
Impacts of the Brown Tree Snake: Patterns of Decline and Species Persistence in Guam's Avifauna

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Abstract: Predation by brown tree snakes (*Boiga irregularis*) devastated the avifauna of Guam in the Mariana Islands during the last half of the twentieth century, causing the extirpation or serious reduction of most of the island's 25 resident bird species. Past studies have provided qualitative descriptions of the decline of native forest birds but have not considered all species or presented quantitative analyses. We analyzed two sets of survey data gathered in northern Guam between 1976 and 1998 and reviewed unpublished sources to provide a comprehensive account of the impact of brown tree snakes on the island's birds. Our results indicate that 22 species, including 17 of 18 native species, were severely affected by snakes. Twelve species were likely extirpated as breeding residents on the main island, 8 others experienced declines of $\geq 90\%$ throughout the island or at least in the north, and 2 were kept at reduced population levels during all or much of the study. Declines of $\geq 90\%$ occurred rapidly, averaging just 8.9 years along three roadside survey routes combined and 1.6 years at a 100-ha forested study site. Declines in northern Guam were also relatively synchronous and occurred from about 1976 to 1986 for most species. The most important factor predisposing a species to coexistence with brown tree snakes was its ability to nest and roost at locations where snakes were uncommon. Large clutch size and large body size were also related to longer persistence times, although large body size appeared to delay, but not prevent, extirpation. Our results draw attention to the enormous detrimental impact that brown tree snakes are likely to have upon invading new areas. Increased containment efforts on Guam are needed to prevent further colonizations, but a variety of additional management efforts would also benefit the island's remaining bird populations.

Key Words: birds, *Boiga irregularis*, brown tree snake, declines, extinction, extirpation, Guam, introduced species, islands, populations, predation

Impactos de la Culebra Arbórea Parda: Patrones de Declinación y Persistencia de Especies en la Avifauna de Guam

Resumen: La depredación de culebras arbóreas pardas (*Boiga irregularis*) fue devastadora para la avifauna de Guam en las Islas Marianas durante la segunda mitad del siglo XX, causando la extirpación o reducción severa de la mayoría de las 25 especies de aves residentes de la isla. Estudios anteriores han proporcionado descripciones cualitativas de la declinación de aves nativas de selva, pero no han considerado a todas las especies ni presentado análisis cualitativos. Analizamos dos conjuntos de datos obtenidos en el norte de Guam entre 1976 y 1998 y revisamos fuentes no publicadas para proporcionar información integral del impacto de *Boiga irregularis* sobre las aves de la isla. Nuestros resultados indican que 22 especies, incluyendo 17 de 18 especies nativas, fueron afectadas severamente por las culebras. Doce especies probablemente fueron extirpadas como residentes reproductores de la isla principal, 8 más presentaron declinaciones de $\geq 90\%$ en toda la isla o por lo menos en el norte, y 2 permanecieron en niveles poblacionales bajos durante todo o buena parte del estudio. Las declinaciones de $\geq 90\%$ ocurrieron rápidamente, promediando solo 8.9 años a lo largo de tres

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rutas de monitoreo combinadas y 1.6 años en un sitio de 100 ha de selva. Las declinaciones en el norte de Guam también fueron relativamente sincrónicas y ocurrieron entre 1979 y 1986 para la mayoría de las especies. El factor más importante que permitió a las especies coexistir con culebras fue su capacidad de anidar o descansar en sitios en los que las culebras no eran comunes. Una nidada grande y tamaño corporal grande también se relacionaron con tiempos de persistencia más largos, aunque el tamaño corporal grande aparentemente retrasaba, pero no evitaba, la extirpación. Nuestros resultados llaman la atención acerca del enorme impacto negativo que pudiera tener la culebra arbórea parda si invade nuevas áreas. Se requieren mayores esfuerzos de contención en Guam para prevenir futuras colonizaciones, pero una variedad de esfuerzos de manejo adicionales también pudieran beneficiar a las poblaciones de aves restantes en la isla.

Palabras Clave: aves, *Boiga irregularis*, culebra arbórea parda, depredación, extinción, extirpación, especies introducidas, Guam, islas, poblaciones

Introduction

Invasive species are widely recognized as one of the greatest threats to global biodiversity (Office of Technology Assessment 1993; Vitousek et al. 1996; Cox 1999; Mack et al. 2000). Invasion by alien species often has pervasive ecological repercussions in both continental and insular situations, but island species appear to suffer especially high rates of extinction and population decline (Johnson & Stattersfield 1990; D'Antonio & Dudley 1995). Several attributes of island species, including small geographic range and population size, low fecundity, and a lack of coevolution with the invading species and extensively altered habitats, may predispose island species to displacement by exotics (Pauley 1994; Cronk & Fuller 1995; Simberloff 1995; Martin et al. 2000). Furthermore, islands usually have fewer species than mainland areas and thus have fewer predators and competitors that might prevent establishment by invading species (Cronk & Fuller 1995).

The introduction of brown tree snakes (*Boiga irregularis*) to the island of Guam in the tropical western Pacific Ocean is a classic example of the deleterious effects that an alien predator can have on an insular ecosystem (Savidge 1987; Conry 1988; Jaffe 1994; Rodda et al. 1997, 1999a, 1999b; Fritts & Rodda 1998). Tree snakes were accidentally introduced to Guam shortly after World War II (Rodda et al. 1992). The expansion and growth of their population during the next 40 years closely coincided with a precipitous decline of Guam's forest birds and culminated in the extirpation of 8 of the island's 11 species of native forest birds in the 1980s (Savidge 1987; Engbring & Fritts 1988; Beck & Savidge 1990). Alternate explanations for these declines, such as disease, pesticide poisoning, habitat alteration, overhunting, typhoon mortality, and competition or predation from other exotic species, have been rejected as major contributing factors, except possibly for the Mariana Swiftlet (see Table 1 for scientific names) (Maben 1982; Jenkins 1983; Grue 1985; Savidge 1987; Beck & Savidge 1990; Savidge et al. 1992; National Research Council 1997; Fritts &

Rodda 1998). Tree snakes have also decimated other vertebrate species on the island, including flying foxes (*Pteropus mariannus*), several small non-native mammals, and several lizards (Savidge 1987; Wiles 1987; Rodda & Fritts 1992). As a result, snakes have created "empty forests" (Redford 1992; Jaffe 1994) on Guam, which may well be impossible to restore because of the ecological repercussions associated with so many missing species, such as reduced seed dispersal and pollination (Rodda et al. 1999b). There appear to be few other documented instances (e.g., Nile perch [*Lates spp.*] in Lake Victoria; Goldschmidt et al. 1993) where a single introduced vertebrate predator has produced such sudden and extensive declines among a host of prey species and dramatically altered existing food webs (D'Antonio & Dudley 1995; Williamson 1996; Fritts & Rodda 1998).

Although researchers have demonstrated that brown tree snakes are responsible for extirpations of native forest birds, little attention has been given to the effects of snakes on nonforest-dwelling birds, and no quantitative analyses have addressed such issues as how rapidly declines occurred and which species seemed most and least susceptible. We investigated these issues by analyzing a 23-year data set from roadside surveys in northern Guam and a 7-year data set from Pajon Basin, the last area occupied by all forest birds on the island, and by reviewing unpublished data on Guam's birds. We asked three questions: (1) How many species were affected adversely by brown tree snakes and how seriously? (2) How fast, and how synchronously, did major declines and extirpations occur? (3) What species' traits were associated with persistence times? Our general objective was to provide useful lessons from Guam for managers on other islands who may soon have to respond to invasion by brown tree snakes.

Study Area

Guam (lat. 13°27'N, long. 144°47'E) is the largest and southernmost of the Mariana Islands, with a total land

area of 541 km². The northern half of the island is dominated by a large, uplifted limestone plateau, with elevations of 90–185 m, bordered by cliffs and steep slopes and narrow coastal benches 30–1000 m wide. The southern half has volcanic soils and more relief, with a maximum elevation of 406 m. Guam's climate is tropical. Temperatures are warm and uniform during the year, ranging from 22° to 33°C. Average annual rainfall is 218 cm, most of which falls from July to November. A population of 155,000 people resides primarily in moderately to heavily urbanized settings in the central and northern parts of the island. Cocos Island, a small (38 ha), atoll-like island that is probably still free of snakes, lies 2.5 km southwest of Guam.

Population History of the Brown Tree Snake

Brown tree snakes became established throughout Guam by about 1968 or 1970 (Savidge 1987; Rodda et al. 1992). Dense populations were first detected in the 1960s near the snake's point of colonization in the south, then spread progressively northward across the island during the 1970s and early 1980s at an average rate of about 1.6 km/year (Fig. 1; Savidge 1987; Rodda et al. 1992). Unfortunately, snake abundance was not determined for any location until after most bird declines were largely completed, making it impossible to correlate the declines to various thresholds of snake density. However, based on measurements of 20–49 snakes/ha (with 95% confidence intervals ranging from 7 to 73 snakes/ha) at several sites from 1985–1992, it is likely that densities of 50–100 snakes/ha occurred during the peak of the initial irruption (Rodda et al. 1992, 1999c). A sharp reduction in the body-condition indices of snakes from northern Guam since 1985 supports the belief that current densities are smaller than the peak abundances of the 1970s and early 1980s (G. Rodda, personal communication). These densities are up to an order of magnitude higher than those known for any other snake away from dens or water (Rodda et al. 1997). Furthermore, they exceeded by four times the aggregate maximum densities of Guam's birds in their most preferred habitats and represent a population with the capacity to consume about 18–30 times the biomass of the adult birds at any site under optimal conditions (Rodda et al. 1997, 1999c).

Methods

Species Affected and Extent of Declines

We investigated the decline rates of bird species during the irruption of the brown tree snake by examining the results of roadside surveys conducted from the mid-1970s until 1998. The surveys were made by conservation officers from the Division of Aquatic and Wildlife

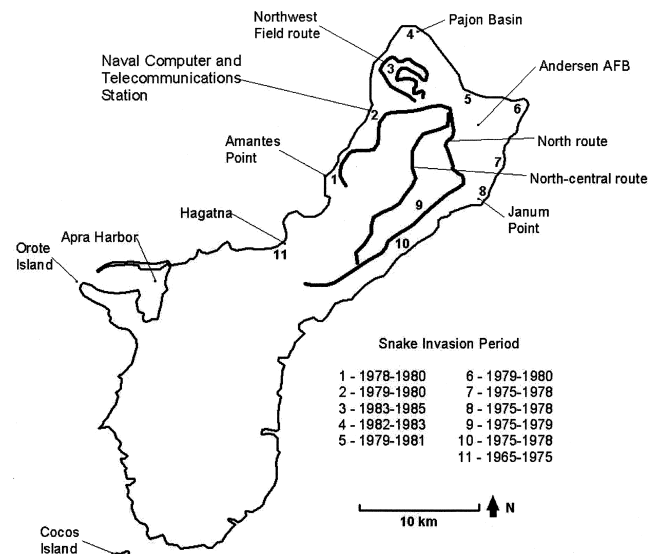


Figure 1. Map of Guam, with locations of survey routes and other sites mentioned in the text. Snake invasion period indicates the earliest and latest possible dates that high densities of brown tree snakes became established at specific locations in northern Guam, based on the loss of native forest bird species from those areas as shown by Jenkins (1983) and Savidge (1987).

Resources along three routes in northern Guam (Fig. 1). The Northwest Field route (19 km long) and the north route (40 km long) were established in 1974, and the north-central route (22.5 km) was established in 1976. The routes were driven twice per month at 20–30 km/hour, beginning at sunrise. Numbers and species of all birds seen by two observers (including the driver) were recorded. Approximately 25 different observers participated in the program. Survey routes followed roads and jeep trails through a variety of habitats, including mature and secondary stands of native limestone forest, groves of the small exotic tree *Leucaena leucocephala*, scrubby thickets of disturbed vegetation, grassy and weedy fields, and one urbanized area. See Fosberg (1960) and Engbring and Ramsey (1984) for descriptions of these plant communities. Surveyed areas were considered representative of the general habitat of northern Guam. Survey routes did not include savannas, which are extensive only in the south.

We estimated trends in the numbers of birds detected over time using linear regression during periods in which the trends approximately fit a linear model as determined by visual inspection. We viewed the three routes as comprising a single population and made statistical inferences only to this area. We did not view routes as primary sampling units because they were not selected randomly, and with only three routes the power to extrapolate findings to other areas would have been too low to be useful.

For 10 species not recorded in sufficient numbers on roadside surveys, information on population trends and status was deduced primarily from unpublished sources and the field observations of G.J.W., R.E.B., and C.F.A., each of whom worked extensively on the island from the late 1970s or early 1980s until 2000.

Speed and Timing of Declines

We investigated the speed and timing of declines by examining the roadside survey data and the results from a separate point-count survey conducted during 1981–1987 at Pajon Basin (Fig. 1). The Pajon study area was a narrow, 100-ha bench of mature limestone forest located at the base of a 130-m-tall cliff near the northern tip of the island. It was bordered by adjoining tracts of forest on three sides and ocean on one side. Surveys there were conducted once annually between January and June, except in 1983, when monthly counts were made from May to October and in December. Birds were surveyed by variable circular-plot counts (Reynolds et al. 1980). Observers worked in pairs, with each recording all birds seen or heard at 10 stations spaced 150 m apart along a transect. Counts lasted 8 minutes and were conducted from sunrise to 1000 hours. Results were expressed as the number of individuals recorded per survey. We defined the period of decline as the number of years between (i.e., starting with) the year in which a decline was first evident and the first year in which the count was $\leq 10\%$ of the pre-decline value. Separate calculations were made for (1) all roadside surveys, which indicated duration of the declines for most of northern Guam, (2) each roadside survey, the mean from which indicated duration of declines at an intermediate scale, and (3) Pajon Basin, which indicated the duration of declines at a small scale.

Traits Related to Population Trends

For each species, we recorded body mass, clutch size, origin (native or introduced), and nesting habitat (caves, cliffs, forests, grasslands, shrubby and open habitats, urban and suburban habitats, various forest and open habitats, and wetlands) (Baker 1951; Jenkins 1979, 1983; Conry 1987; N. Drahos, unpublished data). Additionally, species were assigned a population trend score indicating how seriously they were affected by brown tree snakes, as follows: 1, extirpated; 2, nearly or temporarily extirpated; 3, declined by $\geq 90\%$ and not recovering; and 4, little if any decline or partially recovering. To investigate the relationship between habitat and population trend score, we also assigned a habitat score to each species, as follows: 1, urban; 2, other; and 3, forest.

We calculated correlation coefficients between the population trend score and the continuous independent vari-

ables (body mass, clutch size) and the mean population trend score for categorical variables (e.g., forest species). Variables with significant relationships to the population trend score were used in a multiple-regression analysis, with the population trend score as the dependent variable, to investigate the relative importance of different correlates in predicting the impact of brown tree snakes.

Results

Species Affected and Extent of Declines

Guam's main island historically supported about 23 native resident bird species (Baker 1951; Jenkins 1983). By 1968, five of these species had been extirpated for reasons unrelated to snakes, while an additional seven non-native species had become established. The resident avifauna of Guam thus included 25 species, 18 natives and seven exotics, that were potentially vulnerable to brown tree snakes (Table 1).

Roadside surveys provided trend information for 15 of these species in northern Guam (Fig. 2). All except Eurasian Tree Sparrows and Brown Noddies showed pronounced declines along survey routes. Ten species were lost entirely from count areas, while four of the five surviving species declined by $\geq 90\%$. For the routes combined, all trends were significant ($p < 0.05$), except those for Tree Sparrows and noddies. Eleven of the trends were significant at $\alpha = 0.01$ and seven at $\alpha = 0.001$. Trends were consistent among the three individual routes, with all species except Tree Sparrows having negative trends on all routes. Thirty-six of the 42 declining trends were significant at $\alpha = 0.05$, 35 were significant at $\alpha = 0.01$, and 23 were significant at $\alpha = 0.001$. Only two species showed any population growth during the surveys, with Yellow Bitterns and Eurasian Tree Sparrows both increasing in abundance during the mid- to late 1990s (Fig. 2).

Ten species were not recorded on roadside surveys or were detected in numbers too small to permit analysis. Guam Flycatchers and Bridled White-eyes were already uncommon in the survey area by the mid-1970s, when counts began, and were extirpated from northern Guam at the same time as most other native forest birds (Table 1). Occasional sightings of Blue-breasted Quail, an introduced species inhabiting grasslands, on survey routes during 5 of the first 7 years suggest that it also subsequently declined in the north during the late 1970s or early 1980s. Quail abundance appears unchanged in southern Guam since 1980, but no survey data are available with which to evaluate this impression.

Three species with small, localized populations were lost at dates that approximately corresponded with the times that brown tree snake densities increased in their areas. Several factors were probably involved in the historic demise of Nightingale Reed-Warblers, but their fi-

Table 1. Impacts of brown tree snakes on resident birds of mainland Guam.^a

Population status	n	Species	Body mass (g)	Clutch size	Native/introduced ^b	Nesting habitats ^c
Extirpated ^d	12	White-tailed Tropicbird, <i>Phaethon lepturus</i>	294	1.0	N	Cl
		Brown Booby, ^e <i>Sula leucogaster</i>	1100	2.0	N	Cl
		Guam Rail, <i>Gallirallus owstoni</i>	244	3.5	N	V
		White-throated Ground-Dove, <i>Gallicolumba xanthonura</i>	124	2.0	N	F
		Mariana Fruit-Dove, <i>Ptilinopus roseicapilla</i>	91	1.0	N	F
		Micronesian Kingfisher, <i>Todiramphus cinnamominus</i>	63	2.0	N	F
		Guam Flycatcher, <i>Myiagra freycineti</i>	12	1.5	N	F
		Rufous Fantail, <i>Rhipidura rufifrons</i>	9	2.0	N	F
		Nightingale Reed-Warbler, ^e <i>Acrocephalus luscini</i>	30	2.0	N	W,S
		Micronesian Honeyeater, <i>Myzomela rubratra</i>	14	2.0	N	V
		Bridled White-eye, <i>Zosterops conspicillatus</i>	10	2.5	N	F
		Chestnut Munia, <i>Lonchura atricapilla</i>	13	5.5	I	S
		Brown Noddy, ^f <i>Anous stolidus</i>	193	1.0	N	V
Nearly or temporarily extirpated	3	White Tern, ^f <i>Gygis alba</i>	109	1.0	N	F,U
		Mariana Crow, <i>Corvus kubaryi</i>	249	2.0	N	F
		Island Collared-Dove, <i>Streptopelia bitorquata</i>	149	2.0	I	S,U,F
Decline of ≥90% and not recovering	4	Mariana Swiftlet, ^g <i>Aerodramus bartschi</i>	7	1.0	N	Ca
		Black Drongo, <i>Dicrurus macrocercus</i>	50	4.0	I	V,U
		Micronesian Starling, <i>Aplonis opaca</i>	87	2.5	N	F,U
		Yellow Bittern, <i>Ixobrychus sinensis</i>	94	3.5	N	S,U,W
Little if any decline or partially recovering	6	Black Francolin, <i>Francolinus francolinus</i>	453	10.0	I	G,S
		Blue-breasted Quail, <i>Coturnix chinensis</i>	35	6.0	I	G
		Common Moorhen, ^g <i>Gallinula chloropus</i>	315	6.0	N	W
		Rock Dove, <i>Columba livia</i>	270	2.0	I	U
		Eurasian Tree Sparrow, <i>Passer montanus</i>	22	5.0	I	U,S

^a Four other species were extirpated for causes unrelated to brown tree snakes: Wedge-tailed Shearwater (*Puffinus pacificus*), Mariana Mallard (*Anas platyrhynchos oustaleti*), Micronesian Megapode (*Megapodius laperouse*), and White-browed Crake (*Poliolimnas cinereus*). The Pacific Reef-Egret (*Egretta sacra*) may have nested on Guam, but records are lacking.

^b Abbreviations: N, native; I, introduced.

^c Nesting habitats listed by frequency of use at present: Cl, cliff; V, variety of forest and open habitats; F, forest; W, wetlands; S, shrubby and open habitats; U, urban and suburban; Ca, cave; and G, grassland.

^d Extirpation dates are based on last confirmed records in the wild, as follows: White-tailed Tropicbird, 1982; Brown Booby, 1979; Guam Rail, 1987; White-throated Ground-Dove, 1986; Mariana Fruit-Dove, 1985; Micronesian Kingfisher, 1988; Guam Flycatcher, 1984; Rufous Fantail, 1984; Nightingale Reed-Warbler, 1969; Micronesian Honeyeater, 1986; Bridled White-eye, 1984; and Chestnut Munia, 1994.

^e Original population decline occurred prior to arrival of brown tree snakes, but snakes were likely responsible for the final extirpation, and for the Brown Booby they appear to be preventing reestablishment.

^f Brown Noddies and White Terns became extirpated on Guam's main island in 1982 and about 1985, respectively. Both resumed nesting there during the early to mid-1990s.

^g Original population decline probably caused by factors other than brown tree snakes.

nal disappearance from a marsh in Hagatna in 1969 is most likely attributable to snakes (Reichel et al. 1992). Guam's only colony of White-tailed Tropicbirds, located in the sea cliffs at Amantes Point, held an estimated 20 birds in 1980 (A. Maben, unpublished data) but was deserted by about 1982, soon after the area lost its forest birds (Fig. 1). Similarly, a colony of about 40 Brown Boobies nested at Janum Point in 1975, but was nearly absent in 1976 and gone entirely in 1977 (N. Drahos, unpublished data). This coincided well with the decline of forest birds in the area, but other causes such as human disturbance cannot be ruled out. Another small nesting colony of 20–30 boobies disappeared suddenly from Orote Island in about 1979, whereas nesting by Brown Noddies apparently ceased there sometime during the 1980s. Snakes are present on Orote Island (Perry et al. 1998a), but their date of establishment is unknown. Al-

though both seabird species continue to roost on Orote Island (boobies in very small numbers), neither has resumed breeding there during the past two decades. Thus, even if snakes were not responsible for the initial losses at this site, it seems likely they are preventing a resumption of breeding in both species.

Mariana Swiftlets were common until the late 1960s and early 1970s, when an island-wide decline occurred. The decline's causes are unknown, but its pattern of occurring almost simultaneously throughout Guam and on the adjacent island of Rota was unlike that of any other bird. Thus, we speculate that former pesticide use is a more likely factor in the original decline of this species than snake predation, although some predation may have in fact occurred at colonies in southern Guam. From 1980 to 2000, only three roosts totaling 250–900 swiftlets remained on the island. Recent studies indicate

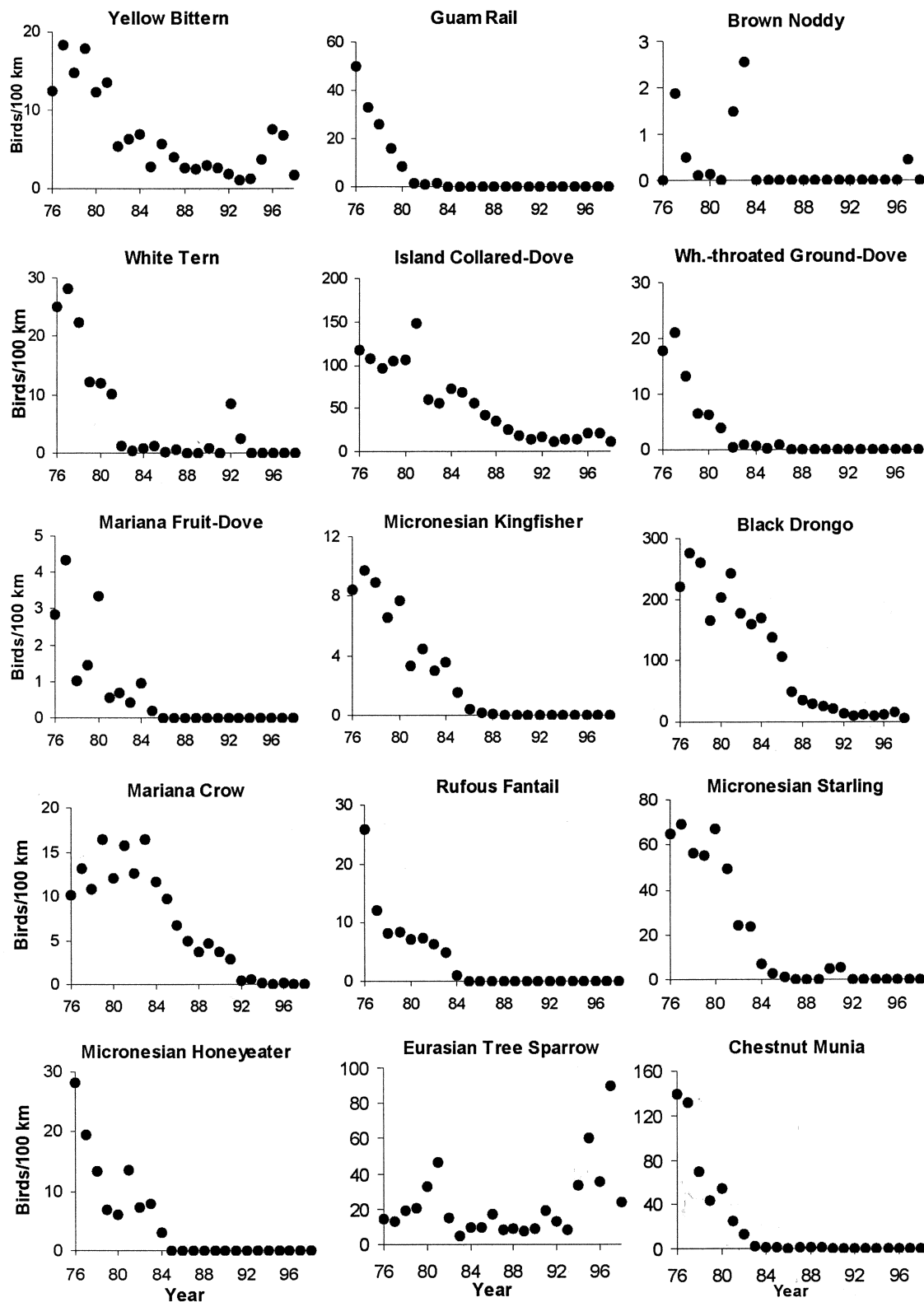


Figure 2. Population trends for Guam birds as indicated by roadside surveys, 1976–1998.

that snake predation is a regular event at the largest colony (G.J.W. and J. Morton, unpublished data) and is likely preventing any recovery by the species. Only those birds nesting and roosting on high, smooth walls and ceilings are able to avoid snakes.

Three species may not have been seriously affected by brown tree snakes. Black Francolin, another introduced bird of open landscapes, and Common Moorhens, a native wetland inhabitant, appear to be relatively stable on much of the island, although quantitative documentation is lacking. Francolin are fairly common, whereas moorhens are restricted by habitat (Stinson et al. 1991). Francolin successfully colonized parts of northern Guam during the 1990s and currently appear to be expanding in abundance there. Rock Doves are uncommon on the island, occurring in urban and suburban areas. Numbers fluctuate with the intensity of control efforts, but population size is probably <1000 birds. No indication exists that brown tree snakes are greatly depressing the populations of these species.

Little information exists on the effects of snakes on Guam's migrant birds. We detected a significant ($p < 0.001$) overall decline in roadside surveys in Pacific Golden-Plovers (*Pluvialis fulva*), the only migrant for which data are available. Abundance was highest along the north-central roadside route, where numbers declined significantly ($p < 0.01$), but a nonsignificant decline on the northern route and a significant increase on the Northwest Field route also occurred.

Speed and Timing of Declines

Population declines proceeded rapidly once started (Fig. 2). For all roadside surveys combined, the numbers of 13 species fell by $\geq 90\%$ during a mean period of 8.9 years (Table 2). Several species may have started declining before the surveys began, so the actual period of decrease may be longer than 8.9 years. Declines progressed more quickly at the scale of a single roadside route, with a mean duration of 6.9 years. They were fastest at the local scale, as indicated by the results from Pajon Basin, where species declines of $\geq 90\%$ averaged just 1.6 years.

Declines were fairly synchronous, although some variation among species was evident. Most birds showed substantial decreases in the number of detections from 1976 or 1977 until the mid-1980s (Fig. 2). Nine of the 10 species that eventually disappeared from the survey routes were seldom if ever recorded beyond 1986, with Mariana Crows being the last species lost in 1997. Declines occurred somewhat later among species that persisted on routes. Yellow Bitterns, Island Collared-Doves, and Black Drongos were all still fairly common in 1986 and did not reach their lowest numbers until the early 1990s.

The detailed results from Pajon Basin (Table 3) provide additional information about the speed and timing

Table 2. Duration (years) of bird declines^a at three spatial scales on Guam.

Species	Spatial scale		
	northern Guam ^b	single route ^c	Pajon Basin
Yellow Bittern	17	8.7	—
Guam Rail	5	6.7	—
White Tern	6	5.0	—
Island Collared-Dove	12	14.3	1
White-throated Ground-Dove	6	5.7	1
Mariana Fruit-Dove	9	4.3	2
Micronesian Kingfisher	10	5.7	2
Black Drongo	15	10.3	—
Mariana Crow	8	8.5	2
Guam Flycatcher	—	—	1
Rufous Fantail	8	4.3	3
Micronesian Starling	5	5.7	2
Micronesian Honeyeater	9	5.3	1
Bridled White-eye	—	—	1
Chestnut Munia	7	6.0	—
Mean	8.9	6.9	1.6

^a Number of years from first evidence of a decline until first year in which number recorded was <10% of the predecline mean.

^b Decline for the three roadside routes analyzed as one "super route."

^c Average of the route-specific declines.

of declines at the local scale. The basin was the last area on Guam to support the full ensemble of native forest birds at historic densities. Count results were high and relatively consistent for the nine species of forest birds present in 1981 and 1982. Declines were first detected in May 1983, when Mariana Fruit-Doves and Bridled White-eyes fell sharply in abundance, and were well underway by May 1984, when four species had been extirpated and two others were in rapid decline. Three native species remained in January 1985, with only Mariana Crows continuing to occur in numbers resembling pre-snake densities. Island Collared-Doves were present in the area from June 1983 to January 1985 following the decline of Mariana Fruit-Doves but were absent in 1986 and 1987. No birds of any species were recorded on the transect, in 1986 and only three crows were detected in 1987.

Surveys at Pajon Basin during 1983, the only year with multiple counts, indicated that some declines occurred within just a few months. Fantails decreased 72% (from 21.5 to 6 birds) in 1 month and 91% (from 21.5 to 2) in 2 months. Guam Flycatchers decreased 88% (from 8 to 1) in 2 months. Micronesian Honeyeaters decreased 73% (from 15 to 4) in 2 months.

In summary, declines were rapid and fairly synchronous, even at larger spatial scales. Extirpated species began decreasing a few years before some species that persisted. At a local scale, differences in speed and timing among species were evident and declines occurred much more quickly, with some abundant populations disappearing in only a few months.

Table 3. Results of bird surveys at Pajon Basin in northern Guam, 1981–1987.*

Species	1981	1982	1983	1984	1985	1986	1987
Island Collared-Dove	0.0	0.0	1.5	9.5	0.5	0.0	0.0
White-throated Ground-Dove	0.5	1.5	2.3	2.5	0.0	0.0	0.0
Mariana Fruit-Dove	5.5	9.5	1.5	0.0	0.0	0.0	0.0
Micronesian Kingfisher	14.5	8.5	17.5	13.0	2.0	0.0	0.0
Mariana Crow	14.0	16.5	23.3	18.0	25.5	0.0	3.0
Guam Flycatcher	3.0	11.5	5.5	0.0	0.0	0.0	0.0
Rufous Fantail	36.5	27.5	21.8	0.0	0.0	0.0	0.0
Micronesian Starling	76.0	79.5	67.3	35.5	3.5	0.0	0.0
Micronesian Honeyeater	15.5	16.5	16.3	1.0	0.0	0.0	0.0
Bridled White-eye	54.0	49.0	0.8	0.0	0.0	0.0	0.0

*Values are the average number of individuals detected per survey. One survey was made per year except in 1983, when seven surveys were made.

Traits Related to Population Trends

The correlation between body size and population trend score for all species was $r = 0.003$, indicating that no simple, strong relationship existed. Among forest species, however, the correlation was $r = 0.54$, indicating that larger species persisted longer. Among smaller species, the correlation between body size and population trend score was also positive. For example, $r = 0.49$ for the nine species weighing ≤ 50 g. The Mariana Swiftlet was an influential point because it was the lightest species but had a trend score of 3. When this point was excluded, $r = 0.64$.

The correlation between clutch size and population trend score for all species was $r = 0.54$, indicating that species with larger clutches were less affected by brown tree snakes than those with small clutches. The high correlation was caused by group 4 (little if any decline or partially recovering), which had a mean clutch size of 5.4 and four of the five species with clutch sizes of ≥ 5 . Mean clutch sizes for species with other population trend scores were 2.3, 1.3, and 2.4 for groups 1, 2, and 3, respectively, indicating no relationship across this range of scores.

Population trend scores averaged 1.6 for forest species versus 2.6 for nonforest species, and 1.7 for native species versus 3.3 for introduced species. Chestnut Munias were the only introduced species with a population trend score of < 3 . The average score was 3.3 for urban species and 1.7 for other species. Four of the seven urban species were introduced, so it is difficult from statistical analysis alone to separate the effects of occurring in urban areas from those of being introduced. However, brown tree snakes are believed to be less common in some urban locations, so habitat is probably of more direct importance than origin of the species. Origin may be important because it predisposes species to move into urban or other disturbed areas.

Habitat was the variable most strongly related to population trend score. Forest species had the lowest scores and urban species the highest scores. The order of pre-

cedence for species occurring in more than one habitat was urban, forest, and other. We used multiple regression to evaluate habitat score, body size, and clutch size as predictors of population trend score. The habitat score entered first and produced an adjusted r^2 of 0.40. Clutch size entered second and increased the adjusted r^2 to 0.59. Clutch size alone was significant, but the r^2 was only 0.26. Including body size after entering either habitat, or habitat and clutch size, reduced the adjusted r^2 , and the coefficient for body size was not significant ($p > 0.40$).

In summary, among the variables we investigated, habitat was most strongly related to the impact of brown tree snakes. Forest species were most affected and urban species least affected. Once habitat was taken into account, clutch size had a significant effect, with species having larger clutch sizes declining less than species with small clutches. Body size was related to the impact of snakes on smaller species, but not for the entire suite of species. Among small species, the smaller ones were more vulnerable to brown tree snakes.

Discussion

Species Affected and Extent of Declines

Although past studies focused on the impact of brown tree snakes on Guam's native forest birds (Jenkins 1983; Engbring & Ramsey 1984; Savidge 1987) and Island Collared-Doves (Conry 1987, 1988), our results indicate that 22 of the 25 species extant when tree snakes became distributed island-wide in 1968 were in fact severely affected. Twelve species were likely extirpated as breeding residents, eight experienced declines of $\geq 90\%$ throughout the island or at least in the north, and two (Mariana Swiftlet and Eurasian Tree Sparrow) were kept at reduced population levels during all or much of the study. These include 17 of Guam's 18 native species. No systematic surveys are available for Black Francolin, Common Moorhens, or Rock Doves, so we do not know the effects of snakes on their populations. However, all

three are believed to be stable or increasing at present. Yellow Bitterns and Tree Sparrows are also currently increasing in abundance, at least in part because of their adaptability to urbanized environments.

Although 13 species continue to reside on the main island of Guam, several are still at risk of extirpation, including the Mariana Crow, Micronesian Starling, Mariana Swiftlet, Brown Noddy, and White Tern. The most seriously threatened are the crow, which is being maintained only by a capture and release program because all individuals in the original population are past reproductive age (National Research Council 1997; C.F.A., unpublished data); the noddy, which has only a few pairs nesting on Andersen Air Force Base; and the starling, which remains at only two sites on the main island, with an estimated 50–100 birds present (Wiles et al. 1995). It appears that six of the island's seven introduced species will probably persist. Thus, in terms of species richness, brown tree snakes may yet convert Guam's avifauna from a largely native community to a largely introduced one.

In addition to reducing the population sizes and distributions of most of Guam's resident birds, brown tree snakes have also been a major selective influence on the habitat associations of surviving species. Yellow Bitterns appear to have altered their predominant breeding habitat in response to snake predation, changing from wetlands in the late 1970s (Jenkins 1983) to urban areas and islets by the mid-1990s. Brown Noddies, White Terns, Island Collared-Doves, Black Drongos, and Micronesian Starlings formerly occurred in a wider variety of habitats (Jenkins 1983; Conry 1987) but, on mainland Guam, are now concentrated in urban and suburban environments. Noddies and terns also occur on islets that tree snakes have not reached. Mariana Swiftlets are under substantial selective pressure to nest high on smooth cave walls and ceilings, which provide the only locations safe from snakes.

The impact of brown tree snakes on Guam's migratory birds, primarily shorebirds and waterbirds (Stinson et al. 1997a, 1997b), is unclear. Most visiting shorebirds frequent beaches or mowed fields, which snakes probably avoid. Migrants have not been found in the gut contents of snakes, nor have predation attempts by snakes on migrants been witnessed (Savidge 1988; G. Rodda, personal communication; G.J.W. and C.F.A., personal observation). However, direct observations of snake predation on any of Guam's birds have been few. Changes in the availability of open habitat, rather than snake presence, may be the most plausible explanation for the decline in detections of Pacific Golden-Plovers along roadside survey routes. Thus, at present we have little knowledge of how, if at all, migrants have been harmed by snakes.

Speed and Timing of Decline

Brown tree snakes devastated Guam's avifauna during a period of 35–40 years. Initial patterns of bird declines in

southern Guam are poorly understood, but extirpations of all resident forest species except the Micronesian Starling (a few birds continued to immigrate to Guam from Cocos Island until about 1992) and still extant Mariana Swiftlet were apparently completed in the south within 27–32 years of the snake's introduction. Localized disappearances there were initially detected in 1963 (N. Drahos, unpublished data), but they were perhaps overlooked for several years and were largely completed by about 1973–1975. The last breeding populations to be lost were seven species that persisted in very small numbers along the southeastern coast until about 1977 or 1978 (Jenkins 1979, 1983; N. Drahos, personal communication). In northern Guam, which is similar in size to southern Guam (south = 304 km², north = 237 km²), 10 species with substantial populations were extirpated during an average of 11.2 years. The difference in time span between the two regions primarily reflects the additional period required in the south for snake abundance to reach levels causing localized bird extinctions.

Declines at Pajon Basin, where nine forest species vanished in an average period of just 2.1 years, illustrate how rapidly losses can occur. Declines there, however, likely occurred faster than in similar areas invaded earlier by snakes because bird populations in the basin were probably not supplemented by immigrants from neighboring areas, most of which were already depleted of birds. Although forest birds entering any snake-rich locality probably survived only briefly, the dispersal of a few such individuals may have prolonged some species' presence in those areas by up to several years.

Traits Related to Population Trends

Our results suggest that the most important trait predisposing a species for coexistence with brown tree snakes is its ability to nest and roost in locations that snakes seldom reach. High fecundity and prior exposure of a species to predators are apparently also helpful, thus supporting the contention of Rodda et al. (1997, 1999b) that a lack of coevolution with predators was an important contributing factor in the declines of many native birds. Body size may be important for smaller species, with the smallest ones disappearing more rapidly, presumably because brown tree snakes take the adults, eggs, and nestlings of these species (Savidge 1987). However, the virtual disappearance of Mariana Crows and the losses of White-tailed Tropicbirds and Brown Boobies indicate that large body size may only delay extirpation, not prevent it.

Our results highlight the importance of urban and other disturbed areas as refugia for birds from brown tree snakes. At urban locations, birds are able to nest and roost in or on buildings, electrical power poles, ornamental trees and shrubs, and vegetation on vacant lots. Similar types of sites are also present in large lawns

and mowed fields measuring 0.5 to >300 ha in size, which occur at military bases, golf courses, community parks, school yards, and airfields. Isolation from larger vegetated plots, in which snakes invariably occur, appears to be a requirement for successful nesting sites and safe roosts, with paved roads, buildings, parking lots, lawns, and larger expanses of short grass being the likely habitat features that discourage snake intrusion.

Nevertheless, many of the island's urban and other disturbed environments currently support relatively low bird densities and thus should not be considered high-quality habitat for most species. Some urban nesting and roosting sites are used only briefly, with bird occupancy declining or ending within a few years. Snake predation may be responsible, but other problems—such as human disturbance and human-related mortality (e.g., collisions with vehicles); predation by dogs (*Canis familiaris*), cats (*Felis catus*), and rats (*Rattus* spp.); and stochastic factors associated with small populations—may also contribute to site abandonment or loss of isolated subpopulations. For example, small remnant populations of five to eight Micronesian Starlings disappeared from downtown Hagatna and the Naval Computer and Telecommunications Station in the late 1980s and early 1990s, respectively, for uncertain reasons. The navy base was eventually recolonized by one or two pairs of birds in about 1998. Thus, while several species now persist largely or exclusively in developed areas, the long-term viability of these populations is not assured.

The extirpation of the Chestnut Munia is somewhat anomalous, given that it was introduced, produced relatively large clutches, and last occurred in southern Guam. However, its flocking behavior and group-nesting habits probably made it more vulnerable to snake predation than nonaggregating species.

Conservation Implications

Guam is the largest island in Micronesia and is substantially larger than the neighboring Mariana Islands of Rota (85 km²), Tinian (102 km²), and Saipan (123 km²), all three of which are at high risk of being invaded by brown tree snakes (Fritts et al. 1999). Because extirpations are likely to occur more rapidly in smaller areas, bird species can be expected to disappear sooner on these and other smaller islands. Rapid declines leave little time for conservation efforts. On Guam, plans for captive propagation of Guam Flycatchers, Rufous Fantails, and Bridled White-eyes failed because these species disappeared sooner than expected.

Successful control of brown tree snakes is Guam's highest conservation priority. Although eradication of snakes from the entire island appears unlikely at this time, snakes may eventually be eliminated over limited areas through various control measures (Engeman & Lin-

nell 1998; Perry et al. 1998b; Rodda et al. 1998; Engeman et al. 2000; Savarie et al. 2001). This will reduce the risk of snake dispersal from Guam and will allow the restoration of extirpated species in treated areas (e.g., Vice & Pitzler 1999).

Guam's offshore waters provide birds with a variety of small refugia for roosting and nesting, including Cocos Island, about 25 smaller islets ranging in size from 0.05 to 3.4 ha, smaller nearshore rocks, and shipping buoys in Apra Harbor. These sites, nearly all of which are snake-free (Perry et al. 1998a), retain Guam's largest breeding aggregations of Brown Noddies, White Terns, and Pacific Reef-Egrets, at least four nesting colonies of Yellow Bitterns, a seasonal roost of up to 3500 Black Noddies (*Anous minutus*) (Wiles et al. 1993), and a sizable Micronesian Starling population on Cocos Island. Preventing brown tree snakes from reaching these sites, especially Cocos Island, should be a high priority. To enhance Guam's urban bird populations, we recommend judicious increased plantings of ornamental trees and shrubs and continuation of a nest box program for starlings on Andersen Air Force Base.

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