FLOCK STABILITY IN RELATION TO SOCIAL DOMINANCE AND AGONISTIC BEHAVIOR IN WINTERING DARK-EYED JUNCOS

MARTHA HATCH BALPH
Department of Wildlife Science, UMC 52, Utah State University, Logan, Utah 84322 USA

ABSTRACT.—This paper examines some consequences of changes in the membership and location of winter flocks of Dark-eyed Juncos (*Junco hyemalis*). Among captives, intragroup social relationships seldom were affected by separation from or subsequent reunion with another portion of the home flock, by amalgamation with or separation from a foreign flock, or by changes in flock location. Foreign flock members usually were subordinate to, and preferentially attacked by, residents. Juncos rejoining their home flocks after a 1-week separation retained their previous social positions but engaged temporarily in a disproportionate amount of agonistic behavior with former flockmates. Some proximate and ultimate implications of winter flock stability in juncos are discussed in the light of these and other findings. Social and ecological costs that may be incurred by juncos attempting to change their flock membership or home range during the winter should select for behavior that reduces the likelihood of such changes, including geographic differentiation in the migratory habits of the sexes. *Received 12 March 1979, accepted 31 May 1979.*

WINTERING Dark-eyed Juncos (*Junco hyemalis*) are well known to form small- to medium-sized flocks of relatively stable membership and location and to exhibit social hierarchies (e.g. Sabine 1949, 1955, 1956, 1959). Juncos may enjoy various advantages by living in groups rather than as isolates during the winter (see Balph 1977). Presumably juncos also may benefit by maintaining constant inter-individual associations and by localizing their winter activity. In this paper I explore the latter possibility by examining some consequences of changes in the membership and location of groups of wintering juncos. My first objective is to present the results of experiments testing the following null hypotheses:

1. Members of a dispersing segment of an established resident flock maintain constant dominance-subordination relationships among themselves: (a) if they live apart from other juncos; (b) if they join a foreign flock; or (c) if they subsequently rejoin their home flock.
2. After part of a resident flock disperses, remaining flock members maintain constant dominance-subordination relationships among themselves: (a) if they are not joined by other juncos; (b) if they are joined by a foreign flock; or (c) if they are rejoined by former flockmates.
3. Members of an incoming, foreign flock are as likely to be dominant to residents as the reverse.
4. Dominance-subordination relationships between resident flock members and former members returning after a 1-week absence are the same before and after the separation period.
5. Agonistic encounters are equally likely to occur between as opposed to within incoming and resident flocks: (a) if the introduced birds are foreign; or (b) if the introduced birds are former members of the resident flock.
6. The ratio of high- to low-intensity agonistic encounters is the same between and within incoming and resident flocks: (a) if the introduced birds are foreign; or (b) if the introduced birds are former members of the resident flock.

A further objective is to integrate my findings and those of others into a discussion of some proximate and ultimate implications of winter flock stability in juncos.

METHODS

Twelve Dark-eyed Juncos (*J. h. montanus*) were captured on 21 November 1973 in North Logan, Utah, and 6 birds were placed simultaneously in each of 2 large (3.05 × 9.14 × 2.14 m) outdoor flight pens. Each six-member "flock" consisted of first-year birds of both sexes; age was determined by skull examination at capture and sex by gonadal examination after behavioral studies were completed. Resources, including ample quantities of bird seed, water, perches, brushy cover, and natural substrate, were identically distributed in both pens. The sides of each pen were covered to effect visual (although not auditory) isolation.

Over an 8-day period in January 1974, three randomly selected members of each flock were transferred (1) from their home pen to an identical pen containing no birds, (2) to the home pen of the other flock, (3) once again to the empty pen, and (4) back to their home pen (subgroups A_1 and B_1, Table 1). All transfers were accomplished during the first hour after official sunrise. The remaining three birds of each flock resided in their respective home pens throughout (subgroups A_2 and B_2, Table 1). Each subgroup contained either 2 males and 1 female (A_2, B_1, B_2) or 1 male and 2 females (A_1). None of these birds was used in the individual-transfer experiments reported by Balph (1977).

Data on the frequency and form of agonistic behavior at various resources were collected for each resident flock from a blind in December (described in detail by Balph 1977). Similar data were gathered for each subgroup or combination of subgroups during all phases of the transfer experiments in January. A total of 2,374 agonistic interactions was recorded during 476 5-min observation periods (see Table 1); excluded are a few interactions (<2%) for which either or both of the participants or the form of agonistic behavior could not be identified. Interactions in which one bird pecked, chased, or threatened another (i.e. pecking attacks, flight pursuits, fights, and head dances) were called "high intensity," whereas avoidance encounters (i.e. supersedences and ground approaches causing escape) were classified as "low intensity" (see Balph 1977). One individual was considered socially dominant to another if it caused the other to retreat in most or all of their agonistic interactions. Reverse wins were rare (<3% of observed interactions), as were encounters with a tied outcome (<1%).

Behavioral data were analyzed with Chi-square tests of goodness of fit and Chi-square two-way contingency table tests of independence. In testing hypothesis 5 (above), expected values were weighted to reflect relative numbers of within-group and between-group bird pairs (i.e. 6 within-group versus 9 between-group pairwise combinations for a 6-member composite flock containing two 3-member subflocks).

RESULTS

Juncos (subgroups A_1 and B_1) that "dispersed" from the two captive flocks exhibited a constant order of dominance among themselves prior to and throughout the transfer experiments. The same was true for one of the resident subflocks (A_2). In the other (B_2), however, a male that had dominated both other individuals of the B_2 subgroup in December was subordinate to both during all phases of the transfer experiments. Whether this change occurred prior to or as a result of the separation of subgroup B_1 from B_2 is not known. Perhaps importantly, both shifts of dominance involved bird pairs in which one individual pursued the other in flight, whereas the other won all other forms of agonistic encounter (see Balph 1977), even though this type of dominance-subordination relationship was rare (3 of 48 pairwise relationships in the present study). In sum, intragroup social relationships appeared to be affected slightly or not at all by separation from or subsequent reunion with another portion of the home flock, by amalgamation with or separation from a foreign flock, or by changes in flock location (see hypotheses 1 and 2).

Members of foreign subgroups joining resident subgroups (A_1 into B_2 and B_1 into A_2) were dominant to residents in only 3 of 18 pairwise relationships, a result dif-

TABLE 1. Summary of experimental design.

Date of manipulation	Pen	Subgroup(s) Present	Subgroup(s) Introduced	Date(s) of observation	5-min samples (n)	Agonistic encounters recorded (n)
21 Nov.	A	None	A_1, A_2	1–23 Dec.	72	385
21 Nov.	B	None	B_1, B_2	1–22 Dec.	72	332
17 Jan.	A	A_2	None	17–18 Jan.	25	103
17 Jan.	B	B_2	None	17–18 Jan.	25	64
17 Jan.	C	None	A_1	17–18 Jan.	25	61
17 Jan.	D	None	B_1	17–18 Jan.	25	48
20 Jan.	A	A_2	B_1	20 Jan.		
				0–4 h[a]	15	106
				4–9 h	18	158
21 Jan.	B	B_2	A_1	21 Jan.		
				0–4 h	15	218
				4–9 h	18	154
21 Jan.	A	A_2	None	22–23 Jan.	25	56
21 Jan.	D	None	B_1	22–23 Jan.	25	68
22 Jan.	B	B_2	None	22–23 Jan.	25	76
22 Jan.	C	None	A_1	22–23 Jan.	25	32
24 Jan.	B	B_2	B_1	24 Jan.		
				0–4 h	15	167
				4–9 h	18	136
25 Jan.	A	A_2	A_1	25 Jan.		
				0–4 h	15	126
				4–9 h	18	84

[a] Refers throughout to elapsed time since introduction of a subgroup.

fering significantly from the 8.04 of 18 expected by chance (assuming that males should dominate females in 82% of cases; see Balph et al. 1979) ($\chi^2 = 5.71$, df = 1, $P < 0.025$). These three relationships involved an originally high-ranking male (subgroup A_1) that dominated all members of subgroup B_2. All other foreign birds, regardless of sex or previous social rank, were subordinate to all residents. Conversely, juncos reunited with their home flocks after 7–8 days of separation (A_1 into A_2 and B_1 into B_2) invariably retained their original social positions relative to each former flockmate.

The frequency and form of agonistic encounters appeared to vary importantly according to the degree of familiarity between individuals. Agonistic behavior between and within subgroups did not differ for either resident flock prior to the transfer experiments (Table 2). When foreign subgroups joined resident subgroups, however, agonistic behavior was significantly more frequent between than within the subgroups (Table 2), even though the introduced birds appeared often to evade residents by seeking cover (which probably decreased the probability of meetings between foreign and resident birds). The form of agonistic behavior also differed significantly between birds unfamiliar and familiar with each other (Table 2), with high- to low-intensity encounter ratios of 1.6:1 and 1.0:1 between foreign and resident subgroups as compared to 0.7:1 and 0.3:1 within these subgroups in pens A and B, respectively. Heightened aggression between foreign and resident juncos continued for at least 9 h, when my observations ended. Intermediate behavior was evident when former residents were reintroduced to their home flocks: The frequency and (in one flock) the intensity of agonistic encounters were significantly greater between than within subgroups for the first 4 h but not after this time (Table 2). Thus, foreign juncos joining resident flocks tended not only to occupy inferior social positions but also to become involved in disputes throughout the day with resident birds, whereas juncos rejoining their home flocks after a 1-week separation showed no loss of social status and engaged only temporarily in a disproportionate amount of agonistic behavior with former flockmates (see hypotheses 3–6).

DISCUSSION

Dark-eyed Juncos that disperse from an established winter flock may suffer a variety of costs. A junco that emigrates to live as an isolate stands to lose several hypothesized benefits of flock membership, such as increased efficiency in locating food or early detection of predators. Whether moving singly or as a group, dispersing juncos may attract the attention of predators through their heightened activity (see Gauthreaux 1978) and, once detected, may be less able to escape due to their lack of familiarity with new areas. Such birds also may risk starvation in their search for suitable unoccupied habitat.

Wintering juncos that leave the home flock to join a new flock may encounter problems beyond those of emigration *per se*. In earlier experiments (Balph 1977), foreign juncos introduced individually to a captive resident flock usually were subordinate to the residents (25 of 30 pairwise relationships) and engaged in a disproportionate number of high-intensity agonistic encounters with them. Introducing foreign juncos in groups of three to three-member resident flocks in the present study produced similar results, suggesting that outsiders gained little or no social advantage relative to residents by arriving with familiar flockmates rather than arriving alone. Were newcomers to outnumber resident juncos, however, one might expect the dominance advantage of residents to be lessened somewhat (as in domestic fowl, reviewed by Guhl 1962).

In field studies of juncos, Sabine (1949, 1955, 1959) found that foreign individuals or flocks joining resident winter flocks generally were subordinate to most residents and retained this social status throughout the period of association, which ranged from less than a day to several months. Sabine did not see heightened aggression between foreign and resident juncos; her assessment was qualitative, however, and (as she pointed out) incoming and resident juncos might have interacted prior to her observations. In my studies, the most dramatic encounters between foreign juncos and residents typically occurred within minutes of the newcomers' introduction; after this time, behavioral differences between birds familiar and unfamiliar with each other were statistically significant but qualitatively less obvious. Fretwell (1969) observed pronounced aggression not associated with food among free-living juncos that had recently arrived on their wintering grounds. I have noted similar behavior (including head dances and fights, which often occur when captive juncos first meet) in postbreeding montane populations shortly before migration and in newly arrived winter populations in northern Utah. I believe these observations may indicate heightened aggression in the wild between juncos unfamiliar with each other. Such aggression should favor constancy of flock membership and also might limit the size of wintering junco flocks, as social relationships maintained by individual recognition may become less clear as flock size increases (see Balph 1977).

Wintering juncos that leave and subsequently rejoin their home flock may be treated as outsiders upon their return, to a degree probably dependent upon the length of absence. A breakdown of individual recognition might be expected to increase aggression between residents and former residents, whereas lessened familiarity with the home range should place emigrants at a dominance disadvantage

TABLE 2. Chi-square analysis of the frequency and form of agonistic encounters between as opposed to within junco subgroups under varying social conditions.[a]

	Replication		χ^2					
			Number of encounters between versus within subgroups			Ratio of high- to low-intensity encounters between versus within subgroups		
Social context	Pen	Subgroups	0–4 h	4–9 h	Total	0–4 h	4–9 h	Total
Resident flock (control)	A	A_1, A_2	–	–	0.04	–	–	0.01
	B	B_1, B_2	–	–	0.34	–	–	1.66
Foreign flock introduced to resident flock	A	$B_1 + A_2$	18.00***	6.92**	22.31***	2.20	3.58(*)	7.92**
	B	$A_1 + B_2$	15.20***	12.62***	27.78***	11.91***	8.08**	19.92***
Former residents reintroduced to resident flock	A	$A_1 + A_2$	5.08*	0.01	2.86(*)	0.005	0.66	0.39
	B	$B_1 + B_2$	14.13***	0.59	10.94***	13.46***	2.16	14.82***

[a] (*) = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$. For all relationships significant at the 0.1 level or better, between-group values were greater than expected.

upon their return. In the present study, former residents rejoining their home flocks after a 1-week absence maintained their original social positions, but apparently only through active defense. Presumably longer absences might have produced further aggression and perhaps a reduction in the social status of returning birds (as in domestic fowl, Guhl and Allee 1944). Baker and Fox (1978) noted that juncos removed from captive flocks to regain lost weight usually dropped in social rank upon their return several weeks later; however, because these workers determined social rank from win-to-loss ratios rather than from dominance-subordination relationships between individuals, it is unclear whether differential aggression, reversals of dominance, or both factors produced this change.

In some winter-flocking species, intraspecific differences in plumage coloration or pattern may signal potential dominance status and permit birds to change flocks with relative impunity (Rohwer 1975, 1977). Plumage characteristics associated with high social rank in captive junco flocks, however, appeared to confer little or no short- or long-term dominance advantage upon foreign individuals joining resident flocks, and aggression between residents and newcomers was pronounced (although possibly less than if juncos were alike in appearance) (Balph et al. 1979). Results from the present study are consistent with these earlier findings: Foreign juncos were dominant to residents significantly less often than predicted by relative hood darkness ($\chi^2 = 8.94$, df = 1, $P < 0.005$) or tail whiteness ($\chi^2 = 4.97$, df = 1, $P < 0.05$). Although intraspecific plumage differences may function as imperfect cues to sex- or age-related fighting ability at the time of initial hierarchy formation, prior residency apparently overshadows such an effect, which should discourage juncos from changing their flock membership during the winter (see Balph et al. 1979). Plumage variability in juncos might additionally serve to facilitate individual recognition after dominance-subordination relationships have been established (see Balph et al. 1979), which should further promote stability of flock membership.

Dispersal from an established flock, although costly, may have compensating benefits for some juncos under certain conditions. In studies of captive junco flocks, Baker and Fox (1978) found that subordinate individuals were more likely than dominants to die when food was restricted. Fretwell's (1969) results, although more difficult to interpret, may indicate the same for free-living juncos. If food within a junco flock's home range becomes scarce or inaccessible, flock members (particularly those of low rank) might increase their chances for survival by emigrating to new areas, even if these areas are occupied by other juncos; for example, Sabine (1955) noted that foreign juncos joined a resident flock at a feeding station during a period of low temperatures and snowfall, then disappeared during a thaw. If subordinates leave their home flock as a group and are successful in finding unoccupied habitat of adequate quality, they may further enjoy the advantage of a relative increase in dominance status (see Gauthreaux 1978). My experiments indicate that social relationships between individuals are not changed by movements to unfamiliar areas; thus, fighting potentially associated with intragroup dominance reversals can be discounted.

Fretwell (1969) predicts that dominant juncos should force subordinates to disperse to habitats of inferior quality early in the winter so that dominant flock members are assured an adequate food supply through the winter. Because high-ranking juncos usually are males and those of low rank females (Balph 1977, Baker and Fox 1978, Ketterson 1979a), however, the evolution of winter dominance behavior as a mechanism for population regulation (as proposed by Fretwell) should lead to shortages of females of the species for breeding and thus might be to the long-term detriment of males as well as females. Moreover, Fretwell assumes that juncos are able each year to assess the adequacy of winter food supplies in various habitats from fall seed reserves; yet over much of this species' wintering range, winter temperatures and snowfall may increase energy demands and decrease food accessibility to an unpredictable degree.

A sequence of events different from that proposed by Fretwell seems possible, at least in regions such as northern Utah, where winters are relatively cold and snowy but of variable severity. Some recent findings suggest that, in established junco flocks, agonistic encounters occur most frequently among males (Ketterson 1979a) and between birds of similar plumage coloration (Balph et al. 1979) or similar social rank (discussed by Sabine 1949 and tested by Ketterson 1979b). Although differential spacing of dominants and subordinates within flocks quite likely influenced some or all of these results, differential aggression also might be indicated. Because closely ranked juncos are likely to be similar with respect to such correlates of dominance as sex, age, and various morphological features (see Fretwell 1969, Balph 1977, Baker and Fox 1978, Balph et al. 1979, Ketterson 1979a), juncos of similar social status may be the closest competitors ecologically. In this event a high-ranking junco (usually large, adult, and/or male) should gain by directing more aggression toward its immediate inferiors than toward low-ranking birds, as the latter (usually small, immature, and/or female) provide equal benefits associated with flocking at less competitive cost to the dominant. Such behavior could have the added (perhaps indirect) benefit of enhancing the survival of females for breeding. To the extent that high-ranking juncos may be tolerant of flockmates much lower in rank, subordinates should profit by remaining in their home flocks as long as possible—probably throughout the flocking season in a mild winter.

During a severe winter, however, when food becomes limited, low-ranking juncos may starve within their home flocks or disperse to new areas in search of food, perhaps to die there also. Certain factors may facilitate subordinate flock members' access to food during periods of snow cover and low temperatures and perhaps delay their death or departure, including the possibility of differential aggression (see above), decreases in individual distance with decreasing temperature (Pulliam et al. 1974), and a tendency for subordinates to challenge dominants more readily (sometimes with success) as conditions deteriorate (Ketterson 1978 and references cited therein). Nevertheless, energy output may exceed intake at such times due to heightened metabolic demands, increased time spent searching for food, and a rise in the frequency of agonistic behavior induced by crowding at scarce resources (which may outweigh the effect of a possible decrease in individual distance; see results of Balph 1977 and Ketterson 1978). Subordinate members of junco flocks are smaller and less fat on the average than dominants (Fretwell 1969); thus, as Ketterson (1979a) points out, they may be less able than dominants to survive periods in which energy expenditures exceed energy gains.

The difficulties potentially encountered by juncos attempting to change their flock membership or home range during the winter should select for behavior that reduces the need for such changes. In view of their low social status in bisexual flocks, female juncos may be more likely than males to die or disperse in periods of adverse weather and food scarcity. Among eastern-wintering juncos (*J. h. hyemalis*), females winter farther south on the average than males and may thereby avoid competing with males at latitudes where such competition is most likely to harm females (Ketterson and Nolan 1976, Ketterson 1979a). Geographic segregation of the sexes is not complete, however, for various reasons discussed by Ketterson and Nolan (1976). I believe three additional factors might prevent complete sexual segregation: (1) males possibly are more tolerant of females than of other males, which should lessen the cost to female juncos of intersexual competition; (2) a male junco always should benefit socially by flocking with females rather than with other males; and (3) selective pressures acting upon females may vary between years, such that the cost of an extended southward migration in the fall is outweighed by increased overwinter survival if the ensuing winter in northerly regions is severe, but not if the winter is relatively mild. Strongly biased sex ratios among juncos wintering in northern Utah (primarily *J. h. montanus*) suggest that differential sexual migration also may occur in western North America (Balph 1975). However, because western-wintering juncos are taxonomically diverse (see Miller 1941), and because some junco races or species dominate others socially in areas of winter sympatry (pers. obs. and Moore 1972), I suspect that inter-racial or interspecific competition may interact with intersexual competition to affect sex ratios in western regions.

In conclusion, it appears that stability of flock membership and location could be of considerable survival value to wintering juncos. A variety of proximate and ultimate factors may interact in complex ways to promote such stability. Several of these factors are speculative, however, and much remains to be learned concerning the relative importance of each under various environmental conditions.

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The **third joint meeting of the Cooper Ornithological Society and the Wilson Ornithological Society** will be held at the La Quinta Motor Inn in Corpus Christi, Texas, on **19–23 March 1980.** Paper sessions are scheduled to start the morning of 20 March. The announcement of schedule and arrangements and a call for papers will be mailed to members of COS, WOS, and AOU using the new Ornithological Societies of North America mailing labels around 1 December 1979. The sponsoring organizations of the meeting are Corpus Christi State University and the Coastal Bend Chapter of the National Audubon Society. Chairpersons of the committees on arrangements and on scientific program are, respectively, Brian R. Chapman, Division of Biology, Corpus Christi State University, Corpus Christi, Texas 78412; and Jerome A. Jackson, Department of Zoology, Mississippi State University, Mississippi State, Mississippi 39762.

The **XVIII International Ornithological Congress** will take place in Moscow, USSR on 16–25 August 1982. Professor Lars von Haartman (Finland) is President and Professor Valery Ilyichev (USSR) is Secretary-General. The program is being planned by an international Scientific Program Committee chaired by Professor J. Aschoff (Germany). Current plans are to have a plenary lecture each morning followed by symposia; hopefully, only three symposia will run concurrently at any time. One mid-congress day will be free. Postcongress excursions are planned to many interesting ornithological localities, such as Baikal, Samorkand, and Bochara. If sufficient interest exists, a group flight will be arranged for North American ornithologists.

Inquiries about the congress and requests for application forms should be addressed to:

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Secretary General
XVIII Congressus Internationalis Ornithologicus
Ringing Centre 117312
Moscow, Fersman Street 13
USSR

Questions and suggestions (including the program and flight plans) may be sent to:

Dr. Walter Bock
Department of Biological Sciences
Columbia University
New York, N. Y. 10027