A Selfish Herd of Martins

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Hamilton's (1971) "selfish herd" model demonstrated that an individual can benefit from group membership because of reduced probability that it will become the victim of predator attack. Basically, he showed that an individual can increase its safety by diminishing the distance between itself and conspecifics (alternative targets for predators); that is, individuals achieve safety by crowding. We present evidence that night-roosting birds show preferences for being on the "inside" of flock structure, as predicted by the hypothesis.

We studied a night roost of Gray-breasted Martins (*Progne chalybea*) in downtown Manzanillo, Colima, Mexico (19°2'N, 104°21'W) on the evenings of 9 and 10 January 1982 and 4, 5, 6, and 8 January 1985. Approximately 10,000 birds roosted nightly on utility wires over city streets in the vicinity of the downtown square. During the 1982 study observers were scattered over the roosting area, and in 1985 2 observers concentrated on approximately 3,000 birds within 10–20 m of a park bench. The birds were distributed evenly along 14 main powerlines and several smaller lines 7–10 m above the street. An obvious distinction could be made between edge and center zones within each line of birds (see Fig. 1). Movements and defensive behavior could be monitored separately for each zone.

We predicted generally that competition would be more intense for central roosting positions. Specifically, *contested arrivals* (which occurred when one bird tried to usurp an already-occupied position) were expected to be more common and less successful in central zones compared with edge zones. *Uncontested arrivals* were expected to be more common at the edges. Finally, we predicted that individuals would depart *voluntarily* (i.e. without being supplanted) more often from the edges, presumably as they tried to move inward (comparable to the "leap frogging" of Hamilton 1971).

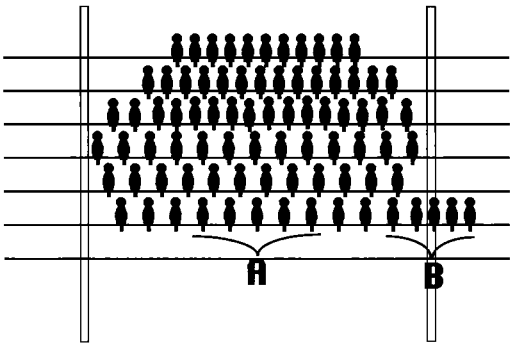

Fig. 1. Simplified representation of distributions of birds within a night roost of Gray-breasted Martins on powerlines. Two focal zones of 5 birds each are indicated: (A) center zone, (B) edge zone.

Observations were made during roost formation (between 1900 and 2000 PST). Focal zones, defined as 5 bird positions the first night in 1982 and 10 thereafter, in the centers or at the edges of lines were monitored simultaneously by two observers for 5-min periods. An edge focal zone contained the 5–10 birds on the end of a string of birds and the spaces vacated by them, if any, during the 5 min. A center focal zone contained 5–10 birds in the central region of a line of birds that was usually more than 100 birds long (see Fig. 1). All supplanting attempts (whether successful or not), departures, and arrivals were recorded for a total of 51 edge and 51 center samples in 1982 plus 16 edge and 16 center in 1985. No two samples were from the same focal zones on any one night.

As predicted, bird arrivals in the central positions were more likely to be contested than those in the edge zones (Table 1). In 1982, 82.5% of 63 central

TABLE 1. Summary of Gray-breasted Martin roost traffic Manzanillo, Mexico.

Wire position	Unforced departures	Arrivals		Percentage successfully contested
		Uncontested	Contested	
1982				
Center	15	11 (17.5%)	52 (82.5%)	0.0%
Edge	73	104 (80.6%)	25 (19.4%)	20.0%
1985				
Center	0	4 (21.1%)	15 (78.9%)	6.7%
Edge	126	155 (81.6%)	35 (18.4%)	45.7%

arrivals were disputed vs. just 19.4% of 129 edge arrivals (G with Williams' correction = 72.69, df = 1, $P < 0.001$). In 1985 the comparable frequencies were 78.9% of 19 center vs. 18.4% of 190 edge (G with Yates' correction = 26.17, df = 1, $P < 0.001$). Also, contested arrivals in central zones were less likely to be successful [in 1982, 0 of 52 center attempts vs. 5 of 25 edge attempts: G (Yates) = 7.80, df = 1, $P < 0.01$; in 1985, 1 of 15 center vs. 16 of 35 edge: G (Yates) = 6.29, df = 1, $P < 0.01$]. In both years most uncontested arrivals occurred at edge zones (Table 1). Finally, unforced departures were more common in edge zones than in the center. In 1982, 83% of all voluntary departures were from edge positions (binomial test against extrinsic hypothesis of equal likelihood, $z = 6.19$, $P < 0.001$), as were 100% of 126 departures in 1985 ($z = 11.22$, $P < 0.001$).

In summary, the martins gave three indications of preferring the center of the roost. Central positions were defended more consistently, defended more successfully, and less likely to be vacated voluntarily. Furthermore, central positions were taken quickly when vacancies appeared (we collected no latency data, however). Although we observed no actual predator attacks on these urban birds, our findings are consistent with the hypothesis that this preference evolved as an antipredator strategy in natural roost sites. Of the other selective advantages hypothesized for group living (e.g. Wilson 1975), only increased warmth would seem to predict strong behavioral preference for crowded central positions; this seems unlikely to confer a significant benefit in the tropics.

Brown (1984) reported on a preroost gathering of breeding Purple Martins (*P. subis*) in Arizona in which the birds preferred positions on the uppermost wires rather than lower wires. Also, in his study of a dimorphically colored species, light-breasted birds displaced dark-breasted birds more frequently than expected by chance. In our study of a monomorphic species, we could not distinguish age or sex of individual birds; however, once a bird was located in a central position it rarely lost to an intruder. These centrally located birds could be socially dominant because of age or sex, or they could be "winners" because of resident status. Such brief, asymmetrical contests among animals in which the resident "always" wins have been reported previously (e.g. Davies 1978) and are expected to occur primarily when the opponents are physically mismatched or when the perceived value of the contested resource differs markedly between owner and intruder (Maynard Smith 1982). In the case of powerline position, the asymmetry seems most likely to stem simply from the physical advantage of having a firm grasp on the preferred resource. The benefit for attempting intrusions in central zones may stem primarily from finding rare and ephemeral vacancies there or from occasionally startling an incumbent into flight.

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