SURVIVAL RATES FOR VISITED AND UNVISITED NESTS OF BICOLORED ANTBIRDS

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ONE often wonders, when studying nests, if predators find the nests by following the observer. In other words, are survival rates lower in visited nests than in unvisited ones? In a study of Bicolored Antbirds (*Gymnopithys bicolor*) on Barro Colorado Island in Panama (Willis 1967), I found a way to see if survival rates are similar in visited and unvisited nests.

Nests are in small cavities in stumps or sheathing leaf bases of palms near the ground (Willis 1967: 82); the bird sits low and is concealed except from above. In passing by watched nests on infrequent visits (never over once per day), I looked down briefly to check nest contents. Normally the parent flushes when one is still distant and chirrs only at a distance from the nest. If the parent flushed noisily from the nest, I walked off and wandered about, passing the nest and checking its contents on one leg of the wandering. At one nest young were weighed daily until some predator took them.

Unvisited nests can be monitored by watching the color-banded adult birds at swarms of army ants, which adults follow for most of their food (Willis 1967). During the nesting season, April (rarely March) to December, the male regularly feeds the female before a nesting, and never feeds her when a nesting is in progress. Just before eggs are laid, some of the courtship feedings end in copulations. Occasionally the pair wander away from the ants and search for nest sites. During the last few days before egg-laying, the pair are occasionally absent from swarms for an hour or two—especially early in the morning. They may carry nest material as they leave the ants.

The day the first egg is laid (day 0), the female or both birds are late—about 09:00—arriving at the swarm of ants. Unless the male disappears for an hour or two later in the day or the next day to sit on the single egg, there is no way to tell whether the pair are building or egg-laying. On day 2, however, the female lays the second egg during an absence before 09:00, and incubation begins. On the first day of incubation, the male and female are absent irregularly, usually alternately. Until this day, one is uncertain that eggs have been laid; it is thus possible to check survival at unwatched nests mainly after the second egg is laid.

From day 4 to days 17–19, when the young hatch, incubation is regular—only the female is at the ant swarm to about 11:00 or 12:00 (unless the male visits briefly about 07:00–08:00); then loud songs herald the

arrival of the male from the direction of the nest. The male feeds and preens busily while the female rests; she moves off toward the nest with faint songs between about 11:30 and 13:00. Later in the day the male or female are together at the swarm only briefly; they alternate going to the nest.

When the first young hatch this regularity breaks down. The male appears over the ants in midmorning, feeds hastily, and later he or the female or both carry food off in the direction of the nest. Were the nest destroyed at any stage, he would take the food and feed the female for the next nesting instead (on the first day of nest loss, the birds sometimes also disappear irregularly and probably are sitting on or wandering around the empty nest, as other antbirds sometimes do). Later in nesting the male and female often forage together, but eventually one or both carry food in the direction of the nest. When the young leave on day 31 or 32, the parents lead them toward the ant colony. Feeding rates become very high as soon as the young leave, and within 2 days the two young can be discovered sitting in separate tangles behind the ant swarm. Soon after the young leave the nest, the female carries food in one direction and the male in another, for she feeds one young and he feeds the other.

This regularity of behavior makes it possible to tell reasonably accurately when a pair have eggs, young, or fledglings by watching at ant colonies and not visiting nests at all. Figure 1 shows differences in survival and mortality at 61 such unvisited and 16 visited nests in my annual visits to Barro Colorado Island in 1960–71. Calculations are based on the method suggested by Ricklefs (1969). For each day, nests that survived to the next day and ones that did not are tallied separately. (As nests are more frequently successful in certain months, I divided each record by the number of months I was on Barro Colorado at that month of the year; April nests are divided by 1.0, July nests by 8.1, etc. Otherwise the facts that July nests rarely succeed and that I was on Barro Colorado often in July would bias survivorship curves.) The percent surviving for that day is then the number of surviving nests divided by the total number of nests. Percentages for successive days are multiplied together and graphed in Figure 1. Nests are not tallied before discovery, even if later hatching or fledging of young made it obvious that the nest had been in existence before I found the nest or the parents showing nesting behavior. Survival rates at visited and unvisited nests of Bicolored Antbirds are very similar, and indeed slightly more of the visited nests fledged one or more young than did unvisited nests (the difference is not significant). Final survivorship in the 76 nests was 11.7 percent, which lies above both survivorships of watched and unwatched nests because of a crossover on day 22.

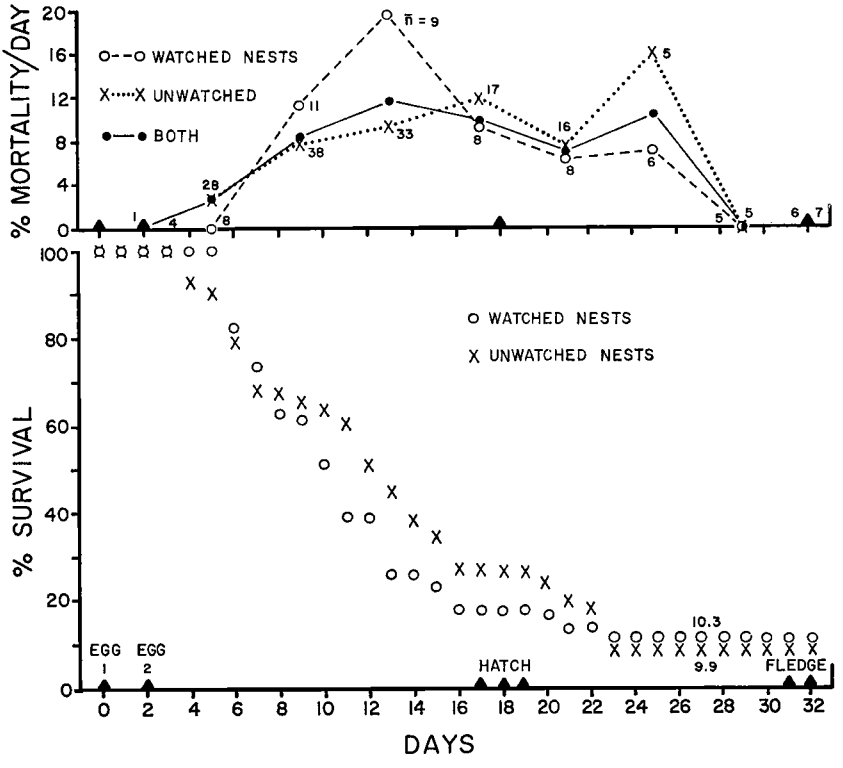

Figure 1. Success of unwatched and watched nests of Bicolored Antbirds. Above, daily nest mortality rates averaged over 4-day periods. Below, percent nest survival, based on the same original data.

Data are too few to reveal much about mortality rates, but averaging mortalities over 4-day intervals shows that watched nests had high mortality rates early in the nesting cycle, while mortalities rose in both kinds of nests, but especially in unwatched nests, after the young hatched. Mortalities were near zero the first and last week of nesting. These patterns suggest that predators become more adept at finding Bicolor nests the longer they have been in use, that they find most of the easily discoverable nests by late in incubation, that nests then are predated less, and that the growth of the young quickly reveals to predators some nests that until then were hard to discover. Soon all the discoverable nests are robbed, and young Bicolored Antbirds are in relatively safe nests if they have managed to survive the first week after they hatch.

At watched nests it seemed that my visits accelerated the destruction of easily discovered nests, but had little or no effect on the final percentage

of nests surviving. Watching nests would thus be an advantage to the population, giving more time for renestings (Willis 1961). However, discovered nests may be easier for predators to find than are undiscovered nests, so that I may have had little influence on predation.

The most likely predator would be one that hunts by scent, which would accumulate over the first few days the birds use the nest, then stabilize until young hatch when it would rise again and stabilize. The effect of my visits could be to show inquisitive predators, probably opossums (*Didelphis marsupialis*) or other nocturnal mammals, the nests early. At one nest a mammal probably got the young, for several feathers of the female were scattered about, and when she reappeared at the ant swarms after a few days absence, she was missing some tail feathers and probably a lot of body feathers. Similar nocturnal predation of the female and young in another cryptic low nest, that of Chestnut-backed Antbirds (*Myrmeciza exsul*), is noted in Willis and Oniki (1972). As females are on the nest at night, this may explain why female Bicolored Antbirds have high mortality rates (Willis MS) and populations show a surplus of males.

It is also possible that a persistent predator might search repeatedly for a Bicolor nest near which it once flushes a bird, gradually homing on the nest by repeated attempts. Possibly, also, the antbirds sit more tightly as the nesting progresses, so that they flush late in nesting only when the predator is very near. They brood little after the young are 6 days old, which could cause the low predation rate thereafter. If they flush at distant predators early in nesting, they should go off the nest more often then, which is a behavior pattern that was never detected and which should show the nest to other predators anyway.

Easily detected cup nests, of Spotted Antbirds, *Hylophylax naevioides* (Willis 1972) and of Slaty Antshrikes, *Thamnophilus punctatus* (Oniki MS), have a mortality pattern in which rates of predation are very high as the eggs are laid and the first few days thereafter. Predation rates then drop off to the time the young hatch, and rise rapidly as the young grow—until the day they can leap out if a predator appears. These birds have very short nestling periods, 9 to 11 days, rather than the 12–14 day nestling periods of Bicolored Antbirds. The differences in predation rates on older nestlings may be the cause. Snakes (*Pseustes poecilonotus*) are the main known predators on these nests. Females can easily escape these predators, which probably hunt by sight or heat and come in the daytime; female Spotted Antbirds survive about as well as do males (Willis MS). These nests have the disadvantage of slightly lower survival rates—9 percent for Spotted Antbirds, about 10 percent for Slaty Antshrikes—than the 11.7 percent for cryptic nests of Bicolored Antbirds.

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LITERATURE CITED

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contrib. Zool. No. 9.

WILLIS, E. O. 1961. A study of nesting ant-tanagers in British Honduras. Condor 63: 479–503.

WILLIS, E. O. 1972. The behavior of Spotted Antbirds. Ornithol. Monogr. No. 10.

WILLIS, E. O. 1967. The behavior of Bicolored Antbirds. Univ. California Publ. Zool. No. 79: 1–132.

WILLIS, E. O., AND Y. ONIKI. 1972. Ecology and nesting behavior of the Chestnut-backed Antbird (*Myrmeciza exsul*). Condor 74: 87–98.

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