

Constant density and stable territoriality in some tropical insectivorous birds

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Summary. Four species of understory antbirds (Formicariidae: *Myrmotherula fulviventris*, *M. axillaris*, *Microrhophias quixensis*, and *Thamnophilus punctatus*) had stable populations over eight rainy seasons on Barro Colorado Island, Panama. The co-defended territories of *M. fulviventris* and *Microrhophias quixensis*, were essentially identical from year to year on our intensive study site, despite a moderate turnover of territory owners. The location of the territories of *T. punctatus* was also similar between years. This stability occurred in the face of considerable annual variation in the survivorship of adult *M. fulviventris* and *T. punctatus*. This variation was not significantly correlated with patterns of rainfall. Stable territoriality has rarely been reported from relatively-short-lived insectivorous birds. The annual production of young was significantly variable only in *M. axillaris*. Because BCI is an island comprised of one habitat (tropical forest) and so supports a closed population of antbirds, and because it is unlikely that natality equaled mortality on our study site during the entire eight years of the study, we suggest that these breeding populations are socially regulated at a constant level below the limits directly set by food supply.

Population stability remains a cornerstone of theories concerning the ecological differences between tropical and temperate zone birds (see, for example, Cody 1966). A major reason for suggesting that tropical populations are relatively stable is that temperatures remain nearly constant throughout the year, and thus tropical forests are climatically less seasonal than woodlands of temperate latitudes. Furthermore, the specter of large scale climatic events reducing population levels during a winter period seems less likely. It is now well established, however, that variation in rainfall and related cycles in soil moisture may make tropical forests quite seasonal. Fluctuations in rainfall can profoundly influence patterns of leaf, flower, and fruit production, which in turn, can affect population levels of arthropods (Janzen 1973; Fogden 1972; Frankie et al. 1974; Foster 1982a; Wolda 1978a, b; Leigh and Windsor 1982; Levings and Windsor 1982). In addition, certain climatic events, such as cold fronts and El Nino (southern oscillation), induce unusual rainfall patterns that can change nor-

mal phenological events (Foster 1982b). Although it remains unclear how such variability affects animals at higher trophic levels, some studies indicate that insectivorous vertebrates are subject to notable year-to-year changes in abundance, natality, and survivorship (Andrews and Rand 1982), which are in part related to climatic events.

Birds are among the most conspicuous and easily censused of insectivorous vertebrates in tropical forests. Few studies, however, have explicitly examined the degree of between-year variation in density and demography of tropical bird species. Notable exceptions include Willis' studies of ant-following birds on Barro Colorado Island, Panama (BCI) (Willis 1974, 1980) and Karr and his associates' examination of the dynamics of the "mist-nettable" avifauna of a Panamanian forest (Karr 1980; Karr et al. 1982). In our study we have concentrated on monitoring the density, home-range configuration, and demographic features of populations of a few understory birds on BCI to examine the degree to which inter-annual variation relates to variation in climate (rainfall) and food supply. The study species, Checker-throated Antwren (*Myrmotherula fulviventris*), White-flanked Antwren (*M. axillaris*), Dot-winged Antwren (*Microrhophias quixensis*) and Slaty Antshrike (*Thamnophilus punctatus*), are among the most abundant insectivorous birds on BCI (Willis 1980; Greenberg 1984) and adjacent Canal Area forests (Karr 1971).

We examined patterns of rainfall to see if annual mortality was correlated with this indicator of climate. Good reasons exist to predict that variation in rainfall during the late rainy or dry season might affect the survivorship of insectivorous birds on BCI. Karr (1982) suggested that the dry season is a particularly stressful time for forest birds, and that many use mesic refugia to survive periods of drought. Wolda (1978b) showed that unusual rains during the dry season may depress the population of certain arthropod groups. Hespeneide (1980) demonstrated that the late rainy season was a period of particularly low insect abundance. The amount of rain during the late rainy season may also influence the availability of prey, and affect hunting time (for similar arguments see Foster 1974).

Study area

The research was conducted on BCI, an island created in 1911 when the Chagres River Valley was flooded to create Gatun Lake. The island reserve protects approximately

15 km² of lowland tropical forest, which receives about 2,600 mm rain per year (Rand and Rand 1982). The rainfall is quite seasonal with 92% occurring during the rainy season, which generally lasts between early May and mid-December. The western half of the island is covered with "old forest" which may have been undisturbed by human activity for up to 300–400 years (Foster and Brokaw 1982). The eastern half of the island is covered with second-growth forest approximately 70–100 years old. The island is crossed by 40 km of trails which provide access to most of the forested area of the island. Our study involved censuses along the entire trail system, as well as intensive work on a 12 ha plot near the eastern edge of the center of the island (the BCI "plateau").

Methods

Trailside census

Each mid-rainy season (Aug–Sept) from 1977 to 1983 we hiked 10–30 km of trail (at approximately 1 km per hr) and recorded the composition of family groups of the three antwren species located within 15 m of the path. Each trail was censused only once per year. Young antwrens can be assigned to several crude age classes based on a few morphological and behavioral features (e.g., 1 month, 1–2 months, > 2 months from fledging).

From these censuses we could derive an estimate of the density of antwren groups in the BCI forest. To do this we assumed that for each 1 km covered that we were counting antwrens over a 3.0 ha area (15 × 1,000 × 2 m). This assumption is supported by the observation that we detected no significant reduction in the number of groups sighted at increasing distances from the trail. In 1983 we recorded estimates of such distances and found that 20 groups were located within 0–5 m, 23 at 6–10 m, and 16 at 11–15 m (χ^2 for departure from equal observations per cell = 1.35, *d.f.* = 2, n.s.). In addition, we assume that our rate of movement along the transect is rapid compared to the speed of antwrens; our extensive following of antwren groups shows that they are quite slow (Gradwohl and Greenberg 1980).

We also derived an estimate of the natality based on the number of groups sighted with fledglings during the early to mid rainy season. While this does not include all young produced in the population each year, it probably includes the peak breeding season for antwrens (Willis and Eisenmann 1979; Gradwohl and Greenberg 1982). We therefore use these data as an index of annual reproduction, rather than a direct estimate. We present the frequency of groups with young rather than total young because the presence of young in a group is more accurately determined than actual number of young present (clutch size is two for all species of antbirds).

Intensive plot

Each year from October 1977 through September 1983 we mist netted and color-marked birds on a 6–12 ha study plot on the BCI plateau (the initial 6 ha plot was expanded by addition of an adjacent 6 ha to 12 ha in 1980). The plot was gridded and marked at 20 m intervals with forestry flagging; we also used the grid system of the tree census plot established by S. Hubbell for the 1980 addition. Each

year we netted at 30–60 sites preselected as likely spots for capturing members of mixed species flocks in ground-level mist nets. Our netting effort allowed us to color band 82 Checker-throated, 51 White-flanked, 8 Dot-winged Antwrens, and 85 Slaty Antshrikes. We spent over 3,200 person hrs during the six year study slowly moving over the plot resighting color-marked birds and recording their position on maps based on the gridded coordinates. From 1981 to 1984 we followed Checker-throated Antwren groups for 2 hr increments (never more than one such tracking session per group per day). We spread out the flock following over a number of days because antwrens use much, but not all of their territories during one day (Gradwohl and Greenberg 1980). The territory maps in Figure 2 do not include 1980, in which we obtained too few data.

Although we had only eight color-marked Dot-winged Antwrens, the observation of family groups with unusual composition indicates that their territories always coincide with the territories of associated Checker-throated Antwren pairs (Gradwohl and Greenberg 1980); over the eight years of the study, we have been able to distinguish 25 "unusual" Dot-winged antwren groups on the plot. We determined the number of territorial adults of Checker-throated and White-flanked antwrens and Slaty Antshrike that survived from one late rainy season to the next. With the exception of the first year of the study, which began in October, all other censuses of surviving color-banded birds were conducted in early September. We searched areas adjacent to the 12 ha plot to locate marked birds that had moved off the study area. In the analyses, we assumed that all adults that disappeared had died.

Rainfall measurements

The analysis of the seasonal distribution of rainfall is based on the summaries of daily precipitation recorded at a rain gauge in the laboratory clearing of BCI (Environmental Sciences Program of the Smithsonian Institution). Because the bird censuses were conducted in August and September, we present the rainfall data in years that begin 16 September. We further break down rainfall into three periods: late wet season (16 September–30 November), dry season (1 December–15 April), and early wet season (16 April–15 September). The periods include the beginning of the rainy and dry seasons for most years of the study.

The abundance of Katydid and Roaches

Large orthopterans comprise 40–60% of the nuptial or nestling prey items for the four study species (Greenberg 1981; Gradwohl and Greenberg 1982). We present tallies of katydids and roaches from the ultra-violet light traps operated by H. Wolda (Environmental Sciences Program) on BCI as an estimate of the yearly abundance of breeding food resources. The U.V. lights, operated at 7 and 17 m heights in the forest understory, are more fully described by Wolda (1978a).

Results

Density of Antwrens and Antshrikes on BCI

The estimates of the number of antwren pairs per km² based on trailside censuses during the five rainy seasons

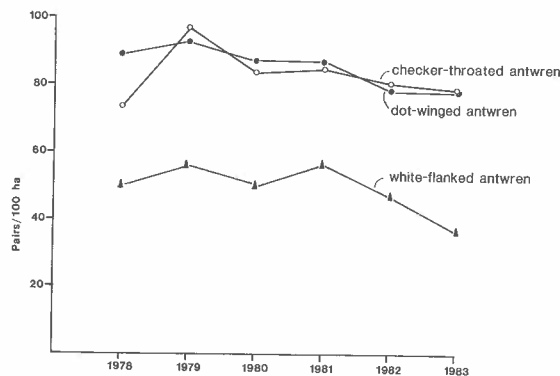


Fig. 1. The number of antwren groups per km² based on trailside censuses conducted late July through early September. The number of km censused per year were 10 (1979), 18 (1980), 27 (1981), 23 (1982), 29 (1983)

is presented in Fig. 1. Both the abundance and relative abundance of the three species has remained fairly constant; the coefficient of variation of density over the different years was 6% for Dot-winged, 8% for Checker-throated, and 15% for White-flanked Antwrens.

The number of pairs of Checker-throated and Dot-winged Antwrens (which co-defend identical territories on BCI) remained constant on the intensive study plot (Table 1). On the 6 ha study plot (1977–1983) we found 4 groups of each species, and on the 12 ha plot (1980–1983) we censused 9 groups of each species each year (8 total and 2 partial territories). The density estimate from our study plot was 75 groups per km² which is quite similar to the overall mean of 82/km² found on the trailside censuses.

The number of White-flanked Antwren groups varied on the intensive study site from 1–3 (6 ha) and 2–7 (12 ha). The overall mean density from the 12 ha plot was 42/km², which is only slightly less than the 49/km² derived from the trailside censuses.

Slaty Antshrike densities, measured only on the intensive plot, remained constant; 8 pairs on the 6 ha and 16 pairs on the 12 ha plot over eight years. The density estimate on the plot was 133 pr/km², which agrees well with the estimate of 108 pr/km² obtained by Oniki (1975) during the early 1970s.

Adult survivorship

Checker-throated Antwrens had variable and high adult survivorship (Table 2). The grand mean percent survivorship for all years was 62%, but the range was 9–93%. The chi-square for the homogeneity of adult survivorship between years was 29.3 (*df* = 6, *P* < 0.001). Although the sample size for survivorship values for White-flanked Antwrens is very small, the same general pattern emerges: high but variable survivorship (\bar{X} = 64%, 15–100%, χ^2 = 11.6, *df* = 6, 0.05 < *P* < 0.10). Slaty Antshrikes showed moderate and variable annual survivorship (\bar{X} = 54%, range = 35–92%, χ^2 = 11.8, *df* = 6, 0.05 < *P* < 0.10).

Natality

Both Dot-winged and Checker-throated antwrens had moderate and similar proportions of groups with young each

Table 1. The number of pairs or family groups of Checker-throated (and Dot-winged) Antwrens, White-flanked Antwrens, and Slaty Antshrikes on the 6 and 12 ha study site (6 ha is included within the expanded 12 ha plot; numbers are rounded to the 1/2 pair)

Year	Species		
	Checker-throated 6/12 ha	White-flanked 6/12 ha	Slaty Antshrike 6/12 ha
1977	4/?	1/2	6/?
1978	4/?	2/6	6/?
1979	4/?	2/6	6/?
1980	4/?	3/6	6/?
1981	4/9	3/7	6/15
1982	4/9	2/4.5	6/15
1983	4/9	1.5/4	6/15
1984	4/9	3/5	6/15
\bar{X}	4/9	2/5	6/15
C.V.	0/0	31%/33%	0/0

Table 2. The annual survivorship of settled adult antwrens and antshrikes on the intensive study site. Numbers are the percent survivorship from year 1 to year 2 with the number of birds marked in year 1 in parentheses

Year	Species		
	Checker-throated	White-flanked	Slaty Antshrike
1977–1978	9 (11)	100 (3)	42 (12)
1978–1979	64 (11)	100 (3)	47 (15)
1979–1980	66 (12)	30 (10)	53 (15)
1980–1981	50 (14)	66 (3)	92 (12)
1981–1982	93 (15)	60 (10)	35 (20)
1982–1983	89 (19)	83 (6)	60 (15)
1983–1984	57 (21)	15 (6)	41 (17)
\bar{X} (s.e.)	62 (11)	64 (12)	54 (11)
χ^2	29.3 (<i>P</i> < 0.01)	11.6 (<i>P</i> < 0.10)	11.8 (<i>P</i> < 0.10)

The percentage of color-marked birds that survived from September of year 1 to September of year 2, with the exception of 1977–1978 when the censuses were conducted in early November

Table 3. The percentage of antwren groups located on trailside censuses (conducted during August and September of each year) with young juveniles (< 2 months old). The numbers are the percentage of groups with young and the number of censused groups in parentheses

Year	Species		
	Dot-winged	Checker-throated	White-flanked
1979	13 (54)	23 (56)	50 (40)
1980	17 (42)	11 (30)	24 (30)
1981	30 (60)	27 (50)	50 (40)
1982	24 (50)	28 (46)	40 (35)
1983	21 (48)	24 (54)	27 (37)
\bar{X} (s.d.)	21 (6.5)	23 (6.8)	38 (12.3)
χ^2	3.8 n.s.	1.3 n.s.	10.6 <i>P</i> < 0.05

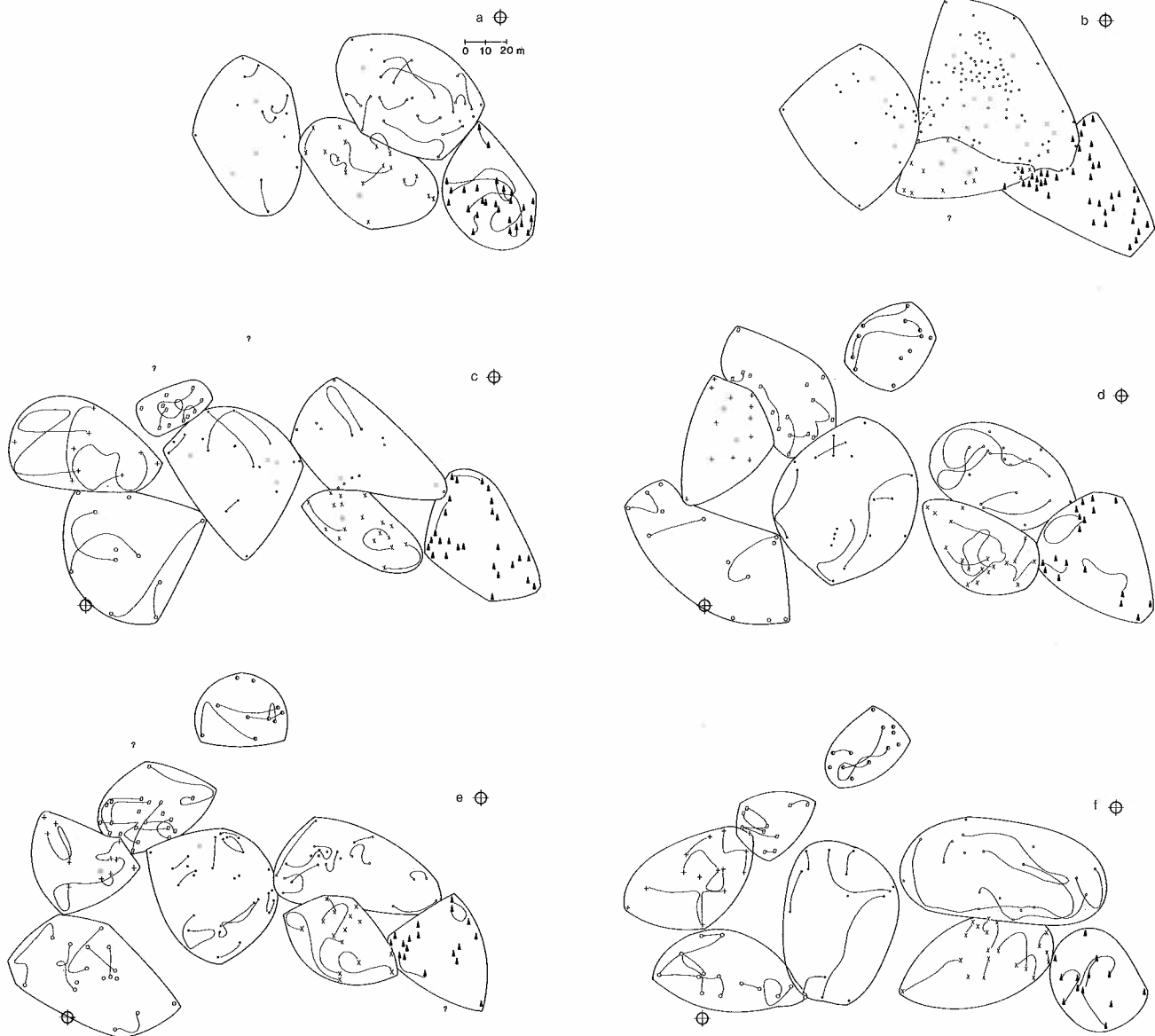


Fig. 2a-f. The home-ranges of Checker-throated (and Dot-winged) Antwren groups for each year of the study. Each point denotes a resighting; points connected by lines indicate 2 h followings (no more than one resighting is recorded per 6 h period). Different symbols represent different groups within a year only. The study area increased from 6 to 12 ha in 1980. The register mark is placed at the same point in the grid for each Figure. Solid triangles indicate the group that suffered mortality in 1977. ? indicate areas where no antwren groups were seen and too little time was spent to determine if these regions are true hiatuses: **a** 1977-78, **b** 1978-79, **c** 1981, **d** 1982, **e** 1983, **f** 1984

year (Table 3). White-flanked Antwren, however, had a high and significantly variable proportion of groups with young ($\bar{X} = 33\%$, 21-50%, $\chi^2 = 10.36$, $P < 0.05$).

Territory location

Checker-throated Antwren territories remained almost identical over the seven breeding seasons of the study. The four territories on the 6 ha and the eight territories on the 12 ha plot are depicted in Fig. 2. The territory maps are the outline of all observations made during the rainy season each year. The areas of variability are almost always those for which few observations of adjacent groups were made, so that boundaries could not be mapped from border interactions.

Territories of White-flanked Antwren groups are much more variable in their location from year to year (not depicted). Slaty Antshrike territories are more difficult to map because the birds remain localized and patrol their territory boundaries less frequently. Because of this, we have only been able to determine that the number and general location of territorial pairs has remained constant, although the apparent boundaries varied in location more than those of Checker-throated/Dot-winged Antwren territories.

Rainfall

Rainfall varied considerably from year to year in amount and seasonality (Table 4). Two climatological extremes occurred during the study: a very dry, dry season December

Table 4. Rainfall (mm) recorded for the laboratory clearing on Barro Colorado Island (courtesy D. Windsor)

Year	Season			
	Late rainy	Dry	Early rainy	Total
1977-1978	1,084.5	194.0	1,163.4	2,441.9
1978-1979	687.7	92.4	1,551.3	2,331.4
1979-1980	719.9	464.6	1,863.9	3,048.4
1980-1981	802.0	736.0	2,269.8	3,807.8
1981-1982	1,182.6	833.2	1,017.4	3,033.2
1982-1983	640.5	60.0	1,614.9	2,315.4
1983-1984	850.5	362.4	1,479.3	2,692.2

Table 5. The total capture of katydids and roaches at the ultra-violet light traps on Barro Colorado Island 1977-1983 (data courtesy H. Wolda)

Year	Season		
	Early rainy	Late rainy-Dry	Total
1977-1978	3,258	2,436	5,694
1978-1979	2,077	1,686	3,763
1979-1980	1,978	912	2,890
1980-1981	1,877	1,313	3,190
1981-1982	2,067	1,100	3,176
1982-1983	1,742	1,386	3,131
\bar{X} (c.v.)	2,167 (25%)	1,472 (37%)	3,640 (29%)
\bar{X} (c.v. 1978-1983)	1,948 (7)	1,280 (23)	3,230 (10)

Early rainy is 16 April-15 September and late rainy-dry is 16 September-15 April

1982 to May 1983 (resulting from El Niño) and a very rainy period during late 1981 and early 1982.

The Abundance of Orthopterans

The number of orthopterans captured in the light traps was remarkably constant from year to year, with the exception of a notably large catch during the 1977-1978 sample (Table 5). For the years of this study, the coefficient of variation of annual capture was 29%; for 1979-1983 the c.v. was only 10%. The capture rate during the main breeding season, April to September, was particularly constant (c.v. was 25% for all years, and 6% for the last six years).

Relationships between rainfall patterns and adult survivorship

We found no correlation (Fig. 3a) between the amount of rainfall during the dry season (December 1-April 15) and percent survivorship in either Slaty Antshrike ($r_s = +0.11$) or Checker-throated Antwren ($r_s = -0.25$); White-flanked Antwren mortality figures were not used, as they were based on very small sample sizes. The data do suggest a possible correlation between the amount of rainfall in the late rainy season (Fig. 3b) and the adult survivorship during the following year. While the correlations are not significant (Slaty Antshrike $r_s = -0.60$, Checker-throated Antwren $r_s = -0.17$), these results are heavily influenced by one outlying point for each species. If the high survivorship values for

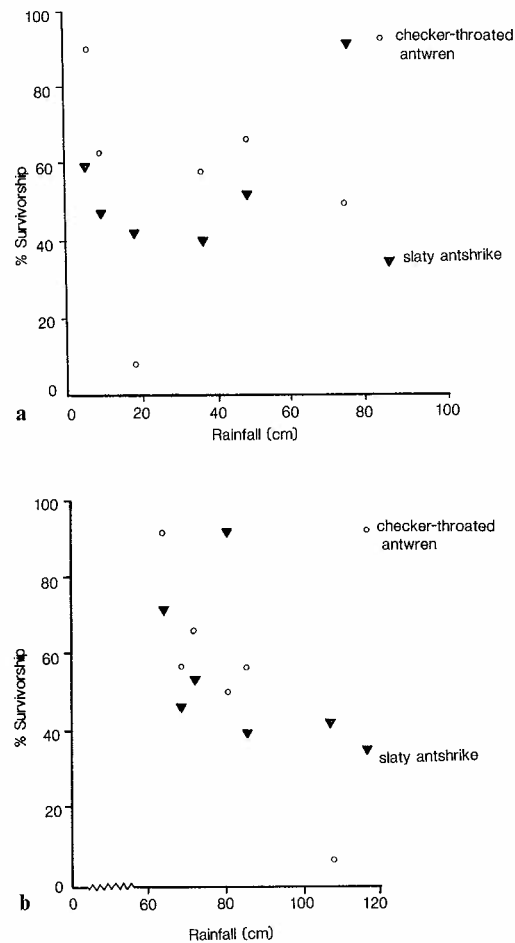


Fig. 3a, b. Survivorship of settled adult Checker-throated Antwrens and Slaty Antshrikes from September to September plotted against rainfall in **a** dry season, 1 December-15 April and **b** late wet season, 16 September-30 November

the antwren (1981-1982) and the antshrike (1980-1981) are removed, the remaining correlations are quite high (-0.97 , -0.77). Clearly the sample of seven years is insufficient to establish the correlation, but the possibility of such a relationship deserves further study.

Discussion

Stable density

The four species of antbirds we studied had stable populations over the eight breeding seasons. In fact, the number of pairs of Dot-winged and Checker-throated antwrens and Slaty Antshrikes on our intensive study site showed no annual variation at all. For the Checker-throated and Dot-winged Antwrens the island-wide census data had an overall coefficient of variation of only 6-8%, indicating a small degree of annual change in island-wide abundance. Only the White-flanked Antwren showed any variation in the number of pairs present on the study plot, and it had somewhat more variable island densities as well (c.v. = 15%). The trailside census technique should be more greatly affected by census conditions and random fluctuations than the censuses based on maps of color-marked (or otherwise

recognizable) birds. Territorial maps provide a highly accurate estimate of density based on a small sample of birds; the trailside censuses provide a broad, yet crude confirmation of the stability observed on the smaller study plot.

Rigid territoriality

The locations of territory boundaries for the Checker-throated/Dot-winged Antwren territories and the general locations of Slaty Antshrike territories were generally constant over the entire study. This constancy might be based on stable habitat features. These three species are particularly strongly associated with areas of dense vine-tangles, which occur in areas of old forest disturbance. The Checker-throated/Dot-winged Antwren territories generally contain two such areas between which the antwren groups shuttle (see Gradwohl and Greenberg 1980 for a territory-use map and vegetation analysis for a focal antwren group). Slaty Antshrike pairs are associated with one area of dense vine-tangles. The core areas of the territories on the 6 ha plot remained largely unchanged 1977–1983, suggesting that such areas may be stable features of a tropical forest. One exception was the creation of a new center of vine-tangled vegetation with a large tree fall in late 1979. The gap became heavily overgrown with vine vegetation by 1983, but was incorporated into existing Checker-throated-Dot-Winged Antwren and Slaty Antshrike territories with little shift in boundaries. An alternative hypothesis for the basis of stable territories is that they are traditional and conservative, and not based on particular habitat features. Boundaries are maintained upon the disappearance of a bird or a pair by the continued presence of the mate, neighbors and other species sharing the boundaries. Territories would have to be conservative in the sense that they are of sufficient size to guarantee enough area of disturbance.

Turn-over in territorial adults

Despite the apparent rigidity of the territories of the two antwren and antshrike species, the actual territorial holders have shown considerable turnover. Adult mortality averaged 25–46% per year for these species; the year to year variation in mortality has been high, and in some years a majority of all marked adults of a species have disappeared. By 1980, for example, none of the adults of these species marked in 1977 were still present on the study area.

Natality

We were able to detect significant annual variation in the proportion of groups with fledged young only in the White-flanked Antwren. Considering the low productivity of tropical birds, such variation, were it to occur, might take very large samples of censused groups to detect. At the resolution of this study, Checker-throated and Dot-winged antwrens seem to produce a fairly constant number of young per year. This constancy occurs despite a nearly two-fold range in the amount of rainfall during the early rainy season (Table 4), which probably includes the peak breeding effort of the antwrens. On the other hand, the number of orthopterans used by antwrens extensively when feeding young (Gradwohl and Greenberg 1982), was nearly constant for the early rainy seasons in the years that we censused juveniles (1979–1983).

Stable territoriality and social regulation of Antwren and Antshrike populations

We suggest that, in a proximate sense, the rigid territorial system found in Checker-throated and Dot-winged Antwrens and perhaps the Slaty Antshrike, regulates their populations on BCI. When considering the regulation of these forest birds, we assume that the island has closed populations. Insularity combined with the hesitancy that most antbirds show toward crossing water gaps (Willis 1974) make any significant amount of emigration or immigration to or from BCI unlikely. Further, BCI is covered by forest, and alternative "buffer" habitats are essentially non-existent.

It is possible that natality counterbalances mortality closely enough to give the appearance of a stable population regulated by territoriality. The observation of the fate of fledged young antwrens argues against this proposal. In Dot-winged Antwrens, young remain with parents for a period up to a year. Independent young of both sexes are found with about half of the pairs throughout the non-breeding season; this suggests that in this species a reservoir of potential territorial birds exists (Greenberg and Gradwohl 1985). Young of the Slaty Antshrike and Checker-throated Antwren usually spend less time when parents (Oniki 1975; Greenberg and Gradwohl 1985), but young of these species are often observed dispersing onto our study plot during the late rainy and dry seasons. We have particularly detailed notes on the occurrence of interloping Checker-throated Antwren young (immatures are distinguishable by their gray, rather than brown or gold irides – Gradwohl and Greenberg 1980). During each August and September we observed on the average of five immature antwrens (s.e. = 3.2) on our intensive study site; these young were observed displaying against members of their own sex (members of established territorial pairs) for long periods. Young of both sexes were involved: six females and seven males. Such dispersal appears to be quite local; six of the ten fledglings marked on our study site eventually settled as new pair members in established territories on our study site.

We were unable to conduct removal experiments on territorial birds on our study site. However, on one occasion (see Gradwohl and Greenberg 1980) a mist-netting accident removed a pair of Checker-throated Antwrens from a previously mapped territory (see territory marked by dark triangles in Fig. 2). After a succession of two immature females and three immature males temporarily occupied the territory, a pair eventually remained to maintain a territory with similar boundaries to the removed pair. In the subsequent six years, the territory had two new males and three new females resulting from vacancies left by natural mortality, and the boundaries remained similar to those of the original territory.

Our argument, that the territoriality of antwrens and antshrikes maintains the breeding population at a constant level in the face of a seasonal surplus of young, seems to contradict our natality data which, when compared with adult mortality shows a short-fall of young each year. However, the census of young antwrens was not meant to completely census the production of young, but to assess the proportion of groups with young at the peak of the breeding season.

The observation of rigid territoriality in the face of at

least occasional surpluses of immatures of both sexes, combined with the lack of any buffer habitat, suggests that the populations of these species are probably socially regulated. The ultimate factors that determine territory size and hence underlie regulation of the breeding population are not known. The dense vine-tangle areas apparently represent a discrete and indivisible resource to these birds. The defense of one or two such areas may provide the minimum safe area for foraging and thus be a conservative response to potential fluctuation in foraging conditions. This view would be similar to the one proposed for the Dunlin (*Calidris alpina*) by Holmes (1966). On the other hand, the birds may be defending areas that insure a necessary reduction in the level of nest predation, if nest predation is density dependent (Yom-tov 1974). Whatever the ultimate basis of the territorial system, the birds do not track the subtle variability in feeding conditions. Although the abundance of preferred nestling food, orthopterans, is relatively stable (based on light trap data), the capture for the first year of the study was nearly double the mean annual capture for the subsequent years. We observed no change in the density of antwrens and antshrikes on our study plot between the first year and subsequent years. In addition, many other groups of arthropods show large year to year fluctuations in capture rate at light traps on BCI (Wolda 1978a, b). Antwrens should experience variation in the availability of these alternative prey. These results support the proposal of Schoener (1985) that insectivorous birds and lizards have more stable populations than their arthropod prey.

Such stable territorial systems have been reported for a variety of long-lived birds such as Tawny Owls (Southern 1970), crows (Charles 1972, Yom-tov 1974) and Oystercatchers (Harris 1970). Stable territories are reported from one tropical forest primate (Lemurs, Jolly 1978). To our knowledge stable territorial systems have not been explicitly described for forest passerines, although the multispecific territorial systems described by Munn (1985) for Amazonian forest birds strongly suggest that territoriality regulates population densities for many tropical species.

Other studies

Few studies of tropical birds provide long-term data that are comparable to those we have presented. Willis (1974, 1980) presented a survey of the populations of ant-following birds monitored on BCI for 10 years. In this study he found a general trend towards very stable populations with a few notable exceptions. The exceptions, however, include two antbird species that displayed long-term systematic declines rather than marked annual fluctuations.

Another line of evidence that many tropical bird species display population stability in the face of environmental variation is the data presented by Wright (1979) on bird abundances on small islands and mainland forests around Lake Gatun in Panama (including BCI). He showed that most insectivorous understory birds did not differ significantly in abundance between various study sites, despite demonstrated differences in food availability and the species density of potential competitors. Wright attributed the lack of adjustment of bird density to resources to foraging stereotypy, but it could just as well be a result of rigid territorial systems.

Karr (1980) and Karr et al. (1982) have emphasized the

dynamic nature of tropical bird populations based on the number of mist-net captures over a ten year period on a study site in the Panama Canal Area. Although it is well known that some tropical forest species, such as the Slaty Seedeater (*Sporophila schistacea*), show dramatic fluctuations in abundance (Willis and Eisenmann 1979), the studies of Karr provide the only data that suggest that a number of forest birds show such fluctuations. The emphasis in his papers on the dynamic nature of tropical forest bird populations does not necessarily contradict the picture of stability that we portray in this paper. We have selected species that, by the nature of their territorial behavior, are more tractable for population studies. In addition, Karr (1983) has suggested that the most severely fluctuating species populations may have already gone extinct from BCI. Still, we suggest that the mist-netting sampling technique which generated the data presented in Karr (1978) and Karr et al. (1982) will tend to overestimate the degree of population fluctuation for the following reasons:

1. Behavioral variables affect the probability that birds will be captured. Variation in behavior can cause fluctuations in capture rate even when population size is constant. A seasonal or annual shift in foraging height distribution of a species, for example, would result in a pseudo-fluctuation in its estimated abundance.

2. In these studies, the mist nets cover a relatively small area (2 ha). A plot of this size is only slightly larger than some of the smallest territories found in a tropical avifauna (our studies, Willis 1974). The estimates derived from netting will be influenced by local variation involving relatively few birds and hence may not be generalizable to entire populations (a problem noted in Karr 1983).

3. The data are presented as the number of captures per species for a given netting period. The number of individuals captured is probably smaller than the number of captures. Because the study site is small, the statistical independence of each capture is questionable. More importantly, critical biological information is lost because immatures are not distinguished from adults, even in species for which such determinations are easily made (i.e., Checker-throated Antwren). Fluctuations in capture rate may reflect variation in family group size or in the rate of dispersal onto the plot from other areas, rather than changes in the number of settled territorial (potentially breeding) adults.

We conclude that at least some species of tropical forest birds have very stable populations in the face of environmental fluctuations. How true this is for tropical birds in general cannot be determined until more detailed population studies are conducted on species in a variety of ecological guilds.

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