

USE OF TIME AND SPACE BY CHESTNUT-BACKED ANTBIRDS

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ABSTRACT.—Foraging accounted for over 90% of the activity of two pairs of Chestnut-backed Antbirds (*Myrmeciza exsul*) during a one month study of their daytime time budgets in the Pacific lowlands of Costa Rica. We also documented in detail their use of territorial space and preference for dense vegetation where foraging was most productive. Our results support previous findings that tropical insectivores may have to devote much effort to foraging and that dense cover is the best microhabitat for foraging by antbirds.

Daily time budgets reflect a bird's allocation of time to essential self-maintenance and to options such as reproduction and migration (King 1974). Breeding seasons, reproductive effort, and pair bonds are shaped in part by the foraging requirements of individuals.

The proportion of the daylight hours devoted daily to foraging ranges from less than 10% to nearly 100%. At one extreme, hummingbirds and tropical frugivores obtain adequate food in rather little time by feeding on conspicuous, energy-rich foods (D. Snow 1963, B. Snow 1970, Wolf and Hainsworth 1971, Wolf et al. 1975). At the other extreme, small landbirds in the far north feed almost continuously during short winter days to accumulate the energy required for survival (Gibb 1956, 1960). Remaining to be determined, however, is how much time each day tropical insectivores feed. Does the time they require to find enough energy and nutrition constrain other activities or somehow dictate seasonal cycles in the availability of productive energy?

With the exception of the Mangrove Swallow (*Tachycineta albilinea*; Ricklefs 1971) and Checker-throated Antwren (*Myrmotherula fulviventris*; J. Gradwohl and R. Greenberg, unpubl. data), the daily foraging time budgets and space use patterns of insectivorous tropical birds remain unquantified. Mangrove Swallows with nestlings devote 80–100% of the morning and late afternoon hours to the capture of aerial insects. Mid-day foraging apparently is limited by heat stress. Checker-throated Antwrens forage 80–90% of the day most of the year and 30–50% of the day when food is most abundant. Studies on both of these birds reveal substantial daily foraging effort as well as seasonal variation. The widespread impression that tropical insects are abundant and, therefore, that finding adequate insect food may not require much time seems erroneous.

We undertook to document further the importance of foraging effort in the daily activity

patterns of the Chestnut-backed Antbird (*Myrmeciza exsul*). This species is common in lowland forest undergrowth and second-growth forest from Nicaragua to western Ecuador (Willis and Oniki 1972, Ridgely 1976). It typically inhabits old (3–6 years) gaps in the forest with dense shrub and sapling growth, or edges of man-made clearings with similar vegetation (F. G. Stiles, in litt.). The bird does not habitually associate with antswarms.

Willis and Oniki (1972) suggested that in Chestnut-backed Antbirds, conflicts between self-maintenance and the demands of parental care are resolved by active male participation in all aspects of nesting. Plentiful supplies of food in dense cover also may provide some relief. We wished to obtain more precise information on foraging effort and the importance of dense vegetation to this species.

METHODS

We conducted this study from 12 June to 5 July 1981 in Corcovado National Park on the Osa Peninsula of Costa Rica. Allen (1956) has described the Tropical Wet Forests (Slud 1964: 17) of this park. Our study site, 100 × 200 m, was at the edge of rain forest near the park headquarters at La Sirena. The site, a recently abandoned pasture edge, was second-growth vegetation, 3–4 years old with a canopy 4–8 m tall, composed of *Ochroma lagopus* (Bombacaceae), *Trema micrantha* (Ulmaceae), *Piper auritum* (Piperaceae), *Heliocarpus appendicatus* (Tiliaceae), and *Inga* sp. (Leguminosae), *Heliconia imbricata* (Musaceae), *Heliconia curtispatha*, *Calathea* sp. (Amaranthaceae), and dense thickets of *Acalypha* sp. (Euphorbiaceae) were the principal understory plants (D. H. Janzen, pers. comm.).

We spent 56 h observing one pair (A) of Chestnut-backed Antbirds color-marked with celluloid leg bands and 6 h observing a second pair (B), only one of which was color-marked. The antbirds were followed nearly continu-

TABLE 1. Time budget of a pair of Chestnut-backed Antbirds.*

	N = 726 min 05:00 07:00	890 min 07:00 09:00	590 min 09:00 11:00	130 min 11:00 13:00	665 min 13:00 15:00	378 min 15:00 17:00
Forage	90.4 ± 11.6	98.3 ± 9.4	92.0 ± 9.4	80.3 ± 14.4	97.3 ± 4.4	100.0 ± 0.0
Rest ^b	0.7 (1)	0.0 (0)	7.6 (2)	11.0 (0)	0.0 (0)	0.0 (0)
Agonistic behavior	4.0 (4)	1.9 (1)	0.0 (0)	8.3 (1)	2.9 (2)	0.0 (0)
Advertisement	4.9 (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)

* Percentage of time devoted to the activity ± 1 standard deviation.

^b The number of times activity was observed per observation period is in parentheses.

ously during each observation period in the dense thickets of their territory via trails we cut and also those of peccaries.

Breeding preceded our observations. The principal pair (A) had a fledgling with them in mid-June at the onset of our field work, but the fledgling disappeared shortly before we color-marked the adults and started to monitor them. We did not see any signs of reneating, including feeding of the female by the male.

The birds followed a daily routine throughout the study with only minor variations. Both pairs of antbirds were territorial and regularly engaged in disputes with their neighbors or with intruders. The territory boundaries did not change during the study.

Observation periods ranged from 30 to 285 min, and usually started shortly after dawn at 05:15 to 05:45, when the antbirds began calling. The percent of time foraging during each

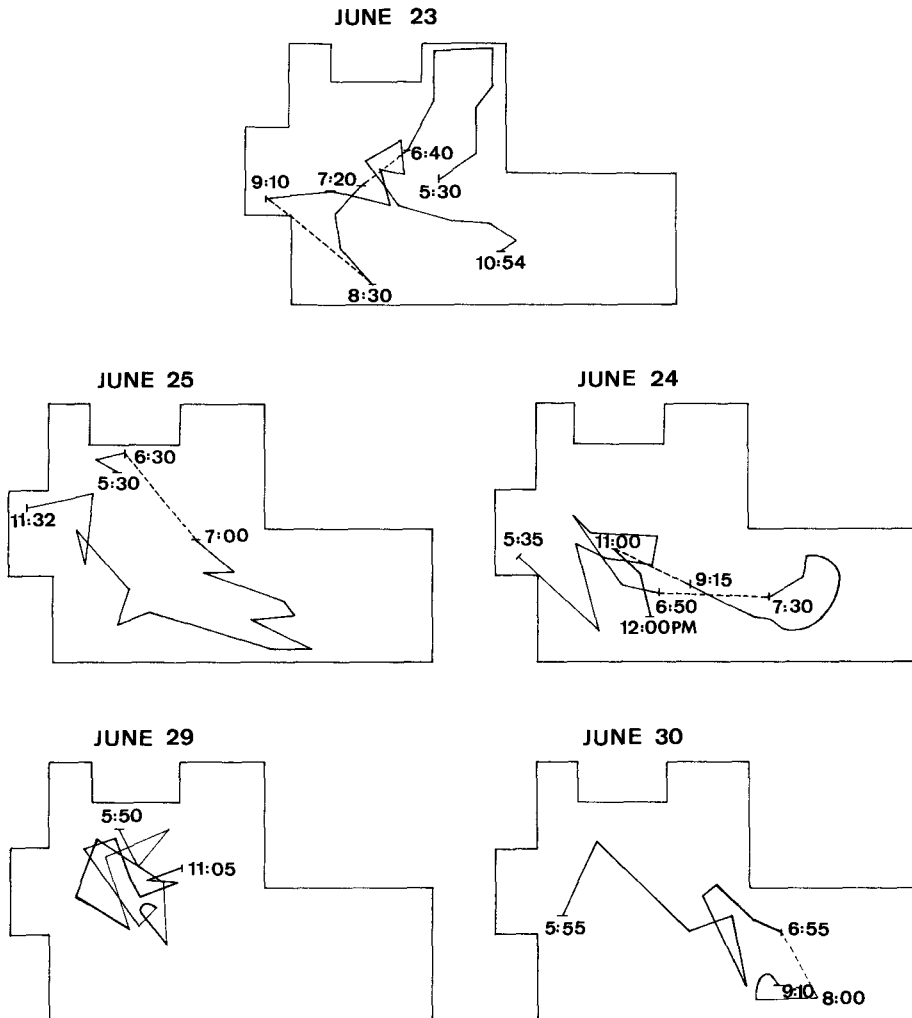


FIGURE 1. These maps show the movements of pair A during the mornings of June 23–25 and 29–30. Dotted lines connect points between observation periods and may not be actual routes of the birds.

		7			11	15				
	122	(222)	57	15	31					
15	70	142	119	(71)	48					
5	(55)	(194)	(170)	(70)	(65)	(33)	18	18	4	
	(16)	(72)	(132)	(58)	(101)	(91)	(75)	26	8	
	(2)	(84)	49	3	22	(166)	(61)	18	5	

FIGURE 2. Use of territorial space in terms of total time (minutes) spent by pair A in each quadrat. Times spent in quadrats with dense vegetation are indicated within circles. The rest had open vegetation. Scale: 2 cm = 25 m.

observation period proved to be independent of the duration of that period. Days were divided into 2-h periods. Two-thirds of our data were obtained before 11:00. Therefore, we treated the average foraging times for each period equally to estimate average daily foraging effort. We recorded the birds' activity, precise location on the mapped territory, frequency of pecking at possible food, and general behavior.

We classified the antbirds' activities as "Foraging," "Agonistic Behavior," "Advertising," and "Resting." Foraging referred to time spent actively procuring food as described for this species by Slud (1964), Skutch (1969), and Willis and Oniki (1972). "Agonistic Behavior" accompanied territorial disputes and included displays, attacks, chases, actual fights, and escaping. "Advertising" refers to singing on exposed branches while clearly not foraging. The antbirds also sang throughout the day while foraging. "Resting" refers to sitting quietly with preening. Sometimes at mid-day the antbirds disappeared into small, dense thickets only to reappear ca. 20 min later; we assumed they were resting inside these thickets.

We divided the territory of pair A into 42 quadrats each 20 m on a side. Total time, number of visits, and average time per visit were computed for each quadrat. We also classified the vegetation in each quadrat as "open" or "dense." What we categorized as "dense vegetation" consisted mostly of an understory of *Acalypha* thickets. "Open vegetation" was pri-

marily an understory of *Heliconia* and scattered *Calathea*.

RESULTS

DAILY TIME BUDGETS

Considering the proportions of the six 2-h periods spent foraging as equal measures, despite the difference in total observation time in each, our data show that the antbirds of pair A spent an average of 93% of their time foraging (range was 80–100% per 2-h period; Table 1). Non-foraging activities comprised less than 20% of any 2-h period and less than 6% of the total daylight hours. Foraging effort was least at mid-day and was particularly intense in the late afternoon. The variations in foraging efforts among the 2-h periods, other than mid-day, were minor.

USE OF TERRITORIAL SPACE

The antbirds used only part of their territory each day. They usually started the day in the center of the territory, moved out to the periphery, and then returned to the center before mid-morning. The daily foraging paths themselves, however, varied greatly in coverage of sections of the territory (Fig. 1). On some days (e.g., June 23, 26, 28), the antbirds moved rapidly over large sections of their territory, but on other days (e.g., June 29), they restricted their activities to smaller sections.

The antbirds preferred certain parts of their

territory; their time was not distributed evenly among the available quadrats (Fig. 2). Low-use quadrats were peripheral, whereas most high-use quadrats were centrally located. Intensities of use in the morning were significantly correlated with such intensities in the afternoon ($r = 0.5$, $P < 0.01$).

Total time per quadrat reflected both the frequency of revisitation and the average amount of time per visit to a quadrat. High-use quadrats usually were visited at least once daily, low-use quadrats only once a week. The distribution of these visits was not random (Chi-square for comparison to Poisson distribution with mean of 2.43 = 14.65, $df = 7$, $P < 0.05$). Average times per visit to high-use quadrats (14.3 ± 5.6 min) and average-use quadrats (12.2 ± 5.2 min) were similar, but average time per visit to low-use quadrats was less (7.6 ± 5.1 min).

"Open" vegetation covered 440 sq. m of the territory whereas "dense" vegetation covered 400 sq. m. A two-way analysis of variance showed that the antbirds averaged more time per visit in quadrats with dense vegetation than in quadrats with open vegetation, no matter where these quadrats were located (Fig. 2) ($F_{1,37} = 6.73$; $P < 0.01$). Times per visit in "dense edge" versus "dense center" quadrats were not significantly different ($F_{1,37} = 1.05$; $P < 0.31$), but more total time was spent in dense center quadrats than in dense edge quadrats (Chi-square = 5.11, $df = 1$, $P < 0.005$). Similarly, more total time was spent in open center quadrats than in open edge quadrats (Chi-square = 39.8, $df = 1$, $P < 0.005$).

The antbirds' preference for quadrats with dense vegetation reflected their apparent foraging success. The frequency of pecking at actual or potential prey was significantly higher in dense areas (1.30 pecks/min ± 0.44) than in open areas (0.84 pecks/min ± 0.48) ($t = 4.17$, $df = 26$, $P < 0.05$). We are unable to tell from our data whether more frequent use of center territories reflected better foraging or simply geometry of the territory.

DISCUSSION

Our results, plus those of Gradwohl and Greenberg for *Myrmotherula* antwrens, indicate that the foraging can be the principal daytime activity of tropical insectivores even when they are not feeding nestlings. Tropical antbirds thus join tits (*Parus* spp.), Goldcrests (*Regulus regulus*), and Rock Pipits (*Anthus spinoletta*) wintering in northern Europe (Gibb 1956, 1960) as examples of birds with limited time for activities other than foraging. Such effort is the more surprising because antbirds have nearly 3 h more daylight each day than

Goldcrests in England, and they do not face comparable metabolic demands on stored reserves, owing to long, cold nights.

We could not determine why the Chestnut-backed Antbirds spent most of the day foraging. Conceivably, they were eating more than was necessary for maintenance in order to accumulate reserves for reneating. This possibility seems unlikely because we did not see any courtship feeding of the female by the male, as would be expected if this were happening (Willis 1972, Willis and Oniki 1972, Greenberg and Gradwohl 1983). Masses of the three individuals weighed at the beginning of this study were typical of the species—28, 28, 27 g (see also Willis and Oniki 1972).

Most likely, the foraging effort we documented reflected the difficulties of finding prey in a lowland tropical forest where insects are exceedingly cryptic and often distasteful or inedible (Fogden 1972, Janzen 1980). The abundance of litter-dwelling arthropods varies seasonally on Barro Colorado, Panama, increasing during the rainy season (Levings and Windsor 1982). June, therefore, should not have been a period of food scarcity at Corcovado, although the seasonality of litter arthropod abundance has not been studied at this site. Willis and Oniki (1972) suggested that the penchant of these antbirds for dense cover indicates better foraging in such microhabitats. Our data show not only a bias of foraging time towards patches of dense cover within the territory, but also greater foraging activity in this microhabitat as indicated by frequency of pecking.

Confirmation of such substantial foraging efforts by tropical insectivores will complement the growing body of evidence that breeding by tropical birds is proximately constrained by their ability to accumulate adequate protein and fat reserves (Jones and Ward 1976, Fogden and Fogden 1979). Comparative studies of the time budgets of tropical birds may also provide a productive route to understanding of the adaptive basis of monogamy and the evolution of pair bond diversity in tropical birds.

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RECENT PUBLICATIONS

Common bird songs. Songs of eastern birds. Songs of western birds.—Donald J. Borror. 1984. Three sets, each containing a 50-minute cassette and a 64-page booklet. Dover Publications, Mineola, NY. \$7.95 per set. These are cassette versions of field recordings that were first issued as phonodiscs in 1967-1971. Their age notwithstanding, the sound quality is good, though with a little more white noise background than one would like. Each cassette presents sixty species, with no duplication among them. The species are arranged more or less according to the general character of the vocalizations, from simple to complex. Birds with similar songs are grouped together as an aid to comparison. Most species are represented by two or more cuts, thus a fair sample of their vocal quality and characteristics. Each species is introduced simply by name and its cuts by number. The accompanying booklet describes the songs in the same sequence as on the cassette; the accounts focus on features that serve for identification and are much fuller than the remarks in field guides. A table showing the locality and month in which the songs were recorded is appended. These cassettes are certainly effective aids for learning bird songs, better yet for refreshing one's memory before spring migration. They are good value for the money, but eastern birders will have to buy the first two sets in order to get better coverage.

The Peterson Field Guide Series. A field guide to bird songs of eastern and central North America. Second edition.—Cornell Laboratory of Ornithology. 1983. Available in albums of either two phonodiscs or two cassettes. Houghton Mifflin Co., Boston. \$19.95 per set. Here, in a completely revised edition, are field recordings of the voices of 250 species of birds. They are arranged systematically, i.e., following the sequence in the fourth edition of Peterson's eastern *Field Guide*. Each species is announced by name. Calls and/or songs are given, though not as separately identified cuts. An index to the recordings, including their locality and a page reference to the species account in the book, is given on the phonodisc album and a booklet with the cassettes. Both formats have their advantages: discs are easier for finding particular species, whereas cassettes can be used in the field. As compared with the Dover sets mentioned at left, these offer many more species, though some of them are questionably necessary for recognition. The trade-off is that the samples for each species tend to be fewer and briefer, thereby presenting less of the variability and the sometimes-characteristic pattern of pauses in singing. The Cornell sets sound slightly clearer, though they have a low background hum in place of white noise. Being keyed to the *Field Guide*, they enable an observer to check a bird's appearance, habits, and range along with its voice. Borror's booklets, on the other hand, go into more detail about the vocalizations. A choice between them depends on one's budget and the kind of help one needs in learning bird songs.