Pacific Science (1992), vol. 46, no. 1: 46–57

Origin and Population Growth of the Brown Tree Snake, *Boiga irregularis*, on Guam[1]

GORDON H. RODDA,[2] THOMAS H. FRITTS,[3] AND PAUL J. CONRY[4]

ABSTRACT: After the accidental introduction of the Brown Tree Snake, *Boiga irregularis*, to the island of Guam after World War II, the snake became exceedingly numerous, and most of Guam's native vertebrates either became endangered or disappeared from the island. In this paper we summarize what is known about populations of this snake on Guam and the likely origin of the Guam population. Scale counts and transportation records suggest that the Guam population originated in the Admiralty Islands, about 1500 km south of Guam. It was probably transported to Guam in ships that transported salvaged war materiel after World War II. For ca. 35 yr after its introduction, the presence of the snake on Guam was documented only by popular accounts, occasional photographs, and a few museum specimens, indicating that the snake's distribution was fairly limited initially, but ultimately a period of sharp population growth and wide dispersal occurred, with the snake reaching all parts of the island by the late 1960s. Peak population levels were attained about a decade or more after each area was colonized. Mark-recapture and removal data indicate that the capture of 50 snakes per ha at one site in northern Guam during 1985 probably represented a population density of around 100 snakes per ha, but by 1988 this population had declined to around 30% of the 1985 density. However, this reduction may not be permanent. In central Guam, where the snake irrupted decades ago, the snake's numbers have continued to fluctuate, and in some cases it has attained densities in excess of 50 per hectare.

THE INTRODUCTION OF A SPECIES provides an opportunity to evaluate ecological relationships within a community by monitoring the trajectories of the component populations as a new equilibrium is established. This process is most observable in communities with few species and major perturbations, conditions that facilitate interpretation of causation. The accidental introduction of the Brown Tree Snake, *Boiga irregularis*, on Guam is believed responsible for the nearly complete extirpation of native bird species (Savidge 1987, Engbring and Fritts 1988), for hundreds of power outages (Fritts et al. 1987), for loss of domestic and pet animals (Fritts and McCoid in press), for envenomation of human babies (Fritts et al. 1990), and for the probable extirpation of native bat and lizard populations (Wiles 1987, Fritts 1988). Thus, Guam's vertebrate population ecology is of great interest not only to researchers and island biologists but also to managers responsible for the control and containment of the snake.

Only recently has any attempt been made to document the numbers of the snake. Population size measurements were not undertaken before 1985, but some information exists on the date of initial colonization and the chronology of the spread of the snake across the

[1] Funding for this research was provided by the U.S. Department of the Interior, Technical Assistance Program, the U.S. Navy, and the U.S. Air Force. Manuscript accepted 5 April 1991.

[2] Arizona Cooperative Fish and Wildlife Research Unit, Biological Sciences East Room 210, University of Arizona, Tucson, Arizona 85721.

[3] U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.

[4] Guam Division of Aquatic and Wildlife Resources, P.O. Box 2950, Agana, Guam 96910. Present address: Hawaii Division of Forestry and Wildlife, 1151 Punchbowl Street, Honolulu, Hawaii 96813.

island (Savidge 1987). These data are useful for predicting the possible time course of *Boiga* colonizations on other islands and for evaluating the snake's ability to disperse from extralimital populations. Minimum estimates of the snake's density (Savidge 1987, Fritts et al. 1989) based on the number of snakes removed from two trap grids in 1985 had not been corrected for the number of snakes that eluded capture or those that might have been inactive during the sampling periods. Those two studies used different trap technologies at different sites, and the information is not closely comparable. Thus we did not use these trap data in our detailed analyses of historical trends in snake numbers.

A population assessment program is needed to: (1) assess the predatory threat resulting from the snake, (2) identify the factors that influence the snake's ecological success, (3) predict the snake's future population cycles, and, (4) provide baseline data for quantifying the effectiveness of management efforts to control the snake. This paper is a review of available information on the origin and growth of the snake's populations on Guam before 1985, and subsequent attempts to estimate population trends by visual censuses and mark-recapture studies.

MATERIALS AND METHODS

Study Sites

The study sites were located in central and northern Guam (Figure 1). Censuses at two of the sites involved counts of snakes on chain-link fences (Andersen Fence and Airport Fence); the other transects were in secondary limestone forest (Stone 1970) with a roadside border of the tree *Leucaena leucocephala*. Details of their locations and plant species composition are given in the following section. Transect sampling durations are given in Table 1.

Transect Descriptions

The habitat descriptions for the sites studied in 1988 are based on an average of 337 point samples of the vegetation per site. These point samples of vegetation were collected during routine snake censuses by noting the species of plant being viewed at the instant when an unpredictable timer sounded.

The Airport Road site (13° 29.64′ N, 144° 47.58′ E), along the entrance road leading to Guam International Airport (Guam Route 10A), extended for about 0.7 km southeast from the airport and along the edge of a forest consisting of about 71% *Leucaena leucocephala*. No other tree species was abundant. This isolated patch of forest in an urban area is at the bottom of the cliff on which the Airport Fence census line was located. These two lines were about 100 m apart at their nearest point.

The Northwest Forest transect made a triangle, with a perimeter length of about 2.4 km, to the southeast of 13° 38.10′ N, 144° 50.76′ E ca. 2.4 km southwest of Ritidian Point on the northern end of Guam. Much of this transect was along a narrow path through a second-growth forest, including three common trees: *Leucaena leucocephala* (28%), *Scaevola taccata* (32%), and *Casuarina equisetifolia* (18%).

The Communications Site transect was near a cliff edge at 13° 34.8′ N, 144° 49.8′ E immediately inland from Haputo Beach on the Naval Communication Area Master Station–Western Pacific. This was the most diverse site botanically, with 16 genera of common forest trees that were abundant and only 20% *Leucaena*.

The Weapons Storage transect, in the Conventional Weapons Storage Area of Andersen Air Force Base, was 2.9 km northeast of Pott's Junction at 13° 36.06′ N, 144° 53.22′ E. The transect ran along 1.5 km of roadside forest edge similar to that found at Northwest Road.

The Andersen Fence transect (13° 35.1′ N, 144° 56.52′ E) was a 1-km-long chain-link fence at the eastern end of the main flightline of Andersen Air Force Base. The fence ran along the edge of cleared areas at 4 to 30 m distance from typical limestone forest.

Airport Fence was a 2.3-m-high chain-link fence extending along the cliff line above the Airport Road site (13° 29.64′ N, 144° 47.58′ E), near the Guam International Airport. Compared to Andersen Fence, it was longer

FIGURE 1. Outline map of Guam and the locations of study areas.

TABLE 1

NUMBER OF HOURS OF CENSUSING CONDUCTED AT EACH TRANSECT

TRANSECT	1985	1986	1987	1988	1989	1990
Airport Fence	7.0		10.2	14.4	13.7	5.0
Airport Road			10.6	2.5	1.3	1.9
Andersen Fence		20.4	22.7	25.9	31.5	31.5
Northwest Forest	9.0			49.2		
Northwest Road	66.0	55.5	9.1	31.0	16.5	5.9
Orote	4.0		1.5	20.4	17.1	45.5
Weapons Storage	34.0	3.5	14.5			

(3.3 km) and usually closer to the adjacent vegetation (2–4 m).

The Orote transect was a relatively short transect (0.7 km) through an almost pure (95%) stand of *Leucaena* located on the tip of Orote Peninsula (13° 26.58′ N, 144° 37.32′ E) adjacent to Apra Harbor, where the snake first became established on Guam. Unlike the other transects, which had about 0.5% vine cover, Orote had extensive viney areas (10%).

The Northwest Road site was near the Northwest Forest site 2.5 km southwest of Ritidian Point. It was usually searched for 2.0 km to the southwest from 13° 38.10′ N, 144° 50.76′ E. Like most sites it was dominated by *Leucaena* (72%), with no other species of tree being conspicuous.

Origin of the Guam Population

Our information on the colonization of the Brown Tree Snake on Guam was based on newspaper reports, photographs, museum specimens, sight records from herpetologists visiting Guam, and postwar books and magazine articles describing the fauna of Guam. To identify the most probable source of the colonizers, we compared standard scale counts of specimens from Guam with those of specimens from various parts of the snake's native range. We also reviewed records of human activities and interviewed naval and civilian personnel who monitored or handled shipments originating in the snake's native range. We studied preserved material at the National Museum of Natural History (USNM), California Academy of Sciences (CAS), University of Kansas (KU), Los Angeles County Museum (LACM), Carnegie Museum (CM), and the American Museum of Natural History (AMNH).

Relative Abundance

To estimate the relative abundance of this nocturnal arboreal snake, we conducted timed visual searches. Population trends were inferred from changes in the annual averages of snakes seen per hour. Most visual censuses were conducted while walking slowly (mean walk rates ranged from 0.8 to 1.1 km/h) along the edge of a road at night and looking for snakes on fences or in the vegetation from a distance of 2–4 m. Most of the forests censused were "typhoon climax" assemblages of second growth (Fosberg 1960), rarely exceeding 10 m in height.

Two transects, Airport Fence and Andersen Fence, were along chain-link fences, instead of being along forested roadsides. The fences were usually observed from a slow-moving vehicle (e.g., Airport Fence mean = 4.8 km/hr). Snakes are relatively easy to spot against the regular symmetry of a chain-link fence, allowing higher censusing speeds. However, the earlier censuses of Airport Fence were usually done on foot, and car and foot censuses are not equatable on a per-hour basis. Thus, annual comparisons of sightings at fence sites were based on the mean number of snakes seen per census instead of snakes seen per hour.

Different searchers have different proficiencies in seeing snakes in the forest. This factor was statistically controlled by entering "searcher" as a separate main effect in the analysis of variance (ANOVA) that was used to compare years. Time-of-year effects were not significant in any of 12 preliminary ANOVAs conducted to identify important censusing variables; therefore, data from a wide variety of months were pooled for the annual comparisons. The data to be analyzed were log transformed to eliminate a weak correlation between means and variances, but results are reported in untransformed values. All statistical procedures except absolute population estimates (see following section) were carried out using the SAS (Statistical Analysis System) computer package (SAS Institute Inc. 1988). The SAS General Linear Model program was used to fit least squares means to each site-year combination, to estimate standard errors for these, and to test for differences between adjacent years at each site with a t test.

Absolute Population Estimates

We made three absolute population estimates for sites that were sampled concurrently

for relative abundance: Orote, 1988; Northwest Road, 1985; and Northwest Road, 1989. In addition, we reanalyzed the removal trapping data of Savidge (1986) to provide an unaccompanied absolute population estimate for Communications Site, 1985. The computer program CAPTURE (White et al. 1982) was used for maximum likelihood estimates of absolute population size at Communications Site, 1985; Orote, 1988; and Northwest Road, 1989, but the Northwest Road, 1985 data, collected for another purpose (Fritts et al. 1989), were not suitable for analysis with CAPTURE.

We used two methods to extrapolate absolute population estimates for Northwest Road, 1985. In the first, the ratio of number-captured to total-estimated-population in the comparable mark-recapture study at Orote, 1988 provided a visibility correction multiplier to extrapolate from the number of captures for Northwest Road, 1985 to a total estimated population for Northwest Road, 1985. In the second method, we estimated the relative population decline at Northwest Road, 1985–1988 from visual censuses and extrapolated back in time from the absolute population estimate of Northwest Road, 1989.

To temporarily mark snakes, we painted small numbers on their heads using paint pens. For the mark-recapture effort at Northwest Road in 1989, we also clipped the edges of two unique combinations of ventral scales. On four occasions we captured active snakes that had been painted earlier in the same evening; from these captures we concluded that paint marking did not cause the snakes to hide. We painted 12 snakes that were maintained in captivity for the duration of the 1989 marking study to evaluate the marking techniques. None of these lost either their paint markings or scale clips during the mark-recapture time interval. Both marks were visible on all marked animals recaptured.

RESULTS

Origin of the Guam Population

As denoted by its name, *B. irregularis* is an extremely variable species in scutellation and coloration. Few specimens exist from selected parts of its range, and no complete analysis of the geographic variation in the species is available. However, our preliminary comparisons suggest that the snakes on Guam are more similar to snakes from the Admiralty Islands north of New Guinea than to those from elsewhere in the range. The number of dorsal scales at three positions on the body show significant (t test, $P < .05$) differences between snakes on the Admiralty Islands and those of New Guinea (Table 2). In each

TABLE 2

VARIATION IN NUMBERS OF DORSAL SCALE ROWS COUNTED AROUND THE BODY FOR THREE SAMPLES OF BROWN TREE SNAKES

SAMPLE SITE	NO. OF SCALE ROWS	NEW GUINEA	ADMIRALTY IS.	GUAM
Neck	21	15 (37)		1 (3)
	23	26 (63)	1 (20)	9 (29)
	25		3 (60)	21 (58)
	26		1 (20)	
Midbody	19	2 (5)		
	21	37 (90)		1 (3)
	23	2 (5)	4 (80)	27 (88)
	24			1 (3)
	25		1 (20)	2 (6)
Posterior body	15	41 (100)		
	17		5 (100)	31 (100)

NOTE: Values are number of specimens exhibiting the scale counts indicated (percentages of sample in parentheses). The New Guinea sample includes small islands immediately offshore, but excludes the Bismarck Archipelago and Admiralty Islands.

of three scale counts (Table 2), the Guam sample is not statistically distinguishable from the Admiralty Island sample, but does differ significantly from the mainland New Guinea sample ($P < .05$). The number of scale rows tends to be higher in specimens from Guam and the Admiralty Islands at all three sites on the body, but the presence of 17 scale rows around the posterior body at a longitudinal position 10 scale rows anterior to the vent is the most conspicuous single character distinguishing the Guam and Admiralty Island populations from snakes elsewhere. There are obvious differences in coloration among specimens from Guam, and the Admiralty Islands, and many localities on New Guinea, where the species is quite variable in coloration. A more thorough analysis of geographic variation by one of us (THF) is under way.

Initial Colonization

The date of initial colonization cannot be determined unequivocally. No evidence exists for the presence of a snake (other than the worm snake *Ramphotyphlops braminus*) on Guam before the Japanese invasion in 1941 and the American invasion in 1944. Although record keeping was impaired during the Japanese occupation, several American soldiers made extensive collections of reptiles on Guam following the occupation and the only snakes encountered were worm snakes (collections at USNM, CAS, KU; Smith 1949, Dryden and Taylor 1969). The earliest written or photographic evidence for large snakes potentially identifiable as *B. irregularis* on Guam is a cryptic statement by Stevens (1953) that "there have been persistent rumors during recent years of some [snakes] in the vicinity of Apra Harbor. Allegedly they were brought inadvertently to the island from a ship berthed in Apra Harbor. There are no native snakes, and if any do exist they are merely strays brought in from the outside." That this statement refers to the Brown Tree Snake is confirmed by a statement published two years later (Guam, Office of the Governor 1955): "During the past four years eight snakes have been captured in the area adjoining Apra Harbor. They ranged from four to eight feet in length and were all of one specie [sic]. The specie [sic] has been identified as *Boiga irregularis*, a rear-fang snake ... believed to have entered the Territory from visiting ships."

We found no historical evidence indicating that the initial colonization near Apra Harbor spread quickly. The Guam newspapers published numerous photographs of large *B. irregularis* from the Santa Rita area near the harbor during 1958–1962. Although *B. irregularis* does not occur in the Philippines, the Guam snake was erroneously known as the Philippine Rat Snake and was assumed to have arrived on Guam from the Philippine Islands. Captions indicate that the early newspaper photos were published to disprove the popular notion that Guam had no snakes. Several articles indicated that snakes were known only from the Santa Rita/Naval Magazine area of Guam. A U.S. Navy publication in 1962 (Anonymous 1962) was unusual for this era in that it correctly identified both the snake and its mild venom: "There are a couple of species of snakes, the rear-fanged *Borja Irregularis* [sic] of the Santa Rita area being slightly poisonous." This misspelling of *Boiga* may have been due to a subliminal slip by a herpetologically naive typesetter; "Borja" is a common surname on Guam.

Evidence for the presence of snakes increased rapidly after 1960. In 1960 the first museum specimen was collected (USNM). Savidge (1987) reported that many people in the southern and central parts of the island had seen a large snake by the end of the 1960s. Based on reported sightings in 1968 and 1970, snakes soon reached the northern end of the island. Savidge (1987) compiled the evidence indicating a progressive outbreak of the snake in the northern part of the island in the 1970s and 1980s.

Northern Guam, 1985–1989

Snake population trajectories are available for four sites in northern Guam for 1985–1989 (Figure 2). Relative population estimates for the nonfence sites are least squares means for each site-year combination from an

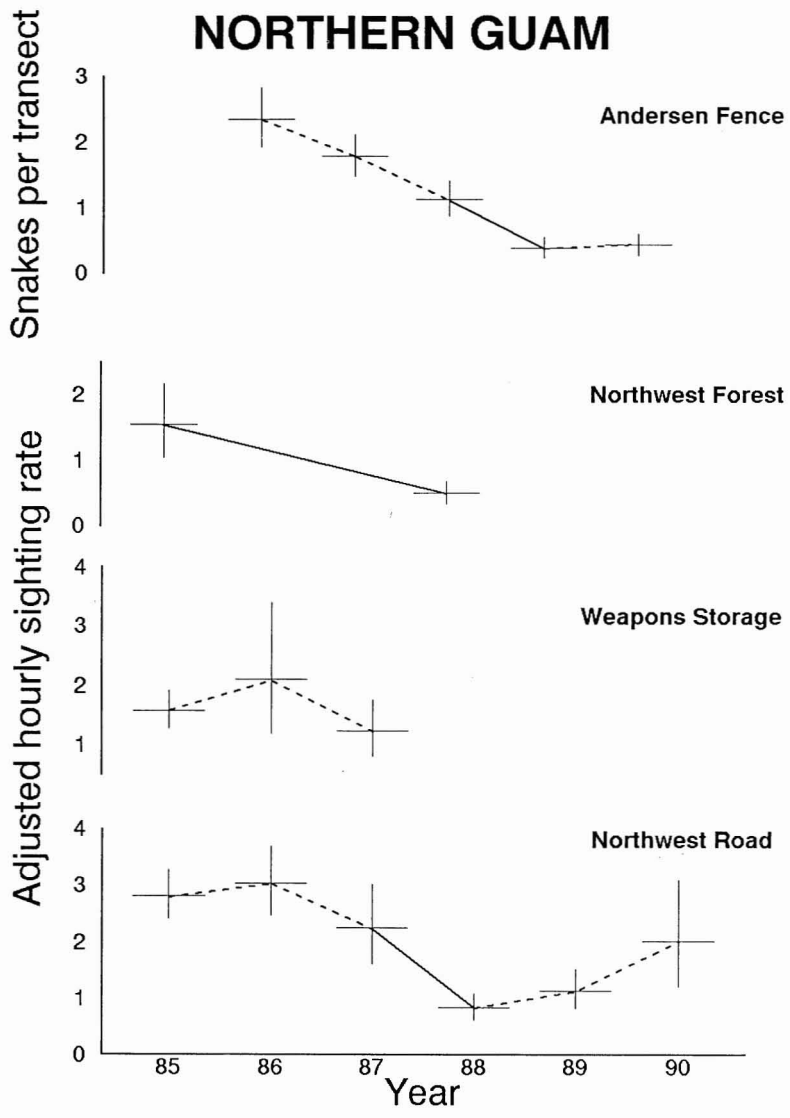

FIGURE 2. Annual mean relative population counts (± 1 SE) for sites in northern Guam. Temporally adjacent samples are connected by solid lines if the annual means differed significantly at $P = .05$ level. Nonfence sites are hourly sighting rates adjusted for differences in searcher proficiency.

ANOVA based on the effects of searcher ($F = 4.34$, df = 7,194, $P = .0002$) and the site*year interaction ($F = 3.57$, df = 19,194, $P < .0001$). No significant differences have been detected among searchers censusing fence lines ($F = 0.54$, df = 6,83, $P = .8$). Therefore the fence transects have been analyzed separately, considering only the effect of year ($F = 7.85$, df = 4,84, $P < .0001$).

The Weapons Storage site was sampled only for the period 1985–1987, and no differences in counts were detected. The three other sites registered significant reductions in snake sightings from 1985 to 1988 (Figure 2).

Three absolute population estimates are available for the northern end of Guam. Savidge's 1985 data (Savidge 1986) from Communications Site reanalyzed through

CAPTURE indicated a population density of about 20 snakes per ha (95% CI, 16.5–24.0), based on 35 removals from a 1.88-ha area. Our 1989 mark-recapture data from Northwest Road gave an estimate of 35 snakes per ha (95% CI, 7–62), based on four recaptures out of 20 animals marked in a 1.5-ha plot (CAPTURE detected no violations of the mark-recapture assumptions in this estimation; for evidence of geographic closure, see Orote results that follow). In 1985, Fritts et al. (1989) removed 50 snakes from a 1.0-ha plot at Northwest Road. Using the 0.42 ratio of captures to estimated population total from an extremely similar trapping effort at Orote in 1988 (similar traps, bait, length of effort), we tentatively extrapolated this figure to a total population size of around 119 snakes per ha for Northwest Road, 1985. Using the 3.2-fold decline from 1985 to 1988 in relative population counts at Northwest Road and the above estimate of 35 per ha at Northwest Road in 1989, we can tentatively calculate another absolute population estimate for Northwest Road, 1985 of around 112 snakes per ha.

Central Guam, 1985–1989

Relative population estimates in central Guam are available for only three sites: Airport Road, Orote, and Airport Fence (Figure 3). The site near Apra Harbor (Orote) showed a significant increase in 1988 over the pooled samples from 1985 to 1987, a significant decrease for 1988–1989, and an increase for 1989–1990. The two sites along the cliff near the commercial airport produced contrary results. Populations at Airport Fence generally increased throughout the period 1985–1989, whereas those at Airport Road declined significantly from 1987 to 1988.

An absolute population estimate calculated for Orote in October 1988 was based on a 12-day period during which we captured 39 snakes, including six animals that had been previously marked within the 12-day interval. These animals were all captured within a 2-ha plot and recaptured within the same area. Additional evidence for geographic closure comes from a total of 16 recaptures that were obtained by visually censusing the 2-ha plot and an additional 2 ha surrounding the plot over a 40-day period. None of the recaptured snakes moved from outside of the 2-ha plot to inside the plot or vice versa, nor did any move out of the 1-ha subplot in which they were initially captured. The average detected total movement distance of these snakes was 38 m. The Schumacher technique estimated a population density of 63 per ha for the 2-ha study area (95% CI, 45–108); the best available model under program CAPTURE gave a population estimate of 58 per ha (95% CI, 18–97). Program CAPTURE tests all the assumptions used in mark-recapture population estimation. For the Orote data set, all assumptions were violated. However, on a scale of 0 to 1, where 1 is the perfect estimator, the null model that CAPTURE used for the above estimate rated 0.96. Therefore, the violations were minor ones.

DISCUSSION

Establishment of the Snake on Guam

The Brown Tree Snake probably arrived on Guam as a passive stowaway in vehicles or other material transported to Guam from the Admiralty Islands in the years immediately after World War II. From 1946 to 1950 the U.S. military endeavored to salvage many shiploads of damaged war materiel that had been abandoned in Melanesia (Cdr. M. Dodge, pers. comm.). The vast naval base at Manus in the Admiralty Islands was used for staging this materiel to Guam (see Mead 1956, Lightbody and Wheeler 1985). The correspondence of scale counts between the snakes of Guam and snakes from the Admiralty Islands is therefore consistent with the most likely means of introduction. The passage quoted from Stevens (1953), indicating a stowaway arrival of a snake at Apra Harbor on Guam several years before 1953, is also consistent with this chronology. The attraction of the snake to small, dark places (Pendleton 1947) leaves little doubt that some snakes were sequestered in the large number of objects brought to Guam from the Admiralties.

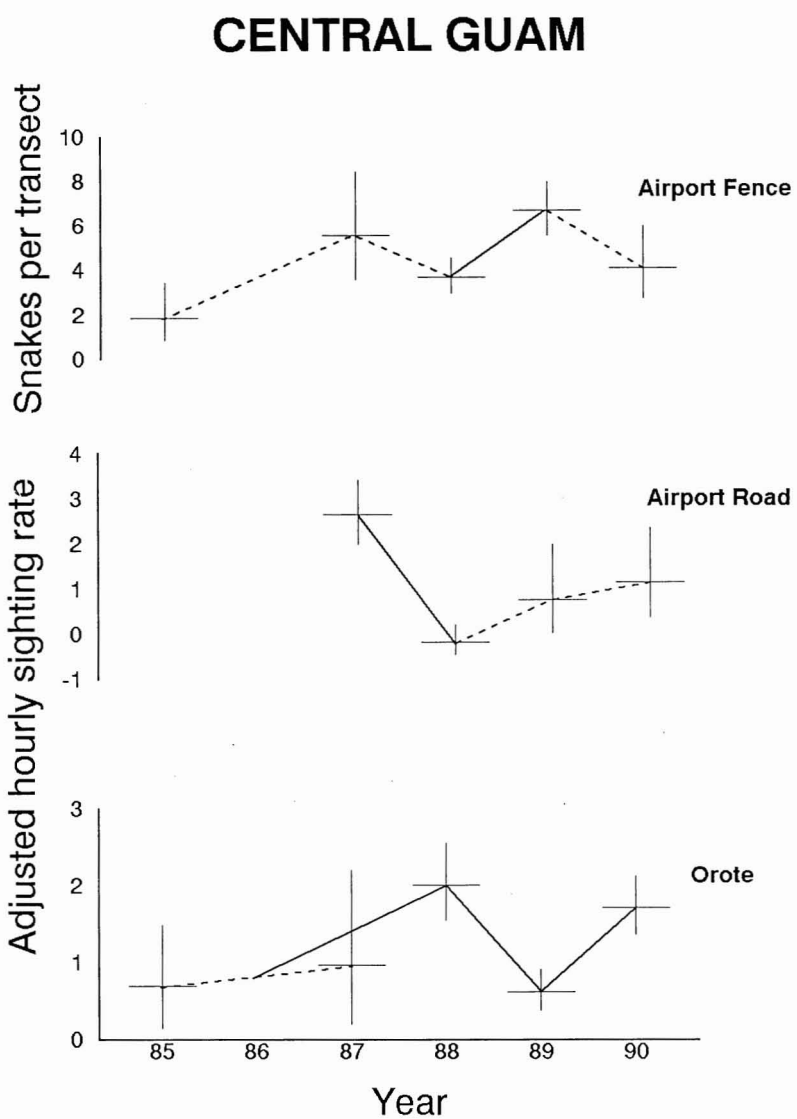

FIGURE 3. Annual mean relative population counts (±1 SE) for sites in central Guam. We pooled the 1985 and 1987 samples at Orote to assemble a sufficient sample size for comparison to 1988 samples. All other symbols as in Figure 2.

The plausibility of accidental transport of snakes in cargo is also suggested by the discovery of a snake on Wake Island in 1946. This snake, discovered in a tree, was incorrectly assumed by Downs (1949) to have been a Brown Tree Snake and presumed to have arrived in material brought from the Admiralty or Solomon islands. The snake was later identified as a North American snake (*Pituophis*) by R. Crombie and one of us (THF), but the fact that Downs called it a Brown Tree Snake and explained its presence as a stowaway in military cargo from the South Pacific suggests that the Brown Tree Snake had been accidently translocated on other occasions known to Downs.

The initial colonization of the snake on Guam received little attention, in part because of the displacement of the island's human residents from the port area after the American invasion in 1944. For two decades after the war, the entire Apra Harbor area was a Navy base off-limits to civilians at night, when the snakes are active. In contrast to the resident civilians, many soldiers had grown up and traveled extensively in places where the presence of snakes was not noteworthy. The snakes may already have been established in military areas for nearly a decade before their appearance in the civilian areas around Santa Rita stimulated newspaper photos in the late 1950s. The snake did not spread far from Apra Harbor–Santa Rita until the 1960s (e.g., Anonymous 1962).

Dispersal and Irruption of the Snake throughout Guam

The rapid spread of the snake after 1960 is unexplained. It is plausible that some people might have intentionally spread the snake to suppress rat populations, which were very high on Guam before establishment of the snake (Beardsley 1964, Savidge 1986).

The rapid spread of the snake in the 1960s probably resulted in the snake occurring islandwide by 1970. The pattern of bird extirpations suggests, however, that numbers of snakes in northern Guam did not peak until a decade or more later (Savidge 1987). The gravid snakes that have been found on Guam usually have clutches of only three or four eggs (M. J. McCoid, pers. comm.). Even if production of two or more clutches in a season is possible, this species does not have an especially high reproductive rate (see also Zwinnenberg 1978). In northern Guam, the first population increase of snakes does not seem to have peaked until the mid 1980s.

Peak densities of Brown Tree Snakes in northern Guam probably approached 100 per ha around 1985. The 50 removed from a single hectare by Fritts et al. (1989) probably included a few individuals that had strayed into the study plot during the course of the removal. However, there is no evidence for the kind of territorial pressure that promotes rapid immigration to a depleted area. Specifically, home ranges of *Boiga* overlap enormously (recapture locations from this study and radiotelemetry work by Manuel Santana, pers. comm.). *Boiga* use communal refugia (Pendleton 1947), and snakes apparently often encounter each other without animosity (unpubl. data). The extrapolations we have made from the 50 removed in 1985 (Fritts et al. 1989) are rough estimates. However, it is noteworthy that the two methods gave comparable results (112 versus 119). We cannot put confidence intervals on the value used for the ratio of captured snakes to estimated total population that was used for the extrapolation, but 0.42 seems reasonable in comparison to the 0.38 ratio that applies to the 1989 Northwest Road trapping program. Less capture effort was applied in 1989 at Northwest Road, thus it was expected that the 1989 ratio would be slightly lower.

At the time that measurements were begun in 1985, the population density of snakes in northern Guam was high, approaching 100 per ha at Northwest Road. However, the population may already have been declining when the first measurements were taken. Therefore, the estimate of maximum density must be considered a lower bound. Although the peak density of 100 snakes per ha seems reasonable in light of the relative population estimates made since that time, it is much higher than has been recorded for other large colubrids that are not clustered around water or hibernacula (Parker and Plummer 1987). Such a high density is expected to result in the local depletion of food sources, which is consistent with the observed concurrent extirpations of birds, bats, and lizards (Savidge 1987, Wiles 1987, Fritts 1988).

The differences in snake abundances among sites did not seem to reflect habitat differences as much as prey availability as influenced by the length of occupancy by snakes. The density of 20 snakes per ha at Communications Site in 1985 probably reflects a longer occupancy by the snake and therefore greater prey depletion at that site than at Northwest Road. Both sites are in northern Guam, but Communications Site is 6.5 km closer to the site of initial colonization and must have lost

its bird population earlier than the more northern site. Densities of snakes at Communications Site probably peaked before 1985.

The trajectories of snake populations in central Guam are more complicated than those in the north. The initial wave of snakes probably passed through the central Guam study areas one or two decades before 1985. Therefore, the 1985–1989 measurements in central Guam may be indicative of conditions after the initial irruption had passed. During our study, native birds and bats were absent from the central Guam study areas, as were most native lizards. However, introduced vertebrates were present at those sites. In particular, the introduced gecko *Hemidactylus frenatus* reached very high densities, especially on man-made objects such as road signs, utility poles, and buildings where lizards were inaccessible to the snake. In these areas the snake has demonstrated an ability to reattain high densities, at least temporarily.

In 1988 the Orote study area had the highest density of forest lizards (mostly the introduced species *H. frenatus* and *Carlia fusca*) known to us on Guam. The snake's peak density of over 50 per ha in 1988 may have resulted in the depletion of prey resources, for the numbers of both predator and prey declined in 1989.

The opposing trajectories exhibited by snakes along the Airport Road/Airport Fence cliff transects may reflect long-term shifts of snakes between the forest (Airport Road) and the fence (Airport Fence). Snakes may have moved to prey on the high density of *H. frenatus* living within the security of man-made structures along the fence transect (Airport Fence).

The general conclusions that we draw from these data are that: (1) snake populations on Guam have expanded irregularly over a period of more than 35 years, with increases in numbers and area of distribution; (2) snake densities probably approached 100 per ha in some areas when the snake was reaching its peak for the first time; and (3) snakes may again reach high densities in areas that have already experienced loss of most native prey and sharp declines in snake numbers.

ACKNOWLEDGMENTS

Among the many people who assisted with the fieldwork were J. A. Savidge, H. Muna, J. P. Guerrero, R. J. Rondeau, E. W. Campbell III, S. W. Gotte, M. J. McCoid, G. J. Wiles, B. E. Smith, D. E. Wilson, G. R. Grimm, M. J. Altenbach, G. Neubauer, and N. J. Scott. Guam's Division of Aquatic and Wildlife Resources has generously provided support, unpublished data, and facilities for researchers on Guam. O. E. Maughan and J. L. Oldemeyer provided administrative support. The military services have provided logistical support as well as ready access to their bases. E. P. Collins and R. J. Rondeau prepared the figures. The encouragement of C. Imamura and E. Kosaka has been important to our continued study of this snake. M. J. McCoid, O. E. Maughan, R. J. Rondeau, and E. A. Kay suggested improvements to the manuscript.

LITERATURE CITED

ANONYMOUS, 1962. Glimpses of Guam 1962. U.S. Navy Relief Fund Drive, Agana, Guam.

BEARDSLEY, C. 1964. Guam past and present. C. E. Tuttle, Tokyo.

DOWNS, B. H., Jr. 1949. Snakes in paradise! One found in Wake. Honolulu Advertiser, 6 March 1949.

DRYDEN, G. L., and E. H. TAYLOR. 1969. Reptiles from the Mariana and Caroline islands. Univ. Kans. Sci. Bull. 48:269–279.

ENGBRING, J., and T. H. FRITTS. 1988. Demise of an insular avifauna: The Brown Tree Snake on Guam. Trans. West. Sect. Wildl. Soc. 24:31–37.

FOSBERG, F. R. 1960. The vegetation of Micronesia. Bull. Am. Mus. Nat. Hist. 119:1–75.

FRITTS, T. H. 1988. The Brown Tree Snake, *Boiga irregularis*, a threat to Pacific islands. U.S. Fish Wildl. Serv., Biol. Rep. 88(31).

FRITTS, T. H., and M. J. MCCOID. In press. Predation by the brown tree snake on poultry and other domesticated animals in Guam. Snake.

FRITTS, T. H., M. J. MCCOID, and R. L. HADDOCK. 1990. Risks to infants from the bites of the Brown Tree Snake (*Boiga irregularis*) on Guam. Am. J. Trop. Med. Hyg. 42(6): 607–611.

FRITTS, T. H., N. J. SCOTT, Jr., and J. A. SAVIDGE. 1987. Activity of the arboreal Brown Tree Snake (*Boiga irregularis*) on Guam as determined by electrical outages. Snake 19:51–58.

FRITTS, T. H., N. J. SCOTT, Jr., and B. E. SMITH. 1989. Trapping *Boiga irregularis* on Guam using bird odors. J. Herpetol. 23: 189–192.

GUAM, OFFICE OF THE GOVERNOR. 1955. Annual report of the Governor of Guam. Office of the Governor, Agana, Guam.

LIGHTBODY, M., and T. WHEELER. 1985. Papua New Guinea, a travel survival kit. Lonely Planet, South Yarra, Victoria, Australia.

MEAD, M. 1956. New lives for old: Cultural transformation—Manus, 1928–1953. Wm. Morrow, New York.

PARKER, W. S., and M. V. PLUMMER. 1987. Population ecology. Pages 253–301 *in* R. A. Siegel, J. T. Collins, and S. S. Novak, eds. Snakes: Ecology and evolutionary biology. Macmillan, New York.

PENDLETON, R. C. 1947. A snake "den" tree on Guadalcanal Island. Herpetologica 3:189–190.

SAS INSTITUTE INC. 1988. SAS/STAT™ user's guide, release 6.03 ed. SAS Institute Inc., Cary, North Carolina.

SAVIDGE, J. A. 1986. The role of disease and predation in the decline of Guam's avifauna. Ph.D. diss., University of Illinois, Urbana-Champaign.

———. 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68:660–668.

SMITH, A. G. 1949. Notes on the herpetology of Guam, Marianas Islands. Nat. Hist. Misc. (37): 1–2.

STEVENS, R. L. 1953. Guam, U.S.A., birth of a territory. Tongg Publishing Co., Honolulu.

STONE, B. C. 1970. The flora of Guam. Micronesica 6:1–659.

WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, and D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, New Mexico.

WILES, G. J. 1987. Current research and future management of Marianas Fruit Bats (Chiroptera: Pteropodidae) on Guam. Aust. Mammal. 10:93–95.

ZWINNENBERG, A. J. 1978. Die Braune Nachtbaumnatter *Boiga irregularis*. Aquar. Terrar. Z. 31:177–179.