

TERRITORIALITY IN THE PURPLE MARTIN

CHARLES R. BROWN

Studies on the breeding biology of the Purple Martin (*Progne subis*) have defined territory in the martin as one or several rooms of a martin house which the birds defend with decreasing intensity as the breeding season progresses. Allen and Nice (1952:617) state that a male martin selects 1 room of a house and sometimes "part of a house;" and Johnston and Hardy (1962:247, 253) note that territory consists of "one or two" and "more than one" martin house compartment. Olmstead (1955) wrote of a minimum territory of 1 compartment, although he observed that some males may attempt to dominate more than 1 room. Gaunt (1959) mentioned a "pairing territory." However, there have been no detailed, quantitative studies of territoriality in the Purple Martin. From 1968-1977, in Texas, I studied territoriality in martins.

STUDY AREA AND METHODS

My studies were conducted at 2 martin colonies in Sherman, Grayson Co., north-central Texas, Colony A from 1968-1977 and Colony B in 1977. These colonies consisted of both wooden and aluminum martin houses. In 1968-70, Colony A contained a 6-room house; in 1971, a 24-room and a 6-room house; in 1972, a 24-room and a 12-room house; in 1973, a 24-room, a 6-room, and two 12-room houses; in 1974, same as 1973 plus another 24-room house and a 14-room house; in 1975-76, same as 1974 plus another 12-room and a 6-room house; in 1977, two 24-room houses and two 12-room houses. Colony B contained an 18-room, a 12-room, and two 6-room houses.

Resident male martins at the colonies were captured in specially constructed trapping houses, or as nestlings, and marked with colored and painted bands. The number of birds marked varied from year to year, but 30 to 50% were commonly marked. Present capture techniques used for adult martins have rather low yield, and it was impossible to capture all birds in the colonies; the way is clear for development of high-yield techniques. Although Klimkiewicz and Jung (1977) reported a capture technique which they used with success in Maryland, in Texas I have not had great success with their method. Their technique requires certain architectural styles of martin houses and cannot be used widely until eggs are laid, which is too late in the season for complete studies of territoriality. Fortunately, most unmarked individuals could be recognized by plumage characteristics or distinctive behavior. During each year of the study I spent 900-1000 h observing the colony(ies). Arrival dates for all resident martins were recorded, and throughout the season a file was kept on all individuals, indicating the extent of their territories from day to day. Glossy blue-black male Purple Martins were termed "adults" and light-breasted yearling males were termed "subadults."

RESULTS

Territorial data were recorded for all 158 male Purple Martins occupying the study colonies. Extent of territory in martins at Colonies A and B consisted of martin house compartments and the porches adjoining those

TABLE 1
NUMBER OF MALE PURPLE MARTINS AND THEIR MAXIMUM AND MINIMUM TERRITORY SIZES WITH MALES' MONTHS OF ARRIVAL

Month of arrival		Territory size (no. of rooms)														Mean size	
		1	2	3	4	5	6	7	8	9	12	14	18	24	30		36
February	maximum	0	0	0	2	0	6	0	1	0	5	0	0	4	1	0	12.5
	minimum	5	2	8	2	0	1	0	1	0	0	0	0	0	0	0	2.8
March	maximum	4	4	8	9	2	18	0	4	2	10	0	5	2	0	1	7.8
	minimum	15	12	19	10	0	9	1	0	2	0	0	1	0	0	0	3.3
April	maximum	8	6	9	9	0	5	0	2	0	0	1	0	0	0	0	3.5
	minimum	21	8	5	2	0	4	0	0	0	0	0	0	0	0	0	2.1
May	maximum	7	6	8	1	1	2	0	3	1	1	0	0	0	0	0	3.6
	minimum	11	9	6	0	2	1	0	1	0	0	0	0	0	0	0	2.3
Total	maximum	19	16	25	21	3	31	0	10	3	16	1	5	6	1	1	6.5
	minimum	52	31	38	14	2	15	1	2	2	0	0	1	0	0	0	2.6

rooms. Roofs of martin houses were not defended, and no territorial defense was observed away from the martin houses. I distinguished maximum and minimum territories in martins. Maximum territory was the number of rooms a male defended upon his arrival and establishment at the colony. Minimum territory was the number of rooms a male defended at the end of the season, i.e., while he was feeding young.

The number of male Purple Martins that claimed each maximum and minimum territory size, along with the males' months of arrival, are shown in Table 1. Male martins' mean territory sizes also are shown in Table 1. For 48 (30.3%) males the maximum and minimum territory sizes were identical ($\bar{x} = 4.1$ rooms). Although Finlay (1971) implied that Purple Martins commonly claim only 1 room in Alberta and Rohwer and Niles (1977) apparently assumed the same in their discussion of spring arrival hypotheses, only 20 males (12.6%) defended 1 room as both their maximum and minimum territories. Of males that claimed multi-room maximum territories, 34 (21.5%) claimed only 1 room as their minimum territories. The largest maximum territory defended by a male was 36 rooms for 12 days after his arrival; the largest minimum territory claimed by a male was 18 rooms.

For some males, the progression from maximum to minimum territory was gradual. These males slowly abandoned parts of their maximum territories as the nesting season progressed. At times, males relinquished portions of their maximum territories in response to strong challenges by other males, but generally males seemed to be unaffected by challenges

from intruders. In other males, the progression from maximum to minimum territory was abrupt; one day a male vigorously defended his maximum territory, and the following day he inexplicably confined his defense to his minimum territory. In this study I never recorded a male attempting to enlarge his territory after he restricted his activities to his minimum territory. Males seemed to restrict their territories most frequently while feeding young. Male Purple Martins do not actively build nests or incubate, so when these activities are ongoing, males loaf in the colonies extensively and thus are able to easily defend their territories at this time.

Once established in their territories, neighboring males seldom fought or trespassed onto a neighbor's territory. Observations of banded birds indicated that some neighboring males learned to recognize each other and uttered distinct "greeting" vocalizations when they approached each other at the martin house. There even appeared to be a type of "mutual defense" mechanism in neighboring males. On at least 65 occasions, I observed a male that was established on a territory defend a neighbor's territory while that neighbor was absent. In these cases an intruding male appeared in a territory while the owner was away. A neighboring male, apparently recognizing the intruder as foreign, chased the intruder away and then quickly returned to his own territory. In 32 cases when the legitimate owner returned while the neighbor and intruder were fighting, the owner repelled both neighbor and intruder. An intruding male could become established on a territory in a very short time (<10 min), and then fights between the "established" intruder and owner (when the owner returned) could be quite severe and long-lasting (see Brown [1977a]; Purple Martins are capable of inflicting appreciable injury in intraspecific fighting). Nonetheless, mutual territorial defense may promote stability in the colony by keeping intruders away.

Although Allen and Nice (1952) and Johnston and Hardy (1962) indicated that adult male Purple Martins often tolerated, or were less aggressive toward subadult males, I detected no differences in behavior between these 2 age classes. Adult males treated subadults in much the same way as they treated other adults, and I observed vicious fights when subadults intruded into adults' territories. For descriptions of aggressive behavior used in territorial defense see Allen and Nice (1952), Johnston and Hardy (1962) and Brown (1977a).

Although much attention was directed toward males, I also observed territorial behavior in female Purple Martins, though no quantitative data were collected. In many instances territorial defense in females was identical to that of their mates. A female defended the maximum territory while her mate did so, and she restricted her defense to the minimum territory when her mate restricted his defense. No female maintained a

minimum territory larger than her mate's minimum territory. But since pair formation in Purple Martins is largely a choice by the female of a territory and attending male, some females briefly held maximum territories that were larger than their eventual mate's maximum territory. In such cases females claimed territories that included more than 1 male. Apparently the females in these instances were still "indecisive" about which male and territory they "wanted."

While no female maintained a larger minimum territory than did her mate, many males claimed larger minimum territories than did their females. A female frequently confined her minimum territory to the nest hole when laying or incubating, while her mate continued to claim several rooms. This disparity in territory size sometimes results in polygyny (Brown 1975).

My studies (unpubl.) of polygyny in Purple Martins show that this mating system is fairly regular in north-central Texas. Preliminary studies suggest that about 20% of males may engage in polygynous relationships during at least the early part of the nesting season, but only about 5% continue as polygynists throughout the entire season. The remaining 15% claim 2 or more females for varying lengths of time while they control their maximum territories, later "releasing" all but 1 female to other males. All but 1 polygynous male have been adults that arrived in February and March; the exception was a May-arriving subadult bird (Brown, unpubl.). Studies on Purple Martin polygyny are continuing and results will be published later.

Once established, females, like males, seldom fought among themselves. Females also displayed mutual defense of neighboring territories. In Purple Martin pairs, the male generally chased away intruding males and the female chased away intruding females, but females were more likely than males to chase away occasionally intruders of the opposite sex. Firmly paired males usually encouraged intruding females.

Table 1 illustrates that males arriving in February and March claimed larger maximum territories than April and May males ($P < 0.05$, Student's *t*-test), while minimum territory remained the same for all males ($P < 0.05$). All males that arrived in February and March were adults; 21 of 40 (52.5%) April-arriving males were adults; 5 of 30 (16.6%) May-arriving males were adults.

Since I define minimum territory in Purple Martins as the rooms claimed by a male at the end of the breeding season, minimum territory is an indicator of how much of the colony was controlled by the resident male martins (see Table 2). Rooms used by House Sparrows (*Passer domesticus*) and Starlings (*Sturnus vulgaris*) were not included in any male's minimum territory. For 1968–1977, the mean percentage of rooms controlled by male

TABLE 2
TOTAL APARTMENT-ROOMS CONTROLLED BY MALE PURPLE MARTINS, FEBRUARY–JULY

Year	Rooms in colony	No. of males present	Rooms controlled by males	Percent rooms controlled
1968	6	2	5	83.3
1969	6	3	3	50.0
1970	6	2	5	83.3
1971	30	8	24	80.0
1972	36	8	33	91.6
1973	54	17	48	88.8
1974	92	20	70	76.1
1975	110	25	80	72.7
1976	110	33	75	68.2
1977A	72	26	51	70.8
1977B	42	13	35	83.3

martins was 77.1%. No figures were obtained for the remaining rooms not controlled by martins, but most of them were used by sparrows and Starlings.

DISCUSSION

Anyone attempting an analysis of avian territoriality is confronted with a body of literature (e.g., references in Brown 1969, Wilson 1975) in which few, if any, hypotheses to explain territoriality may be found that have attained general acceptance (Nice 1941; Hinde 1956; Tinbergen 1957; Wynne-Edwards 1962; Brown 1964, 1969; McLaren 1972; Wilson 1975; Verner 1977).

The Purple Martin's territory fits Nice's (1941) Type D1 territory—a colonial species restricted to the immediate vicinity of the nest. In martins, the significant aspect of territoriality is the contraction of territories as the nesting season advances. Nice (1941) recognized that such contraction occurs in some species, and suggested a density-limiting function for territoriality. Density-regulation was advocated by Wynne-Edwards (1962), but such group selection has generally been rejected by other contemporary evolutionary biologists (Brown 1964, 1969; Wilson 1975; Verner 1977). I reject density-limitation as a function of territoriality in Purple Martins, but I concede that it may occur as an incidental effect. Density of nesting martins in colonies can be controlled by the size of the established males' maximum and minimum territories (and by the number of apartment-rooms available for occupancy).

Regarding the functions and evolution of territoriality in Purple Martins, I will consider 2 theories of territoriality: McLaren's (1972) view that territoriality has evolved in most species to promote polygyny, and the "super-territory" hypothesis of Brown (1964) and Verner (1977). I favor McLaren's hypothesis to explain territoriality in general, despite the absence of confirming evidence for some species and certain problems of the hypothesis which McLaren admits exist.

McLaren's (1972:203) thesis is that males "with breeding territories are would-be polygynists." But polygyny is kept at a low incidence through competition in populations of evenly matched males with equal sex ratios, despite strong Darwinian sexual selection for polygyny. McLaren notes that it is incorrect to assume that a female, given a choice of sharing a mate or having exclusive use of one, will always opt for the exclusive use of a male. Some males may be inherently superior in attracting mates, and, by mating with one of these polygynous males, a female produces young that also are superior in attracting mates (McLaren 1972:201).

The low incidence of polygyny that I noted in Purple Martins suggests to me that breeding territory has evolved to promote polygyny, as McLaren hypothesizes. This hypothesis is supported by the temporal contraction of martin territories. As the nesting season advances, fewer potential mates are in the population, and males more profitably may restrict their territories and assist their mates in nesting duties. This is confirmed by my observations that males restricted their territories often when the young hatched, which was after most birds in the population had found nesting sites and few additional mates were available. Earlier in the season during nest-building and incubation (in which they do not participate), males are free to compete for more mates. Following McLaren (1972), my unpublished value of 5% polygynous males in martins meets Verner and Willson's (1969) criteria for classifying a species as "normally polygynous."

According to Brown's (1964) and Verner's (1977) super-territory model, male birds that defend territories larger than that needed in terms of resources accrue a selective advantage by preventing conspecifics from breeding. These super-territory holders thus increase their relative genetic contribution to future generations by preventing conspecifics in the same population from contributing any genes (Verner 1977). Furthermore, Verner's super-territory model "predicts that the maximum area should be defended early in the breeding season." Since more individuals attempt to find territories early in the breeding season rather than later, a super-territory holder must maintain his large territory at that time, in order to exclude other males. As the nesting season continues, defense of the territory becomes unimportant, since few males attempt to establish themselves late in the season. This prediction is verified for Purple Martins. In Feb-

ruary and March, male martins' maximum territories are much larger than in April and May.

But the super-territory hypothesis for Purple Martins faces difficulties not encountered by McLaren's polygyny model. When Purple Martins nested in woodpecker holes, before European man installed birdhouses, it is probable that many nested singly, or in very small colonies. It seems doubtful that the super-territory would have been adaptive in those primitive circumstances, simply because populations probably were small and scattered and males may not have had opportunities to exclude others. Presently, colonies are large and population density is high in artificial martin houses, and it is possible that the super-territory now could operate. But since there are many nesting cavities in birdhouses available to martins, it is debatable if a super-territory holder really excludes any birds from nesting. Evidence suggests that non-breeding floaters that exist in martin populations move in and replace lost breeders (Brown 1978). But are these floaters excluded from nesting by super-territory holders, or by interspecific competition (Brown 1977b, 1978) from House Sparrows and Starlings? I think the latter possibility is more likely.

On the other hand, the polygyny hypothesis holds for martins that nested in primitive conditions as well as for those nesting in artificial birdhouses. This hypothesis is based on the inherent superiority of some males in attracting mates. We have no records of martin breeding biology prior to the arrival of Europeans in North America, and it is not known if polygyny in martins occurred then. But, following McLaren (1972), if polygyny did not occur then, territoriality was reduced accordingly. In recent times, more nesting cavities in martin houses have allowed the superior males to compete more noticeably (and more successfully?) for mates, and territoriality is expressed.

About 65% of the male Purple Martins in my study defended more than 1 room as their minimum territory. This is curious, because if, at the end of the season, males no longer try to attract additional mates, the defense of more than the nest hole at the end of the season seems energetically wasteful. But multi-room minimum territories may simply be attributed to artificial nesting houses. Perhaps Purple Martins have not completely adapted to the high apartment-room density of birdhouses. Optimal adaptation to birdhouse nesting will consist of a maximum territory of several rooms to facilitate competition for mates, and then a restriction to 1 room when it becomes unprofitable to compete for mates. Also, many males roost in a separate room while their mates are incubating or brooding. Males may defend a minimum territory of more than 1 room to provide themselves with such a sleeping place, although this may be a recent adaptation (in primitive nesting, there were probably few potential roosting holes adjacent to the nest hole).

Since only 12.6% of the males in my study defended a single room throughout the season, it is surprising that Johnston and Hardy (1962:253) found that more than half of their males in Kansas claimed only 1 room. Perhaps Johnston and Hardy confused actual room occupancy with mere male control of rooms. In Texas, while martins never nested in every room in my colonies, most rooms were controlled by either male martins as part of their territories or House Sparrows and Starlings. There have been few "spare" rooms in colonies. The maintenance of minimum territories larger than 1 room assures that colonies cannot have Purple Martins breeding in all the available rooms.

SUMMARY

Territoriality in Purple Martins in north-central Texas was studied at 2 martin colonies. Two types of territory were distinguished: maximum—the number of rooms males claimed upon their arrival at the colony; and minimum—the number of rooms males claimed at the end of the season. Maximum territories were larger than minimum ones; males arriving in February and March claimed larger maximum territories than males that arrived in April and May. Territory in females closely paralleled territory in males. Unpublished studies suggested that polygyny occurred in about 5% of male Purple Martins in Sherman, Texas. Resident male martins controlled about 75% of all available rooms in a martin colony, with House Sparrows and Starlings using the remaining rooms.

It is suggested that territoriality in Purple Martins has evolved to facilitate polygyny. Polygyny remains at a low incidence because competition among evenly matched males in the population overrides strong sexual selection for polygyny. This hypothesis applies to martins that nested in woodpecker holes before man provided birdhouses and to martins presently nesting in martin houses. Polygyny, as a function of territory, is further supported by the temporal contraction of martin territory. As fewer potential mates are available in the later part of the breeding season, males may profitably restrict defense of their territories and assist their mates in feeding young. Territoriality in Purple Martins resembles the "super-territory" model, which postulates that increased territory size in the early part of the nesting season serves to exclude conspecifics from nesting, increasing the territory-holder's relative genetic contribution. But this model is weakened for Purple Martins because it is doubtful that the super-territory holders exclude any conspecifics from breeding. The maintenance of minimum territories larger than 1 room may indicate that Purple Martins have not adapted completely to the high apartment-room density of artificial birdhouses, or may be an adaptation for males' holding a roosting room.

ACKNOWLEDGMENTS

I thank Erik J. Bitterbaum, Warren M. Pulich, R. Douglas Slack, and C. R. Woodrow for advice on the manuscript. I am most grateful to The Wilson Ornithological Society for providing me with a Margaret Morse Nice Award.

LITERATURE CITED

- ALLEN, R. W. AND M. M. NICE. 1952. A study of the breeding biology of the Purple Martin (*Progne subis*). *Am. Midl. Nat.* 47:606-665.
- BROWN, C. R. 1975. Polygamy in the Purple Martin. *Auk* 92:602-604.

- . 1977a. A record of intraspecific injury in the Purple Martin. *Bird-Banding* 48:273.
- . 1977b. Purple Martins versus Starlings and House Sparrows in nest site competition. *Bull. Texas Ornithol. Soc.* 10:31–35.
- . 1978. On early spring arrival of Purple Martins. *Bird-Banding* 49:130–133.
- BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160–169.
- . 1969. Territorial behavior and population regulation in birds, a review and re-evaluation. *Wilson Bull.* 81:293–329.
- FINLAY, J. C. 1971. Breeding biology of Purple Martins at the northern limit of their range. *Wilson Bull.* 83:254–269.
- GAUNT, A. S. 1959. Behavior in the Purple Martin. *Kansas Ornithol. Soc. Bull.* 10:14–16.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98:340–369.
- JOHNSTON, R. F. AND J. W. HARDY. 1962. Behavior of the Purple Martin. *Wilson Bull.* 74:243–262.
- KLIMKIEWICZ, M. K. AND P. D. JUNG. 1977. A new banding technique for nesting adult Purple Martins. *N. Am. Bird Bander* 2:3–6.
- MCLAREN, I. A. 1972. Polygyny as the adaptive function of breeding territory in birds. *Trans. Conn. Acad. Arts Sci.* 44:191–210.
- NICE, M. M. 1941. The role of territory in bird life. *Am. Midl. Nat.* 26:441–487.
- OLMSTEAD, R. 1955. Observations on Purple Martins. *Kansas Ornithol. Soc. Bull.* 6:8–10.
- ROHWER, S. AND D. M. NILES. 1977. An historical analysis of spring arrival times in Purple Martins: a test of two hypotheses. *Bird-Banding* 48:162–167.
- TINBERGEN, N. 1957. The functions of territory. *Bird Study* 4:14–27.
- VERNER, J. 1977. On the adaptive significance of territoriality. *Am. Nat.* 111:769–775.
- AND M. F. WILLSON. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. *Ornithol. Monogr.* No. 9.
- WILSON, E. O. 1975. *Sociobiology*. Harvard Univ. Press, Cambridge, Massachusetts.
- WYNNE-EDWARDS, V. C. 1962. *Animal dispersion in relation to social behavior*. Hafner, New York, N.Y.

2601 TURTLE CREEK, SHERMAN, TEXAS 75090. ACCEPTED 21 AUG. 1978.