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EXTINCTION OF AN ISLAND FOREST AVIFAUNA BY AN INTRODUCED SNAKE[1]

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Abstract. The island of Guam has experienced a precipitous decline of its native forest birds, and several lines of evidence implicate the introduced brown tree snake (*Boiga irregularis*) as the cause of the range reductions and extinctions. The range expansion of *B. irregularis* correlated well with the range contraction of the forest avifauna. Exceptionally high predation by snakes on bird-baited funnel traps occurred in areas where bird populations had declined. Little or no snake predation occurred in areas with stable bird populations. Several factors have contributed to *Boiga*'s success in decimating the avifauna on Guam. Although most common in forests, *B. irregularis* has occupied a variety of habitats on Guam, and few effective barriers to its dispersal exist. Prey refuges are present only in urban areas, on concrete or metal structures, and in the savanna. *Boiga*'s nocturnal and arboreal habits and an apparent keen ability to locate prey, make roosting and nesting birds, eggs, and nestlings vulnerable. Besides birds, *B. irregularis* feeds on small mammals and lizards. By including the abundant small reptiles as a major component in its diet, *Boiga* has maintained high densities in forest and second-growth habitats while exterminating its more vulnerable prey. This is the first time a snake has been implicated as an agent of extinction.

Key words: Boiga irregularis; *endangered species; extinction; Guam; island avifauna; predation.*

INTRODUCTION

In certain situations, usually following introductions of exotic species by humans, predators have driven prey to extinction (see Greenway 1967 for examples). Most avian extinctions within the past 200 yr have been of insular species. About half of these extinctions are presumed to have been caused by introduced predators, particularly rats (*Rattus* spp.; Diamond 1984). Predation as the cause for extinction has generally been surmised only after the fact, and is thus based primarily on correlations derived from attempts to reconstruct past events (for examples, see Atkinson 1973, 1977). Rarely have data been gathered during the extinction process. Consequently, the dynamics of the process usually have not been documented.

Study area and historical background

The island of Guam offered a rare opportunity to study the decline and impending extinction of an entire forest avifauna. Guam is one of the Mariana Islands, a north-south chain of 15 islands halfway between Japan and New Guinea. It is ≈45 km long and 6–13 km wide. Second-growth forest dominates the northern limestone plateau, but primary forest remains in cliff areas; the vegetation in southern Guam is largely savanna with ravine forest in the river valleys (Stone 1970). Cocos Island is a small (1800 × 250 m) island 2.5 km south of Guam. The western half of the island is dominated by mixed forest and strand vegetation, whereas the eastern half is a tourist development. Before the recent declines and extinctions, the resident avifauna of Guam consisted of 18 native birds: 12 land birds, 3 breeding seabirds, 2 wetland species, and a reef-heron, and 7 introduced species (Table 1). Seven of these species (Pacific Reef-heron, *Egretta sacra*; Yellow Bittern, *Ixobrychus sinensis*; Brown Noddy, *Anous stolidus*; White Tern, *Gygis alba*; Philippine Turtle-dove, *Streptopelia bitorquata*; Eurasian Tree-sparrow, *Passer montanus*; and Micronesian Starling, *Aplonis opaca*) also occur on Cocos Island.

Historically, most forest birds were common to abundant throughout Guam (Seale 1901, Baker 1951). However, populations of Guam's forest species plummeted in recent decades, while bird populations in savanna habitat on Guam, on Cocos Island, and on Rota, Tinian, and Saipan, islands 71–127 km north of Guam, remained relatively stable. Bridled White-eye (*Zosterops conspicillatus rotensis*) populations on Rota have declined also (J. Engbring, *personal communication*), but the pattern of decline on Rota (disappearance from low elevations) is different from that on Guam. Except for the Vanikoro Swiftlet (*Aerodramus vanikorensis*), a cave nester, all the other 10 forest species of birds on Guam have followed a similar pattern of decline (Table 1). These birds disappeared from southern ravine forests in the 1960's and gradually their ranges contracted and populations declined progressively to

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TABLE 1. Resident birds of Guam. Native forest species that have followed a similar pattern of decline on Guam are in bold print.

Scientific name	Common name	Status on Guam*	Nesting habitat
Phaethon lepturus†	White-tailed Tropicbird	N; R	Coastal cliffs
Egretta sacra	Pacific Reef-heron	N; U	Coastal areas
Ixobrychus sinensis	Yellow Bittern	N; C	Wetlands, grasslands, scrub
Francolinus francolinus	Black Francolin	I; C	Savanna
Coturnix chinensis†	Blue-breasted Quail	I; C	Grasslands/agricultural areas
***Rallus owstoni*‡**	Guam Rail	N; <50	Forest, second-growth, scrub
Gallinula chloropus guamii§	Common Moorhen	N; R	Wetlands
Anous stolidus	Brown Noddy	N; U	Coastal islets
Gygis alba‖	White Tern	N; R	Coastal areas (nests in trees)
Columba livia	Rock Dove	I; U	Urban
Streptopelia bitorquata‖	Philippine Turtle-dove	I; C(n)	Second-growth, forest
Gallicolumba x. xanthonura	White-throated Ground-dove	N; Last seen in Jan. 1986	Forest, second-growth
Ptilinopus roseicapilla	Mariana Fruit-dove	N; Last seen in 1985	Forest, second-growth
Aerodramus vanikorensis bartschi†	Vanikoro Swiftlet	N; R	Caves
Halcyon c. cinnamomina	Micronesian Kingfisher	N; <50	Forest, second-growth
Acrocephalus l. luscinia¶	Nightingale Reed-warbler	N; Extinct by 1970	Wetlands
Rhipidura rufifrons uraniae	Rufous Fantail	N; Last seen in 1984	Forest#
***Myiagra freycineti*‡**	Guam Flycatcher	N; Last seen in 1984	Forest#
Zosterops c. conspicillatus	Bridled White-eye	N; Last seen in 1983	Forest#
Myzomela cardinalis saffordi	Cardinal Honeyeater	N; Last seen in Jan. 1986	Forest, second-growth#
Lonchura malacca†	Chestnut Mannikin	I; U	Grasslands
Passer montanus	Eurasian Tree-sparrow	I; C	Urban
Aplonis opaca guami	Micronesian Starling	N; <100	Forest, second-growth#
Dicrurus macrocercus‖	Black Drongo	I; C(n)	Second-growth, forest edge, urban
Corvus kubaryi	Mariana Crow	N; <100	Forest, second-growth

* Information taken from unpublished data provided by the Guam Division of Aquatic and Wildlife Resources and Jenkins (1983). I = Introduced; N = Native; C = Common; C(n) = Common in northernmost Guam, uncommon to rare in central and southern Guam; R = Rare; U = Uncommon.
† Species appears to have declined but causal factors have not been investigated.
‡ Species endemic to Guam.
§ Species appears to have declined because of loss of wetland habitat.
‖ Species has followed a pattern of decline similar to that of the forest birds.
¶ Reasons for extinction have not been identified. Baker (1951) comments that the species was never very abundant on Guam and that the absence of natural enemies, especially snakes, may have been one of the principal reasons why the Reed-warbler had been able to survive.
\# Historically reported in most habitats except savanna.

the north (see The Role of *Boiga* in the Decline: Prediction 1). Ralph and Sakai (1979) described southern Guam as the most massive avian desert they had seen. By early 1983, all 10 forest species occurred together only in 160 ha of mature forest beneath the cliffline at the northern tip of Guam, with a few species still occupying parts of the northern plateau. Bridled White-eyes (*Z. c. conspicillatus*) have not been seen on Guam since summer 1983, and are presumed to be locally extinct. Guam Flycatchers (*Myiagra freycineti*), an endemic species, and Rufous Fantails (*Rhipidura rufifrons*) may also be extinct on Guam. Since July 1985, only three Guam Rails (*Rallus owstoni*), an endemic species found in forest and second-growth vegetation on Guam, have been located in the wild (R. E. Beck, Jr., *personal communication*). The remaining forest avifauna is extremely rare (Table 1).

Other native and introduced species have declined in a pattern similar to that of the forest birds (Table 1). The endemic White Tern was described as common over the whole island in 1961 (Hartin 1961). By the early 1980's, it was restricted mainly to the northern coastline of Guam (Engbring and Ramsey 1984). This species has remained abundant on Cocos Island. Introduced Black Drongos (*Dicrurus macrocercus*) are rare in southern and central Guam (Engbring and Ramsey 1984). Philippine Turtle-doves, a species introduced by the Spanish, have undergone >80% decline since the 1960's in southern and central Guam (P. Conry, *personal communication*).

POSSIBLE CAUSES OF THE DECLINE

Various factors including pesticide contamination, overhunting, interspecific competition with introduced birds, habitat modification, exotic diseases, and predation by introduced vertebrates have been proposed as causal agents for the decline.

Pesticides

Pesticides were used extensively in the past for vector control on Guam (Baker 1946*a*). In 1981, an intensive pesticide survey was conducted by Patuxent Wildlife Research Center (United States Fish and Wildlife Service). A variety of animals was collected and most were essentially free of organochlorine pesticides (Grue 1985). Residues found in one sample of skinks and in shrews were at levels less than those known to adversely affect birds or small mammals (Grue 1985). Grue concluded that neither past nor present use of pesticides on Guam appeared to be responsible for the continuing decline in the island's native bird populations.

Hunting

Although the Micronesian Kingfisher (*Halcyon c. cinnamomina*) and Mariana Crow (*Corvus kubaryi*) were largely unprotected until 1981, the majority of the forest birds have been legally protected on Guam since the turn of the century. Birds have declined also on military land, where hunting of native species was prohibited and tight security minimized illegal hunting (Savidge 1984). Hunting may have produced additional stress on certain populations, but no evidence suggests it was responsible for the major declines.

Competition with exotic species

Seven exotic avian species have been introduced to Guam. The only species that could be competing with forest birds is the Black Drongo, an aggressive species first found on Guam in 1960 (Hartin 1961). However, Maben (1982) concluded that because of differences in habitat utilization, foraging techniques, and dietary preferences, the Black Drongo was not competing with native birds on Guam. Furthermore, drongos are relatively rare in southern Guam and are more abundant in northern Guam, corresponding with the present distribution of the native birds (Engbring and Ramsey 1984).

Loss of habitat

During World War II, large areas of vegetation were cleared and some habitat was destroyed in heavy fighting (Fosberg 1960). Since 1945, there has been an increase in weedy species, particularly *Leucaena leucocephala*. Nonetheless, substantial native habitat remains in southern and northern Guam, and birds have disappeared from forests that previously supported healthy bird populations (Savidge 1984). Furthermore, major habitat disturbances have also occurred on Tinian and Saipan yet avian populations on those islands have remained relatively stable.

Disease

In cooperation with the National Wildlife Health Laboratory (United States Fish and Wildlife Service), a variety of domestic, native, and introduced birds on Guam were sampled for bacteria, viruses, and parasites between 1982 and 1985. Native forest birds were basically free of disease and no blood parasites were detected (Savidge 1986). A sentinel study exposing four species of birds to potential disease vectors was also conducted in 1984 to detect pathogenic diseases in the habitat of remaining forest birds (Savidge 1986). Chickens at one site developed lesions consistent with poxvirus, but the virus appeared to be host specific. None of the other sentinel species developed the virus. Neither the survey nor the sentinel study revealed evidence suggesting that infectious diseases were extirpating the forest birds on Guam (Savidge 1986).

Predation

Feral dogs, cats, rats (*Rattus exulans, R. rattus,* and probably *R. norvegicus*), and monitor lizards (*Varanus indicus*) are present on all major islands in the Marianas. Feral dogs and cats are relatively restricted in distribution on Guam. Rats have been implicated in avian extinctions on other islands (Atkinson 1973, 1977). However, trapping indicates that rat populations are actually rare in many habitats on Guam (see The Role of *Boiga* in the Decline: Prediction 3; Savidge 1986). Monitors have been present on Guam for several hundred years (Moore 1983), and invertebrates constituted ≈70% and birds and bird eggs only 4% of food items found in 54 monitor stomachs collected on Guam between 1962 and 1964 from areas where birds were abundant (Dryden 1965).

The recently introduced brown tree snake *Boiga irregularis* is the only known predator on birds unique to Guam in the Marianas. This snake (hereafter referred to as *Boiga*) is native to Australia, New Guinea and adjacent archipelagos, and the Solomon Islands. It was probably transported to Guam as a passive stowaway in military cargo in the late 1940's or early 1950's. It is nocturnal and both arboreal and terrestrial (Savidge 1986). Snakes have been implicated previously as major predators at bird nests (Nolan 1963, Skutch 1966, Best 1978), but no bird extinctions or dramatic range reductions have been attributed to reptiles. The remainder of this paper evaluates the hypothesis that *Boiga* is responsible for the decline of Guam's avifauna by preying on eggs, nestlings, or adult birds.

The Role of *Boiga* in the Decline

To address the hypothesis that *Boiga* is responsible for the avifauna decline, three predictions were tested: (1) the spatial and temporal distribution of *Boiga* on Guam should be correlated with the avian range contraction; (2) predation rates on Guam should be higher where birds have been decimated than where bird populations are stable; and (3) alternative prey of *Boiga* should show a pattern of decline similar to that of Guam's birds.

Prediction 1

To address the prediction that the range expansion of *Boiga* should be correlated with the avian range contraction, historical records were searched, and a questionnaire was developed and distributed to Guamanians. Three hundred and fifty-two people responded to the questionnaire (147 in northern, 113 in central,

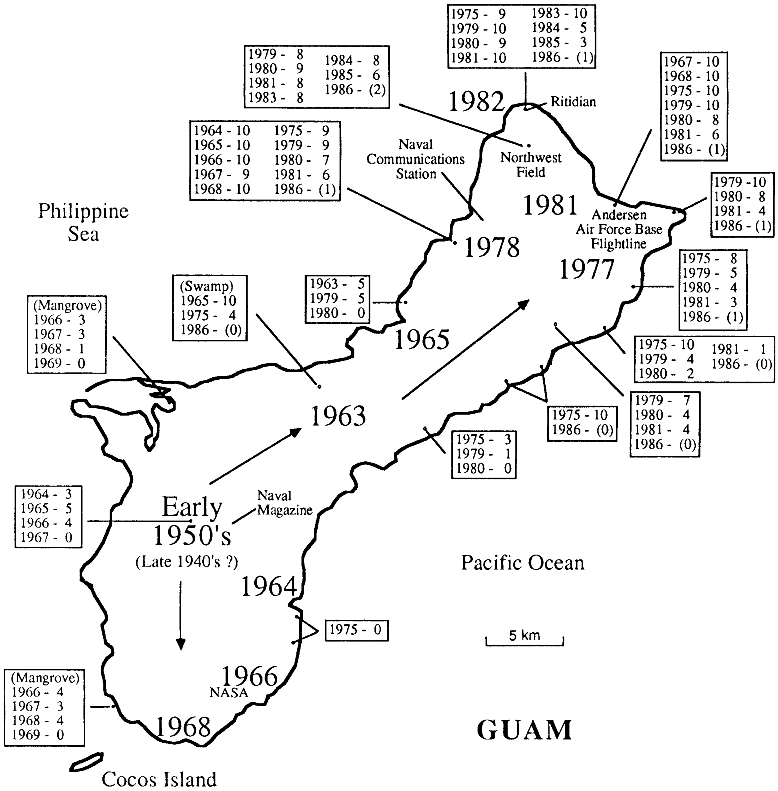

FIG. 1. Map of Guam showing location of study areas and the range expansion of *Boiga* in relation to the forest bird decline. Years in large print are snake records from the Guam Division of Aquatic and Wildlife Resources (DAWR), newspaper articles, or from questionnaire data. Years based solely on questionnaire data were derived by calculating the average of the years in which snakes were first recorded by poultry owners in the specific location. All years for snake presence should be considered approximate (it is likely snakes were not detected in the various locations until snake populations reached higher densities). Arrows indicate the general direction of snake movement. Years in small print are followed by the number of forest bird species, out of 10 possible, recorded in bird censuses conducted in that year by DAWR biologists (DAWR, *personal communication*). For years with zero species recorded, subsequent surveys also revealed no forest species. Except where indicated, bird censuses were in forest or second-growth habitat. Number of species recorded in 1986 is in parentheses to indicate data are incomplete for the year.

and 92 in southern Guam). Many local people farm or raise poultry, or both, and are generally closely associated with the land. Because they were unfamiliar with large snakes before *Boiga*'s introduction, many individuals of the indigenous population paid close attention to *Boiga*'s range expansion. The only other snake that occurs on Guam is the small, vermiform blind snake *Rhamphotyphlops braminus*, which is rarely observed.

Newspaper articles, field records from the Guam Division of Aquatic and Wildlife Resources (DAWR), and questionnaires documented the spread of *Boiga* throughout Guam over the past three decades (Fig. 1). *Boiga* was first reported in south-central Guam in the early 1950's. It spread throughout the south and into central Guam and then moved north in the 1970's. Ritidian, at the northwest tip of Guam, and the second-growth areas within the flightline at Andersen Air Force Base (AAFBF) in northeast Guam were the last areas infiltrated. The snake expanded its range at a rate of $\approx$1.6 km/yr. In addition to increased snake sightings over the past decade, the Guam Navy Public Works reported a substantial increase in snake-caused power outages in their central to northern circuit before they installed snake guards in 1983 (15 outages in 1978, 23 in 1979, 31 in 1980, 67 in 1981, and 82 in 1982). This suggests that *Boiga* increased in abundance within its range as well.

The range expansion of *Boiga* was correlated closely with the range contraction of the forest avifauna (Fig. 1). Birds disappeared from southern Guam at the same time *Boiga* populations were expanding. In 1964, white-eyes, flycatchers, fantails, and honeyeaters (all small birds) were absent in suitable habitat at Naval Magazine (DAWR, *personal communication*), which was within 3–4 km of the first *Boiga* sightings. Although this is not documented, there is no reason to doubt that these species were present in this expanse of ravine forest prior to *Boiga*'s arrival. By the early 1970's, snakes were found throughout southern and much of

TABLE 2. Predation at bird-baited traps placed in various areas (see Fig. 1 for locations) on Guam and Cocos Island for 14-d intervals during the indicated months. Percent predation is in parentheses. Areas trapped between May 1984 and April 1985.

	NCS [May 1984]	NWF [May 1984]	Naval Magazine [Oct 1984]	Ritidian* [Jul 1984]	AAFBF [Dec 1984]	Cocos Island [Dec 1984]	NASA [Apr 1985]
Habitat	Second-growth	Second-growth	Ravine forest	Limestone forest	Second-growth	Mixed forest	Savanna
Approximate date of snake arrival	mid-1970's	1980's	1950's	1980's	1980's	...	1960's
Bird population	Extinct	Rare	Extinct	Declining	Declining	Stable	Stable
No. prey taken/no. traps	20/20 (100.0)	30/32 (93.8)	27/30 (90.0)	8/21 (38.1)	10/16 (62.5)	0/15 (0.0)	15/24 (62.5)
Predators†							
Snake	20 (100.0)	23 (76.7)	27 (100.0)	8 (100.0)	9 (90.0)	...	2 (13.3)
Monitor	...	6 (20.0)	...	...	1 (10.0)	...	...
Rat	...	1 (3.3)	...	...	...	...	13 (86.7)

* Birds exposed only at night.
† Both snakes and monitors generally were retained by the traps. Rats gnawed through the trap mesh.

central Guam, and almost all native birds were restricted to the northern half of the island. By 1981, native birds were largely restricted to the Northwest Field (NWF) and Ritidian areas. Ritidian was the last area to have all 10 forest species. It was also one of two known areas last invaded by *Boiga*. The other area, a 28-ha patch of second-growth vegetation at AAFBF, maintained the last population of Guam Rails (DAWR, *personal communication*); a surrounding expanse of asphalt may have served as a partial deterrent to snake colonization.

Cocos Island is a natural exclusion experiment. Birds are thriving despite development on one-half of the island (Engbring and Ramsey 1984). Rats are present on Cocos, but monitors and snakes are absent.

Prediction 2

Moors (1983) argues that to implicate a predator as the cause of avian extinctions, it is necessary to show that losses from predation cause mortality in excess of annual recruitment. However, it is virtually impossible to evaluate quantitatively the mortality and recruitment rates for a complex of birds, particularly when they are near extinction. An alternative approach to Moors' suggestion is to use an empirical measure of the intensity of predation. Bird-baited traps can approximate normal night conditions for roosting and nesting birds that are sedentary.

To test the prediction that predation by snakes would be higher where bird populations had declined, I established seven transects in different locations on Guam and Cocos Island (Fig. 1). The locations included two areas with normal levels of bird populations. The first area, Cocos Island, has maintained stable populations of both native and introduced birds. Introduced Black Francolin (*Francolinus francolinus*) and Blue-breasted Quail (*Coturnix chinensis*) and native Yellow Bitterns were common at the second site (NASA, land surrounding an installation of the National Aeronautics and Space Administration) located in savanna habitat on Guam. Additional transects were located in areas on Guam where: (1) forest birds were locally extinct (Naval Communications Station [NCS] and Naval Magazine, both large military installations with abundant forest); (2) there were only rare occurrences of individual birds (the perimeter of Northwest Field [NWF]); and (3) bird populations were declining (Ritidian and Andersen Air Force Base flightline [AAFBF]). Primary forest dominated the Ritidian site, whereas vegetation within NWF and AAFBF was largely second-growth.

Each transect had 15–32 funnel traps baited with Coturnix Quail (*Coturnix coturnix*). The traps were made of a 5-mm plastic mesh and were 23 cm in diameter by 62 cm in length. A movable door, which allowed entry but not exit, was hinged to the small end of the funnel entrance. Seed and water were provided for the birds. Traps on Guam were placed at 160-m intervals; Cocos Island traps were 50 m apart. The number of traps per transect depended on habitat availability. Most traps were exposed to predators throughout the day and night. However, at Ritidian, where predation by monitor lizards on birds in the traps was high in the initial experiments (18 of 21 traps were disturbed by monitors), birds were exposed only to nocturnal predators.

Because *Boiga* is primarily arboreal and all the forest species except the rail roost and nest in trees, all traps within forest habitat were hung with nylon cord from branches ≈1.5–3.7 m above the forest floor. Traps were placed on the ground in the savanna because there are few shrubs and trees and savanna birds nest near or on the ground. The bait was checked daily or every other day over 14-d intervals. Once a bait was eaten, it was not replaced.

Virtually all quail in traps placed in forest habitat on Guam where native birds were extinct or rare were preyed on by *Boiga* (Table 2). Excluding predation by monitors and rats, 75% of the birds were killed by snakes within four nights of exposure at NCS, seven

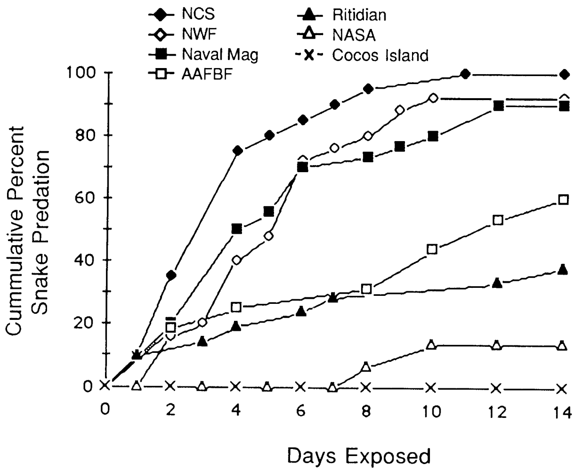

FIG. 2. Predation by snakes on birds in traps exposed for up to 14 d at seven different locations. Once the bait was preyed on, it was not replaced. See Table 2 for trapping dates and number of traps. Predation by rats and monitor lizards was excluded from analyses.

nights at NWF, and nine at Naval Magazine (Fig. 2). Within 11 d, all birds in funnel traps at NCS were preyed upon by snakes. Frequencies of predation at these three sites were not significantly different (χ^2 = 2.04, 2 df, $P > .05$).

Birds in traps where avian populations were declining and snakes had become established more recently (Ritidian and AAFBF) had significantly lower predation by snakes than at NCS, NWF, and Naval Magazine (χ^2 = 33.69, 3 df, $P < .05$; χ^2 = 14.13, 3 df, $P < .05$) but were not significantly different from each other (χ^2 = 1.69, 1 df, $P > .05$). The lower predation at these two sites may have been due to the availability of alternative prey or because snake numbers had not had time to increase to a high density or both. Although only 38% predation by snakes on birds in traps was recorded at Ritidian, birds had been virtually eliminated from the area.

Predation by monitors was high on birds in traps exposed during the day at Ritidian, but under normal conditions monitors are not a significant cause of avian mortality. This species forages during the day when most birds can easily escape capture, and invertebrates are its primary prey (Dryden 1965). It is unknown why predation by monitor lizards was substantially lower in all other locations than in Ritidian. *Boiga* may be impacting monitor lizards. Monitor lizard eggs have been found in snake stomachs (Savidge 1986), and *Boiga* may also consume the young.

The AAFBF location is particularly interesting. Rails occupied all suitable habitat in February 1984. By September 1984, the range of the rails was reduced by 50%. Fifteen bird-baited snake traps maintained by the Guam Division of Aquatic and Wildlife Resources (DAWR) within the remaining occupied habitat revealed zero predation over a 30-d period in September 1984. By December 1984, my traps, located throughout the area, revealed 63% predation in 14 d, mostly by *Boiga* (Table 2). Further range contraction of the rails within the remaining flightline area was associated temporally with this increase in predation.

One case of predation by a rat was recorded on the six forest transects. However, rats accounted for 87% of the predation at the NASA site (Table 2), which was in savanna habitat. On the basis of direct observations and predation rates obtained from the transects, numbers of *Boiga* appeared to be highest in forest habitat and lowest in savanna. On Cocos Island, there was no mortality in the experiment due to predators.

Prediction 3

Brown tree snakes within their native range eat small mammals and lizards as well as birds (Worrell 1963, Cogger 1975, McCoy 1980). To address the prediction that alternative prey of *Boiga* declined in a pattern similar to that of Guam's birds, densities of small mammals before and after invasion by snakes were compared. Published estimates of small-mammal densities before snakes invaded were available for various locations (Baker 1946*b*, Barbehenn 1974*a*, *b*), and I retrapped five similar areas using methods comparable to those used in the earlier studies. Methodologies and the vegetation composition of the study areas are described in Savidge (1986).

Barbehenn (1974*b*) trapped year-round on Guam in savanna and various field habitats from 1962 to 1964, before the snake had invaded or become firmly established in these locations, and found an average of 42.5 small mammals/ha. My comparable trapping effort during the dry seasons of 1984–1985 in field habitats yielded 2.8 mammals/ha, a 94% decline (Savidge 1986). *Mus musculus* and *Rattus rattus* were the only species I caught in these areas. In contrast, savanna habitat yielded 109 mammals/ha (Savidge 1986). Small mammals caught in savanna included *M. musculus*, *R. rattus*, and *Suncus murinus*.

Although more extensive trapping may reveal seasonal or annual fluctuations in small-mammal densities, the present data indicated that small mammals have undergone dramatic declines in fields, but remain abundant in savanna. Snakes are commonly found in small fields (J. Savidge, *personal observation*), but, as indicated by low snake-trap success, are uncommon in savanna. At least during the dry season, savanna habitat may be unsuitable for *Boiga* because the large expanses of swordgrass (*Miscanthus floridulus*) do not provide adequate cover during the day. The grassy fields provide varying amounts of shrubby growth and are relatively near forest or second-growth habitat to which *Boiga* can retreat. The reduced numbers of small mammals at my field sites were probably not caused by natural cycling, as I found small mammals abundant in savanna; nor were they due to asynchronous cycling betwen the habitats, as several species with different diets (an insectivore and two omnivores) were similarly affected.

Suncus was Barbehenn's most common species. Shrews are the second most frequent small mammal consumed by *Boiga*, and I caught shrews only in savanna (Savidge 1986). In 1981, Grue and Fecko (1986) ran a series of transects throughout Guam to obtain shrews for pesticide studies. They concluded that, with the exception of urban areas, the abundance and distribution of *Suncus* were similar to that of the native birds, further supporting the prediction that alternative prey should show a pattern of decline similar to Guam's forest avifauna.

Lastly, predation experiments with artificial nests containing quail eggs in northern forest on Guam suggested snakes had impacted rat populations in the study location. Rats were the major predators on nests prior to snake arrival (31% of 51 nests were preyed on, with rats accounting for 88% of the predation), but 28 mo after snake colonization, snakes were responsible for 100% of predation on artificial nests (37% of 30 nests; J. Savidge, *personal observation*).

Discussion

Pattern of local bird decline or survival in relation to predation by Boiga

Smaller forest birds disappeared first from areas on Guam (DAWR, *personal communication*). Trapping and general field collecting indicate that most snakes are in the smaller size classes ($\approx$120 cm snout–vent length or less; Savidge 1986), and thus predation pressure would be greatest on the small birds because they could be swallowed by both small and large snakes. White-eyes, the smallest and the first of the forest birds to become extinct on Guam, are a gregarious, flocking species. Captive individuals that I maintained in a large outdoor cage always slept shoulder to shoulder and could be removed one at a time at night without the others taking flight. Presumably a nocturnal predator could consume several individuals at a roost. *Boiga* could take roosting white-eyes as well as nesting adults and their eggs. One relatively small snake (66 cm) consumed three white-eyes and killed a fourth in one night when it forced its way through an air conditioner and into a laboratory holding birds for disease studies (J. Savidge, *personal observation*). No doubt snakes take adult fantails, flycatchers, and honeyeaters, but because these species are slightly larger than white-eyes and are nongregarious, the impact on them was initially less severe. Since they are unable to swallow large birds (J. Savidge, *personal observation*), small snakes probably prey on the eggs and nestlings of the remaining forest species. Micronesian Kingfishers, Micronesian Starlings, Guam Rails, and Mariana Crows were the last forest birds to decline in local areas on Guam. In addition to their larger size, Micronesian Kingfishers and Starlings are both tree-cavity nesters. Tree-cavity nesters have lower rates of predation than species nesting in the open (Lack 1954, Nice 1957, Skutch 1966, Oniki 1979). The crow and rail are the largest of the native forest birds on Guam. Not only would adults of these species be difficult for most snakes to consume, but these larger birds presumably live longer and would therefore be detectable for a greater period of time even if there were no recruitment to their populations.

Observations on surviving Guam birds reveal factors that reduce their susceptibility to predation by *Boiga*. Yellow Bitterns, the most common of the native terrestrial species, typically nest in wetlands or savanna, areas with reduced densities of *Boiga*. When scrub habitat is utilized for nesting, it is generally surrounded by grass or asphalt. The introduced Black Francolin is restricted to open savanna habitat, and clutch size ranges from six to eight eggs (Baker 1920) compared with clutches of one to two eggs for most forest birds (Jenkins 1983). It is also a large bird. Black Drongos mainly nest on concrete telephone poles in northern Guam. The introduced Eurasian Tree-sparrows are largely restricted to urban locations and usually nest on concrete or metal structures inaccessible to snakes.

The mechanisms of overexploitation of prey by Boiga

Murdoch and Oaten (1975) summarize a variety of mechanisms that can lead to stability in natural predator–prey systems, including refuges for prey, invulnerable prey classes, barriers to predator dispersal, and the existence of alternative prey combined with predator switching. How then has *Boiga* been able to overexploit the avian and mammalian fauna on Guam and not in its native range?

1) *Boiga* has few competitors and no significant predators to limit its populations on Guam. Surveys and field trapping indicate the snake occurs in high densities, with a conservative estimate of about 16 snakes/ha in northern forests (Savidge 1986).

2) Theoretically, if refuges of adequate size were present, some number of prey would be safe. However, on Guam, refuges are present only in urban areas, on human-made structures and in savanna, habitats unsuitable for resident forest species. Additionally, the forest canopy on Guam is relatively low, usually < 15 m. This simplified vertical structure may facilitate *Boiga*'s access to prey species throughout the canopy. In the native range of *Boiga* (e.g., Solomon Islands and New Guinea), forest canopy may extend above 40 m (Kent 1972, Bell 1982). Though no data are available on snake densities at increasing canopy heights, the greater complexity of taller forests may provide additional prey refuges.

3) Bird densities appear naturally lower on Guam than in the native range of *Boiga*, possibly due in part to the simplified vertical structure of the forest. J. Engbring and F. L. Ramsey (1984 and *personal communication*), using the circular count method, esti-

mated 24.9 birds/ha in Ritidian before snakes invaded and 17.2 birds/ha in comparable habitat on Rota. In contrast, using a variety of census techniques, Bell (1982) estimated 69 birds/ha in lowland rainforest in New Guinea. Even if predator densities were comparable between Guam and New Guinea (no data are available on *Boiga* densities in New Guinea), with a lower density of birds on Guam, the impact of predation on bird populations would be greater.

4) *Boiga*'s generalized food habits and the availability of alternative prey have contributed to the maintenance of high populations of the snake. Small reptiles, particularly skinks and geckos, are major constituents of the diet of the brown tree snake (Savidge 1986). Small lizards are exceedingly common on Guam and apparently their reproductive potential is high enough to withstand the predation pressure. Young snakes probably grow and maintain themselves on small lizards until they are large enough to take birds and small mammals. Even then, lizards make up a major portion of the snake's diet in areas where birds and small mammals have declined (Savidge 1986). For the larger snakes, the birds (eggs to adults) and small mammals are probably preferred prey items because they provide a greater reward. By utilizing this abundant lizard prey resource, *Boiga* can maintain high densities while decimating its more vulnerable prey (birds and small mammals). As indicated by the high predation intensity (90% within the exposure period), the high population levels of *Boiga* in Naval Magazine, an area supporting snakes since the 1950's and without birds for nearly two decades, attest to the importance of alternative prey in maintaining snake densities.

Two additional characteristics make *Boiga* an effective predator. First, *Boiga* may have the ability to locate bird prey other than by random encounter. As indicated by Guamanians responding to the questionnaires, snakes predictably enter chicken and pigeon coops shortly after eggs are laid. Secondly, a characteristic that makes *Boiga,* and snakes in general, effective predators even if prey populations decline is that snakes can go for long periods without feeding. If taken alone, this latter characteristic would interject an increased level of instability into the system. However, since *Boiga* can utilize alternative prey, the lag time before snake populations decline is even further accentuated.

The future of Guam's avifauna

It is questionable whether any of the forest species will maintain populations on Guam. Even the introduced Philippine Turtle-dove, which utilizes forest edge, is experiencing high nest mortality. P. Conry (*personal communication*) monitored 12 turtle-dove nests in forest habitat and concluded that the loss of reproduction for turtle-doves caused by predation appears to be so severe (the daily mortality rate of nests was calculated at 13.5% and nest success at 0.7% using the Mayfield [1975] method) that annual recruitment probably cannot replace natural attrition. Only three native forest species, the Vanikoro Swiftlet, Mariana Crow, and Micronesian Starling, are not near extinction. The population of swiftlets, a cave nester, is estimated at ≈ 400 birds (G. Wiles, *personal communication*). Swiftlets have declined on Guam and throughout the Mariana Islands. Since the pattern of decline of swiftlets on Guam was different from the patterns of the rest of the forest birds, it is unclear what role, if any, *Boiga* played. However, the present nesting cave appears relatively immune to snake predation because it has a smooth ceiling. Crows are estimated at <100, and no successful reproduction has been recorded at nests monitored since 1985 (R. E. Beck, Jr., *personal communication*). One might predict that crow populations will eventually decline to extinction from lack of recruitment. Starlings have recently been observed nesting on artificial structures, and populations might be augmented using nestboxes placed on concrete telephone poles. Both the Micronesian Kingfisher and Guam Rail appear to be breeding successfully in captivity. However, snake populations will need to be reduced on Guam before these species can be reintroduced. Since snakes have never been controlled at this scale, it will probably be many years before effective control measures are developed and enacted.

In summary, the data clearly suggest that predation by the introduced snake *Boiga irregularis* is responsible for the decline of 10 species of native forest birds as well as several other types of birds on Guam. This is the first time a reptile has been implicated in the decimation of an avifauna, and the example shows how rapidly exinction can ensue under the appropriate ecological circumstances.

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NOTE ADDED IN PROOF

Ronald I. Crombie (Smithsonian National Museum of Natural History, Washington, D.C., *personal communication*) observed a brown tree snake near Ritidian in 1968. Because of the large expanse of time between this and other northern Guam records, it is possible that a small population was established, either by natural immigration or accidental transport in military equipment, and that this population went locally extinct. Alternatively, the snake population may have been at low densities throughout the north prior to general detection. If the latter is true, this and the rapid crash of the bird population in the north (five species disappeared from Ritidian within a year) suggest that either (1) the northern snake population gradually increased until a critical density was reached and then the population irrupted to detectable levels, and/or (2) as the nucleus snake population increased in central Guam, there was a larger immigration of snakes to the northern part of the island. The significance of the snake movement information in Fig. 1 remains unchanged as it reflects the general abundance of the expanding snake population. These higher snake densities were responsible for the native forest bird population decline.