

# SEXUAL ROLES IN THE DOT-WINGED ANTWRN (*MICRORHOPIAS QUIXENSIS*), A TROPICAL FOREST PASSERINE

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**ABSTRACT.**—Dot-winged Antwrens maintain long-term pair bonds on year-long territories in tropical forests and woodland of Central and South America. Pairs partition breeding-related activities nearly equally. Like other antbirds (Formicariidae), both sexes incubate and brood. Both sexes participate equally in territorial maintenance behavior, which primarily involves active border displays. Initial investment in offspring is possibly equalized by long-term nuptial feeding of females by males. Overall, both sexes contribute equally to nestling care, although considerable variation is observed between nests, much of which probably results from variation in the foraging ability of parents. Females feed young consistently less often than do males during the early part of the nestling period and may be recovering from depletion of reserves resulting from egg production. In most pairs females bring more spiders than do males. This difference in prey type is unexpected, because the pair forages close together in the same microhabitat and their bill size is similar. Pairs are distinct in their interactions: some pairs have a rigid feeding order, and others do not. *Received 8 January 1982, resubmitted 3 January 1983, accepted 24 May 1983.*

LONG-TERM associations of male and female passerines occur frequently in tropical areas (Kunkel 1974), particularly in forests (Willis 1972). These stable pair-bonds, often occurring on year-long territories, have features that should promote the evolution of equal sex roles. The annual establishment of pair bonds and territories, so integral a part of temperate-zone bird life, is far less prevalent in tropical forest avifaunas. The division of labor between members of long-term monogamous associations has been quantitatively described for only a few bird species, notably species of antbirds (Formicariidae, Willis 1967, 1972; Oniki 1975). We describe in this paper the sexual roles of the Dot-winged Antwren (*Microrhophias quixensis*) with emphasis on territorial maintenance and nestling care.

Dot-winged Antwrens, ranging from Mexico to Bolivia and Brazil (Meyer de Schauensee 1970), are common in dense vine-tangled vegetation in the low-elevation woodlands and forests of Panama (Ridgely 1976). Dot-winged Antwrens are dimorphic in plumage: males are predominantly black, and females have bright

rusty underparts. These birds have qualities that make them particularly appealing for studies of nestling care. Adults are noisy and tame around the nest, often parading for several minutes with prey items carried at the tip of the bill. The approach to the nest is accompanied by constant "pew" notes and often involves rapid maneuvers that resemble hover-gleaning. This boldness near the nest distinguishes this species not only from other local antwrens but from all forest birds in Panama with which we are familiar. This conspicuous behavior, which includes occasional singing from the nest, may be related to the relatively inaccessible location of Dot-winged Antwren nests (Gradwohl and Greenberg 1983). The nests on Barro Colorado Island are usually suspended from thin vines over dense vine tangles and may be safe from most mammalian predators. In the few instances of nest predation that we observed, the contents were removed and the nest remained intact; we attributed this predation to snakes.

## METHODS

We observed several antwren pairs or family groups almost daily, from November 1978 to September 1979, on our intensive study area on the plateau of Barro

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Colorado Island (BCI), Panama (see Gradwohl and Greenberg 1980). Each month we walked 10–30 km of trail on BCI, recording the composition and activity of antwren groups, paying particular attention to whether or not the groups were involved in territorial border interactions (described in Gradwohl and Greenberg 1980).

To study nestling care, we observed 10 nests of eight pairs for a period spanning the wet (breeding) season, May–August 1979. The nestling period lasts approximately 9 days. Roughly half (85 h) of the observations were made during days 1–5 and half (74) during days 6–9 of the nestling period. We were able to observe the nests from 2 to 3 m without blinds; birds showed only brief disturbance at our presence. From this vantage point we could identify 74% of the arthropods carried by adults to order (and family in Orthoptera) and estimate the size of 80%. We estimated the length of prey by comparison with the exposed culmen of the antwren. These estimates were converted to crude live biomass estimates by using the length–weight regression of BCI arthropods of Zug and Zug (1978). For arthropod groups not included in their analysis (larvae), we estimated the weight based on known arthropod groups with similar gross shapes. Most common groups, comprising 90% of our recorded prey, were included in their analysis.

We determined the degree of sexual dimorphism in bill size in Dot-winged Antwrens by measuring adult specimens collected from Central America. Bill length was measured from the front of the nares to the tip, and width was measured at the front to the nares.

## RESULTS

*Territorial defense.*—Territorial defense occurs year round and can make up a substantial portion of the activity budget of an antwren pair (total time spent in display = 21.5%,  $n = 906$  total observations, monthly range = 13–37% in display). The proportion of Dot-winged Antwren groups in border displays was consistent throughout the year, with a peak in March ( $\bar{x} = 31\%$ ) and April ( $\bar{x} = 37\%$ ), preceding the start of the wet season. We found that boundary displays occurred two to three times daily and usually lasted 10–30 min (occasionally hours) in the groups that we followed for long periods (Gradwohl and Greenberg 1980, Gradwohl in prep.). Both sexes displayed simultaneously, but, occasionally, only males or females would display for long periods. This was particularly common during the breeding season when only one bird in a pair was present; presumably, the other bird was incubating or brooding. With

only a few exceptions, all displays were oriented toward birds of the same sex. On several occasions, however, we observed females chasing solitary males.

*Initial reproductive investment.*—Females contribute heavily to the initial reproductive-investment effort through the formation of eggs. Nuptial feeding, during which males present the females with large prey items, is common and occurs through long periods of the breeding season. Nuptial feeding preceded all seven copulations observed. This contribution might help to equalize the initial parental investment in offspring (Smith 1980b). This phenomenon is difficult to study in Dot-winged Antwrens but is more conspicuous in the Checker-throated Antwren (*Myrmotherula fulviventris*). Gradwohl (unpubl. data) estimates that a male Checker-throated Antwren provided a female with 46% of her food during the period preceding egg production.

*Nest building.*—During the course of our trail-side censuses, we observed nest building by 37 pairs. In all cases the building occurred when the mixed-species flock with which the antwrens were traveling moved close to the nest site; both pair members rapidly gathered and added material to the nest.

*Incubation.*—As in all antbirds studied so far (Skutch 1949, 1969; Willis 1967, 1972; Oniki 1975), both sexes of Dot-winged Antwrens participate in incubation. We have few periods of continuous observation of nest attentiveness, but, during checks of Dot-winged Antwren nests throughout the day, we found the male on the nest roughly half of the time ( $n = 6/14$  nest checks).

*Brooding.*—Both sexes brood the young during the first few days of the nestling period. During our daytime nest observations, males brooded more than females in three out of four nests (Table 1). We do not suggest that males in general do more brooding than females. Our data provide no basis, however, for the proposition that there is a female bias in brooding, which is a more common pattern in passerines (Kendeigh 1952).

*Nestling feeding.*—We spent considerable time quantifying the type and amount of food brought into the nest by each sex, because for birds the feeding of nestlings is presumably one of the most demanding aspects of parental care. For all of the nests except one, both sexes made approximately the same number of visits

TABLE 1. Frequency and length of brooding by different sexes at Dot-winged Antwren nests on Barro Colorado Island.

| Nest | Hours of nest watch | Frequency and time of brooding |              |
|------|---------------------|--------------------------------|--------------|
|      |                     | Male (min)                     | Female (min) |
| 1    | 22.75               | 7 (222)                        | 17 (203)     |
| 2    | 13.50               | 2 (20)                         | 1 (1)        |
| 3    | 9.75                | 3 (193)                        | 2 (40)       |
| 4    | 19.75               | 4 (35)                         | 5 (49)       |

(Table 2). In these nine nests male visits comprised 51% of the total; the range was great (35–69%). In one nest the male made essentially all (47/48) of the observed visits. The overall mean, including this outlier, was 55% male visits.

This large variation could result, in part, from the portion of the nestling period during which particular nests were watched. When watches conducted at an early stage (days 1–5) were separated from those conducted at a later stage (days 6–9), a distinct sexual difference emerged (Table 2). Males made 53–98% of the visits during the six early watches and 35–52% of the visits during late watches (Mann Whitney *U*-test; 6, 7;  $U = 21$ ,  $P < 0.01$ ).

Dot-winged Antwrens brought primarily orthopterans (crickets, katydids, and roaches) and spiders to their nestlings. Consistent differences were noted in the major prey taxa brought by males and females (Table 3). Females brought in significantly more spiders overall (21% versus 11%). This bias occurred in six of the eight nests that had large enough sample sizes for a comparison (Wilcoxon Signed-Rank Test  $s = 3$ ,  $n = 8$ ,  $P < 0.05$ ).

Males brought in significantly longer prey items in three of the eight nests (Table 4, *T*-test corrected for multiple comparisons). When estimates of feeding rates and prey size are combined to form an estimate of biomass brought to the young, the bias toward males is slight ( $\bar{x} = 55\%$ ) and the variability great. This variability results both from the number of trips and the relative size of prey brought in. No attempt was made to distinguish early from late watches, because the sample size of prey-size estimates was too small.

*Behavioral interaction within pairs.*—After brooding ceased, male and female Dot-winged Antwrens foraged together while capturing

TABLE 2. Percentage of trips to nest by male Dot-winged Antwrens visiting nests on Barro Colorado Island.

| Nest            | Months | Time watched (h) | Percentage of trips |                   | Total |
|-----------------|--------|------------------|---------------------|-------------------|-------|
|                 |        |                  | Early <sup>a</sup>  | Late <sup>a</sup> |       |
| 1 <sup>b</sup>  | May    | 25.75            | 66 (83)             | —                 | 66    |
| 2               | May    | 13.5             | 53 (25)             | 39 (39)           | 45    |
| 3               | May    | 13.5             | —                   | 35 (38)           | 35    |
| 4               | July   | 4.0              | —                   | 44 (39)           | 44    |
| 5               | July   | 15.5             | —                   | 47 (112)          | 47    |
| 6 <sup>b</sup>  | July   | 12.5             | —                   | 52 (82)           | 52    |
| 7               | July   | 12.25            | 56 (18)             | 46 (35)           | 49    |
| 8 <sup>b</sup>  | Aug    | 9.75             | 71 (14)             | —                 | 69    |
| 9               | Aug    | 19.75            | 60 (15)             | 49 (94)           | 53    |
| 10 <sup>b</sup> | Aug    | 9.75             | 98 (48)             | —                 | 98    |

<sup>a</sup> Percentage of trips by males (number of trips observed).

<sup>b</sup> Nest 1, 8 by one pair and 6, 10 by another pair.

food for nestlings. Under most circumstances, it was hard to discern any structured relationship, such as dominance, between members of the pair (see Smith 1980a). In some pairs, however, there was a distinct order in which nestlings were fed. This order could be discerned in the behavior of the pair when they returned from long trips (>10 m), which comprised 30–90% of the total forays. Short forays usually occurred rapidly, in bursts between long trips (mean trip time was 5 versus 22 min); an order to these feedings was hard to determine. In three nests, one pair member consistently fed first after returning from long trips (Table 5). On occasion, the antwren without priority would wait, insect in bill, for its mate to capture and bring in a prey item before it visited the nest. The order had no apparent sexual bias; in two pairs the male had priority, and in one the female had priority.

We have no evidence that this ordered relationship involved dominance. Buzzing and chasing displays, which were prevalent in territorial border interactions, were observed between members of some pairs when they foraged near the nest. This presumably aggressive behavior occurred most frequently after one member of the pair had seized a fecal sac from the nest. Birds might compete for fecal sacs (Skutch 1976) and visiting the nest first after a long absence might guarantee access to the fecal sacs (fecal sacs were often eaten by adult Dot-winged Antwrens). Our observations (Table 5) indicate that there was no sexual bias as

TABLE 3. Percentage of prey types brought by male and female Dot-winged Antwrens to nests on Barro Colorado Island.

| Nest                       | Sex    | n<br>(arthropods) | Percentage of prey |          |             |         |
|----------------------------|--------|-------------------|--------------------|----------|-------------|---------|
|                            |        |                   | Orthoptera         | Spider   | Caterpillar | Beetle  |
| 1                          | Male   | 40                | 65                 | 0        | 25          | 10      |
|                            | Female | 19                | 53                 | 26       | 0           | 11      |
| 2                          | Male   | 23                | 52                 | 13       | 17          | 9       |
|                            | Female | 32                | 50                 | 25       | 3           | 6       |
| 3                          | Male   | 26                | 69                 | 4        | 19          | 4       |
|                            | Female | 40                | 65                 | 8        | 3           | 5       |
| 4                          | Male   | 12                | 66                 | 17       | 8           | 8       |
|                            | Female | 15                | 27                 | 15       | 13          | 7       |
| 5                          | Male   | 31                | 81                 | 16       | 0           | 0       |
|                            | Female | 38                | 63                 | 13       | 5           | 13      |
| 6                          | Male   | 35                | 71                 | 11       | 9           | 6       |
|                            | Female | 38                | 66                 | 24       | 3           | 0       |
| 7                          | Male   | 20                | 45                 | 5        | 20          | 10      |
|                            | Female | 21                | 57                 | 24       | 14          | 0       |
| 9                          | Male   | 48                | 48                 | 23       | 10          | 6       |
|                            | Female | 39                | 38                 | 31       | 10          | 8       |
| Grand mean percentage (SE) |        |                   |                    |          |             |         |
|                            | Male   |                   | 62 (4.4)           | 11 (2.7) | 11 (2.6)    | 7 (1.2) |
|                            | Female |                   | 52 (4.8)           | 21 (2.8) | 6 (1.9)     | 6 (1.6) |

to which birds got the fecal sac, nor did the individual feeding first usually get the fecal sac.

#### DISCUSSION

*Sexual roles in Dot-winged Antwrens.*—Dot-winged Antwren pairs exhibit an equal division of nesting labor. Some of this reflects patterns found among antbirds generally. That Dot-winged Antwrens share incubation and brooding, for example, is not surprising, because it is a general pattern in all antbirds studied. On the other hand, territorial defense is usually not shared equally between sexes in other antbirds. Spotted Antbird (*Hylophylax naevioides*) and Slaty Antshrike (*Thamnophilus punctatus*) males give distinct advertising songs more often than do females (Willis 1972, Oniki 1975). Even among other antwrens for which border display is the dominant mode of territorial maintenance behavior (Munn and Terborgh 1979, Gradwohl and Greenberg 1980), a bias occurs in the frequency of participation of the sexes (fewer female-female border displays). On BCI, two species of *Myrmotherula* have predominantly male-male border displays.

The overall contribution to nestling feeding is nearly equal for both sexes in Dot-winged Antwrens. It is hard to evaluate how widespread such equality is among antbirds, because the data available are presented in terms of trips to nest only and are based on one nest per species or on data lumped from several nests (Skutch 1949; Willis 1967, 1972, Oniki 1975). Slaty Antshrike males made the same number of feeding trips as females (Oniki 1975) but brought in larger prey items. In Spotted Antbirds males visited more than females, except in the first few days of nestling life (Willis 1972). Our observations of the care of post-fledgling White-flanked and Checker-throated antwrens (*Myrmotherula axillaris* and *M. fulviventris*) are that females are more closely associated with the young and feed juveniles more often than do males. The equal contribution of male and female Dot-winged Antwrens is not surprising for several reasons: (a) through nuptial feeding, the initial investment of males and females in their offspring may be equalized; (b) because each sex performs other activities, such as territorial defense, with equal frequency, there is no differential competition with other aspects of time-activity budgets; and (c) both

TABLE 4. Mean length (mm, SD in parentheses) of prey brought by males and females to Dot-winged Antwren nests on Barro Colorado Island.

| Nest <sup>a</sup> | n <sup>b</sup> | Male                    | Female     | Estimated percentage biomass by male |
|-------------------|----------------|-------------------------|------------|--------------------------------------|
|                   |                |                         |            |                                      |
| 1                 | 55, 28         | 10.8 (4.7)              | 10.5 (5.5) | 66                                   |
| 2                 | 29, 35         | 11.3 (3.5)              | 10.9 (3.9) | 44                                   |
| 3                 | 27, 51         | 11.9 (4.7)              | 11.9 (6.1) | 34                                   |
| 4                 | 17, 22         | 9.7 (3.9) <sup>c</sup>  | 8.1 (4.9)  | 48                                   |
| 5                 | 53, 59         | 9.5 (4.6)               | 9.6 (4.8)  | 47                                   |
| 6                 | 43, 39         | 9.2 (3.8)               | 9.0 (3.5)  | 54                                   |
| 7                 | 25, 26         | 12.0 (5.8) <sup>c</sup> | 9.9 (7.5)  | 66                                   |
| 9                 | 53, 47         | 8.4 (3.9) <sup>c</sup>  | 7.3 (3.7)  | 61                                   |

<sup>a</sup> Sample size too small for one or both sexes in nests 8 and 10.

<sup>b</sup> Male, female.

<sup>c</sup> Significant difference between sexes ( $P < 0.05$ ); *t*-test corrected for multiple comparisons.

sexes forage together and actively defend the territory against individuals of the same sex, so parentage of the offspring is unambiguous.

*Variation in relative feeding rates through the nestling period.*—The consistent increase in female participation in feeding from early to late in the nestling period is puzzling, because unlike other species in which this occurs (Royama 1967), both sexes of Dot-winged Antwrens brood. Females may be restoring their body condition from depletion that it may have suffered during egg production. Because predation on nestlings may be high (Skutch 1949, but see Oniki 1979), females may need to develop reserves for future clutches. Although nuptial feeding by males may tend to equalize prezygotic energetic investment, females probably suffer additional stress from actual egg production. As the probability of successful fledging increases, females may increase their investment in the nestlings. This shift indicates that even if overall contribution is equal, subtle differences may exist between sexes in the timing of parental care.

*Variation between pairs.*—Even within stages in the nestling period, considerable variation was observed in the relative contribution of each pair member. In the last 3 days of the nestling period, for example, male contribution ranged from 35 to 52% of the feeding trips. Dot-winged Antwren parents invariably forage together, even when gathering food for nestlings

TABLE 5. Sex that feeds the nestlings first in feeding bouts (with at least a 10-min gap from previous feeding).

| Nest | Sex feeding first |        | $\chi^2$ probability | Fecal sacs removed |        |
|------|-------------------|--------|----------------------|--------------------|--------|
|      | Male              | Female |                      | Male               | Female |
| 1    | 24                | 8      | 0.005                | 3                  | 7      |
| 2    | 9                 | 10     | N.S.                 | 4                  | 2      |
| 3    | 4                 | 26     | 0.005                | 4                  | 2      |
| 4    | 3                 | 6      | N.S.                 | —                  | —      |
| 5    | 24                | 5      | 0.001                | 2                  | 2      |
| 6    | 12                | 7      | N.S.                 | 3                  | 8      |
| 7    | 12                | 8      | N.S.                 | 1                  | 1      |
| 9    | 20                | 11     | N.S.                 | 7                  | 6      |

(unless one parent is brooding). The variation in contribution between mates does not result from time invested in foraging but from the variation in the rate at which prey are brought to the young. This was most apparent in short trips where one pair member consistently brought in several prey items during a period in which the other brought in only one.

Variation in pair behavior was most clearly seen in the ordered relationship of feeding parents. The relationship was well defined in a few pairs and showed no consistent sexual bias. This may relate to the relative age or experience of the pair members more than to a consistent sexual role.

*Difference in prey brought by males and females.*—The taxonomic differences in prey brought by males and females is surprising, as members of pairs forage in close proximity. In many passerines, males and females forage in different microhabitats during the breeding season (Morse 1968, Williamson 1971); this has not been shown to result in different diets (Robins 1975). The differences between the sexes of Dot-winged Antwrens in prey brought to the young apparently do not reflect differences in the size of prey (e.g. Orthoptera tend to be larger than spiders), because pairs that showed no difference in the size of prey taken had large differences in prey taxa.

No difference in bill size or shape correlates with differences in prey brought by males and females: bill length was 93.3 mm (SE = 0.9) in males and 91.3 (0.9) in females ( $t_{18,20} = 1.58$ , n.s.) and bill width was 37.4 mm (1.1) in males and 38.7 (0.8) in females ( $t_{18,20} = 0.89$ , n.s.).

*Possible significance of sexually dimorphic plum-*

age.—Plumage may not operate in different contexts in male and female Dot-winged Antwrens, but dimorphic plumage may facilitate sexual and individual recognition. This may be critical in Dot-winged Antwrens, because territorial border interactions involve high-speed chasing through dense tropical foliage. Contrasting plumages may allow individuals to concentrate their displays and rapid chasing toward individuals of the same sex, rather than wasting time chasing mates.

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