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SETTLEMENT PERIOD AND FUNCTION OF LONG-TERM TERRITORY IN TROPICAL MANGROVE PASSERINES[1]

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Abstract. We studied the territorial behavior of four insectivorous passerines residing in a tropical mangrove of northeastern Venezuela. Data were obtained through mist-netting and direct observation of color-banded individuals, regularly scheduled over two complete annual cycles. Seasonal variation in food resources (arthropods) and the birds' diet also were evaluated. A chronological cluster analysis was used to determine the settlement periods of territories, the former being illustrated by the probabilistic Jennrich-Turner method. Three of the four species hold year-round territories. These long-term territories were settled only once a year, immediately after the breeding season when food was abundant. The territorial settlement was synchronous among all individuals of a species, favoring strong modifications of the territorial mosaic. Considering the absence of territorial settlement prior to breeding and the high stability of territorial mosaics even during periods of low food abundance, territoriality during the non-breeding season primarily appears to ensure a breeding site for the next reproductive period. These results contrast with those from temperate regions where territoriality over the non-breeding season primarily enhances the survival of individuals during periods of food shortage.

Key words: Conirostrum bicolor; Fluvicola pica; Certhiaxis cinnamomea; Lepidocolaptes souleyetii; *territoriality; breeding; song activity; mangrove; Venezuela.*

INTRODUCTION

Although most studies of bird territoriality have been conducted during the breeding season (Baker and Mewaldt 1979), many species occupy territories year-round (hereafter referred to as "long-term territories"). This behavior is particularly well-developed in the tropics (Robinson 1945, Powell 1980, Karr 1981). For example, Rowan (1966) found that long-term territories were held by nearly 40% of the resident passerines of a tropical region of South Africa. Most studies of the function and settlement periods of long-term territories, however, have been conducted in temperate regions, where temporal stability and predictability of food resources are quite different. Here, most passerines holding long-term territories feed on vegetable matter during the winter months and, in the absence of renewal (Buskirk 1976), their food resources gradually decrease. Consequently, long-term territories in temperate regions may enhance the survival of individuals during periods of food shortage (Gibb 1960, Brown 1969). Two territorial settlement periods occur annually, one before and one after the breeding season (Gibb 1960, Brown 1969, Knapton and Krebs 1974).

In the tropics, however, most passerines with long-term territories are insectivorous (Rowan 1966, Buskirk 1976, Powell 1980). Arthropods generally have a more uniform spatial distribution and are more or less constantly renewed (Buskirk 1976, Buskirk and Buskirk 1976). For birds of seasonal tropical and subtropical habitats in South Africa, Rowan (1966) suggested that a long-term territorial strategy primarily ensured a breeding site for the next reproductive period and allowed initiation of breeding as soon as environmental conditions were favorable. Such long-term territories were constantly contested and modified, advertisement and territorial defense persisting throughout the year. However, in highly seasonal tropical habitats, where food abundance varies greatly over the course of the year, continuous territorial defense seems unlikely. Because costs and benefits motivating territorial defense are influenced by a variety of factors, such as reproductive activities and richness of food supply (Brown 1964), some temporal variation should be expected in territorial aggressiveness.

Here, we examine the territorial strategy of four insectivorous passerines residing in a highly seasonal tropical mangrove habitat: the Bicolored Conebill (*Conirostrum bicolor*: Emberizidae), the Pied Water-tyrant (*Fluvicola pica*: Ty-

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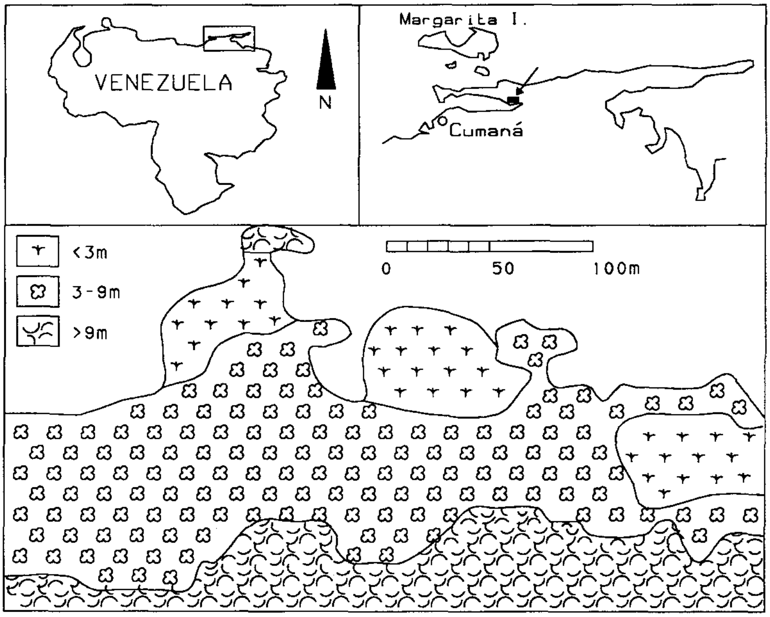

FIGURE 1. Location of the study area and distribution of the vegetation according to cover height.

rannidae), the Yellow-throated Spinetail (*Certhiaxis cinnamomea*: Furnariidae) and the Streak-headed Woodcreeper (*Lepidocolaptes souleyetii*: Dendrocolaptidae). We consider the periodicity of territorial activities in relation to breeding and seasonal fluctuations of food to understand the advantages or benefits of maintaining territories during the non-breeding season. We ask whether long-term territoriality enhances survival over periods of food shortage, ensures possession of a breeding site for the next reproductive period, or both.

STUDY AREA AND METHODS

This study was carried out in a coastal tropical mangrove situated east of Chiguana on the north shore of the Gulf of Cariaco, in the State of Sucre, in northeastern Venezuela (10°29′29″N, 63°45′00″W) (Fig. 1). Located in a semi-arid region (Sarmiento 1976), the study area experiences a dry season from November to May, with less than 25% of the average annual rainfall of 915 mm occurring during this period (cumulative data from the Meteorological Station of Cariaco, Ministério de Obras Públicas, Venezuela).

The mangrove habitat consists of two monospecific stands distributed in parallel belts along the shore. From the coast inland, *Rhizophora mangle*, with a canopy averaging over 10 m in height, is followed by *Avicennia germinans* with an upper layer gradually decreasing from 10 to 1 m in height, and finally by a saline mudflat more or less flooded depending on the season. The study area corresponds to a 5.4 ha plot of *Avicennia* with highly variable canopy height (Fig. 1). Two distinct zones were observed: one consisting of sparsely distributed, low and stubby (0 to 3 m high) trees and shrubs; the other formed of denser and more stratified vegetation (3 to 10 m high) with an extensive ground cover of pneumatophores. The area is regularly flooded by tides except during a 3-week period in March when the ground dries out completely.

The avian community is composed of permanent residents, occasional visitors (primarily from adjacent xeric habitats) and Nearctic migratory warblers. Most species are insectivorous as mangrove propagules are not consumed by passerines (Smith 1987). We report on the four most abundant resident species. The Bicolored Conebill is almost exclusively found in mangrove habitats; the Yellow-throated Spinetail and Pied Water-tyrant are specialists of flooded or near-water vegetation while the Streak-headed Woodcreeper is found in various habitats including mangroves, open woods, plantations, savannas and arid scrubs (Meyer de Schauensee 1970, Phelps and Meyer de Schauensee 1979). The four species have a wide distribution in South America (Guianas, Venezuela, Columbia, Peru,

TABLE 1. Number of individuals, captures, observations and stomach contents for each species.

Species	Number of individuals	Number of captures	Number of observations	Number of stomach contents
Bicolored Conebill	13	92	59	107
Yellow-throated Spinetail	9	31	112	27
Streak-headed Woodcreeper	6	54	26	16
Pied Water-tyrant	15	53	145	17

and Brazil, plus Bolivia, Argentina and Uruguay for some species; Meyer de Schauensee 1970).

SAMPLING

Data were obtained from mist-netting sessions scheduled at 2-week intervals and direct observations over two annual cycles: December 1984 through December 1985, and September 1986 through August 1987.

All mist-netting sessions lasted two days in 1984–1985 and one day in 1986–1987 for a total trapping effort of 5,250 and 5,244 net-hr respectively. Along two transects 50 m distant, we placed 14 mist-nets (14 × 3 m, 32 mm mesh) every 50 m in 1984–1985, and 23 mist-nets every 25 m in 1986–1987. We could thus (1) determine the breeding season of each bird species (by the occurrence of brood patches on adults and the presence of juveniles), (2) mark all captured birds individually with a numbered metal band and a unique combination of four colored plastic bands, and (3) obtain data for territorial cartography using the net location of each captured and recaptured bird.

During 432 hours of observation, the location of each banded individual sighted was noted on a map. A mean point location was used for mobile individuals to eliminate any temporal contingencies between location points, a factor which affects all territorial representation methods (Ford and Myers 1981). The presence of vocalizations (song, calls), nests, pair bonds, familial groups and flocks were also noted.

During each mist-netting session, the abundance of arthropods (the main food resource available) was evaluated by sweep samples. Although this is a questionable method for estimating the absolute value of arthropod abundance, it is very useful in assessing seasonal fluctuations (Janzen 1973). The first three meters of vegetation surrounding mist-nets were swept for 10 min using a standard muslin insect net. By this method, we captured primarily the arthropods exploiting the foliage, twigs, and bark. The diet of each species was evaluated once a month by forcing captured birds to regurgitate through the administration of a 1.5% potassium antimony tartrate solution, following Tomback's (1975) method. This part of the study was conducted 500 m away from the primary mist-netting site to avoid any disruption of territorial activity.

DEFINITION OF TERRITORY

In this paper, the term territory is used in the ecological context of an exclusive area, as advanced by Pitelka (1959) and adopted by many authors (Kaufmann 1983). As defined by Schoener (1968), "the fundamental importance of territory lies not in the mechanisms by which the territory becomes identified with its occupant (i.e., overt defense or any other action), but rather in the degree to which it is in fact used exclusively by its occupant." This ecological definition is well-adapted to tropical resident birds which rarely sing and are involved in only scarce agonistic territorial interactions (Orians 1969, Karr 1981), particularly species holding long-term territories (Willis 1972, Nunn and Terborgh 1979, Beehler and Pruett-Jones 1983, Greenberg and Gradwohl 1986). Thus, although some territorial aggressiveness was occasionally observed, it was not distinctly used in delimiting territorial boundaries.

REPRESENTATION OF TERRITORY

Territorial areas were determined by the method suggested by Jennrich and Turner (1969) and Mazurkiewich (1969). Using all location points obtained through mist-netting and direct observation, the two principal axes translating the greatest variance of the cloud of points were identified to define an elliptical area based on binormal distribution. This method has been widely used for home range studies in mammals (Rodgers and Martin 1986, Anderson 1988), reptiles (Schoener and Schoener 1982), fish (Tytler and Holliday 1984) and even insects (Brakefield

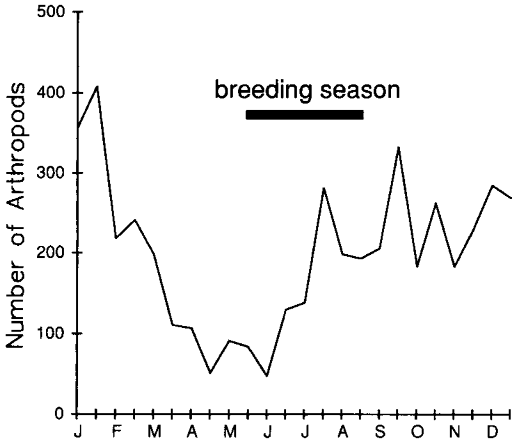

FIGURE 2. Seasonal variation in the number of sweep-netted arthropods (pooled data for both years). The horizontal bar corresponds to the period of breeding activities of the four species.

1982). Because of its lack of bias and high statistical stability, the Jennrich-Turner method clearly surpasses the minimum convex polygon technique (Jennrich and Turner 1969, Ford and Myers 1981, Worton 1987, White and Garrott 1990) traditionally used in bird studies (Ruth and Root 1970, Franzblau and Collins 1980, Village 1982, Loman 1984, Woltom 1985, Yamagishi and Ueda 1986, Smith and Shugart 1987).

STATISTICAL ANALYSIS

All individuals selected for representation of territories were adults observed or captured at least four times within a two month period (Table 1). We calculated a mean location point for each individual and each fourteen day period and submitted these coordinates (grouped by bird species and by year) to an agglomerative chronological cluster analysis (CCA) (Legendre and Legendre 1984). The CCA is useful for identifying discontinuities exhibited by data collected along a temporal gradient. Discontinuities could either represent territorial settlement periods (departure, arrival, or displacement of many individuals) or modifications in the spatial use of territorial areas (concentration of activities on a part of the territory for a certain period). Therefore, a graphic representation of all territories for each group of dates produced by the CCA was necessary to interpret these temporal discontinuities.

RESULTS

BREEDING ACTIVITY AND FOOD ABUNDANCE

In the four species, breeding activities (nest construction, brood patch development, presence of juveniles and family groups) occurred in both years from late May to late August. This is consistent with results obtained for the same species in Trinidad and Tobago (Herklots 1961, ffrench 1980) and southwestern Venezuela (Herrero 1989).

Variation in food abundance was also highly seasonal (Fig. 2). Arthropod numbers were minimal from mid-March to mid-June and gradually increased until January. Some 60% of all captured arthropods were flying insects (Homoptera, Diptera, Coleoptera, Orthoptera, Heteroptera, Neuroptera and Lepidoptera) whereas the remainder were non-flying arthropods (Formicidae, larvae, Araneae, Isopoda, and Coleoptera). As the proportion of each arthropod taxa found within the sweep samples was positively correlated ($r_s = 0.63$, $P < 0.01$) with the proportions observed in the overall regurgitation samples (Table 2), sweep-netted arthropods should provide a reasonable estimate of the seasonal variation in food abundance to which birds were submitted over the course of the year. Thus, we can assume that the breeding season began when food abundance was minimal and ended when still plentiful.

REPRESENTATION OF TERRITORY

A territory generally represents only part of the home range of an individual (Brown and Orians 1970, Tryon and MacLean 1980, Ferry et al. 1981, Wiens et al. 1985) and, consequently, an exclusive territorial area should include most, but not all, bird activities. As the Jennrich-Turner method is based on a binormal distribution, we could determine a theoretical probability for producing non-overlapping ellipses. After an exploratory treatment of the data, a probability of 60% was selected. These non-overlapping ellipses include 80% of the location points and represent an area where 80% of the activities of territorial individuals were carried out. The difference between the binormal and the observed distributions indicates a more concentrated use of space by individuals, reflecting their attachment to territorial area. These results are con-

TABLE 2. Number of arthropods from each taxa found in bird stomachs and sampled by the sweep-net.

Arthropod taxa	Bicolored Conebill	Yellow-throated Spinetail	Streak-headed Woodcreeper	Pied Water-tyrant	All four species	Sweep-net
Coleoptera	192	12	18	21	243	1,015
Diptera	8	2	0	2	12	1,317
Hymenoptera	46	41	27	33	147	1,794
Homoptera	18	20	0	45	83	1,479
Larvae	95	22	6	2	125	730
Orthoptera	7	4	2	1	14	399
Heteroptera	4	2	0	1	7	382
Isoptera	0	1	118	0	119	0
Lepidoptera	10	9	0	9	28	147
Odonata	0	1	0	3	4	0
Neuroptera	0	0	0	0	0	156
Araneae	24	27	3	9	63	375
Gastropoda	2	0	0	0	2	0
Crabs (*Uca thayeri*)	0	1	1	0	2	0
Acarina	1	0	0	0	1	0
Isopoda	3	0	0	0	3	111
Total	410	142	175	126	853	7,905
Correlation[a]	0.802**	0.752**	0.243	0.720*	0.633*	—

[a] Spearman rank correlation between the proportion of each arthropod taxa found in the bird stomachs and the proportion sampled by the sweep-net.
* $P < 0.01$.
** $P < 0.001$.

sistent with those obtained by Tryon and MacLean (1980) for short-term territorial Lapland Longspurs (*Calcarius lapponicus*), where only 65 to 83% of the activities of individuals were observed within the territory.

TERRITORY SETTLEMENT

All territories occupied during the periods of temporal stability, as identified through the CCA, are presented for each species and both annual cycles (Fig. 3). Only the temporal discontinuities corresponding to territorial settlements are indicated. Periods of stability in the territorial mosaic extended over several months for all four species. Territories are generally paired, with two individuals sharing a large portion of their respective territorial areas, but showing little overlap with neighboring pairs. These associations are considered pairs because, in addition to sharing the same activity area, individuals were feeding or moving together in 30% of the cases we observed. Also, the observation of brood patches (primarily limited to females in passerines) during the second annual cycle showed that seven of the eleven pairs observed that year were male-female associations. Three of the four remaining pairs copulated, used the same nest, or fed the same nestlings.

For Bicolored Conebills in 1984–1985, the CCA identified a single temporal discontinuity corresponding to a territorial settlement period in early September. Prior to this date, four distinct territories were occupied by the pairs AB, CD, FG and the individual E (the latter either unpaired or paired with a non-banded individual). In early September, the territorial mosaic was strongly modified. Individuals A, C, D and E disappeared, and new individuals, H and I, were observed. Two pairs were then identified, BH and FG, the latter holding a much larger territory than they had the previous year. For the second year, the CCA did not identify any temporal discontinuity corresponding to a territorial settlement period. Therefore, the territorial mosaic remained stable from early September to late August, as in 1984–1985. Three pairs were then observed; BJ, KL and GM. Only individuals B and G settled their territories in the same area as the previous year.

For Yellow-throated Spinetails in 1984–1985, a single territorial settlement period occurred in late July. Prior to this date, territories were occupied by the pair AB and the individual C. From the end of July, the previous territory of individual C was occupied by the pair EF and individual B was replaced by D. During the second year, the CCA did not identify any territorial settlement period. From September through Au-

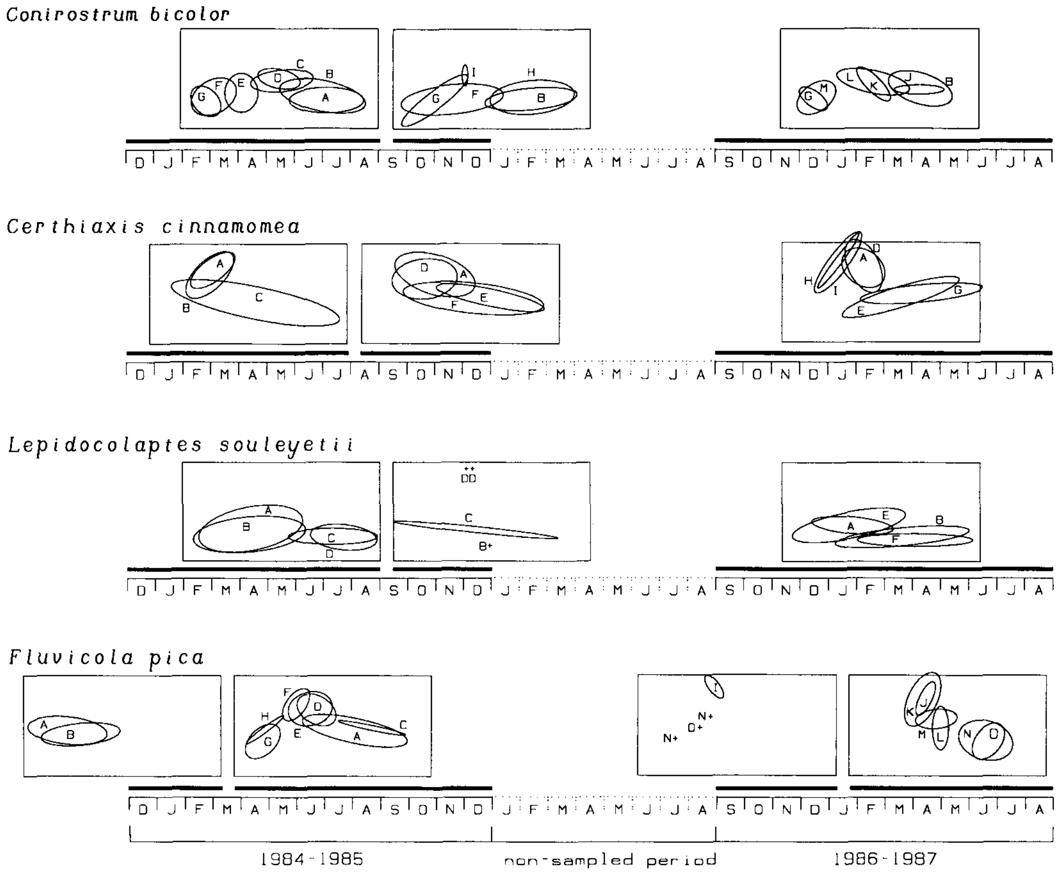

FIGURE 3. Representation of the territorial mosaic of each species over two annual cycles. Rectangles represent the study area and letters refer to individual birds. Ellipses correspond to the territorial areas and, when too few observations were made, the individual location points are represented by "+" symbols. Horizontal bars represent the period of stability of the territorial mosaic as identified by the chronological cluster analysis.

gust, three territories were occupied by the pairs EG, AD and HI, with individuals E, A and D using the same territorial areas as the previous year.

Streak-headed Woodcreepers were observed and captured less frequently than individuals of other species (Table 1). Nevertheless, the CCA identified a discontinuity corresponding to a territorial settlement period in early September 1985. Before this date, two well-defined territories were occupied by the pairs AB and CD whereas after that period, observations of territorial individuals indicated their displacement or desertion. In the second year, no territorial settlement occurred, two territories being occupied by the pairs AE and BF year-round. The 1984–1985 AB pair separated and formed two new pairs in 1986–1987, occupying the entire study area.

The territorial behavior of Pied Water-tyrants was quite different. The CCA identified a territorial settlement period before the breeding season, at different times each year. In 1984–1985, territorial settlement was in mid-March. Prior to this date, only the pair AB had a well-defined territory and after that period, individual B disappeared, individual A moved and formed a new pair with individual C, and a new GH pair and DEF association were observed. In mid-September, after the breeding season, a progressive dismantling of the territorial mosaic led to a temporal discontinuity. However, the latter is not indicated in Figure 3 because it does not correspond to a territorial settlement period, but to a decrease in the size of the territorial space used and the departure of some individuals not replaced. All Pied Water-tyrants finally deserted the study area from mid-November to mid-December. For the second year, the CCA identified a territorial settlement period in mid-January. Preceding this date, only individual I was observed sufficiently to be considered as holding a territorial area, whereas individuals N and O were observed far away from their eventual territory. After mid-January, three well-defined territories were held by the pairs JK, LM and NO. However, not all these individuals were present in the study area in mid-January. In fact, the CCA identified only the onset of the territorial settlement period which actually extended into late February, being a more protracted phenomenon in this species than in the other three.

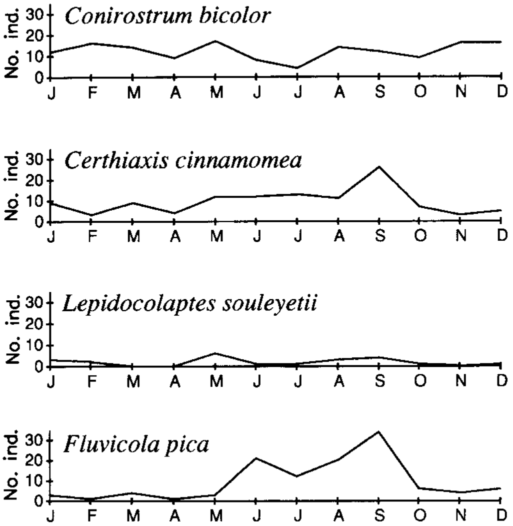

FIGURE 4. Temporal variation in the frequency of vocalizations of each species (pooled data for both years).

VOCALIZATIONS

Temporal variations in the frequency of vocalizations of each species were summed over both annual cycles (Fig. 4). Songs and call notes were pooled because birds rarely sang (38 vs. 622) and the periodicity of both behaviors was similar in all species (G-test, df = 11, ns). The frequency of vocalizations in Bicolored Conebills was relatively high and more or less constant throughout the year, with a slight decrease in the middle of the breeding season (June–July). In Yellow-throated Spinetails, vocalizations varied greatly; they were high during the breeding season, maximal soon after the territorial settlement (September) and minimal during the non-breeding period. Vocalizations were low in Streak-headed Woodcreepers, with a slight increase before the breeding season and over the territorial settlement period. Song levels in Pied Water-tyrants were highly seasonal and largely limited to the breeding season, with a peak during the period of juvenile dispersal. Therefore, the settlement period of this short-term territorial species was not related to a higher rate of vocalizing.

Each species had its own seasonal pattern of vocalizations without regard to territorial strategy. No significant correlation ($r = -0.24$ to 0.54; $n = 12$, ns) appeared between temporal vocalizations of the three species holding long-term territories. In contrast, the analysis revealed a highly significant correlation ($r = 0.85$; $n = 12$; $P < 0.001$) between temporal vocalizations of Pied Water-tyrants and Yellow-throated Spinetails, two species exhibiting different territorial strategies.

DISCUSSION

For each species studied, a single period of territorial settlement occurred during each annual cycle. In the first year, territories of Bicolored Conebills, Yellow-throated Spinetails and Streak-headed Woodcreepers were settled after the breeding season, from late July to early September. For the second year, the territorial mosaic of each species remained stable year-round (from September through August). However, strong modifications in the spatial distribution of birds between December 1985 and September 1986 suggest that new territories were settled during the non-sampled period. Thus, in both years, Bicolored Conebills, Yellow-throated Spinetails and Streak-headed Woodcreepers probably established territories immediately after breeding and maintained them throughout the rest of the year. For Pied Water-tyrants, on the other hand, the territorial settlement took place before the breeding season, from late February through mid-March. After breeding, a decrease in territorial space used and a gradual dispersal of territorial individuals progressively dismantled the territorial mosaic. The use of territory by Pied Water-tyrants is thus a seasonal phenomenon confined to the breeding period.

Most territorial settlements were characterized by marked changes in territory owners as well as in the configuration and location of territories. Modifications of territorial mosaics were especially noticeable in the single species which used a short-term territory: none of the fifteen Pied Water-tyrants maintained the same territory for more than one breeding season compared to 25% (7/28) for species holding long-term territories. This proportion, however, is low compared to the 40% observed by Dowsett (1985) and the 54–75% found by Greenberg and Gradwohl (1986) for tropical resident passerines where territorial modifications were strictly due to individual mortality. An experimental study on Song Sparrows (*Melospiza melodia*) by Knapton and Krebs (1974) revealed that a synchronous territorial settlement, in contrast to a gradual replacement of individuals, involved strong modifications of the territorial mosaic, favoring a higher density in the territorial population. Thus, a long-term territorial strategy, in contrast to a short-term one, may favor territorial individuals by promoting successive reproductions in the same area, while a single period of territorial contest for all birds of a given species could favor non-territorial individuals by increasing modifications in territory owners.

Temporal variation in vocalizations differed greatly among species, regardless of the territorial strategy involved. Moreover, although the breeding season was confined to the same three-month period (May–August), the periodicity of vocalizations was quite variable among the four species. Data such as nest attendance, presence of brood patches and first occurrence of juveniles, thus seem necessary to determine accurately the breeding season of long-term territorial species.

For the three species holding long-term territories, a single settlement period occurred immediately after the breeding season. Territories were not settled again prior to breeding as observed at temperate latitudes (Gibb 1960, Brown 1969, Knapton and Krebs 1974). During the pre-breeding period (April–May), food abundance was minimal in the study area (in contrast to temperate regions) and it would have been difficult for individuals to invest the time and energy necessary for territorial establishment. Alternatively the high population density and food abundance during the dispersal of juveniles immediately after breeding favor an increased competition for space (Brown 1964).

Territorial mosaics in the study area remained stable during periods of low food abundance, in contrast to results from temperate regions (Dixon 1949, Snow 1956, Gibb 1960, Davies 1976). Moreover, breeding was initiated while food abundance was minimal. Thus, food availability is probably not as crucial a limiting factor for these tropical resident species as it is for long-term territorial residents at temperate latitudes.

Consequently, considering the high stability of territorial mosaics even during periods of low food abundance and the absence of territorial settlement before breeding, we suggest that territoriality during the non-breeding period in Bicolored Conebills, Yellow-throated Spinetails and Streak-headed Woodcreepers functions primarily to ensure a breeding site for the following year.

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LITERATURE CITED

ANDERSON, E. M. 1988. Effects of male removal on spatial distribution of bobcats. J. Mammal. 69: 637–641.

BAKER, M. C., AND L. R. MEWALDT. 1979. The use of space by White-crowned Sparrows: juvenile and adult ranging patterns and home range versus body size comparison in an avian granivore community. Behav. Ecol. Sociobiol. 6:45–52.

BEEHLER, B., AND S. G. PRUETT-JONES. 1983. Display dispersion and diet of birds of paradise: a comparison of nine species. Behav. Ecol. Sociobiol. 13:229–238.

BRAKEFIED, P. M. 1982. Ecological studies on the butterfly *Maniola jurtina* in Britain. 1. Adult behaviour, microdistribution and dispersal. J. Anim. Ecol. 51:713–726.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

BROWN, J. L. 1969. Territorial behavior and population regulation in birds. A review and re-evaluation. Wilson Bull. 81:293–329.

BROWN, J. L., AND G. H. ORIANS. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1: 239–262.

BUSKIRK, W. H. 1976. Social systems in a tropical forest avifauna. Am. Nat. 110:293–310.

BUSKIRK, R. E., AND W. H. BUSKIRK. 1976. Changes in arthropod abundance in a highland Costa Rica forest. Am. Midl. Nat. 95:288–298.

DAVIES, N. B. 1976. Food, flocking and territorial behaviour of Pied Wagtail (*Motacilla alba yarrellii* Gould) in winter. J. Anim. Ecol. 45:235–253.

DIXON, K. L. 1949. Behaviour of the Plain Titmouse. Condor 51:110–136.

DOWSETT, R. J. 1985. Site-fidelity and survival rates of some montane forest birds in Malawi, South-Central Africa. Biotropica 17:145–154.

FERRY, C., B. FROCHOT, AND Y. LERUTH. 1981. Territory and home range of the Blackcap (*Sylvia atricapilla*) and some other passerines assessed and compared by mapping and capture-recapture. Stud. Avian Biol. 6:119–120.

FFRENCH, R. 1980. A guide to the birds of Trinidad and Tobago. Harrowood Books, Newton Square, PA.

FORD, R. G., AND J. P. MYERS. 1981. An evaluation and comparison of techniques for estimating home range and territory size. Stud. Avian Biol. 6:461–465.

FRANZBLAU, M. A., AND J. P. COLLINS. 1980. Test of a hypothesis of territory regulation in an insectivorous bird by experimentally increasing prey abundance. Oecologia 46:164–170.

GIBB, J. A. 1960. Population of tits and goldcrests and their food supply in pine plantations. Ibis 102: 163–208.

GREENBERG, R., AND J. GRADWOHL. 1986. Constant density and stable territoriality in some tropical insectivorous birds. Oecologia 69:618–625.

HERKLOTS, G.A.C. 1961. Birds of Trinidad and Tobago. Collins, London.

HERRERO, C. R. 1989. Biología reproductiva de la "Viudita" (*Fluvicola pica*) en el llano Venezolano. Natura (Caracas) 68:22–25.

JANZEN, D. H. 1973. Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distributions. Ecology 54:659–686.

JENNRICH, R. J., AND F. B. TURNER. 1969. Measurement of non-circular home range. J. Theor. Biol. 22:227–237.

KARR, J. R. 1981. Surveying birds in the tropics. Stud. Avian Biol. 6:548–553.

KAUFMANN, J. H. 1983. On the definitions and functions of dominance and territoriality. Biol. Rev. 58:1–20.

KNAPTON, R. W., AND J. R. KREBS. 1974. Settlement patterns, territory size and breeding density in Song Sparrow (*Melospiza melodia*). Can. J. Zool. 52: 1413–1420.

LEGENDRE, L., AND P. LEGENDRE. 1984. Ecologie numérique. Tome 2. La structure des données écologiques. Masson, Paris.

LOMAN, J. 1984. Breeding success in relation to parent size and experience in a population of the Hooded Crow. Ornis Scand. 15:183–187.

MAZURKIEWICH, M. 1969. Elliptical modification of the home range pattern. Bull. Acad. Pol. Sci. Ser. Sci. Biol. 17:427–431.

MEYER DE SCHAUENSEE, R. 1970. A guide to the birds of South America. Livingston Press, Narbeth, PA.

NUNN, C. A., AND J. W. TERBORGH. 1979. Multispecies territoriality in Neotropical foraging flocks. Condor 81:338–347.

ORIANS, G. H. 1969. The number of bird species in some tropical forests. Ecology 50:783–804.

PHELPS, W. H., AND R. MEYER DE SCHAUENSEE. 1979. Una guia de las Aves de Venezuela. Princeton Univ. Press, Princeton, NJ.

PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61:233–264.

POWELL, G.V.N. 1980. Mixed species flocking as a strategy for Neotropical residents, p. 813–819. *In* R. Nohring [ed.], Acta XVII Int. Ornithol. Congr. Deutsch Ornithologen Gesellschaft, Berlin.

ROBINSON, A. 1945. The application of territory and the breeding cycle to some Australian birds. Emu 45:100–109.

RODGERS, A. R., AND C. L. MARTIN. 1986. Diet selection in arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*) demography, home range and habitat utilization. Can. J. Zool. 64: 2717–2727.

ROWAN, M. K. 1966. Territory as a density-regulating mechanism in some South African birds. Ostrich (suppl.) 6:397–408.

RUTH, M. Y., AND R. B. ROOT. 1970. Change in Redstart breeding territory. Auk 87:359–361.

SARMIENTO, G. 1976. Evolution of arid vegetation in tropical America, p. 65–99. *In* D. W. Goodall [ed.], Evolution of desert biota. Univ. Texas Press, Austin, TX.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123–141.

SCHOENER, T. W., AND A. SCHOENER. 1982. Intraspecific variation in home range size in some *Anolis* lizards. Ecology 63:809–823.

SMITH, T. J., III. 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68:266–273.

SMITH, T. M., AND H. H. SHUGART. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology 68:695–704.

SNOW, D. W. 1956. Territory in the Blackbird *Turdus merula*. Ibis 98:438–447.

TOMBACK, D. F. 1975. An emetic technique to investigate food preferences. Auk 92:581–583.

TRYON, P. R., AND S. F. MACLEAN. 1980. Use of space by Lapland Longspurs breeding in arctic Alaska. Auk 97:509–520.

TYTLER, P., AND F.G.T. HOLLIDAY. 1984. Temporal and spatial relationships in the movements of loch dwelling brown trout, *Salmo trutta* L., recorded by ultrasonic tracking for 24 hours. J. Fish. Biol. 24:691–702.

VILLAGE, A. 1982. The home range and density of Kestrels in relation to vole abundance. J. Anim. Ecol. 51:413–428.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press Inc., San Diego, CA.

WIENS, J. A., J. T. ROTENBERRY, AND B. V. HORNE. 1985. Territory size variation in shrubsteppe birds. Auk 102:500–505.

WILLIS, E. O. 1972. The behavior of Plain-Brown Woodcreepers (*Dendrocincla fuliginosa*). Wilson Bull. 84:377–420.

WOLTOM, R. J. 1985. The ranging and nesting behaviour of Wood Mice, *Apodemus sylvaticus* (Rodentia: Muridae), as revealed by radio-tracking. J. Zool. (Lond.) 206:203–224.

WORTON, B. J. 1987. A review of models of home range for animal movement. Ecol. Modell. 38:277–298.

YAMAGISHI, S., AND K. UEDA. 1986. Simultaneous territory mapping of male Fan-tailed Warblers (*Cisticola juncidis*). J. Field Ornithol. 57:193–199.