

FLUCTUATIONS IN FALL AND WINTER TERRITORY SIZE IN THE NORTHERN MOCKINGBIRD (*MIMUS POLYGLOTTOS*)

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Abstract.—Many species of birds track resources contained in their feeding territory. Observations reported here illustrate fluctuations in territory size from fall to winter in perennially territorial mockingbirds in the piedmont of North Carolina. In cold weather, territory size decreased from fall to winter. The decrease was neither a competitive loss of space to intruding conspecifics, nor a direct response to the competitive threat posed by other species relying heavily on winter fruit. During the unusually warm winter of 1984, territory size decreased little if at all. The decrease observed in cold weather may, therefore, be a response to altered energetic demands imposed by cold weather in which decreased territory size minimizes energy expenditure. These observations stress the flexibility of the mockingbird's perennial territoriality in the face of environmental variation.

FLUCTUACIONES EN EL TAMAÑO DEL TERRITORIO DE SINSONTES (*MIMUS POLYGLOTTOS*) DURANTE EL OTOÑO Y EL INVIERNO

Sinopsis.—Muchas especies de aves evalúan los recursos que hay en su territorio de alimentación. Las observaciones que hice en sinsontes en Carolina del Norte, ilustran fluctuaciones en el tamaño del territorio perenne de estas aves durante el otoño y el invierno. El territorio disminuyó en tamaño del otoño al invierno. La disminución no estuvo asociada a pérdida de espacio por competencia con otros sinsontes o como respuesta a la amenaza competitiva por otras especies de aves que dependen en gran medida de frutas durante el invierno. Durante el "tibio" invierno de 1984, los territorios apenas se redujeron en tamaño. Por ende la disminución del territorio observada durante inviernos fríos muy bien pudiera ser una respuesta a la demanda energética impuesta por las bajas temperaturas en donde la reducción del tamaño del territorio reduce también el gasto energético. Estas observaciones recalcan la flexibilidad del territorio perenne de los sinsontes con relación a variables climatológicas.

The adaptive benefit of territoriality depends upon a net advantage that accrues to the resident through exclusive access to resources contained in the defended area (Brown 1964, Davies and Houston 1984, Schoener 1983). Changes in the costs of defense, the value of resources, or the energetic demands of maintenance may alter patterns of territorial defense over both the long and short term (e.g., Carpenter and MacMillen 1976, Hixon et al. 1983). Changes in patterns of territorial defense should be especially pronounced in species exhibiting year-round territoriality in a variable environment. Differences in resource quality or distribution, in weather, and in the nature of competitors may produce altered patterns of territoriality. The observations reported here chart the course of changes in the fall and winter territorial behavior of the Northern Mockingbird (*Mimus polyglottos*).

In the Southern United States, mockingbirds exhibit year-round defense of an all-purpose territory. Throughout the year most of the residents' activities are focused on the defended area (Laskey 1936, Michener and

Michener 1935). However, patterns of resource use may change considerably. For example, demands imposed by breeding are relaxed in the fall and winter, when benefits of territorial defense accrue primarily through food availability (Hailman 1960, Laskey 1936, Michener and Michener 1935). Competitive pressures change as well. In the fall, the number of conspecific intruders increases with the large influx of strange conspecifics attempting to establish territories (Breitwisch et al. 1986, Laskey 1936, Logan et al. 1983, Michener and Michener 1935). In addition, competition with other species may increase in the winter, as mockingbirds vie for increasingly valuable fruit (Moore 1978). Such changes may substantially alter patterns of resource defense.

METHODS

I observed resident wild mockingbirds in Guilford County, North Carolina, in the fall and winter of 1981 and 1984–1985. All territories were located in residential or urban areas on or around the University of North Carolina at Greensboro. This area provides abundant resources for resident mockingbirds that remain in the area year-round. With minor shifts in territorial boundaries, many residents appear to remain in the same area for life.

I engaged in systematic focal animal sampling (Altmann 1974) of 12 males in three sampling periods in 1981 and 1984–1985. Six were observed in 1981 and 6 in 1984–1985. In 1981 observations were collected from 5–27 Sept., from 17 Oct.–7 Nov., and from 28 Nov.–19 Dec. All 6 were color-banded and with one exception, each bird shared his territory with a female. In 1984–1985, observations were conducted from 2–20 Oct., from 30 Nov.–22 Dec., and from 14–31 Jan. Of the 6 birds monitored, 3 were mated and 3 were unmated. One of the mated males and 3 of the unmated males were color-banded. Conspecific aggression peaks during the early fall (Laskey 1936). Therefore, to distinguish conspecific aggression from that directed toward other species different observation periods were used in 1984–1985.

Each sample consisted of 30 min of continuous monitoring of the bird's behavior. During this period, the locations of all activities were recorded on a map drawn to scale representing each bird's territory. I also recorded the temporal sequencing of all behavior observed. The behavioral patterns monitored included conspecific fights, chases and the ritualized dance (Hailman 1960), aggressive interactions with other species, all vocalizations, and all major perch changes and foraging positions. Because fights and chases with conspecific intruders occurred throughout the occupied space, I defined the occupied space as a true territory rather than as a home range. Total numbers of samples obtained in 1981 for each bird in each sampling period were 32, 32, and 18, respectively, totalling 41 h/bird. In 1984–1985, samples totaled 12, 10, and 12/bird, respectively for the three sampling periods. Total sample time was 17 h/bird. As mockingbirds are accustomed to the presence of humans, no blinds were used. However, observers maintained a distance of at least 5 m from the

focal bird. Observations were evenly distributed throughout each sampling period, and nearly equal numbers of samples were obtained during the morning (0800–1200) and afternoon (1300–1700) hours. Territory sizes were calculated by determining asymptotic observation-area curves as defined by Odum and Kuenzler (1955). This method adds the observed area across successive samples to determine the point at which additional samples add no more than 1% to the total area observed. The 1% criterion was used in 1981; in 1984, though fewer samples were used, the number of samples was sufficient to ensure that no more than a 5% increase in area was added with additional samples. Exceptions are noted below. An electronic planimeter was used to calculate territory areas.

RESULTS

Changes in territory size.—Observation area curves calculated from September 1981 forward across successive samples through December 1981 and from December 1981 backward across successive samples indicated stable changes in the size of the 1981 territories. Figure 1 illustrates these changes in 2 of the 6 males. In bird C, two different asymptotic sizes are apparent, one in the fall (calculated from September through December) and one in the winter (calculated from December to September). Bird X exhibited two fall asymptotes, both considerably larger than the asymptotic size of the December territory. A winter decrease in territory size distinguishing the larger fall space from the smaller winter space was observed in 5 of the 6 birds sampled in 1981. In these 5 birds the December space was, on the average, over 50% smaller than the September space (Table 1, $P < 0.06$, two-tailed, Walsh Test [Seigel 1956]). The location of the 6th bird's space shifted continuously throughout the fall and winter of 1981, and no asymptotic value could be obtained. The pair disappeared from the area in the spring of 1982; no data from this pair are included in the analyses below.

The early fall represents the period of greatest conspecific territorial intrusion in mockingbirds inhabiting the Southern United States (Laskey 1936, Logan et al. 1983, Michener and Michener 1935). It is, therefore, possible that the winter loss in territory size reflects a competitive loss of space to conspecifics. Two observations suggest that this is not the case. First, the territories of three adjacent neighbors each shrank away from the other, and no bird occupied the intervening spaces. In the following spring, each bird's territory expanded to include the vacated winter space. Secondly, in 1981, the fall influx of intruding conspecifics peaked before measurable decreases in territory sizes were observed. The number of conspecific intrusions was reduced by 50% during the October sampling period, though sizeable decreases in territory size were not evident until mid-November.

Because fewer samples were conducted in 1984, direct comparisons cannot be made between territory sizes in the two years. However, sizes calculated in 1984 were within the range of variation observed in 1981, and in all but two cases (see Table 1) in 1984 an average of less than

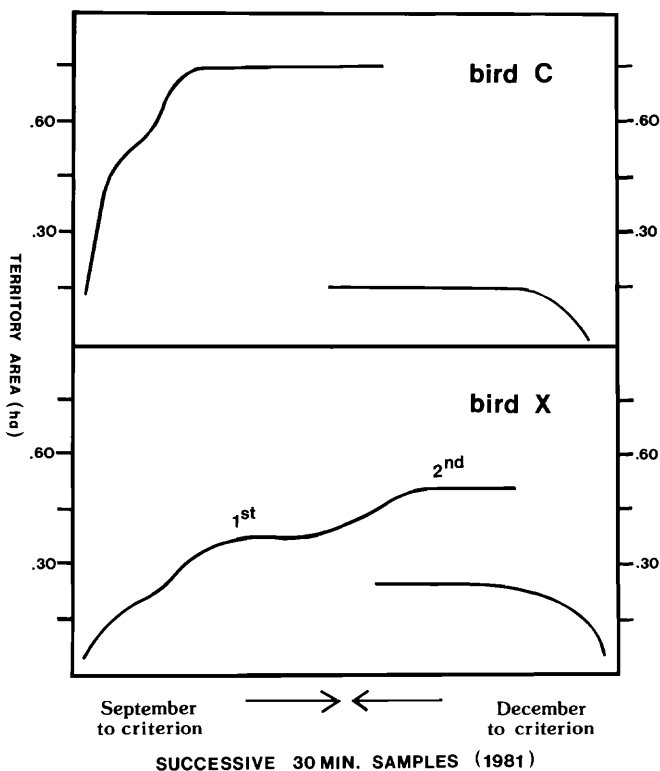


FIGURE 1. Asymptotically large and small territory sizes calculated in 1981 from September forward through December and December backward across successive samples. Samples obtained from bird C indicate one large and one small territory asymptote. Samples obtained from bird X indicate two successive large asymptotes and one small asymptote.

5% of the asymptote was added to the total area in the last three samples obtained. Comparison of the differences in territory size in October versus December, 1984 (Table 1), however, indicates considerable variability among subjects. Across birds, the size of the December territory ranged from 23.5%–107.7% of the October territory size. The change in territory size was not highly reliable ($0.06 < P < 0.094$, two-tailed, Walsh Test). Observations collected during the January sampling period did, however, reveal a significant increase in January over December territory sizes ($P < 0.03$, two-tailed, Walsh Test). January territory sizes ranged from 117.4%–300.0% of December territory sizes (Table 1), and all birds remained stable residents into the spring.

Competitive pressure from other species.—The frequency of conspecific intrusions decreases during the late fall and winter in mockingbirds (Laskey 1936, Logan et al. 1983). However, Moore (1978) reports that in the winter mockingbirds selectively attack and drive from fruiting re-

TABLE 1. Comparison of changes in territory size across fall and winter sampling periods.

Bird	Territory size (ha) ^a in 1981			Dec. as % of Sept.
	Sept.	Dec.		
B	0.47	0.23		48.9%
E	0.62	0.25		40.0%
X	0.37	0.25		67.6%
C	0.72	0.14		19.4%
S	0.49	0.34		69.4%
Mean	0.53	0.24		49.1%
SD	0.14	0.07		20.7%

Bird	Territory size (ha) ^a in 1984/1985				
	Oct.	Dec.	Jan.	Dec. as % Oct.	Jan. as % Dec.
B2	0.34	0.09	0.11	26.5%	117.2%
EF	0.32	0.24 ^b	0.35	75.0%	145.8%
PB	0.57	0.56	0.89	98.2%	158.9%
Z	0.26	0.28	0.40	107.7%	142.8%
G	0.56	0.13 ^b	0.39	23.2%	300.0%
L	0.29	0.16	0.19	55.2%	118.8%
Mean	0.39	0.24	0.39	64.3%	163.9%
SD	0.14	0.17	0.27	35.6%	68.6%

^a Conversion to hectares was performed following statistical analyses.

^b Size criterion in last three samples is <5% added area.

sources other species whose diet consists primarily of fruit. Therefore the December decrease in territory size observed in 1981 may represent a shift from fall defense of a large all-purpose territory against conspecifics to winter defense of a smaller feeding territory against the threat posed by other species of frugivores. As the threat of intrusion by mockingbirds declines (Laskey 1936, Logan et al. 1983) and as other species use increasingly valuable fruit (Moore 1978), territory defense may be concentrated on smaller areas containing fruit.

To determine the relationship between variations in territory size and the frequency of fights with other species, I examined the occurrence of fights and chases directed at other species. The mean number of fights per sample did not change reliably from fall to winter in either 1981 or 1984 ($P > 0.06$, one-tailed, Walsh Test). Combining data on birds observed in 1981 and 1984, I calculated the correlation between the change in a bird's winter territory size and the fall versus winter difference in the average number of fights per sample with other species. The correlation was not statistically significant (Spearman rho [$n = 11$] = -0.349 , $P > 0.14$). Birds with the greatest decrease in territory size did not necessarily engage in more fights with other species (Table 2). However, there was a significant positive correlation between the mean number of fights with other species observed for each bird in the fall and again in the winter (Spearman rho [$n = 11$] = $+0.534$, $P < 0.05$). This suggests

TABLE 2. Relationship between winter/fall ratios of mean intrusions/30 min and the winter/fall ratios of change in territory size.

Bird	Intrusions ^a (w/f)	Territory size (w/f)
C	3.67	0.19
X	55.00	0.68
S	0.39	0.69
B	1.23	0.48
E	1.16	0.40
B2	1.21	0.26
EF	0.96	0.75
PB	1.25	0.98
Z	2.50	1.08
L	3.75	0.55
G	0.48	0.23

^a Includes fights and chases with other species of birds.

that the number of fights with other species is a stable characteristic of either individual mockingbirds or their territories.

DISCUSSION

The observations reported here indicate that the mockingbird's territory size may fluctuate considerably from fall to winter. Moore's (1978) observations suggest that mockingbirds compete selectively with other species for access to winter fruit. My observations indicate that in 1984, over 85% of aggressive encounters with other species were directed toward species ranked by Moore as exhibiting a high percentage of frugivory. However, though mockingbirds compete with frugivores in the fall and winter, because aggression toward other species does not change systematically with changes in territory size, competition with frugivores does not appear to produce changes in winter territory size. Decreased territory size may facilitate efficient competition for fruit. If territories shrink, mockingbirds' activities may be focused on the area of greatest frugivore pressure. That this need not be the case is indicated by two birds in which aggression toward other species increased in December (1984) though territory size either remained the same or increased from fall to winter (see Table 1).

In 1981, the territory sizes of all stable residents decreased to an average of 48.6% of the fall space. In 1984, on the other hand, some decreased, some did not change and some increased. What accounts for the variation in territory size change across seasons? Variations in winter weather are known to affect foraging and spacing strategies in several avian species (Gass and Montgomerie 1981, Grubb 1975, Jorde, Krapu and Hay 1984, Schmidtke and Brandl 1983). Both behavior and metabolism can be affected by changes in temperature and irradiation (DeJong 1979). In the piedmont of North Carolina, the mean temperature drops approximately 16° C from September to December, and virtually all resident

mockingbirds overwinter. The 1981 shrinkage in winter territory size may reflect increased thermoregulatory demands associated with dropping temperatures.

I examined records of daily weather changes for the months of September through December in 1981 and 1984. A correlated *t*-test showed that daily temperatures for December 1984 were considerably higher than the 30-yr norm for that month, while daily temperatures for December 1981 were somewhat colder than the 30-yr norm (Fig. 2, $P < 0.01$). The average daily deviation from normal in 1981 was -1.64°C ; in 1984, the average daily deviation from normal was $+4.59^{\circ}\text{C}$. Direct comparison of the average daily temperatures for only those days in December, 1981 versus December, 1984 on which behavioral samples were taken indicates significantly warmer average temperatures in 1984 (6.03°C versus 2.42°C , $P < 0.05$, *F*-test). Neither month had appreciable amounts of snow or ice, and the months do not differ from one another in the average number of minutes per day with sunshine.

A consistent decrease in the mockingbird's territory size was evident only in the colder year. This suggests that mockingbirds may adapt winter territorial behavior to variation in ambient temperature conditions. The temperature drop associated with colder winters may place a premium on decreased activity as thermoregulatory demands increase. Behavioral adaptation to harsh winter weather has been described in other avian species. During the coldest periods of the Nebraska winter, for example, mallards congregate in warmer canal habitats, returning to riverine areas when temperatures rise. Jorde et al. (1984) suggest that mallards select a microclimate that minimizes energy expenditure for thermoregulation. In mockingbirds, smaller winter territories may reflect a similar weather-driven thermoregulatory strategy. Activity required to patrol the larger area is less and less necessary as conspecific intruder pressure declines. When the temperature drops, as in December, 1981, decreased activity across a smaller area may reduce energetic demands, thereby decreasing the costs of thermoregulation.

Observations collected in the winter of 1984 suggest that as constraints imposed by the drop in winter temperatures are relaxed, individual differences in age, experience and mating status may contribute to differences in territory size. Though they report no differences in territory size, Breitwisch et al. (1986) observed different patterns of fall territory defense in mated versus unmated male mockingbirds in Florida. Comparisons of the size changes in the 3 mated versus the 3 unmated males I observed in 1984, reveal less change in the unmated males (29.8% versus 41.1% decrease). Because unmated males may acquire mates in the fall (unpublished observations), warmer winters may extend the period of mate attraction, possibly entailing larger territories in unmated males. Interactions between two neighboring unmated males, both new to the area, suggest that experience too, may be an important factor. As observations proceeded from October through December, one bird's (EF's) space shifted into that held by another (B) whose territory shrank considerably: the

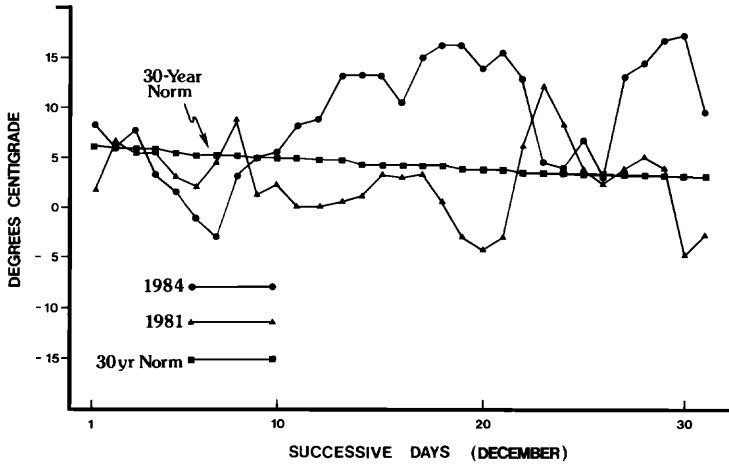


FIGURE 2. Average daily temperatures in the piedmont of North Carolina, for December 1981 (▲—▲) and December 1984 (●—●). The third line (■—■) indicates the 30-yr temperature norm for each December day in the piedmont of North Carolina. Data were provided by the National Weather Service, Greensboro/Winston-Salem/High Point Regional Airport.

December loss of space by B was a result of space yielded to EF. Bird EF did not expand his space into those occupied by his three other neighbors, each a long-time established resident. Rather, he directed his intrusions toward his least experienced neighbor. Together with the above observations emphasize the dynamic nature of mockingbirds' fall and winter territories. As might be expected of year-round territoriality in a variable environment, territorial behavior appears to be finely tuned to local changes in environmental demands.

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