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TERRITORIAL EXCLUSION BY A LONG-DISTANCE MIGRANT WARBLER IN JAMAICA: A REMOVAL EXPERIMENT WITH AMERICAN REDSTARTS (*SETOPHAGA RUTICILLA*)

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ABSTRACT.—To test whether male American Redstarts (*Setophaga ruticilla*) excluded conspecifics from selected habitats on their wintering grounds, we removed territorial individuals from four replicate sites in two different habitats in Jamaica, West Indies, and recorded territory shifts and new colonizations of the vacated areas. In total, 12 American Redstarts (nine after-hatch-year [AHY] or older males, two yearling [HY] males, and one female) were removed, and their vacated territories were re-occupied by 18 neighboring or newly-appearing redstarts (five AHY males, four HY males and nine females). The re-occupation of the vacated areas supports the hypothesis that territoriality in this species acts to exclude conspecifics from certain winter habitat, and shows that American Redstarts compete with conspecifics for habitat in their winter grounds. Moreover, a statistically significant shift in sex composition following removal indicates that AHY males excluded females from mutually acceptable habitats. Such behavioral dominance, if confirmed, could help account for sexual habitat segregation during winter, and could result in differential winter survival rates between the sexes, thereby influencing population structure and regulation in this long-distance migrant. *Received 10 August 1992, accepted 15 December 1992.*

TERRITORIALITY DURING the breeding season is characteristic of many songbirds and its function and impact on population dynamics has been studied frequently (e.g. Brown 1969, Patterson 1985, Beletsky and Orians 1987). Territoriality during the nonbreeding period, however, has received much less attention, especially for migrant species that winter in the tropics. Although winter territoriality has been documented in a number of tropical-wintering songbirds (e.g. Schwartz 1964, Elgood et al. 1966, Willis 1966, Gorski 1969, Nisbet and Medway 1972, Emlen 1973, Rappole and Warner 1980, Morton 1980, Price 1981, Greenberg 1984, Kelsey 1989, Holmes et al. 1989, Winker et al. 1990, Bates 1992), little is known about its function or its potential effects on the population dynamics of such long-distance migrants (Greenberg 1986, Holmes et al. 1989, Winker et al. 1990).

Defense of winter territories among conspecifics implies intraspecific competition for some limiting resource (Greenberg 1986). Such territorial defense may lead to the distribution of individuals evenly through the available habitat or, if despotism is involved, to the differential occupancy of certain habitats by particular sex or age classes (Fretwell 1972). The latter may result in differential survival, thus potentially affecting population structure and size. To demonstrate despotic habitat selection, it must be shown that some individuals are prevented from settling in certain habitats by the behavioral dominance of others. This can best be done through removal experiments (Watson and Jenkins 1968, Krebs 1970, Sherry and Holmes 1989). Thus far, experimental removals of territorial migrants in tropical winter habitats have been attempted only twice, both for Hooded Warblers (*Wilsonia citrina*) in Mexico (Rappole and Warner 1980, Morton et al. 1987).

In this study, we tested for despotism among wintering American Redstarts (*Setophaga ruticilla*), a paruline warbler that breeds across temperate North America and winters in the Neotropics. The redstart is territorial in winter (Rappole and Warner 1980, Holmes et al. 1989, Sliwa and Sherry 1992), and the sexes tend to be segregated among winter habitats (Lopez and Greenberg 1990, Parrish 1991, Sliwa 1991). To test whether territoriality could influence winter habitat distribution patterns of this species, we performed an experiment in which we removed territorial individuals (mostly older males) from two replicate sites in each of two habitat types. Vacated territories were then monitored for territorial shifts by neighboring birds and for colonizations by new individuals, which would be evidence that redstarts were excluding conspecifics from their territories.

STUDY SITES AND METHODS

American Redstarts were permanently removed from four 2.5-ha study sites: two in mangroves and two in dry limestone forest in Jamaica, West Indies. The two mangrove sites were 1 km apart near Luana Point, 13 km west of Black River, St. Elizabeth Parish (see Holmes et al. 1989). These were dominated by black mangrove (*Avicennia germinans*), although white (*Laguncularia racemosa*) and red (*Rhizophora mangle*) mangroves also occurred. These mangrove stands had relatively dense canopies which averaged about 12 m in height and almost no ground or shrub-level vegetation. Both sites were flooded to depths up to 0.5 m when these experiments were conducted.

The two dry limestone forest sites were 13 km SE of Lionel Town and several kilometers inland from the coast at Portland Ridge, Clarendon Parish (elevation 50–100 m). Each was on honeycomb limestone, and was characterized by little ground cover, a dense understory of shrubs, palms, and small trees, and a relatively open canopy, reaching a height of 12 to 20 m. Major tree species included *Bursera simaruba*, *Tecoma stans*, and *Bauhinia divaricata* (Lack 1976).

Each study area was gridded at 25-m intervals to facilitate territory mapping. We caught and color banded most redstarts occupying each site, using song playbacks in combination with mist nets (Holmes et al. 1989). All birds in the hand were then sexed and aged using multiple criteria (skull ossification, retrix patterns and shapes, growth bars, presence of incoming black feathers, breast and wing axillary coloration, and color transition on upperparts) first set forth by Pyle et al. (1987) and further confirmed by Sherry and Holmes (unpubl. data). The few individuals not color banded were identified by unique plumage patterns, particularly the extent and patterning of black on the breast and flanks in the case of the definitive plumage of older or after-hatch-year (AHY) males (Sherry and Holmes 1992), or the degree and patterning of black spotting in the case of yearling (hatch-year or HY) males. HY males, which have femalelike plumage in their first year, were distinguished from females by: (1) scattered incoming black feathers (Rohwer et al. 1983, Pyle et al. 1987), which are evident in many individuals when they arrive in Jamaica (Sherry and Holmes unpubl. data); and (2) the color of the wing axillary and adjacent parts of the breast (yellowish on females, orangish on HY males; Pyle et al. 1987, Sherry and Holmes unpubl. data). Our confidence in identifying males from females in the field during the winter period is based on seven years of observing color-banded individuals of known sexes in Jamaican habitats (Holmes et al. 1989, Holmes and Sherry 1992; Holmes, Sherry, and Marra in prep.). No attempt was made in this study to age females.

The removals were conducted in late October to mid-November, after migration was complete (R. Sutton pers. comm.) and redstarts were settled in winter habitats. Redstart populations in these Jamaican habitats are relatively stable after mid-October, based on evidence from our long-term studies at these sites with color-marked individuals (Holmes et al. 1989, Holmes and Sherry 1992 unpubl. data). Each year since 1986, we have captured and marked all redstarts occupying gridded census plots in several habitats in Jamaica, including some near the sites used in the experiments reported here, mapped their territories, and determined their persistence over the winter period. Redstart abundance and sex and age composition on these sites remain remarkably stable from mid-October through January and into mid-March (Holmes et al. 1989). Individuals of both sex and age classes remain within 30 m of their capture site throughout the winter period, with relatively few disappearing due to mortality and/or dispersal (6–25% between mid-October and mid-January, varying with sex and age; see Holmes et al. 1989). This high stability and low turnover of individuals after mid-October means that any replacement of removed territorial birds demonstrates the effects of territorial exclusion or local shifting into more favorable sites and not the arrival of new migrants.

The locations and territories of all redstarts on each plot were mapped during the two to three days prior to the removals. Mapping of individuals continued until the shape and size of their territories remained constant; this averaged about 9 person-hours per plot (range 8–14 h). Two to four centrally located redstarts were then caught in mist nets and removed from each study site. The experimental plots were examined for redstarts two days following removal, and then territories of all redstarts were mapped extensively after a two-week interval. For this latter process, at least 10 person-hours were spent mapping birds at the Luana sites and 20 person-hours at Portland Ridge during each postremoval interval. The increased effort at Portland Ridge was necessary to obtain accurate maps in this more densely vegetated habitat.

RESULTS

Within two days of removal, territories in both habitats were being settled by neighboring and newly-appearing individuals. Because intensive mapping of territories was not done immediately following the removals, however, we present the territorial patterns showing the replacements after two weeks as the measure of re-occupation of these habitats (Fig. 1, Table 1).

On the first mangrove site (Fig. 1A), 12 territorial redstarts were present of which two older males (labeled AHY-1 and -2) and one yearling male (HY-1) were removed on 24 October 1989. Two weeks later, two bordering females (F-3 and -6) had shifted their entire territories into the newly vacated space (Fig. 1A), one newly appearing AHY male (AHY-6) had established a territory composed of portions of the vacated AHY territories, and a new female (F-7) colonized vacated portions of HY-1's territory. In addition, a fourth female (F-1) shifted her territory to encompass portions of the vacated AHY territories.

On the second mangrove site (Fig. 1B), 12 redstarts were present when we removed two AHY males (AHY-3 and -4), one yearling male (HY-2), and one female (F-3) on 12 November 1989. Within two days, one yearling (HY-1) and two older males (AHY-6 and -7) shifted their territories to occupy portions of the vacated areas, including an area previously occupied by AHY-4. The area left vacant when AHY-6 moved was then re-occupied by a bordering female (F-2). A new female (F-4) colonized part of a vacated AHY (AHY-4) territory.

For both black mangrove sites combined (Table 1), the territories of seven removed redstarts (four AHY males, two HY males, one female) were re-occupied by eight redstarts (three AHY males, one HY male, four females). The proportions of AHY and HY males did not differ significantly before and after removal, nor did the ratio of males to females, even with the increased number of females present after removal (Table 2).

On the first replicate site in dry limestone forest, we removed three AHY males (AHY-2, -3, and -4) of the six redstarts present on 24 October 1990. Portions of their vacant territories were colonized by one neighboring female (F-1), one new female (F-3), two new yearling males (HY-1 and -2), and two AHY males (AHY-5 and -6; Fig. 1C).

The second site in dry limestone forest had eight redstarts present when the removal was conducted on 24 October 1990. Following the removal of two AHY male redstarts (AHY-1 and -2), one female (F-1) and one yearling male (HY-1) shifted their territories onto the vacated areas (Fig. 1D). In addition two new females (F-3 and -4) colonized the study site.

For these two dry limestone sites combined, the removal of five AHY males resulted in subsequent territorial shifts and colonizations by eight redstarts; two AHY males, three HY males, and five females (Table 1). Again, the differences in the proportions of AHY to HY males and of all males to females before and after removal were not statistically significant (Table 2). However, the proportion of females relative to AHY males did increase significantly ($P = 0.03$) after the removals (Table 2).

In all four replicates combined, territories established by the 12 redstarts removed were re-occupied by 18 new or neighboring redstarts (Table 1). With this larger sample size, we found statistically significant increases in the proportions of females relative to all males ($P = 0.02$) and to AHY males ($P = 0.01$), but not between males of different age classes ($P = 0.22$; Table 2). Taken together, these results indicate that male redstarts were excluding neighbors and possibly floaters from these habitats, and that females may have been disproportionately affected.

Discussion

Territoriality in birds has been shown to influence habitat distribution patterns, reproductive success, and survival (Fretwell 1972, Enoksson and Nilsson 1983, Alatalo et al. 1986, Hill 1988, Andrén 1990). Almost all such information, however, is derived from studies of breeding birds and especially of species resident in the temperate zone. In contrast, the potential consequence of territoriality in the wintering season, especially for long-distance migrants, has received little attention. Unlike the breeding season, territoriality in these species in winter is practiced by both males and females (e.g. Nisbet and Medway 1972, Morton 1980, Rappole and Warner 1980, Holmes et al. 1989, Kelsey 1989). Because no breeding occurs during this period, territoriality cannot serve the functions of defense of paternity (Gauthier 1987, Møller 1987) or of spacing to reduce nest predation (Patterson 1985). Rather, winter territoriality seems to function primarily for self maintenance, probably for securing a patch of habitat with dependable food (Price 1981, Greenberg 1985, 1986) and perhaps for providing refuge from predators and inclement weather (Winker et al. 1990). In Jamaica, because there are essentially no bird-hunting predators (Holmes et al. 1989) and climate seems equitable, food would appear to be the primary ultimate factor promoting winter territoriality.

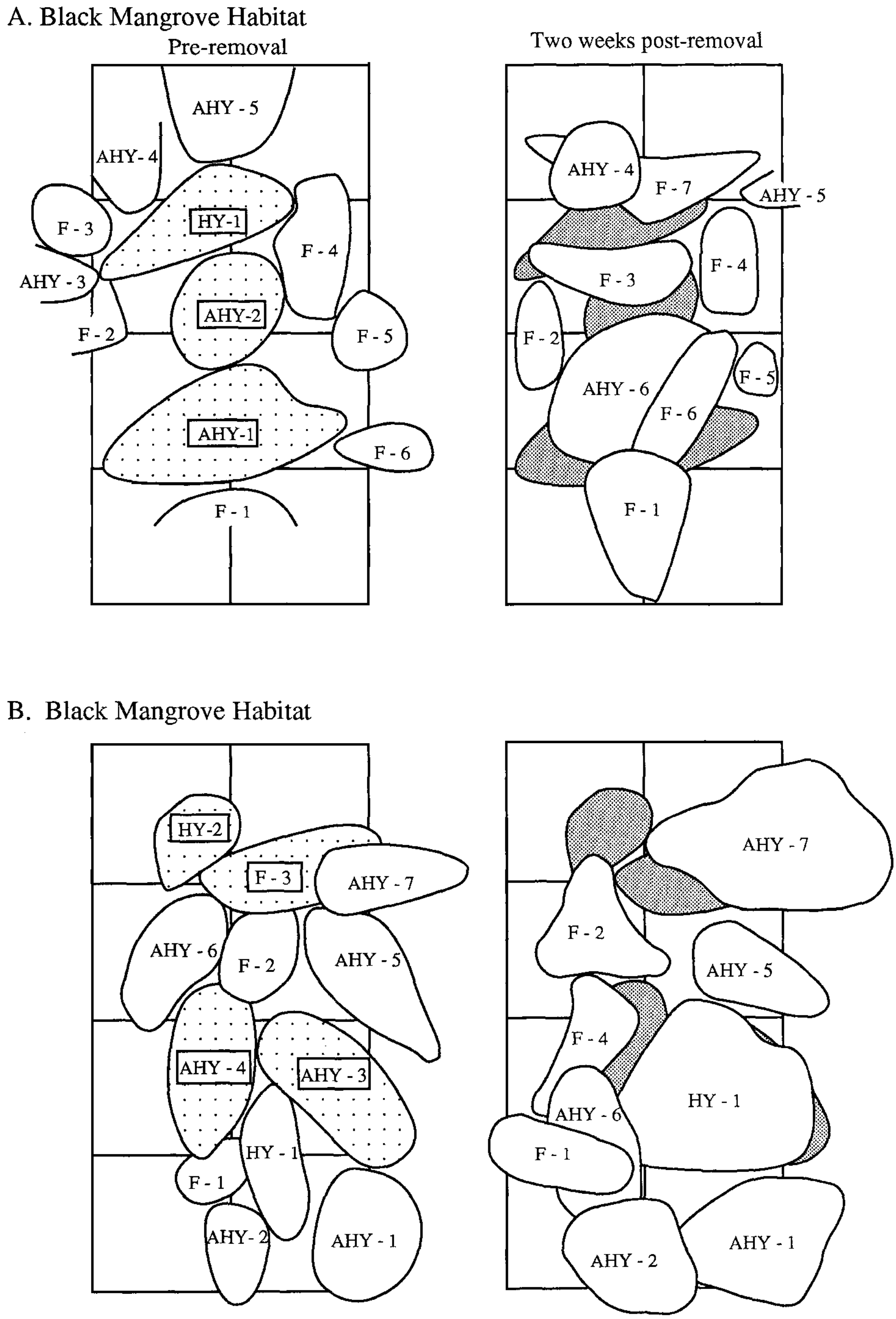
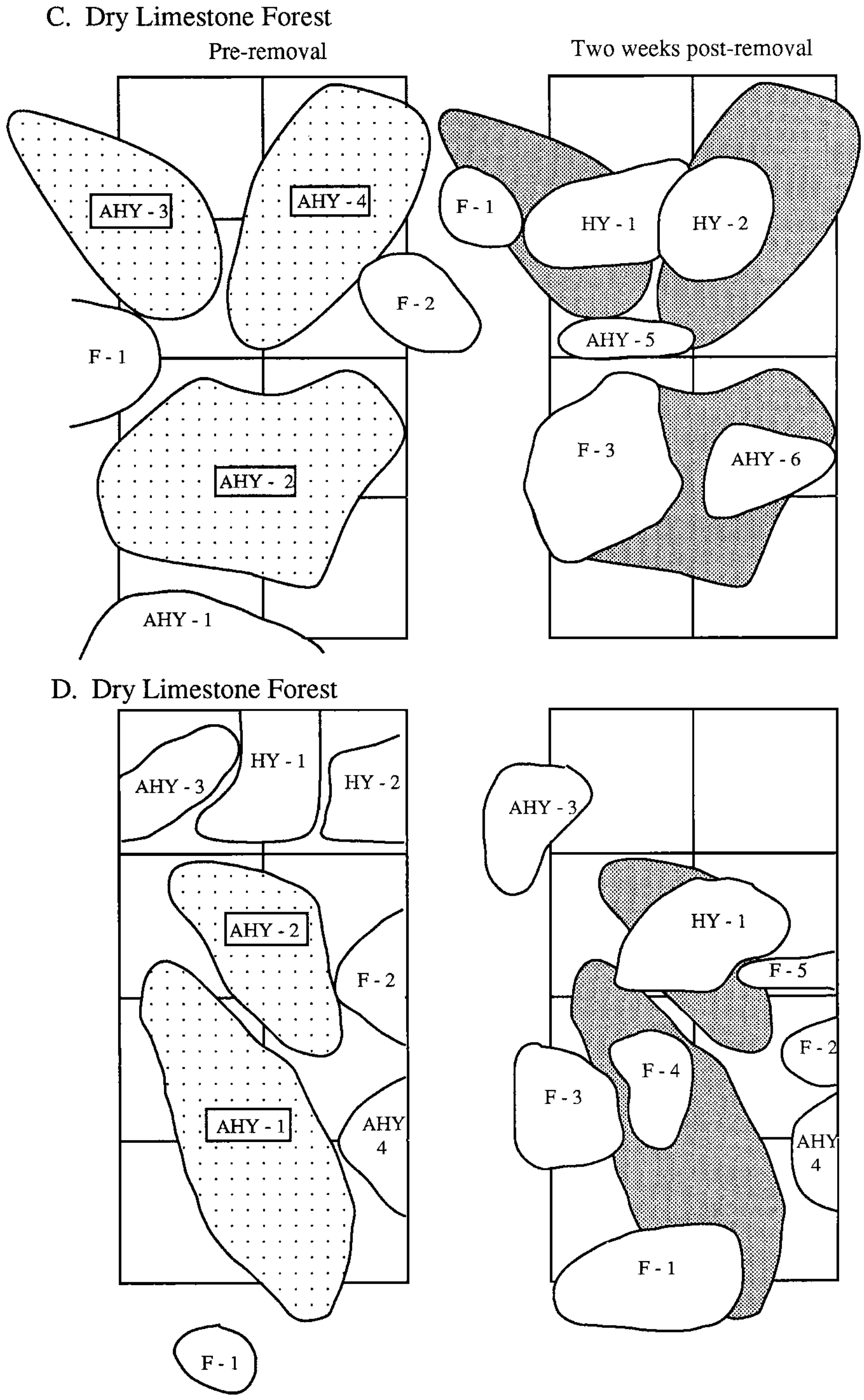


Fig. 1. Territories of American Redstarts on two gridded study sites in black mangrove habitat (A and B) and two in dry limestone forest (C and D) in Jamaica, before and after removals (left and right panels, respectively). Stippled territories are those from which redstarts were removed. Abbreviations: AHY, after-hatch-year or older males; HY, hatch-year or yearling males; F, females.



C. Dry Limestone Forest

Pre-removal

Two weeks post-removal

D. Dry Limestone Forest

Fig. 1. Continued

Behavioral dominance has been implicated as an important regulatory mechanism in a variety of organisms, including birds (e.g. Gauthreaux 1978). The results of our removal experiments with redstarts in Jamaica show intraspecific competition for winter habitat (i.e. at least some winter habitats may be saturated). Similar findings based on observations of color-marked in-

TABLE 1. Numbers of individual American Redstarts removed from winter territories and their replacements in two wintering habitats in Jamaica.

	Black mangrove		Dry limestone		Habitats combined	
	Removed	Replacements	Removed	Replacements	Removed	Replacements
			Male			
AHY	4	3	5	2	9	5
HY	2	1	0	3	2	4
Subtotal	6	4	5	5	11	9
			Female			
	1	4	0	5	1	9
			Total			
	7	8	5	10	12	18

TABLE 2. Results of Fisher's exact tests (probability value) comparing ages and sexes of territory holders removed and their replacements (see Table 1). Significant values ($P < 0.05$) in bold.

Comparison	Black mangrove	Dry limestone	Habitats combined
AHY : HY males	0.67	0.09	0.22
AHY males : females	0.29	**0.03**	**0.01**
All males : females	0.28	0.10	**0.02**

dividuals disappearing and being replaced by "new" birds have previously been reported for Hooded Warblers in Mexico (Rappole and Warner 1980) and for Black-throated Blue Warblers (*Dendroica caerulescens*) and American Redstarts in Jamaica (Holmes et al. 1989). The only previous experimental removals were those of Rappole and Warner (1980) and Morton et al. (1987) for Hooded Warblers, which also showed new individuals moving into the vacancies created, although their sample sizes were small ($n \leq 4$). These results taken collectively demonstrate active competitive exclusion for these migrant species on their Neotropical winter quarters. They also suggest that winter habitat may be limiting and thus of potential importance to the population dynamics of these long-distance migrant bird populations (see below).

Our results also indicate a differential response among sex and possibly age classes, with female redstarts in particular shifting into sites originally occupied by males. This suggests a pattern of social dominance in which males may exclude females from certain winter habitats. The four sites chosen for our experiments contained relatively high densities of AHY male redstarts, suggesting that these sites were optimal winter habitat for this species (Holmes et al. 1989, Sliwa 1991, Sherry and Holmes unpubl. data). If such habitats are indeed preferred and if access to these habitats is limited by the dominance behavior of older and presumably more experienced males, this might help account for the pattern of sexual habitat segregation reported for this species in winter by Lopez and Greenberg (1990) and Sliwa (1991). Although HY males were among the replacements in both habitats (Table 1), our data do not provide an adequate test of whether older males exclude younger males from these habitats.

Our findings for redstarts in Jamaica differ in some respects from those of Morton et al. (1987) for Hooded Warblers in Mexico. In their experiments, females did not invade "male habitat" after males were removed, leading Morton et al. (1987) to suggest that sexual habitat segregation in wintering Hooded Warblers might be due to innate differences, an idea further supported by laboratory experiments with hand-reared birds (Morton 1990). These apparent differences may represent a continuum from a system of behavioral dominance determining sexual habitat selection (American Redstarts) to a more fixed, inherited pattern of habitat preferences among the sexes (Hooded Warblers). Possibly, winter sexual habitat segregation in some species results from both innate sexual differences and periodic behavioral reinforcement in a sexual dominance hierarchy. Further studies involving removals and other experiments that incorporate larger sample sizes of all age and sex classes, as well as replication among habitats and species, are needed to determine both the proximate and ultimate factors influencing sexual habitat segregation in these wintering migrants.

The important question arising from the existence of nonrandom habitat selection for migrant birds in winter is whether, when older males behaviorally exclude other individuals of different sex and possibly age classes from the most suitable habitats, the survival of subordinate individuals is decreased. If this happens regularly, then winter becomes a potentially limiting season. Furthermore, if such density-dependent habitat selection in winter results in higher mortality of subordinate individuals and females in particular, this might explain the male-biased sex ratio during the breeding season in many species (Breitwisch 1989), including redstarts (Sherry and Holmes 1991). Although most explanations of such biased sex ratios focus on breeding season events (Breitwisch 1989), they could also result from behavioral interactions among birds during winter.

Finally, the fact that older male American Redstarts exhibit behavioral dominance on the breeding (Sherry and Holmes 1989) and possibly on the wintering grounds (this paper) suggests that their population dynamics are structured around density-dependent mechanisms acting throughout the year. A dominance-based system in winter, which differentially affects such population parameters as survival and sex ratios, may play a role in structuring events on the breeding grounds. The reverse is almost certainly true, in that reproductive success and survival in the breeding period will influence winter densities, habitat settlement patterns, and perhaps mortality rates (Sherry and Holmes 1991). These conclusions further highlight the need to consider events throughout the annual cycle to understand more completely what factors limit or regulate populations of long-distance migrant birds.

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