AGGRESSIVE BEHAVIOR IN WINTERING DARK-EYED JUNCOS: DETERMINANTS OF DOMINANCE AND THEIR POSSIBLE RELATION TO GEOGRAPHIC VARIATION IN SEX RATIO

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Dark-eyed Juncos (*Junco hyemalis*) residing in central and eastern United States during winter exhibit clinal variation in sex ratio: the percentage of females increases with decreasing latitude from a low of approximately 20% in northern states to a high of about 75% in Texas (Ketterson and Nolan 1976). Similar cases of geographic variation in winter sex ratio have been described in other avian species (Nice 1937, Lack 1944, King et al. 1965, and references cited in Ketterson and Nolan 1976).

Since energetic and other costs of migration presumably increase with distance traveled, it is interesting to inquire about compensating benefits that may accrue to the average female in her more southerly wintering grounds. One obvious possibility is a lessening of intersexual competition during the season when the sexes are not required to reside together and food is likely to be in short supply (Selander 1966, Balph 1975, Ketterson and Nolan 1976).

Recent studies indicate that among captive flocks, male juncos tend to dominate females (Balph 1977) and dominance improves survivorship (Baker and Fox 1978). If food has been limiting and males have tended over evolutionary time to dominate available resources, this may account for the longer migrations of females (Ketterson and Nolan 1976, Gauthreaux 1978). The purpose of the present paper is to corroborate male dominance in free-ranging flocks and to report on other determinants of dominance.

METHODS

The flocks.—Individually marked free-ranging juncos were followed at 2 suburban locations in Bloomington, Indiana, 1 flock during each of the winters of 1971–72, 1972–73, 1973–74. Birds were caught in potter traps, banded with USFWS numbered bands and colored plastic leg bands, weighed (nearest 0.1 g), measured (flattened wing), and aged by the method of skull ossification. Those hatched in the preceding breeding season are referred to herein as immature, those hatched in an earlier year as adult. Skull ossification is a reliable index of age in this species until approximately 1 January at Bloomington (V. Nolan, pers. comm.). Birds first caught after 1 January and possessing completely ossified skulls were categorized as age unknown. Sex was determined as described by Ketterson and Nolan (1976, accuracy ≥95%).

The sex–age compositions of (1) the flocks banded each winter and (2) the sets of birds later observed in aggressive encounters are shown in Table 1; proportions are similar

TABLE 1

SUMMARY OF BIRDS BANDED AND BIRDS INVOLVED IN AGGRESSIVE INTERACTIONS

Birds banded	Males			Females			% male	% Im[b]
	Im	Ad	Not aged	Im	Ad	Not aged		
1971–72	13[a]	2	11	6	1	4	70.3	86.4
1972–73	17	9	6	6	2	4	72.7	67.6
1973–74	19	16	6	12	3	1	71.9	62.0
Birds observed in aggressive interactions								
1971–72	8	2	5	5	1	4	60.0	81.2
1972–73	13	5	0	7	2	0	66.7	74.1
1973–74	6	4	1	3	1	0	73.3	64.3

[a] Numbers given are absolute frequencies except where percentages are indicated.
[b] Percent immatures considering only birds of known age.

to those found by V. Nolan (unpubl. data) who has examined several thousand juncos near Bloomington over the past 15 years.

Observation, behavior, scoring.—From a window 3–7 m distant I used binoculars to observe juncos feeding at heavily baited (cracked corn and commercial wild bird seed), roughly circular feeding areas, 1–1.3 m in diameter. Counting only the time when juncos were present, approximately 100 h were spent in observation.

Each observed encounter in which both participants were individually identified was assigned to one of 4 categories: displacement, tie, withdrawal, and aerial chase. During displacements (see Balph 1977, pecking attack), 1 bird oriented towards another and advanced; the other quickly moved aside or left the feeding area. Occasionally the attacked bird did not yield, but turned to face the initiator until one or the other retreated. These episodes were also classed as displacement and the individual that eventually retreated was the loser. Infrequently both birds retreated after a prolonged encounter, with no apparent winner or loser. I called these ties and arbitrarily recorded ½ of a win for each participant.

Often a junco maintained its distance from others by hopping aside or ahead at another's approach, even though the other bird had not oriented or run in its direction. Such obvious avoidance behavior was classed as withdrawal, and the withdrawing bird was considered the loser (see Balph 1977, escape behavior). Finally, rapid synchronous chases occurred in which the leader appeared to set the pace. These aerial chases (see Balph 1977, flight pursuits) were seen in every month of the study (November–April) and with the sexes in all possible combinations (male chasing female, female chasing male, etc.; compare Balph [1977] who concluded on the basis of a larger sample that among captive juncos, only males pursue). In contrast to the other behaviors described, aerial chases were often initiated at some distance from food. Nevertheless, they are lumped here with other food-related aggressive behaviors, because displacements occasionally escalated into aerial chases.

Data analysis.—Two approaches were employed. First, after checking for seasonal heterogeneity, I combined data across seasons and asked whether members of 1 sex, age, or size class won more encounters than expected on the basis of chance. Secondly, I fit individuals to a linear dominance hierarchy, then noted characteristics of high ranking

birds. Data for this latter effort were sufficient only from the 1972–73 flock. Birds were ordered according to the following criteria (Fig. 1):

(a) Individuals involved in fewer than 5 encounters were omitted.

(b) Individuals were placed above those they displaced or aerially chased or those that withdrew from them; they were ranked below those that displaced or chased them or from whom they withdrew. Results were organized as in Fig. 1, with the smallest possible number of entries below the diagonal.

(c) Individuals that engaged in tied encounters were classed as close together in the hierarchy as possible; however, criterion (b) took precedence to criterion (c).

(d) Application of criteria (a)–(c) produced several equivalent, alternative orders. To choose among these, I selected the one showing the greatest concordance with another measure of dominance, the proportion of interactions won. Thus, birds 6 and 7 could have been interchanged on the basis of criteria (b) and (c), but bird 6 was placed above bird 7 because it won a greater proportion of the interactions in which it was involved. The degree of association between the 2 measures of dominance, rank in the hierarchy and proportion of interactions won, was therefore high (Spearman's $r_s = 0.958$, 1-tailed $P = 0.000$). In this, and in rank order correlations to follow, birds 15, 16, and 17 were all ranked as 16 because they could not be distinguished by any of the criteria used.

RESULTS AND DISCUSSION

Presence of a hierarchy.—Figure 1 indicates the existence of a nearly linear dominance hierarchy in the junco flock studied in 1972–73, and conforms with the findings of Sabine (1949, 1955, 1956, 1959). Nevertheless, rank in the hierarchy and proportion of interactions won were not completely congruous even though proportion won had been used to resolve difficulties in constructing the hierarchy. For example, bird 2 in the hierarchy won a lower proportion of its interactions than did birds 3 or 4. This finding is similar to one reported by Sabine (1959: Fig. 1, compare birds 9 and 10 with 18 and 20). High proportional losses by relatively high ranking birds could result (1) if top dominants tend to deliberately direct more attacks toward individuals ranking close to them, and/or (2) if relatively high ranking birds are more likely than subordinates to approach top dominants. I shall return to this point below.

Determinants of dominance.—Sex, age, body size, plumage coloration, and experience are all variables that might influence an individual's rank (Tordoff 1954; Sabine 1955; Marler 1955, 1956; Brown 1963; Coutlee 1967; Martin 1970; Moore 1972; Rohwer 1975, 1977; Smith 1976; Balph 1977). These potential determinants of rank tend to covary in the junco. Data on Bloomington juncos (Nolan and Ketterson, unpubl. data) indicate that males are larger than females (as measured by wing length), and adult birds are larger than immatures (same measure, both on the average and when site-faithful indi-

FIG. 1. Dominance hierarchy of 17 Dark-eyed Juncos observed the winter of 1972–73 near Bloomington, Indiana. Birds are listed in rank order with the highest rank indicated by the number 1. The wins attributable to each individual appear in the row bearing its number; the losses appear in the column headed by the same number. Displacements are represented by full-size numbers, and withdrawals are designated by superscripts; ties are indicated by double-headed arrows connecting the 2 participants. The birds are further characterized by the information in the right-hand portion of the figure. 'Order ct' signifies order of first capture relative to other members of hierarchy. 'M' signifies male, 'F' signifies female; and 'AD' signifies a bird not hatched in the preceding breeding season, 'IM' signifies a bird that was hatched in that season. Wing lengths are in mm; '# dom' signifies the number of different individuals to which a given individual was dominant. 'Prop won' signifies the proportion of interactions won and 'Σ involv.' signifies the total number of interactions participated in. Totals in the 3 right-most columns are greater than other numbers in the figure might imply, because interactions involving birds not belonging to the hierarchy were included.

viduals are measured in the year of first return). Males are more darkly colored than females (Grant and Quay 1970, Ketterson and Nolan 1976). Age also influences plumage coloration; i.e., males darken with age and adults of both sexes exhibit fewer brown-tipped feathers than immatures. With regard to prior experience at the study site, males are at least as site-faithful as females. The sex–age classes tend to arrive concurrently in the fall; if there is a difference, it is that females predominate among the earliest

arrivals. Except for plumage coloration, which was not measured directly, the importance of these variables as determinants of dominance will be considered first separately, and then interdependently, where possible.

Sex.—Of 64 displacements involving a male and female, 54 were won by males ($\chi^2 = 17.15$, df = 1, P < 0.005, Table 2). Inspection of the hierarchy also reveals male dominance (Fig. 1). Notably, the displacements of males by females all occurred on days when snow was falling; this result concurs with Sabine's (1959) observation that "reverse pecks" were more frequent on cold, snowy days.

The question next arises, what is the impact of the intersexual dominance relationship on flock dynamics? Did males concentrate their attacks on other males and/or did females make any attempt to avoid interaction with males? In other words, were the sexes involved in a greater or lesser proportion of aggressive interactions than expected on the basis of their relative frequency in the population?

Results (Tables 1 & 2) indicate that females were participants in fewer encounters than expected (120 of the 464 participants were female, expected = 158, $\chi^2 = 9.04$, df = 1, P < 0.005). Further, females apparently tended not to interact with each other and male–male interaction was disproportionately frequent.

Such results might be expected if feeding position at a food source varied with dominance rank. Fretwell (1969:7), in a study of wintering juncos (of undetermined sex) in North Carolina, concluded that dominants fed close together over a circular area of baited ground, while "subdominants were more widely separated around the outside of the circle." Subordinate Yellow-eyed Juncos (*J. phaeonotus palliatus*) also feed at the periphery of the flock (Moore 1972). This feeding arrangement would cause dominants to fight among themselves to gain position in feeding areas where there were more birds than positions; subordinates would be repulsed. Although the speed of movement of juncos feeding at my baited areas made it impossible to plot position according to sex, my data would seem to indicate that near Bloomington peripheral juncos were probably female and central ones male. This could also account for the high proportion of losses accumulated by some relatively high ranking birds: males may more often contest feeding positions with central high ranking birds (other males) than with those on the periphery (females).

A study of Varied Thrushes (*Ixoreus naevius*, Martin 1970) suggests that the relationships of sex, dominance, and feeding position may not be specific to juncos. Female Varied Thrushes are usually displaced by males, but intersexual encounters occur relatively less often than male–male encounters because females appear to avoid confrontation with males by feeding at

TABLE 2

INTERACTIONS[a] OF FREE-RANGING DARK-EYED JUNCOS ACCORDING TO SEX

	O[b]	E[b]		$\frac{(O-E)^2}{E}$	
Male, male	127	101	(.66 × .66 × 232)	6.66	
Male, female	77.5	52	(.66 × .34 × 232)	12.43	$\chi^2 = 35.62$
Female, male	12.5	52	(.34 × .66 × 232)	30.06	df = 3
Female, female	15	27	(.34 × .34 × 232)	5.21	P < 0.005

[a] Displacements, withdrawals, ties, and aerial chases; winner's sex named first.
[b] Comparison of observed data (O) to those expected (E) on the basis of relative representation of the sexes among birds observed in aggressive interactions (Table 1).

adjacent, alternate feeding sites (see also Coutlee 1967, Glase 1973, Balph and Balph 1976).

Size.—Size is commonly associated with greater ability to defend resources (Fretwell 1972). Helms et al. (1967) have shown that wing length in juncos is significantly greater in males than females, and that wing length is correlated with lean weight.

Using wing length as an indicator of overall size, bigger juncos won a greater proportion of their interactions (Kendall's tau = 0.881, P < 0.05, Fig. 2). In addition, rank and wing length were significantly correlated in the 1972–73 dominance hierarchy (Kendall's tau = –0.528, P < 0.002). These findings corroborate those of Fretwell (1969) and Baker and Fox (1978), but differ from Moore (1972), who found no significant relationship between wing length and rank in Yellow-eyed Juncos.

Age.—Over 3 years I observed 191 ties, displacements, and withdrawals, and 0 aerial chases where the age class of both participants was known. Represented were 57 juncos; 42 of them were immature (Table 1). The interactions and their expected frequency on the basis of relative abundance of the age classes (74% immature) appear in Table 3. The immature juncos lost a disproportionate number of encounters with adults (consider rows 2 and 3, $\chi^2 = 29.01$, df = 1, P < 0.005), but there was no evidence that immatures avoided interaction with adults (combine rows 2 and 3, compare with 1 and 4, $\chi^2 = 2.75$, df = 2, NS).

Moore (1972) concluded that age contributes positively to rank in Yellow-eyed Juncos. Whether age is important per se, or simply appears important because it is correlated with size or some other determinant of dominance, is not known.

Experience.—Using order of capture as indicative of arrival date and therefore experience, Sabine (1959) reported that rank in her junco hierarchy
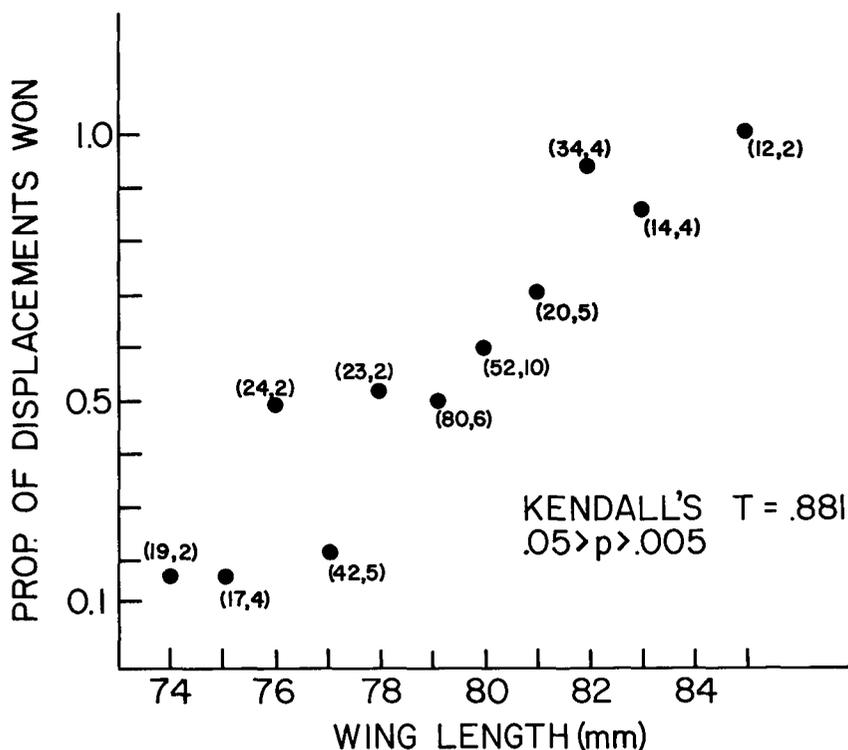
FIG. 2. Relationship between wing length (a size indicator) and likelihood of being dominant in an aggressive encounter. Each point represents the proportion of displacements won when all the displacements involving birds of a given wing length from all 3 seasons were considered. Sample sizes appear in parentheses (number of displacements, number of individuals of that wing length).

was positively correlated with experience; the earlier in the season a bird was caught, the higher its rank. I found a similar correlation between order caught and rank ($r_s = 0.472$, P $= 0.028$, 1-tailed).

Interactions of variables associated with dominance.—Sex, age, and wing length vary interdependently in their effect on dominance; and larger, older, male juncos appear to have the advantage.

What of the effect of each of these variables when the others are not permitted to vary? No displacements involving birds of the same wing length (by 2 mm intervals) and age but of different sex were observed, so it is not possible to test the independent effect of sex on dominance. Displacements in which the 2 participants were of the same sex and age but of different wing lengths numbered 29; 21 individuals, 5 of them females, supplied these data.

TABLE 3

INTERACTIONS[a] OF FREE-RANGING DARK-EYED JUNCOS ACCORDING TO AGE

	O[b]	E[b]		$\dfrac{(O-E)^2}{E}$	
Adult, adult	13	13	(.26 × .26 × 191)	0.00	
Adult, immature	65	37	(.26 × .74 × 191)	21.20	$\chi^2 = 30.12$
Immature, adult	20	37	(.74 × .26 × 191)	7.81	df = 3
Immature, immature	93	104	(.74 × .74 × 191)	1.11	P < 0.005

[a] Displacements, withdrawals, ties, and aerial chases; winner's age named first.
[b] Comparison of observed data (O) to those expected (E) on the basis of relative representation of the age classes among birds involved in aggressive interactions (Table 1).

Of these encounters, 21 were won by birds larger than their opponents, and 8 were won by birds smaller ($\chi^2 = 5.83$, df = 1, P < 0.05). When sex and wing length are held constant, only 4 displacements (involving 7 juncos) were observed between birds that differed in age. In 3 of the 4 cases an adult displaced an immature.

The correlation between rank and order of capture might spuriously arise if males, or adults, or larger birds were the first to arrive; but there is little indication that this was the case. Fourteen of the first 21 juncos caught in 1972–73 were males (67%) and 5 were adults (24%); this agrees well with the ratio of males and adults in the local wintering population (Table 1). The correlation between order of capture and wing length of birds belonging to the hierarchy was not significant ($r_s = 0.169$, P = 0.259), and the fit between rank and order of capture changes little when the effect of wing length is held constant (Kendall's $\text{tau}_{xy} = 0.3197$, Kendall's $\text{tau}_{xy \cdot z} = 0.2991$) (Siegel 1956).

Clearly a multivariate analysis is called for. Employing stepwise regression, I regressed proportion of interactions won by members of the hierarchy on sex, age, wing length, and order of capture, with sex and age written in as dummy variables (male = 0, female = 1, AD = 0, IM = 1). Statements of significance are not wholly appropriate, but the relative values of the regression coefficients (more accurately their *t*-values) do have meaning. The results (Table 4) indicate that among the variables considered, wing length was the most important determinant of dominance, order of capture was also important, age was less important, and sex had little influence. Together the variables explained 63% of the variation in proportion won ($r^2 = 0.633$). These findings overlap somewhat with Baker and Fox (1978) who report that wing length is a better predictor of rank than sex, plumage coloration, genotype, or measures of size other than wing length.

TABLE 4

STEPWISE REGRESSION OF PROPORTION OF INTERACTIONS WON BY MEMBERS OF 1972–73
HIERARCHY ON WING LENGTH, ORDER OF CAPTURE, AGE, AND SEX[a]

Variable	Regression coefficient	Standard error of regression coefficient	*t*	P	Cumulative r^2
Wing length	0.1226	0.0542	2.26	<0.045	.521
Order of capture	–0.0270	0.0133	–2.03	<0.067	.625
Age	–0.1576	0.1269	–1.24	<0.240	.678
Sex	0.1769	0.2704	0.65	<0.520	.690

Constant = –8.879

Anova: F = 6.12, df = 4, 11, P < 0.008

[a] Variables are presented in the order they were entered into the regression.

RELEVANCE TO GEOGRAPHIC VARIATION IN SEX RATIO

The foregoing findings are necessary, but not sufficient, to explain geographic variation in sex ratio in terms of intersexual competition. Although size, not sex per se, is the strongest determinant of dominance identified, the result is that females are subordinate to males where they occur together. If subordinates have lower overwinter survivorship, females should tend to overwinter separately from males.

North Carolina juncos determined in early winter to be subordinate were shown to be less likely than dominants to still be present in the same area at the end of winter (Fretwell 1969). Missing birds may have been dead or they may have moved and joined other flocks (Moore 1972:108). Such moves could affect survival, but relative survivorship of juncos making long or short moves during winter is not known. Nevertheless, independent evidence favors lowered fitness of subordinate juncos: subordinates carry less fat (Fretwell 1969, Moore 1972:112), possess larger adrenals (Fretwell 1969), feed at the periphery of the flock (Moore 1972:120), and apparently expend more energy maintaining individual distance (Moore 1972:115). Baker and Fox (1978) recently found that under conditions of restricted food availability, subordinates showed lower estimated survivorship.

Despite the foregoing, several students of juncos have concluded that subordinate birds are not ultimately prevented from feeding and so may suffer no hardship (Sabine 1959, Moore 1972, for reference to other species see Wing 1941, Dilger 1960, Kessel 1976). Under normal conditions of temperature and food accessibility, losers in aggressive encounters often simply move aside and resume feeding, and under severe conditions (low temperatures,

snow and ice storms that cover food), juncos have been reported to decrease individual distance and reduce the frequency of aggressive behaviors (Sabine 1959; Pulliam et al. 1974; P. Dolan, unpubl. data). Subordinate birds apparently become more persistent in their approach to food, dominants less likely to attack.

How does dominance status influence likelihood of successful overwintering if the very weather conditions that could be critical to survival in fact suppress aggressive responses? An hypothesis is this: Under normal conditions dominants have first access to food, but subordinates too can balance their energy budgets. However, dominants may be able to lay on ample fat reserves during normal conditions, while subordinates cannot (see Baker and Fox, 1978). Several factors may prevent comparable fat deposition in subordinates. Dominants may deny subordinates access to food sufficient for fat accumulation. Alternatively, subordinates may expend more energy than dominants because they engage in more agonistic behaviors requiring locomotion (Moore 1972) or have greater basal metabolic rates as implied by their larger adrenals (Fretwell 1969). That is, subordinates may have less fat, not because they acquire less energy, but because they burn it faster.

For whatever reason, dominants are fatter (Fretwell 1969), and this fat provides the bearer with insurance against periods of high energy requirements and food shortage. In times of severe cold or prolonged snow cover, aggressive behavior may be suppressed as birds concentrate on feeding, not fighting. Nevertheless, if food intake falls short of expenditure, the fatter, i.e. dominant, birds will be more likely to survive until conditions ameliorate. Among White-crowned Sparrows, the heavier a bird at the onset of a period of fasting, the longer it can survive. Notably, males are larger than females and show greater ability to withstand fasting (Ketterson and King 1977). White-crowned Sparrows also show geographic variation in sex ratio (King et al. 1965).

Data reported herein suggest that where the sexes are sympatric, males, being bigger, should be dominant. According to the hypothesis relating dominance status to fitness, periods of high energy demand coupled with limited food accessibility would be most harmful to females. Such conditions occur most frequently in the northernmost regions of the juncos' winter range and this is the region where females are least abundant.

Complete allopatry of the sexes during winter might be expected, if intersexual dominance relations were the only factor influencing choice of a wintering site. However, size distributions of the sexes overlap, and some large females probably dominate some small males. Moreover, factors other than intersexual competition surely play a role in determining choice (Ketterson and Nolan 1976). Nevertheless, geographic variation in sex ratio prob-

ably evolved partially as a means by which females could avoid detrimental interactions with males.

SUMMARY

This paper considers determinants of dominance among free-ranging Dark-eyed Juncos visiting baited feeding stations. The data are evaluated in terms of the insight they provide into factors that may have effected evolution of geographic variation in winter sex ratio.

Dominant juncos near Bloomington, Indiana, tend to be adult males of large body size, as indicated by wing length. Because size varies with sex and age in the junco, the independent effect of these variables on dominance is difficult to determine; however, size appears to be the best single indicator of status. Early arrival on the wintering grounds also contributes positively to status.

Because males are dominant and dominants are reputed to exhibit greater survivorship, females may have responded over evolutionary time to this set of conditions by migrating south of regions of maximal male abundance in order to lessen the effects of intersexual competition.

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LOUIS AGASSIZ FUERTES AND
MARGARET MORSE NICE AWARDS

Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists and students. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic institutions. Each proposal is considered primarily on the basis of possible contributions to ornithological knowledge. Although grantees are not required to publish their studies in *The Wilson Bulletin*, it is hoped that they will submit their manuscripts to the Editor of *The Wilson Bulletin* for consideration.

Most statements applicable to the Fuertes Awards also are applicable to the Nice Award. However, the Nice Award is limited to applicants not associated with a college or university. It is intended to encourage the independent researcher without access to funds and facilities generally available at the colleges. High school students are eligible. In some years 2 Fuertes Awards have been made, in some years, one amount given is $200.00 per award. One Nice Award is made annually in the amount of $200.00. Interested persons may write to Clait E. Braun, Wildlife Research Center, P.O. Box 2287, Fort Collins, Colorado 80522. Completed applications must be received by 1 Feb. 1980. Final decisions will be made by the Council of The Wilson Ornithological Society at the annual meeting of the Society, 19–23 March 1980.

NOTICE OF SYMPOSIUM ON
NEW HAMPSHIRE ENDANGERED SPECIES

A symposium to recommend vertebrate species for the New Hampshire Fish & Game Department's State List of Endangered Species will be held on 1 December 1979 at the Harris Center for Conservation in Hancock, N.H., co-sponsored by the Audubon Society of New Hampshire, the Harris Center, and the New Hampshire Fish and Game Department. Persons with pertinent information on New Hampshire species of mammals, birds, reptiles, amphibians or fresh water fish that should be considered for endangered or threatened status, should contact Carol Smith, Audubon Society of New Hampshire, 3 Silk Farm Road, Concord, New Hampshire 03301 (603-224-9909) by 15 October.