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### HIGH NEST PREDATION BY BROWN TREE SNAKES ON GUAM<sup>1</sup>

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*Key words:* Nest predation; nesting success; snake predation; *Boiga irregularis*; *Streptopelia bitorquata*; avifauna decline; Guam; Pacific islands.

A great deal of attention has recently been focused on the drastic decline of the native avifauna of Guam since the 1960s (Engbring 1983; Jenkins 1983; Engbring and Ramsey 1984; Savidge 1984, 1986, 1987). Populations of once common native forest birds have declined and are now thought to be locally extinct or restricted to the northernmost part of the island (Jenkins 1983; Engbring and Ramsey 1984; U.S. Fish and Wildlife Service, in press). Savidge (1986, 1987) investigated the role of disease and predation in the decline and concluded that the introduced brown tree snake (*Boiga irregularis*) was responsible for the extinction or decline of 10 species of native forest birds on Guam. My report provides direct evidence of the significant impact that snake predation is having on the nesting success and population dynamics of the Philippine Turtle-Dove (*Streptopelia bitorquata*), one of the few wild birds on Guam that remains sufficiently abundant for such a study.

The Philippine Turtle-Dove was probably introduced to the Mariana Islands by the Spanish in the late 1700s (Baker 1951). The species became one of the most abundant birds on Guam and was made a legal game bird (Baker 1947, 1951; Conry 1987). More recently, however, numbers have declined in a pattern similar to that of the native forest birds, though not as severely, and the hunting season for the species has been closed (Engbring and Ramsey 1984, Conry 1987). The turtle-dove is presently uncommon to rare throughout southern Guam, common in localized areas of central and northern Guam, and abundant on Cocos Island, a small snake-free islet 2 km off southern Guam (Conry 1987). The turtle-dove also occurs on the neighboring southern Mariana Islands of Rota, Aguijan, Tinian, and Saipan (Pratt et al. 1987), where its numbers appear stable (T. K. Pratt, pers. comm.) and the brown tree snake does not occur.

#### STUDY AREA AND METHODS

Nesting success of the Philippine Turtle-Dove was studied in forest and urban habitats on Andersen Air

Force Base (AAFB), Guam, from February 1984 to October 1985 and in urban habitat only during May to July 1986. The forest study site is located in the Northwest Field area of AAFB. Northwest Field is an abandoned World War II airfield now occasionally used for training purposes and recreational hunting. The area contains patches of secondary vegetation located inside a network of asphalt runways, taxiways, and roads. The airfield complex is surrounded by primary and secondary limestone forest and scrub forest. This patchy habitat offers a mosaic of grass, shrubs, and trees that provide ample nesting and feeding sites for turtle-doves. Engbring and Ramsey (1984) categorized the area as being 43% primary limestone forest, 50% scrub forest, and 6% urban.

The urban study site is located in the interior of the present-day airfield complex on AAFB. Turtle-doves nest on the corrugated surface of steel-sided, earthen-filled revetments constructed to shelter parked aircraft. Most nesting occurs on one row of revetments in a 24-ha area along the center taxiway of the airfield. Mowed grass, asphalt runways, and roads completely surround the revetments and the closest forest is 0.5 km away. Secondary and primary limestone forest and scrub forest surround the northern two-thirds of the airfield and the remainder of the general area is urban.

Primary limestone forest has a dense canopy 10 to 20 m high and an understory of varying density. Common species include *Ficus*, *Aglaiia*, *Guamia*, *Cycas*, *Neisosperma*, *Elaeocarpus*, *Pisonia*, *Pandanus*, *Wikstroemia*, and *Triphasia*. Secondary limestone forest has a shorter, broken canopy with a dense understory and contains many of the same species as primary forest plus *Hibiscus*, *Leucaena*, *Casuarina*, *Cocos*, *Carica*, and *Morinda*. Scrub forest has similar species composition as secondary forest but is shorter and more open with small grassy patches interspersed with scattered trees and shrubs. The vegetation types of the study areas are described in detail by Stone (1970), Jenkins (1983), and Engbring and Ramsey (1984).

Turtle-doves build shallow, flimsy, platform nests made of small twigs. Nests are typically built in a variety of small trees and shrubs and average 1.8 m in height and 0.9 m distance from the center of the tree (Conry 1987). Nests in forest habitat were located by flushing nesting adults while walking or driving through forested areas, or by searching vegetation. Nests in urban habitat were located by driving the outside perimeter of the U-shaped revetments and observing birds nesting on the structures. All nests on revetments were

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TABLE 1. Survival and cause-specific mortality rate estimates for Philippine Turtle-Dove nests in forest and urban habitat on Guam, 1984 to 1986. Rates are expressed as probabilities. Values in parentheses are the number of nests lost.

Site/period	Days of exposure	Daily rates				Interval rates*			
		Survival	Mortality			Survival	Mortality		
			Snake	Small mammal	Other		Snake	Small mammal	Other
<b>Forest habitat</b>									
1984 [ <i>n</i> = 12]									
Incubation	32.5	0.769 (7.5)	0.215 (7.0)	0.000 (0)	0.015 (0.5)	0.012	0.922	0.000	0.066
Nestling	41.5	0.928 (3.0)	0.048 (2.0)	0.000 (0)	0.024 (1.0)	0.279	0.481	0.000	0.240
					Overall rates:	0.003	0.928	0.000	0.069
<b>Urban habitat</b>									
1984 [ <i>n</i> = 64]									
Incubation	517.0	0.940 (31.0)	0.041 (21.0)	0.014 (7.0)	0.006 (3.0)	0.349	0.441	0.146	0.063
Nestling	426.0	0.966 (14.5)	0.034 (14.5)	0.000 (0)	0.000 (0)	0.555	0.445	0.000	0.000
					Overall rates:	0.195	0.596	0.146	0.063
<b>Urban habitat</b>									
1986 [ <i>n</i> = 23]									
Incubation	108.5	0.825 (19.0)	0.129 (14.0)	0.037 (4.0)	0.009 (1.0)	0.038	0.709	0.203	0.051
Nestling	41.0	0.976 (1.0)	0.024 (1.0)	0.000 (0)	0.000 (0)	0.657	0.343	0.000	0.000
					Overall rates:	0.025	0.722	0.203	0.051

\* Interval rates cover the entire incubation, nestling, and nesting-cycle periods. Incubation and nestling interval rates were calculated from daily survival and mortality rates. Overall nesting-cycle interval rates were calculated by combining interval rates from the incubation and nestling periods (Heisey and Fuller 1985).

visible from a vehicle. Nest sites were marked for observation and rechecked at 2- to 4-day intervals, a few at less frequent intervals of up to 10 days, until the eggs or young were lost or the young fledged. Data were collected on length of incubation and nestling periods, nesting success, and the nature of nesting failures.

Of the potential predators on Guam at the time of this study, the brown tree snake, roof rat (*Rattus rattus*), and monitor lizard (*Varanus indicus*) were judged to pose the greatest threat to nests with the latter present only in forested areas. Possible avian predators on Guam include the Mariana Crow (*Corvus kubaryi*), Micronesian Kingfisher (*Halcyon cinnamomina*), and the introduced Black Drongo (*Dicurus macrocercus*) but none are considered major nest predators (Baker 1951, Maben 1982, Jenkins 1983). At the time of this study, all were extremely rare at the forest study site and, with the exception of the Black Drongo, absent from the urban study site. None of the above avian species were observed harassing dove nests. Feral cats were present at the urban study site but appeared unable to climb the revetments to reach turtle-dove nests.

Nests and surrounding sites were examined thoroughly after the disappearance of eggs or young. Nest failures in which nests appeared virtually undisturbed with no shell fragments or tissue debris present in or around the nest were attributed to snake predation (Best 1978, Best and Stauffer 1980, Aldrich and Endicott 1984, Wheeler 1984). Avian predators may also leave little evidence at nests, but their extreme rarity at the study sites suggested they were not a significant cause of nest loss. Nest failures with evidence of predation such as shell, tissue, or feather fragments left at the site were attributed to small mammals (Best 1978, Moors 1983). Such predation only occurred in urban

habitat. Monitor lizards may also leave signs of predation (J. A. Savidge, pers. comm.), but monitors were not found in urban habitat.

Nesting success was estimated from daily survival rates using the Mayfield method (Mayfield 1975) and modifications of it (Johnson 1979, Hensler and Nichols 1981, Heisey and Fuller 1985). Because nests were usually rechecked on a 2 to 4-day basis, the Mayfield midpoint assumption for determining exposure was considered an appropriate model (Johnson 1979). Estimates of daily survival and cause-specific mortality rates and their sampling variances were used to compute *z*-test statistics and determine differences in nesting success and predation rates within and between sites (Johnson 1979, Hensler and Nichols 1981). Survival and mortality rates over the entire incubation, nestling, or nesting-cycle periods were referred to as interval rates. These rates were calculated from daily survival and mortality rates or by combining rates from multiple intervals (Heisey and Fuller 1985). The loss of a single egg or squab from a normal clutch of two was considered a partial nest loss and recorded as the loss of 0.5 nests. This varies from the method of considering a nest successful if it fledges one young (Mayfield 1975). The method employed here produces a slightly lower estimate of success but accounts for mortality that would otherwise not be recorded such as the loss of one squab from a pair.

## RESULTS

### NESTING BIOLOGY

Four turtle-dove nests were found during the egg-laying period and provided data on the length of the incubation period which varied from 17 to 18 days and

averaged 17.2 days. Data from 14 nests provided information on the length of the nestling period. Young remained in the nest an average of 17.0 days (range = 16–19 days). The entire nesting cycle usually took 34 days. Young birds stayed near the nest site after fledging.

Turtle-doves consistently laid two-egg clutches. No three-egg clutches were found. A single egg was incubated in five of 99 (5%) nests monitored, but a second egg could have disappeared before its presence was noted. In a sample of 35 eggs, egg weight averaged 7.8 g (range = 7–9 g), length averaged 29.5 mm (range = 27.4–32.1 mm), and width averaged 22.1 mm (range = 19.9–23.1 mm).

#### NESTING SUCCESS

Seventy-six active Philippine Turtle-Dove nests were monitored during 1984 to 1985 (hereafter referred to as 1984), with 64 in urban habitat and 12 in forest habitat. During 1986, an additional 23 nests in urban habitat were monitored in a follow-up study. Estimates of daily survival rates (Table 1) were significantly lower during incubation than in the nestling period for both habitats and study periods (forest 1984:  $z = 1.88$ ,  $P = 0.06$ ; urban 1984:  $z = 1.89$ ,  $P = 0.06$ ; urban 1986:  $z = 3.45$ ,  $P = 0.001$ ). Thus, overall nesting success was calculated by combining the probability of success in the incubation and nestling stages.

The moderate nesting success observed in urban habitat during the first phase of the study in 1984 differed dramatically from the extremely low success observed in forest habitat during that year and from the low success at the urban site in 1986 (Table 1). Low overall success appeared to be associated with poor survival during incubation; daily survival rates during incubation were significantly lower in forest than in urban habitat in 1984 ( $z = 2.29$ ,  $P = 0.02$ ) and were significantly lower in urban habitat in 1986 than in 1984 ( $z = 3.03$ ,  $P = 0.002$ ). Survival during the nestling period was more consistent throughout the study and daily survival rates did not differ among sites or periods (forest vs. urban 1984:  $z = 0.93$ ,  $P = 0.35$ ; forest vs. urban 1986:  $z = 1.02$ ;  $P = 0.31$ ; urban 1984 vs. urban 1986:  $z = 0.37$ ,  $P = 0.71$ ).

#### MORTALITY

Predation by brown tree snakes was the major cause of egg and nestling mortality and accounted for daily mortality as high as 21.5% (Table 1). Daily mortality rates from snake predation were significantly higher during incubation than in the nestling stage for forest habitat in 1984 ( $z = 2.10$ ,  $P = 0.04$ ) and urban habitat in 1986 ( $z = 2.60$ ,  $P = 0.01$ ) when nesting success was lowest, but did not differ between stages in urban habitat in 1984 ( $z = 0.56$ ,  $P = 0.58$ ) when nesting success was higher.

Rates of snake predation also varied among sites. Snake-caused daily mortality was significantly higher at the forest site in 1984 ( $z = 2.60$ ,  $P = 0.01$ ) and urban site in 1986 ( $z = 2.64$ ,  $P = 0.01$ ) than at the urban site in 1984, apparently accounting for their poor overall success. Snake-caused daily mortality during the nestling period did not differ ( $P > 0.20$ ) among sites or periods. Overall, snake predation accounted for 93%,

74%, and 74% of all mortality at forest, urban 1984, and urban 1986 sites, respectively.

Small mammals accounted for some losses in urban habitat but only preyed on eggs. Daily mortality rates attributed to small mammals did not differ ( $z = 0.17$ ,  $P = 0.87$ ) between 1984 and 1986 (Table 1). Overall, small mammal predation accounted for 18% and 21%, respectively, of total mortality in urban habitat for 1984 and 1986. Other causes of mortality were relatively rare accounting for 5 to 8% of all mortality and included losses to storm damage, hatching failures, and undetermined causes.

#### DISCUSSION

Predation by the introduced brown tree snake was the major cause for low nesting success of Philippine Turtle-Doves on Guam. The poor nesting success of 0.3% in forest habitat and 2.5% in urban habitat raises doubts whether production is adequate to maintain historic population levels. This indeed appears to be the case as turtle-dove numbers have declined by 80 to 90% throughout most of the island (Conry 1987). Only cursory information is available on nesting success of the Philippine Turtle-Dove from other sources (Baker 1951, Alcalá 1976) and it is of little comparative value in assessing the present rates of nesting success on Guam. However, the Mourning Dove (*Zenaida macroura*), a Nearctic species with similar breeding biology (Edminster 1954), typically achieves far better nesting success in the range of 13 to 77% (Edminster 1954, Hanson and Kossack 1963, Best and Stauffer 1980, Westmoreland and Best 1985). Hanson and Kossack (1963) reviewed nesting studies of the Mourning Dove in various regions of North America and reported average success rates varying from 46 to 70%.

Predation is a major cause of nest loss in many species, particularly doves (Edminster 1954, Best and Stauffer 1980, Westmoreland and Best 1985). Snakes have been identified as contributing to poor nesting success elsewhere (Imler 1945, Best 1978) but not to such a severe extent as on Guam. Best (1978) found that four species of snakes destroyed 65% of all nests on his study area. Imler (1945) found bull snakes (*Pituophis melanoleucus*) preyed on 42% of all nests in his study. In contrast, on Guam, nests in forests and urban sites had a 93% and 72% chance, respectively, of failing due to predation by one species of snake. Savidge (1987) also found exceptionally high predation pressure by snakes on Guam. In trapping experiments using live birds as bait, she recorded predation losses to snakes of 100%, 90%, and 72% (Northwest Field site) at three forest sites in northern Guam. Although based on different techniques, her results seem applicable here because sedentary traps approximate conditions during nesting.

The critical factor causing poor nesting success on Guam appeared to be high snake predation during the 17-day incubation period. Abnormally high snake densities could result in such intense predation. Savidge (1987) found high snake predation early in the 14-day exposure period of her trapping experiments. At a forest site on NCS Naval Base near Northwest Field, snakes visited most of her traps within 4 days and all within 11 days of exposure. She (1986) estimated that snakes occurred in densities of about 16 snakes/ha in northern

forests. Snake densities were apparently very high in forests at Northwest Field. T. H. Fritts (pers. comm.) captured 53 snakes on an 1-ha forest plot within 2 km of my study area. In addition, he captured 101 snakes in eight nights (37 man-hr) along a 2-km stretch of forest road in the same area.

An increase in snake densities at the urban site by 1986 would also explain the decrease in nesting success there. Savidge (1986) reported no snake predation in forest habitat near the AAFB flightline in September 1984 and thought that the flightline area on AAFB was one of the last to be invaded by snakes. However, by December 1984, snake predation had increased to 56%. I found snakes very common at the urban habitat site in 1986. In 14 nights (14 man-hr) during May to September, I captured and removed 39 snakes from a 1.6-km length of fence located 400 m from my study site.

Small mammal predation was not a cause of nest failure in forests during 1984 although rats were possibly the major nest predator prior to the arrival of the snake (Savidge 1987). Similarly, Savidge (1987) found that small mammals accounted for only 3% of her trap losses at Northwest Field and none at four other forested sites during 1984. The extreme rarity of small mammals in forests was apparently the reason for this diminished role. Savidge (1986) caught no small mammals in over 1,000 trap nights at Northwest Field in March 1985 and attributed their scarcity to predation by the brown tree snake. She found that small mammals were more common in savanna and urban habitat. Causes of nest failure other than snake and small mammal predation were minor and similar to levels reported elsewhere (Best 1978, Best and Stauffer 1980).

The small number of nests monitored in this study, particularly at forest sites, raises concerns whether these results reliably reflect actual nesting success and causes of mortality. Sampling predation-prone nests and observer error can bias results toward high predation and low success with this bias further distorted by small sample sizes (Mayfield 1975, Heisey and Fuller 1985). However, the similarity between Savidge's (1987) results and mine, as discussed above, suggests that my estimates of survival and causes of mortality are not seriously biased. Observer disturbance can also bias results by alerting predators to nests by visual, olfactory, or vegetation-disturbance cues. Avian and mammalian predators are thought to use such cues to find nests (Best 1978, Westmoreland and Best 1985) but both were extremely rare in forests and less important in urban habitat, thus any bias associated with these species would likely be small. It is unclear to what extent, if any, human visitation affected snake predation. Best (1985) thought that snakes searched for nests randomly but Savidge (1987) attributed the brown tree snake with the ability to locate bird prey by means other than random encounter. It is unknown if human odors would attract this snake. Human presence was common at both study sites.

In conclusion, severe nest predation by snakes appears to be having a devastating impact on the recruitment of an open-nesting, wild bird population on Guam. This study is the first to document the impact of snakes on a wild bird population on the island and, as such, is useful in analyzing the recent decline of Guam's native forest birds. These data provide evi-

dence that nest predation by snakes and the resulting poor production may have been a far more important factor in the decline of native birds on Guam than previously thought. In light of these findings, any efforts to recover bird populations must recognize the need to implement snake control and nest protection measures if birds are to achieve the reproductive success necessary to coexist with the brown tree snake.

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## FACULTATIVE MIGRATION IN YELLOW-EYED JUNCOS<sup>1</sup>

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*Key words:* Facultative migration; winter flock stability; Yellow-eyed Juncos; *Junco phaeonotus*.

Altitudinal migrants, wintering relatively close to the breeding grounds can assess more precisely when the breeding grounds become favorable for habitation than can long-distance migrants. Altitudinal migrants also have the opportunity to inhabit the breeding grounds early if local weather conditions permit, and then can quickly return to the wintering area if weather conditions deteriorate. The close proximity of refuges from severe climatic conditions at the breeding grounds may permit the timing of spring migration to be highly facultative in these birds.

Yellow-eyed Juncos (*Junco phaeonotus*) are altitudinal migrants in mountain ranges in southern Arizona and throughout Central America (Moore 1972). As part of an ongoing study of the behavioral ecology and demography of Yellow-eyed Juncos, we documented winter site fidelity and spring movements between the

breeding and wintering grounds in a population of juncos in the Chiricahua Mountains, Cochise County, Arizona.

### METHODS

The senior author conducted censuses of individually marked juncos at one high elevation site (Rustler Park, elevation 2,560 m) and at two lower elevation sites (Southwestern Research Station, SWRS, elevation 1,646 m, 8 km from Rustler Park; and Sunnyflat Campground, elevation 1,554 m, an additional 2 km from Rustler Park) between 3 January and 31 March 1986.

A census of banded individuals was carried out at SWRS (36 banded Yellow-eyed Juncos) on 71 days between 16 January and 31 March 1986. The area was not visited on 25 January, 30 January, and 13 February and therefore these dates are not included in Figure 1. At least once every 3 days an extensive search of the research station grounds was made to find banded juncos. We classified individuals as present if they were sighted at least once during the 3-day interval. The senior author also conducted a census of an additional 10 banded Yellow-eyed Juncos at Sunnyflat on 14 February, 20 February, 13 March, and 20 March and searched for banded juncos at Rustler Park (where we had banded 552 Yellow-eyed Juncos during the previous two summers) on 18 January, 19 February, 10 March, 22 March, 28 March, and 31 March.

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