mammals and minute lizards was not as obvious as the disappearance of noisy, colorful birds, the loss of biodiversity was nearly as complete; only three of Guam's lizard and mammal species have stable populations. Moreover, two of the three native bat species vanished in recent decades, leaving only the Marianas fruit bat, *Pteropus mariannus*. Compared with the bat populations on nearby islands that do not have snake populations, nonvolant juvenile bats on Guam suffer near 100% mortality at the age when they are first cached by their foraging mothers (Wiles 1987). An unattended nonvolant bat would be highly vulnerable to brown tree snake predation, and the elevated mortality of nonvolant young is presumed to be

the cause of its continued population decline. For the other two bat species, no population data exist to indicate the cause of their declines on Guam.

Of Guam's 12 historically native lizards, only one species appears to be as dense on Guam as on nearby snake-free islands; six have been extirpated from Guam (Figure 5), three are rare and localized (Figure 6), and two are common but reduced in abundance (Rodda and Fritts 1992b). The interpretation of these population changes is complicated by concurrent introductions of lizard and mammalian predators and competitors, but it is likely that the snake caused the declines of several lizard species (Rodda and Fritts 1992b). All native lizard species persist on Guam's tiny offshore islets, which the snake has not yet reached.

The details of each extinction may be open to debate, but the aggregate impact is unquestionably an astonishing loss of biodiversity. Of the native vertebrates, only one bird and three lizard species retain long-term viability on Guam.

The profound effects of Guam's snakes stand in stark contrast to the earlier generalization that snake populations would be of little ecological consequence to prey populations. That generalization had been based on the relative rarity of most snake species and on the fact that their feeding is seasonal and opportunistic. That is, snakes can eat when prey are abundant and fast when prey are scarce (Pough 1980). This feeding strategy crops the "doomed surplus" (Errington 1956), rather than controlling or depressing baseline prey populations. To discourage the wanton killing of snakes, conservationists often advise farmers to allow snakes to live for the purpose of rodent control. But if snake populations are incapable of controlling the abundances of their prey, their benefit to the farmer will be small. Indeed, there is no evidence that snakes routinely reduce prey populations except on small islands such as Guam.

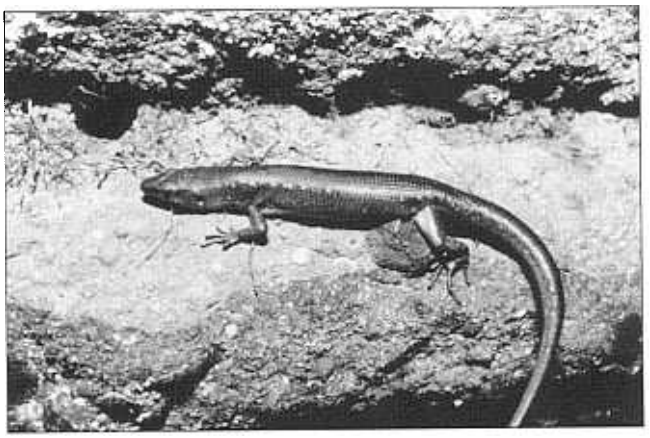


Figure 5. Slevin's skink (*Emoia slevini*) is endemic to the Mariana Islands (an American chain of islands within Micronesia). Guam was the largest of the islands inhabited by this lizard, but it is no longer found there, possibly due to predation by the introduced brown tree snake.

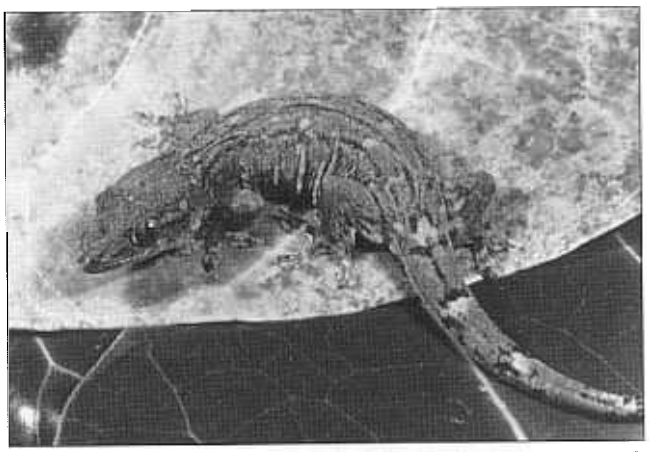


Figure 6. The oceanic gecko (*Gehyra oceanica*) is one of several large geckos that vanished from Guam forests following colonization and irruption of the brown tree snake. This gecko is still occasionally found on ornamental plants in Guam's urban areas. Apparently, the arboreal snake rarely visits these isolated plants.

The fact that snakes normally have little effect on prey populations may be related to another characteristic that most snakes share: low reproductive potential. Snakes have far fewer offspring than rodents, frogs, or other common prey. Snake populations may increase following an irruption of prey, but the subsequent buildup of the predator is limited and slow. In response to a prey population increase, snake populations rarely increase so much that they overtax the food supply and ultimately depress prey abundances. For example, one does not expect to hear of a sudden surplus of garter snakes causing a localized shortage of frogs. The increase in snake numbers, if it happens at all in response to an irruption of prey, is likely to be long term and demographically minor. A good year for rattlers is generally the result of a bumper crop of rodents, rather than the cause of a shortage of rodents. Accordingly, snake numbers are typically regulated by "bottom-up" rather than "top-down" trophic interactions.

By contrast, extinction of prey populations by a predator is a decidedly top-down proposition. What enabled the brown tree snake to have such an impact on so many of Guam's native vertebrates? On one level, it is not necessary for a snake to be an exceptional predator to exert top-down pressure, it is only necessary that the snake be an exception to the generality that snakes are not abundant. On Guam, the brown tree snake was abundant. Before returning to the question of why the brown tree snake became so numerous, we describe how the snake's high population density turned it from an annoyance into a significant problem for the human population.

The strange case of Guam's baby bites

The brown tree snake is a member of the snake family Colubridae, most of which lack the sophisticated venom apparatus and highly toxic venom of the "truly" venomous cobras and vipers. Many of the natricine colubrids (the garter snakes and their allies) have saliva that can be irritating (McKinstry 1983, Minton 1979), but the irritation is usually mild. No herpetologist would hesitate to handle a garter snake. Thus, little credibility was accorded to the early reports of serious snakebites on

Guam. Still, the reports kept coming. There have been more than 160 such cases, or approximately 1 in 200 emergency room visits on Guam, including nine cases of infants who received ventilation or intubation to assist breathing (Fritts et al. 1990, 1994).

What was shocking about these reports was not the seriousness of the bites but rather the circumstances of the encounters. Whereas the modal snakebite victim in North America is a young adult suffused with a dangerous combination of testosterone and alcohol (Minton and Minton 1980), the typical snakebite victim in Guam was a sleeping infant of less than six months of age. In a few cases, the snake appeared to select the young infant in preference to larger children: in 2 of 11 medically serious bites, the victim was an infant sleeping between its parents or older siblings who were not bitten. Even if one includes teenage and adult snakebite victims, 80% of all reported bite victims were sleeping at home, not active or sleeping outside of their homes. In a small percentage of bites to sleeping persons (7%), the victim was being constricted by the snake when discovered. Although constriction may not have changed the medical consequences of any bite cases, the occurrence of constriction is important because it suggests snake feeding behavior rather than self-defense.

Many bite victims also exhibited multiple bites, as if the snake were repeatedly regripping the victim in an attempt to ingest prey that is far too large. Although inferring motivation is always risky, this pattern of snakebites more closely resembles that of predatory strikes than that associated with defensive behavior. Apparently, the brown tree snake stumbles into the corridors of homes at night, willing—although presumably not seeking—to bite exposed infants (Figure 7). This phenomenon, even if it involves only a less venomous rear-fanged snake, has added an entirely new perspective to snakebite. Moreover, this snake's apparent willingness to enter occupied buildings may help explain how it reached Guam; it could have accidentally been transported with shipped goods.

Figure 7. Although most of Guam's brown tree snakes are only approximately 1 m in length, the species reaches a maximum size of more than 3 m, enabling it to kill or seriously harm medium-sized birds and mammals, such as chickens, puppies, and small children.

Foraging by brown tree snakes

Guam's infant envenomations and wildlife extinctions have, not surprisingly, evoked countermeasures by wildlife managers (Fritts 1988). One of the most successful measures has been to trap the snakes (Fritts et al. 1989, Rodda and Fritts 1992a). Perhaps due to their broad diet, brown tree snakes readily enter traps that are baited with prey items, typically laboratory mice (the mice are protected from the snakes and are not harmed by the experience).

In the process of perfecting the trap design, many experiments have been performed to elucidate the searching algorithm that is used by foraging brown tree snakes (Rodda et al. 1992b), which turns out to be different from that used by most other snakes. For instance, whereas most rattlesnakes hunt by ambush and garter snakes typically forage actively, brown tree snakes do both (Rodda 1992). Consequently, the brown tree snake is likely to use different sensory modalities for capturing active and inactive prey. For example, a fleeing lizard presents a strong visual stimulus, but a concealed bird egg offers few visual cues; thus, olfaction probably plays a major role in helping brown tree snakes to locate eggs.

Similarly, actively foraging garter snakes, which often search for immobile or slow-moving prey, rely heavily on chemosensation to identify prey. However, the brown tree snake's foraging decisions appear to be more sophisticated. Unlike garter snakes, which will often attack and attempt to swallow an inappropriate object (e.g., a cotton swab) that has been soaked with an appropriate odor, brown tree snakes may ignore food cues that appear out of context. For example, Chiszar et al. (1988b) found that brown tree snakes ignore isolated odors of mice but will attack olfactory cues in more realistic settings (Chiszar et al. 1992, 1993). In some situations, brown tree snakes will attack mice that they see but do not smell (i.e., mice temporarily placed in airtight but transparent boxes). They will also investigate an odor-infused opaque box, but they will not expend comparable effort on a similar but transparent box (Lankford 1989). Apparently, the visually detectable absence of prey is sufficient to redirect prey-seeking behavior. Similarly, in some captive studies (Chiszar et al. 1988a), airborne olfactory cues have been insufficient to elicit predation, but substrate-borne chemical cues have induced brown tree snakes to follow odor trails to hidden prey. By contrast, Fritts et al. (1989) and Rodda et al. (1992b) found that wild brown tree snakes were attracted to free-hanging traps that were baited with chicken litter but that adding olfactory trails leading to the trap bait did not enhance trap capture success. Thus, brown tree snakes appear to be facultative in their use of chemical, visual, and other types of information. The factors that determine the snakes' reliance on their various sensory modalities are still not understood.

Wild brown tree snakes also do not respond to pungent mammal baits, even though in the laboratory they respond to the same cues with high rates of tongue flicking. Brown tree snakes seem to be adept at distinguishing between live prey and all

artificial prey; we have yet to find an artificial cue that, in nature, elicits more than approximately 5% of the captures obtained with real prey, although in laboratory tests some prey extracts are indistinguishable from live prey. Consequently, disembodied odors are of minimal use for trapping brown tree snakes, even though it is clear from laboratory work that the snakes are aware of these odors and investigate them. Our working hypothesis is that brown tree snakes use multiple cues and avoid traps that do not provide multi-modality cues that confirm the presence of living prey.

Given this sophisticated algorithm for identifying prey, it seems remarkable that brown tree snakes would mistake hopelessly large sleeping infants for potential prey items. However, in laboratory trials, brown tree snakes routinely kill and attempt to eat rodents that are well beyond their gape limits. It is also possible that when searching visually, brown tree snakes fail to comprehend that a portion of the infant is concealed by bedding. For whatever reason, brown tree snake herpetoculturalists have consistently found that this species has poor judgment with regard to the size of potential prey. Brown tree snakes will attack prey that are too large for them to swallow; perhaps some of their attacks on children reflect this error.

Nevertheless, brown tree snakes are capable of prodigious meals (Chiszar 1990). A snake's maximum meal size depends on its taxon: Vipers and other heavy-bodied venomous and nonvenomous snakes are in one class, whereas the more slender species, including the brown tree snake, are in another (Pough and Groves 1983). However, brown tree snakes stand apart from their class in the size of meals ingested; we have found brown tree snakes in the wild with prey equal to more than 70% of their mass. This is without precedent in the nonviper group.

Another unexpected feature of brown tree snake foraging is that the snakes readily consume carrion and organic matter, which are not considered typical snake food. For example, brown tree snakes have been found eating or having eaten dog food, chicken bones, raw hamburger, maggot-infested rabbits, paper towels, spareribs, rotting lizards, ornamental betel nuts, larger conspecifics, dog placentas, and soiled feminine hygiene products. Curiously, many of these items do not have the visual appearance of a traditional prey item. Moreover, some of these items, such as betel nuts, do not have the odor, color, temperature, vibration, or behavior of a traditional live food item (although the nuts do resemble eggs in shape). Perhaps the snake's habit of switching between active and passive foraging modes has preadapted it to a wider, more sophisticated definition of suitable prey or to facultative reliance on sensory systems that are more or less obligate in other, less flexible species. Undoubtedly, the brown tree snake's liberal attitudes about prospective food items has allowed it to successfully colonize new habitats, including Guam.

Snakes as colonists

Brown tree snakes occur naturally in eastern Indonesia, New Guinea, the Solomon Islands, and the north and east coasts of Australia. As soon as sailing ships began to ply the seven seas, rats (first *Rattus rattus* and later *Rattus norvegicus*) began appearing throughout the world, on virtually every island contacted by the ships (Atkinson 1985). By contrast, snakes are not generally considered to be good colonists. With the exception of the widespread parthenogenetic blindsnake *Ramphotyphlops braminus* (every individual is a female, and each is capable of starting a population), few snakes have colonized remote islands. Are brown tree snakes uniquely capable colonists, or is it a myth that snakes are poor colonists?

Brown tree snakes are believed to have been transported accidentally to Guam through the postwar salvage of derelict vehicles and equipment that were deposited in the New Guinea area during World War II (Rodda et al. 1992a). Many of the salvaged items are likely to have housed snakes, including brown tree snakes. Being nocturnal, brown tree snakes would be quiescent and undetected during the day, when salvagers would have collected the materials and loaded them on barges for recycling or disposal on American soil (i.e., Guam). Once on Guam, the material would have been unloaded during the day, and the snake would, naturally, have remained concealed until nightfall, when its dispersal into the jungle would have gone undetected.

Since reaching Guam, the brown tree snake has gained access to other previously snake-free islands. In the last six years, more than 40 snakes have been spotted on the previously snake-free island of Saipan, approximately 175 km north of Guam. We know of seven occasions in which the brown tree snake has been accidentally transported the 6100 km from Guam to Hawaii. Other individuals have been reported from sites such as Diego Garcia Atoll (Indian Ocean); Corpus Christi, Texas; and Spain.

Thus, brown tree snakes seem to experience no difficulty in reaching new locations. But a single stowaway snake is unlikely to lead to a new brown tree snake population, unless it happens to be a gravid female. One feature promoting successful colonization in many snake species is the ability of females to store sperm. Although the brown tree snake has never been tested for this ability, other species of the same genus are capable of storing sperm for at least two years (Groves 1973), and several closely related snakes store sperm for at least six years (Haines 1940). Thus, it is theoretically possible for a single snake to start a population, even if she was not gravid at the time of accidental transport. Scientists do not know how many females were responsible for the Guam population, but it was probably a small number because most stowaways probably died in transit or failed to find mates in the new environment.

If the initial colonizing population was small, then presumably there were special circumstances on Guam that made it possible for a small population to irrupt into an unprecedented infestation. Many explanations have been suggested for the extraordinary irruption, and the consequent exceptional impact, of brown tree snakes on Guam (Pimm 1987, Savidge 1987). Of the reasons that

have been suggested, we are most impressed by the importance of coevolution between predator and prey. The overwhelming predominance of islands in the record of anthropogenic extinctions (Brockie et al. 1988) is consistent with a heightened likelihood of predator irruption and prey extinction when predator and prey lack a shared evolutionary history. An anecdote from Guam illustrates this point. In the process of searching for the hypothesized disease that was eradicating Guam's birds, Savidge (1987) housed a flock of bridled white-eyes (*Zosterops c. conspicillatus*) in a laboratory aviary. While sleeping, these birds roost in aggregation. One night, Savidge discovered that a brown tree snake had found a way into the aviary and, by the time it was discovered, had consumed three of six white-eyes sleeping side by side on a branch. The surviving three remained in place on the branch near the snout of the advancing snake. Unlike birds in other locations, bridled white-eyes on Guam appear not to have evolved the behavior of waking or flying when a neighboring bird is eaten. Had Savidge not intervened, the birds' lack of coevolutionary experience with this predator would likely have cost all six their lives.

With their generalist feeding habits, brown tree snakes were preadapted to find suitable forage on Guam, where prey density was extraordinarily high. Although prey density on Guam was not measured at the time when the snake arrived (i.e., 1950 or so), measurements from 1993 to 1995 indicate that Guam continues to have higher mammal and lizard densities than are found on comparable tropical mainland areas. For example, we recently removed (in a span of days) an average of 55 rats/ha from a forested area of northern Guam. Comparable mainland forests have population densities in the range of 1.5–19/ha (0.8–6 kg/ha) for all rodent species combined (Fleming 1975).

To measure the absolute densities of Guam's lizards, we placed lizard-proof fencing around four 10 × 10 m patches of forest and counted all lizards that we encountered as the vegetation within each patch was removed. A year prior to the lizard sampling, snakes had been eliminated from two of the sites, and lizard densities in these sites averaged 19,650/ha (52.3 kg/ha). In the two areas still occupied by snakes, the average lizard density was lower (13,290/ha; 33.7 kg/ha) but still higher than in comparable mainland areas. For example, Duellman (1987) found an average of 57 lizards/ha (1 kg/ha) in the lowland tropical forests of Cusco Amazonico, Peru. Comparable data for the density of either rats or lizards are not available for the brown tree snake's native range, but our relative counts indicate that nocturnal lizards are approximately five times as abundant, and diurnal lizards approximately four times as abundant, on Guam as in the brown tree snake's native range. The abundance of lizards on Guam is not unique to Guam but has been reported for many islands. Thus, the success of the brown tree snake on Guam may be due as much to the unique characteristics of island environments as to the unique attributes of the snake.

One unique feature of all modern environments is the unprecedented level of human commerce. Guam imports virtually all its food, building materials, and other goods. Almost all of this material comes from localities with snakes and other potentially damaging exotic species. For example, a number of snakes, probably from mainland United States, recently arrived on Guam in a shipment of Christmas trees. Similar introductions are apparent on other islands. Okinawa, for example, has recently been colonized by cobras that have escaped from roadside attractions, and Hawaiian customs authorities have intercepted an inbound snake once every two weeks, on average, in recent years.[1] Island economies are unusually dependent on imports, but most industrial communities also obtain the majority of their goods from elsewhere. Thus, although snakes may not be particularly good colonists under natural conditions, present conditions provide an extraordinary number of opportunities for accidental translocation and colonization.

[1]L. Nakahara, 1992, personal communication. Hawaii Department of Agriculture, Honolulu, HI.

Is the brown tree snake unique?

Our understanding of possible snake behaviors and ecological interactions has been broadened by the study of the brown tree snake. However, it is important not to generalize too much from a single example. Is this species exceptional? Or has our understanding simply been limited by the paucity of opportunities to study tropical snakes, non–North American snakes, or nocturnal arboreal snakes? Does the brown tree snake have attributes that make it different from most other snakes?

Typical pest species often have high reproductive rates; however, the brown tree snake does not. In recent years, the modal size of detected clutches on Guam has been 3–4 eggs. Thus, it is not surprising that it took many decades for brown tree snakes to build dense populations throughout the island of Guam. Unlike the irruption of the zebra mussel, which spread over most of the North American continent in a few years (Benson and Boydstun 1995), the biodiversity crisis on Guam moved relatively slowly. However, as is evident from the history of the human species, even taxa with low reproductive rates can eventually overshoot local carrying capacities, causing the extinctions of vulnerable prey.

The above observations suggest that in comparison to all other potential pests, brown tree snakes have relatively low fecundity, but how do they compare with other snake species? Although natricines and crotalines (rattlesnakes) have somewhat larger average litters than brown tree snakes (Seigel and Ford 1987), neither these taxa nor any other snakes can be described as highly fecund. Yet the brown tree snake case illustrates that an organism need not be highly fecund to be a successful colonist or potential pest. Thus, in terms of reproductive output, the brown tree snake is not unique; many other species of snakes are more fecund and therefore have the reproductive potential to become colonists or pests under appropriate (i.e., undesirable) circumstances.

The brown tree snake is well known for its willingness to eat a diversity of foods. Are other snakes

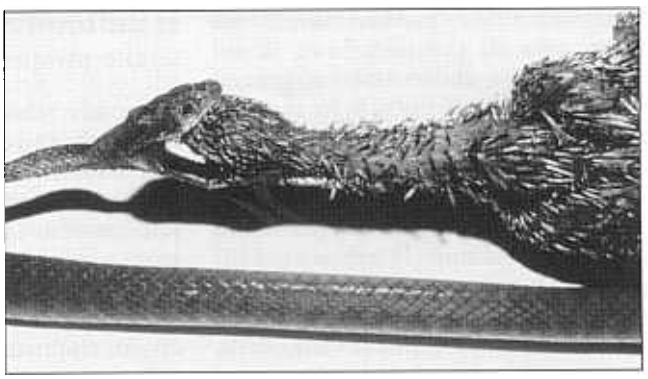


Figure 8. This snake was attempting to eat a baby pigeon out of a nest on a power pole in Guam in 1988 when the weight of the struggling bird caused the snake and its meal to sag enough to contact another electrical conductor. The resulting surge of electricity killed the snake and bird instantly. It also caused in an islandwide power outage that deprived 125,000 Guamanians of electricity for approximately 8 hours. Most of the 1500 power outages caused by the snakes have affected smaller portions of the island.

precluded from becoming pestiferous by the specificity of their dietary requirements? Greene (1989) noted explicitly that the broad diet of the brown tree snake is widely shared by its approximately 30 congeners. Many other snakes, including many crotalines, are also similar to the brown tree snake in exhibiting an ontogenetic shift from ectothermic to endothermic prey. Moreover, the ingestion of carrion is unusual but not unprecedented among snakes. Crotalines, in particular, will eat nonliving, even putrefying, prey (Gillingham and Baker 1981). Brown tree snakes are exceptionally good climbers (Chiszar 1990), enabling them to gain access to food sources that are denied to more terrestrial snakes (Figure 8). But hundreds of arboreal snakes have similar capabilities (Lillywhite and Henderson 1993), and Shine (1983) concluded that food habits of arboreal snakes are similar worldwide. Even the bizarre willingness of brown tree snakes to attack sleeping humans is found in South Asian snakes of the genus *Bungarus* (De Silva 1992, Hati et al. 1988) and, indeed, other *Boiga* species. Thus, the dietary habits of the brown tree snake are not unique.

Other aspects of the brown tree snake's history on Guam are also not unique. The introduction of the brown tree snake to Guam was dependent on humans. Human transport requires of a snake a willingness to be around people and a propensity for entering artificial objects. Many other tropical colubrids, especially several species that have colonized tropical islands, share the brown tree snake's willingness to live alongside people (Fritts 1993). The brown tree snake's tolerance of the ecological disturbance and human environments on Manus after World War II contributed to its arrival to Guam as a stowaway in military traffic.

Successful human-aided colonization requires not only a likelihood of being placed aboard a ship, but also the capability to survive during the sea voyage. Colonization is undoubtedly facilitated in species that can fast during dispersal through inhospitable habitat (e.g., on ships or airplanes), and all snakes appear to have an exceptional ability to fast between meals (Greene 1983, Pough and Groves 1983). A brown tree snake can conceal itself in amazingly small spaces, but this advantage of supple vermiform morphology is not unique to snakes, much less to brown tree snakes. Thus, the brown tree snake is not unique in either its ecology or its behavior.

If the brown tree snake is not unique, we are led to two key conclusions, one applying to herpetology and the other to conservation biology. The herpetological conclusion is that the insights gained through the study of the brown tree snake could have been gained through the study of any number of other snakes. A cursory review of the snake ecology papers appearing in the *Journal of Herpetology* from 1985 to 1995 indicates that approximately half of the research in this area is devoted to just rattlesnakes and natricines, especially garter snakes. Given that there exist over 2600 species of snakes, herpetologists should strive to study a wider diversity of species and clades, particularly tropical species.

For conservation biologists, the inference is that snakes can cause biodiversity crises in a wide variety of contexts. Prey species on islands seem to be especially vulnerable, but many prey species on continents also lack coevolutionary experience with nocturnal arboreal snake predators. If not *B. irregularis*, the culprit could be *Boiga trigonata* (the gamma cat snake, a native of Asia), *Trimorphodon biscutatus* (the lyre snake, a native of North America), or the deadly *Trimeresurus flavoviridis* (the habu, a native of Japan). These three snakes are, like the brown tree snake, venomous, nocturnal, and at least partially arboreal—but so are hundreds of other species. Would the invasion of the Galápagos Islands by a generalized predatory snake that threatened the unique radiation of Darwin's finches differ from what occurred on Guam? More important, could it happen? As the world becomes more tightly united through commerce, the probability of global fauna homogenization and catastrophic snake introductions will grow.

Acknowledgments

Our research has been made possible primarily through the support of the US Departments of the Interior and of Defense. We thank the Guam Division of Aquatic and Wildlife Resources for hospitality and assistance. We greatly appreciate the skill and persistence of the many people who have assisted us in the field. We wish to thank Marie Timmerman, Kathy Dean-Bradley, and Renée Rondeau, who suggested improvements to this article.

References cited

Atkinson IAE. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. Pages 35–81 in Moors PJ, ed. Conservation of island birds. Cambridge (UK): International Council for Bird Preservation. Technical Publication nr 3.

Baker RH. 1946. Some effects of the war on the wildlife of Micronesia. Transactions of the North American Wildlife Conference 11: 207–213.

Benson AJ, Boydstun CP. 1995. Invasion of the Zebra Mussel in the United States.

Pages 445–446 in LaRoe E, Farris G, Puckett C, Doran P, Mac M, eds. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. Washington (DC): US Department of Interior, National Biological Service.

Brockie RE, Loope LL, Usher MB, Hamann O. 1988. Biological invasions of island nature preserves. Biological Conservation 44: 9–36.

Carano P, Sanchez PC. 1964. A complete history of Guam. Rutland (VT): C. E. Tuttle.

Chiszar D. 1990. The behavior of the brown tree snake, *Boiga irregularis*: a study in applied comparative psychology. Pages 101–123 in Dewsbury D, ed. Contemporary issues in comparative psychology. Sunderland (MA): Sinauer.

Chiszar D, Kandler K, Lee R, Smith HM. 1988a. Stimulus control of predatory attack in the brown tree snake (*Boiga irregularis*). 2. Use of chemical cues during foraging. Amphibia-Reptilia 9: 77–88.

_____. 1988b. Stimulus control of predatory attack in the brown tree snake (*Boiga irregularis*) 1. Effects of visual cues arising from prey. The Snake 20: 151–155.

Chiszar D, Fox K, Smith HM. 1992. Stimulus control of predatory behavior in the brown tree snake (*Boiga irregularis*) IV: effect of mammalian blood. Behavioral and Neural Biology 57: 167–169.

Chiszar D, Dunn TM, Smith HM. 1993. Response of brown tree snakes (*Boiga irregularis*) to human blood. Journal of Chemical Ecology 19: 91–96.

Clark DR Jr. 1970. Ecological study of the worm snake *Carphophis vermis* (Kennicott). University of Kansas Publications of the Museum of Natural History 19: 89–194.

Craig RJ. 1994. Regeneration of native Mariana Island forest in disturbed habitats. Micronesica 26: 97–106.

De Silva A. 1992. *Bungarus caeruleus*: its ecology and bite in Sri Lanka. Pages 746–760 in Gopalakrishnakone P, Tan CK, eds. Recent advances in toxicology research. Vol. 1. Singapore: National University of Singapore.

Diamond JM. 1984. Possible effects of unrestricted pesticide use on tropical birds. Nature 310: 452.

Duellman WE. 1987. Lizards in an Amazonian rain forest community (Peru): resource utilization and abundance. National Geographic Research 3: 489–500.

Engbring J. 1983. Forest birds of Guam in critical danger. US Fish & Wildlife Service Endangered Species Technical Bulletin 8: 6–8.

Engbring J, Pratt HD. 1985. Endangered birds in Micronesia: their history, status, and future prospects. Pages 71–105 in Temple SA, ed. Bird conservation. Vol. 2. Madison (WI): University of Wisconsin Press.

Engbring J, Ramsey FL. 1984. Distribution and abundance of the forest birds of Guam: results of a 1981 survey. US Fish & Wildlife Service. Publication nr FWS/OBS-84/20US. Washington (DC): US Fish & Wildlife Service.

Errington PL. 1956. Factors limiting higher vertebrate populations. Science 124: 304–307.

Fitch HS. 1982. Resources of a snake community in prairie–woodland habitat of northeastern Kansas. Pages 83–97 in Scott NJ Jr., ed. Herpetological communities. Washington (DC): US Fish & Wildlife Service Wildlife. Report nr 13.

Fleming TH. 1975. The role of small mammals in tropical ecosystems. Pages 269–298 in Golley FB, Petrusewicz K, Ryszkowski L, eds. Small mammals: their productivity and population dynamics. Cambridge (UK): Cambridge University Press.

Fritts TH. 1988. The brown tree snake, *Boiga irregularis*, a threat to Pacific islands. Biological Report nr 88(31). Washington (DC): US Fish & Wildlife Service.

_____. 1993. The common wolf snake, *Lycodon aulicus capucinus*, a recent colonist of Christmas Island in the Indian Ocean. Wildlife Research 20: 261–266.

Fritts TH, McCoid MJ. 1991. Predation by the brown tree snake on poultry and other domesticated animals in Guam. The Snake 23: 75–80.

Fritts TH, Scott NJ Jr., Smith BE. 1989. Trapping *Boiga irregularis* on Guam using bird odors. Journal of Herpetology 23: 189–192.

Fritts TH, McCoid MJ, Haddock RL. 1990. Risks to infants on Guam from bites of the brown tree snake (*Boiga irregularis*). American Journal of Tropical Medicine and Hygiene 42: 607–611.

_____. 1994. Symptoms and circumstances associated with bites by the brown tree snake (Colubridae: *Boiga irregularis*) on Guam. Journal of Herpetology 28: 27–33.

Gillingham JC, Baker RE. 1981. Evidence for scavenging behavior in the western diamondback rattlesnake (*Crotalus atrox*). Zeitschrift für Tierpsychologie 55: 217–227.

Godley JS. 1980. Foraging ecology of the striped swamp snake, *Regina alleni*, in southern Florida. Ecological Monographs 50: 411–436.

Greene HW. 1983. Dietary correlates of the origin and radiation of snakes. American Zoologist 23: 431–441.

_____. 1989. Ecological, evolutionary, and conservation implications of feeding biology in Old World cat snakes, genus *Boiga* (Colubridae). Proceedings of the California Academy of Sciences, Series nr 4, 46: 193–207.

Groves JD. 1973. Delayed fertilization in the snake *Boiga dendrophila*. Herpetologica 29: 20–22.

Grue CE. 1985. Pesticides and the decline of Guam's native birds. Nature 316: 301.

Haines TP. 1940. Delayed fertilization in *Leptodeira annulata polysticta*. Copeia 1940: 116–118.

Hati AK, Saha SG, Banerjee D, Banerjee S, Panda D. 1988. Clinical features of poisoning by common kraits and treatment with polyvalent antivenin. The Snake 20: 140–143.

Jaffe M. 1994. And no birds sing. New York: Simon & Schuster.

Jenkins JM. 1983. The native forest birds of Guam. Washington (DC): American Ornithologists' Union, Ornithology Monographs 31: 1–61.

Lankford JD. 1989. Stimulus control of foraging in brown tree snakes (*Boiga irregularis*). Journal of the Colorado–Wyoming Academy of Sciences 21: 12.

Lillywhite HB, Henderson RW. 1993. Behavioral and functional ecology of arboreal snakes. Pages 1–48 in Seigel R, Collins J, eds. Snakes: ecology and behavior. New York: McGraw-Hill.

Marshall JT Jr. 1985. Guam: a problem in avian conservation. Wilson Bulletin 97: 259–262.

McKinstry DM. 1983. Morphologic evidence of toxic saliva in colubrid snakes: a checklist of world genera. Herpetological Review 14: 12–15.

Minton SA Jr. 1979. Beware: nonpoisonous snakes. Clinical Toxicology 15: 259–265.

Minton SA Jr., Minton MR. 1980. Venomous reptiles. New York: Charles Scribner & Sons.

Morison SE. 1953. New Guinea and the Marianas, March 1944–August 1944. Boston: Little, Brown and Co.

Parker WS, Brown WS. 1980. Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola*, in northern Utah. Milwaukee Public Museum Publications in Biology and Geology 7: 1–104.

Parker WS, Plummer MV. 1987. Population ecology. Pages 253–301 in Siegel RA, Collins JT, Novak SS, eds. Snakes: ecology and evolutionary biology. New York: Macmillan.

Pimm SL. 1987. The snake that ate Guam. Trends in Ecology & Evolution 2: 293–295.

Pough FH. 1980. The advantages of ectothermy for tetrapods. American Naturalist 115: 92–112.

Pough FH, Groves JD. 1983. Specializations of the body form and food habits of snakes. American Zoologist 23: 443–454.

Reichenbach NG, Dalrymple GH. 1986. Energy use, life histories, and the evaluation of potential competition in two species of garter snake. Journal of Herpetology 20: 131–153.

Rodda GH. 1992. Foraging behaviour of the brown tree snake, *Boiga irregularis*. Herpetological Journal 2: 110–114.

_____. 1993. Where's Waldo (and the snakes)? Herpetological Review 24: 44–45.

Rodda GH, Fritts TH. 1992a. Sampling techniques for an arboreal snake, *Boiga irregularis*. Micronesica 25: 23–40.

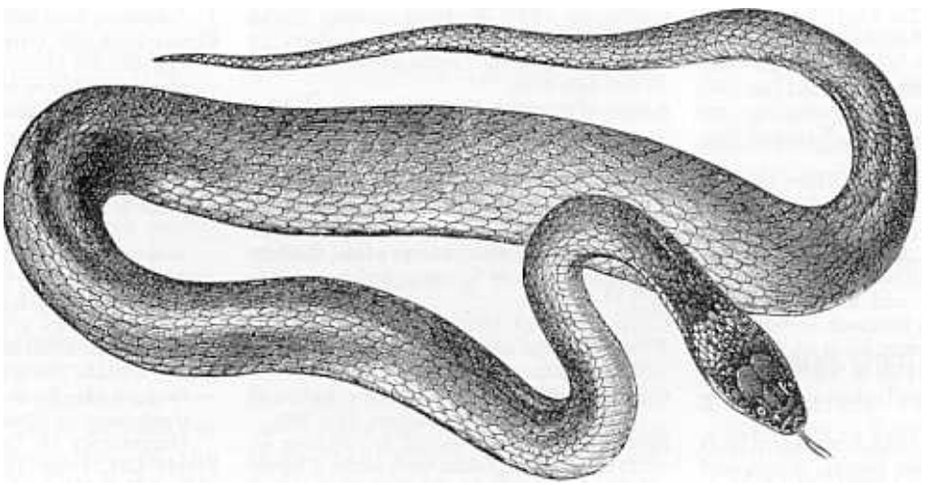
_____. 1992b. The impact of the introduction of the brown tree snake, *Boiga irregularis*, on Guam's lizards. Journal of Herpetology 26: 166–174.

Rodda GH, Fritts TH, Conry PJ. 1992a. Origin and population growth of the brown tree snake, *Boiga irregularis*, on Guam. Pacific Science 46: 46–57.

Rodda GH, Rondeau RJ, Fritts TH, Maughan OE. 1992b. Trapping the arboreal snake *Boiga irregularis*. Amphibia-Reptilia 13: 47–56.

Savidge JA. 1987. Extinction of an island forest avifauna by an introduced snake.

Ecology 68: 660–668.
_____. 1988. Food habits of *Boiga irregularis*, an introduced predator on Guam. Journal of Herpetology 22: 275–282.
Savidge JA, Sileo L, Siegfried LM. 1992. Was disease involved in the decimation of Guam's avifauna? Journal of Wildlife Diseases 28: 206–214.
Seigel RA, Ford NB. 1987. Reproductive ecology. Pages 210–252 in Seigel R, Collins J, Novak S, eds. Snakes: ecology and evolutionary biology. New York: Macmillan.
Shine R. 1983. Arboreality in snakes: ecology of the Australian elapid genus *Hoplocephalus*. Copeia 1983: 198–205.
_____. 1991. Strangers in a strange land: ecology of Australian colubrid snakes. Copeia 1991: 120–131.
Steadman DW. 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. Science 267:1123–1131.
Stickel LF, Stickel William H, Schmid FC. 1980. Ecology of a Maryland population of black rat snakes (*Elaphe o. obsoleta*). American Midland Naturalist 103: 1–14.
van Riper C III, van Riper SG, Goff ML, Laird M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. Ecological Monographs 56: 327–344.
Warner RE. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70: 101–120.
Wiles GJ. 1987. Current research and future management of Marianas fruit bats (Chiroptera: Pteropodidae) on Guam. Australian Mammalogy 10: 93–95.

Harvard University
Bullard Fellowships in Forest Research

Each year, Harvard University awards a limited number of Bullard Fellowships to individuals in biological, social, physical, and political sciences to promote advanced study, research, or integration of subjects pertaining to forested ecosystems. The Fellowships, which include stipends up to $30,000, are intended to provide individuals in mid-career with an opportunity to utilize the resources and to interact with personnel in any department within Harvard University in order to develop their own scientific and professional growth. In recent years, Bullard Fellows have been associated with the Harvard Forest, Department of Organismic and Evolutionary Biology, and the J. F. Kennedy School of Government and have worked in areas of ecology, forest management, policy, and conservation. Fellowships are available for periods ranging from four months to one year and can begin at any time in the year. Applications from international scientists, women, and minorities are encouraged. Fellowships are not intended for graduate students or recent postdoctoral candidates. Further information may be obtained from: Committee on the Charles Bullard Fund for Forest Research, Harvard University, Harvard Forest, P.O. Box 68, Petersham, MA 01366. Annual deadline for applications is February 1.