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Costs of switching social groups for dominant and subordinate dark-eyed juncos (*Junco hyemalis*)

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Abstract I quantified the costs of switching from a familiar to an unfamiliar flock for captive dark-eyed juncos (*Junco h. hyemalis*) by measuring several physiological and behavioral variables before and after flock switching. Birds that were initially dominant dropped in status in unfamiliar flocks, and experienced increased metabolic rates, while subordinate birds appeared to undergo less physiological change when switching flocks. This difference occurred despite a lack of any rank-related differences in the effects of joining a new flock on rates of aggression, weight change, access to food, or plasma corticosterone levels. These results suggest that for dominant, but not subordinate, individuals there is a measurable metabolic cost to joining a new social group, even in the absence of adverse factors such as food limitation. Dominant individuals may be less likely than subordinates to leave familiar flocks because of their higher metabolic costs when joining a new social group.

Key words Flocking · Dominance rank · Flock switching · Group switching · *Junco hyemalis*

Introduction

Much attention has been paid to the advantages of familiarity, particularly in the context of territoriality and group living. Familiarity with a spatial area increases social status, leading to greater success in territorial disputes (e.g., Stamps 1987; Beletsky and

Orians 1991). Familiarity with individuals in a social group or on neighboring territories can also lead to reduced aggression, increased breeding success, and other advantages (e.g., Beletsky and Orians 1989). Seasonally mobile animals, such as migratory birds that winter in flocks, may frequently face a choice of remaining in a familiar social group or switching to an unfamiliar one (e.g., Myers 1983). While there are obvious benefits that might lead an animal to remain with familiar individuals, group stability may also be enhanced by the costs to an individual of joining an unfamiliar group. To better understand the decision faced by an individual with the option of joining a new social group we must consider these potential costs of group switching. In the present study, I measured some of the costs of joining an unfamiliar social group for dark-eyed juncos (*Junco h. hyemalis*), migratory songbirds that spend the non-breeding season in dominance-structured flocks (Sabine 1949). The goal of the experiment was to compare physiological and behavioral changes occurring in high- and low-ranking juncos as the result of establishing new social relationships, to determine both whether there were detectable costs of flock switching, and whether these were related to dominance rank.

Although there is little information on flock dynamics in wintering juncos, several laboratory experiments and field studies indicate that subordinate juncos acquire food less successfully (Caraco 1979), are more likely to lose weight or shift diet during periods of resource limitation (Baker and Fox 1978; Langen and Rabenold 1994), and may disappear (i.e., die or disperse) more frequently during the course of a winter than dominants (Fretwell 1969; Terrill 1987). Higher disappearance rates of subordinates have been demonstrated in several other species of flocking birds in winter (e.g. Kikkawa 1980; Ekman 1990).

If changing flocks is costly, natural selection should act to reduce behavior that leads to group switching,

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unless the benefits of living in a new group outweigh the costs of joining. If the costs of joining a new flock are correlated with dominance rank, natural selection may act differentially, with respect to dominance rank, on behaviors affecting flock fidelity. In at least some species of birds, the characteristics necessary to obtain high or low dominance rank have a genetic component (Ortman and Craig 1968; Boag and Alway 1981). Because some determinants of social status appear to be heritable, evolution could have led to different degrees of flock fidelity in high- and low-ranking juncos, based on rank-related differences in the costs of joining a new social group. Lower flock fidelity among subordinates would be likely if the cost of joining a new flock were lower for subordinate than dominant birds.

Among the many potential variables that might be affected by joining a new social group, I chose to measure dominance rank, oxygen consumption, body mass, access to food, aggressive interactions, and plasma corticosterone (a hormone that is released into the blood in response to a variety of stressors in birds; Harvey et al. 1984). I measured values for these variables before and after single birds were reciprocally transferred between captive four-bird flocks to assess the effect of joining a new social group.

My experimental design ensured that members of the flock receiving a new bird had a competitive advantage because they had prior residence, which is a strong determinant of dominance in this species (Cristol et al. 1990). Therefore I predicted that high-ranking birds would initially exhibit a decrease in rank, with a concomitant increase in aggressive interactions and decreased access to food. The main objective of this study was to determine whether these previously dominant subjects would experience an increase in oxygen consumption and plasma corticosterone levels as they attempted to maintain high social status in the new flock. I expected that subordinates would insert at the bottom of the unfamiliar flock and experience few physiological or behavioral costs of flock switching as they maintained their initial, low social status. Control flocks, in which birds were returned to their familiar flock in a new cage, were included to determine whether high- and low-ranking birds responded differentially to experimental factors other than those caused by the unfamiliar social environment.

Methods

Capture, housing and flock establishment

The general design of the experiment was to record baseline values of variables on a single bird in each of two concurrently established flocks, and then to reciprocally switch these two birds between flocks to measure the values of the variables after flock-switching. The

individuals transferred from each flock will be referred to as *subjects*.

Juncos were captured in mist nets near Bloomington, Indiana, United States, from 12 December 1991 to 2 February 1992. I banded all birds with a U.S. Fish and Wildlife Service aluminum band and three plastic bands of a single color (green, red, orange, or blue, A.C. Hughes). Individuals were classified as either yearling or older (based on skull ossification, rectrix shape, and eye color; Pyle et al. 1987), and sex was determined by wing length and plumage color (Ketterson and Nolan 1976). To establish flocks, birds were combined with three other individuals of the same age, sex, and capture site and placed in small, visually isolated cages ($1 \times 2 \times 2$ m) for a period that varied depending on when wild-caught birds were available with which to setup flocks (range = 18–45 days, $x = 30$ days). Food and water were provided ad libitum.

After this period of isolation, two flocks from different capture sites were placed simultaneously into two much larger, visually isolated test cages ($6.8 \times 2.3 \times 2.0$ m) to be used in concurrent trials. Trials consisted of two parts. On day 1 baseline values of subject's feeding behavior, dominance rank, rate of aggressive interactions, oxygen consumption, and corticosterone while in the familiar flock were assessed. On day 2 these same variables were assessed after reciprocal transfer of two subjects. Eighteen experimental flocks, composed of 72 different birds, were tested from 15 January through 1 March 1992 (Table 1).

I also tested 18 control flocks, composed of 72 additional birds, during the same period. Control trials were identical to experimental trials except that birds chosen as subjects were returned to their familiar flock, in a new test cage, after the oxygen-consumption recordings were made on day 1 (see below). In this way I could measure any effects of handling, transfer into a new cage, blood sampling, oxygen-consumption recording, or other disturbances, uninfluenced by change of social group. Order of experimental and control trials was determined randomly, with the constraint that, to allow reciprocal transfer of subjects, the two flocks initiated on any given day were of the same treatment type. No mortality occurred during this experiment, and all individuals were released at site of capture one day after their testing was completed.

Flock switching

At 1400 hours on the day before the start of observations two test flocks were moved from their isolation cages into test cages. Birds were weighed and stored energy reserves were determined by scoring the sub-cutaneous fat filling the furcula on a subjective scale of 0–5 (0 indicating no visible fat, 5 indicating fat bulging above the ventral surface of the pectoral muscle). Birds then had several hours of daylight in which to familiarize themselves with their new surroundings.

Day 1: familiar flock

Behavioral data were gathered by two observers in blinds adjacent to the test cages. One observer recorded the identity of all birds

Table 1 Number of flocks of each age/sex class in each treatment group, and the dominance rank (high or low) of individual transferred from each flock

	<i>Experimental flocks</i>		<i>Control flocks</i>	
	Rank of bird transferred <i>High</i>	<i>Low</i>	Rank of bird transferred <i>High</i>	<i>Low</i>
Yearling males	2	6	2	6
Yearling females	2	2	2	2
Older males	6	0	6	0
Total	10	8	10	8

involved in aggressive interactions and the outcome of each interaction. The second observer classified, every 30 s, the location of each bird. The test cages were designed to allow analysis of the amount of time that individuals spent on or near the food source. At the center of the cage there was a 0.5-m diameter wooden circle, hereafter referred to as the food disc, on which I placed 100 g of mixed seed before each trial. The food disc was surrounded by a 1.15-m diameter circle marked on the floor of the cage. The location of each bird could be classified as either on the food disc, or within the surrounding circle. The two flocks were observed alternately for four 10 min sessions each, beginning at 0900 hours, with no interruptions. Food was withheld for 10 min before each observation session.

At 1200 hours, after birds had fed undisturbed for 1.5 h, I captured the subject from one flock by hand. Birds were always captured within 1 min after I entered the cage because they voluntarily entered an enclosed capture area when disturbed. I removed approximately 75 μ l of blood from the alar vein. Because corticosterone tends to increase quickly during disturbance and handling (Wingfield et al. 1982) I terminated blood collection within 5 min after entering the cage. After bleeding the subject in one flock, I repeated this procedure with the other flock. Blood was then centrifuged for 5 min to separate the plasma, which was promptly frozen at -20°C for later analysis by radioimmunoassay (see below). All other flock members were captured and held in darkened containers until subjects were returned at 1400 hours (see below).

Following blood sampling, oxygen consumption was measured for the subjects from both flocks using an open-circuit respirometry system. Birds were weighed and placed on non-conductive perches in 1800-ml chambers (fat scores were not determined because of time constraints). Each chamber was made from a pressure-sealed, light-proof, metal container with input and output openings in the lid. The two chambers were connected to separate oxygen analysis circuits and immersed in a constant temperature water bath at 5°C . This temperature was the predicted mean outdoor temperature based on data from the same cages during the previous winter. The pumps in the water bath produced a continuous, low-frequency noise that probably prevented subjects from being disturbed by any external noises. Mass flow controllers (Tylan) ventilated the chambers with 900 ml/min of air dried with drierite. After the air left the chambers, carbon dioxide and moisture were removed by ascarite and drierite, respectively. Oxygen consumption was measured for 1 h (after a 15-min equilibration period) by separate portable paramagnetic oxygen analyzers (Servomex). These, and the flow controllers, were connected by an analog/digital converter to a portable computer that, every 30 s, recorded the flow rate of air entering the chamber and the oxygen content of air leaving the chamber. The temperatures of the chambers were monitored continuously using NiCr-NiAl thermocouples attached to a microprocessor thermometer (Tegam). Subjects' body temperatures were recorded immediately after removal from chambers by inserting a thermocouple 1 cm into their cloacae.

At 1400 hours, after recording oxygen consumption, I carried out the reciprocal switch of the subjects by combining the subject from each flock with the non-subjects of the other flock in the other flock's home cage. Subjects were either the highest- or lowest-ranked individuals in their original flocks, and were always switched with another subject of the same dominance rank. The two flocks used in the reciprocal switches were comprised of birds of the same sex/age class. In control flocks each subject was combined with its familiar flock mates in the other flock's home cage.

Day 2: The unfamiliar flock

On the following morning, the procedure used on day 1 was repeated with the following modification. In addition to previously described data, the time, and number of pecks at food, were recorded during each visit to the food disc by a subject.

Radioimmunoassay

I measured total corticosterone concentration in the plasma samples by direct radioimmunoassay, using the same method and antiserum as Wingfield et al. (1992). The antiserum used has only 5% cross-reactivity with cortisol, and it has previously been demonstrated that cortisol-cross-reacting serum accurately measures corticosterone (Rattner and Eastin 1981). All samples were measured in a single assay and the intra-assay coefficient of variation was 15%. Plasma sample volumes ranged from 10 to 76 μ l ($\bar{x} = 34 \pm 15\text{SD } \mu$ l). Recovery of radioactively labeled hormone was 72–100% ($\bar{x} = 85 \pm 7\%$), and, in a linear regression, was not correlated with volume of the plasma sample ($r^2 = 0.02$, $F = 1.5$, $P = 0.21$). The amount of steroid present was determined by comparison with a standard curve ranging from 4 pg to 2000 pg. All plasma samples ($n = 5$) in which no corticosterone was detected by the assay were assigned the value of 4 pg, as this is the largest quantity that could have remained undetected. The average concentration calculated for these undetectable samples, after correcting for recovery, was 3.3 ± 1.5 ng/ml. To assess accuracy, four standard samples containing 1000 pg corticosterone were assayed together with the unknown samples, and gave an average concentration of 888 ± 135 pg per sample.

Ambient temperature

The ambient temperature was recorded in the shade adjacent to test cages at 0900 and 1200 hours. The average of the two readings was used for the daily temperature, and the two daily temperatures were averaged in some analyses, as noted. All cages were outdoors and unheated, but were protected from wind, snow and disturbance by a partial covering of polyethylene film. Flocks experienced ambient temperatures ranging from -21° to 22°C (0900 hours $\bar{x} = -1.5^{\circ}\text{C}$; 1200 hours $= 2.6^{\circ}\text{C}$; mean for entire experimental period $\bar{x} = 0.3^{\circ}\text{C}$). The mean outdoor temperature at 1200 hours was 2.4°C colder than the constant-temperature water bath, with the result that, on average, metabolic measurements may have been carried out at a temperature slightly warmer than ambient.

Data analysis

I tested flocks of yearling males, yearling females, and older males. Older females were rarely available during this study, as they winter south of other sex/age classes (Ketterson and Nolan 1976). I could find no evidence of sex or age effects on any of the variables measured, including initial body mass (male: 18.36 ± 1.15 g, female: 18.57 ± 0.57 g, $t = 0.5$, $P = 0.6$; adult: 18.34 ± 0.88 g, yearling: 18.44 ± 1.13 g, $t = 0.27$, $P = 0.7$), so I have combined the subjects with regard to sex/age class in all analyses. The balanced design, wherein each experimental flock was matched with a control flock of the same sex/age class, should have eliminated any bias introduced by these factors.

A bird was classified as the winner of an aggressive interaction if it successfully displaced another bird and occupied its space. Win-loss data from these interactions were used to construct dominance hierarchies for each flock using the method of Brown (1975). In every flock I observed two or more displacements between members of each dyad ($\bar{x} = 6 \pm 4$ interactions). In captive junco flocks, if one individual displaces another twice there is a $>90\%$ chance that the loser will not displace the winner in future interactions (D.A. Cristol, unpublished work).

I used a software package (Datacan IV, Sable Systems) to determine the minimum oxygen consumption per subject per hour for the 10 min segment with the lowest mean (hereafter referred to as metabolic rate). The minimum oxygen consumption always occurred at the end of the 1 h-long measurement period, probably because subjects were asleep in the dark chamber. Mean metabolic rates on day 1 for each treatment and dominance rank were

compared using *t*-tests. Changes in metabolic rate between days 1 and 2 were compared using a two-factor ANCOVA (independent variables: treatment group, dominance rank; covariate: average temperature for days 1 and 2). Change in plasma corticosterone between days 1 and 2 was compared using two-factor ANCOVA (independent variables and covariate as above).

Change in mass was calculated as the difference in mass between days 1 and 2 divided by day 1 mass. Time spent on the food disc and in the surrounding circle was measured for all subjects on day 1 and day 2 as the number of 30-s periods in which the bird was present. Pecking rates on day 2 were analysed as pecks per second while on the food disc. Since subjects had been treated alike when the day 1 measurements were made I analyzed day 1 data with a one-factor ANCOVA (independent variable: dominance rank; covariate: average temperature on day 1). Comparisons of day 2 data were made with two-factor ANCOVA, using variables described above for metabolic and corticosterone changes.

Unless otherwise indicated, sample sizes for all analyses are as noted in the totals row of Table 1. Throughout text and tables all means are presented ± 1 SD, and an α level of 0.05 is considered significant.

Results

Dominance rank and aggressive interactions

Assigning dominance ranks was straightforward because in only four dyads (<2%) did the lower-ranked bird win any interactions against a higher-ranked bird, and these reverse interactions were, in each case, greatly outnumbered by the wins of the higher-ranked bird. The social relationships established on day 1 were unchanged on day 2 in all but three dyads (>98%). In 31 of the 36 flocks the hierarchies were linear. In each of the remaining five flocks there was a single non-transitive relationship that persisted on day 2.

Dominant experimental subjects declined an average of 1.8 ± 1.3 ranks on day 2, but it should be remembered that low-ranked subjects could not decline in dominance rank, while high-ranked birds could not increase in rank. Dominant control subjects remained dominant on day 2 in eight of ten control flocks, and became second-ranked in the other two. Subordinate subjects continued to be the lowest-ranked birds in all experimental and control flocks on day 2.

Experimental and control birds did not differ in the number of aggressive interactions on day 1 (experimentals $\bar{x} = 31 \pm 16$; controls $\bar{x} = 32 \pm 12$, $t = 0.2$, $P = 0.8$) or day 2 (experimentals $\bar{x} = 31 \pm 8$; controls $\bar{x} = 34 \pm 10$, $t = 0.8$, $P = 0.4$), and there was no change in the total number of interactions for either of the treatments or ranks (Table 2). Because of the high degree of linearity in the hierarchies, virtually all aggressive interactions involving a dominant subject on day 1 resulted in it winning, and all interactions involving a subordinate subject resulted in it losing. In control flocks this continued to be the case on day 2. In experimental flocks, formerly dominant subjects both won and lost interactions on day 2, while subordinates

Table 2 Total number of interactions ($\bar{x} \pm$ SD) by high- and low-ranking birds in each treatment on days 1 and 2. Statistical comparisons are between days 1 and 2

Rank:	Experimental flocks		Control flocks	
	High	Low	High	Low
Day 1	13.4 \pm 7.8	12.8 \pm 5	17.2 \pm 7.5	15.4 \pm 8
Day 2	13.6 \pm 6.4	16.8 \pm 5.6	15 \pm 5.7	20.2 \pm 9.3
<i>t</i>	0.1	1.2	-1.0	1.0
<i>P</i>	0.9	0.12	0.21	0.40

Table 3 Number of interactions ($\bar{x} \pm$ SD) by high-ranking experimental birds on days 1 and 2 separated as wins and losses. Statistical comparisons are between days 1 and 2

	Wins	Losses
Day 1	13.3 \pm 7.5	0.0 \pm 0.3
Day 2	4.8 \pm 7.0	8.8 \pm 7.8
<i>t</i>	-2.4	3.5
<i>P</i>	0.04	0.007

continued to lose all interactions. Dominant subjects in experimental flocks won significantly fewer, and lost significantly more interactions on day 2 than on day 1 (Table 3).

Metabolic rate

There was no significant difference between the metabolic rates of high-ranking and low-ranking subjects on day 1, before flock switching occurred (dominants: 151.1 ± 26.9 ml O₂/h; subordinates: 146.3 ± 28.1 ml O₂/h, $P = 0.6$) or day 2 (dominants: 140.5 ± 23.1 ml O₂/h; subordinates: 141.5 ± 22.4 ml O₂/h; $P = 0.6$). Experimental subjects tended to have a lower mean metabolic rate than controls on day 1, but this difference was not significant (experimentals: 140.6 ± 24.2 ml O₂/h; controls: 157.3 ± 28.1 ml O₂/h; $P = 0.06$).

Among experimental birds, subjects that were initially high-ranked experienced a 6% increase in metabolic rate between day 1 and day 2, whereas subordinates exhibited a 1% decrease (Fig. 1A, see Table 4 for mean values on day 1). The pattern of change in metabolic rates of experimental subjects was the reverse of that found among controls, as high-ranking controls experienced a 15% decrease in mean metabolic rate and low-ranking controls underwent a 7% increase (Fig. 1B). Thus, the effect of treatment on metabolic rate varied according to dominance rank. This is borne out by the results of the statistical analysis, as the interaction between dominance rank and treatment was significant ($F = 7.3$, $P = 0.01$), although neither treatment nor dominance rank were significant main effects (treatment: $F = 0.20$, $P = 0.66$; dominance rank $F = 1.02$, $P = 0.32$; all other interaction terms $P > 0.1$), and there was no significant covariation with

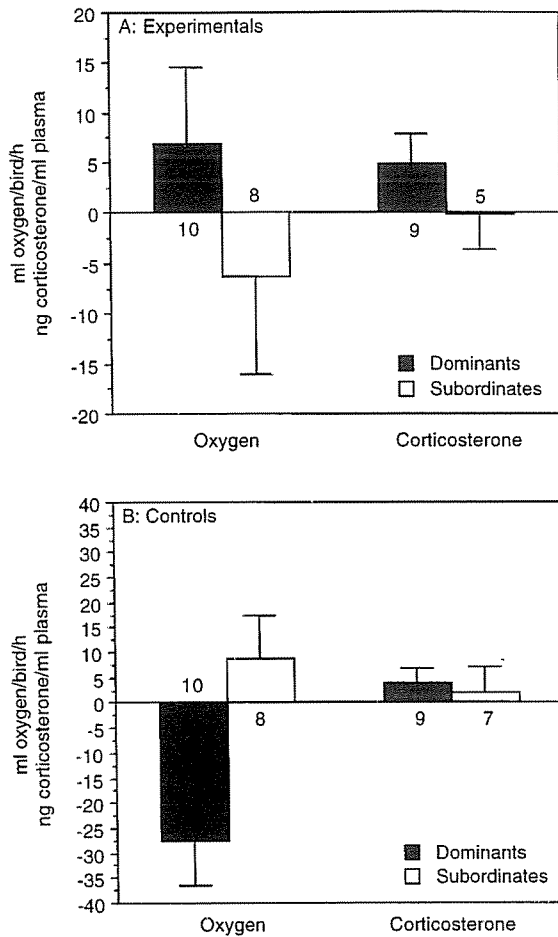


Fig. 1A Change ($\bar{x} \pm SE$) in oxygen-consumption rate (left bars), and plasma corticosterone levels (right bars) between days 1 and 2 for experimental subjects. **B** The same results for control subjects. Sample sizes are indicated at bases of bars. See text for statistical comparisons

temperature ($F = 3.6$, $P = 0.07$). Because this result suggests that ambient temperature may have affected metabolic rate, I performed linear regression and ANOVA on the data for control birds and found that there was no correlation between the change in mean temperatures on days 1 and 2 and the change in metabolic rate on those days ($r^2 = 0.24$, $F = 0.07$, $P = 0.79$).

Table 4 Metabolic rate, corticosterone concentration, and mass, for high- and low-ranking subjects in each treatment group on day 1 ($\bar{x} \pm SD$). Values for both day 1 and day 2 are shown for time spent

Rank:	Experimental High(10)	Low(8)	Control High(10)	Low(8)
Metabolic rate (ml O ₂ /h)	134 ± 15	148 ± 31	167 ± 25	144 ± 27
Corticosterone (ng/ml)	11.5 ± 7.7	15.4 ± 8.3	9.4 ± 4.8	9.8 ± 2.2
Mass (g)	18.7 ± 1.4	18.5 ± 0.81	18.1 ± 0.99	18.2 ± 0.77
Periods feeding:				
Food disc, day 1	12.8 ± 5.7	8.8 ± 3.9	11.7 ± 6.5	8.6 ± 5.3
Food disc, day 2	13.1 ± 9.6	10.6 ± 4.5	10.4 ± 7.4	10.7 ± 4.4
Circle, day 1	2.0 ± 2.1	5.6 ± 5.7	2.4 ± 2.2	7.6 ± 5.7
Circle, day 2	2.3 ± 3.6	9.9 ± 7.7	4.0 ± 5.2	3.9 ± 2.4
Pecking rate (pecks/s)	0.49 ± 0.08	0.50 ± 0.10	0.41 ± 0.08	0.52 ± 0.10

To determine whether conditions prior to testing, as reflected by stored energy reserves, were correlated with metabolic response to flock switching, I performed linear regression and ANOVA on the data for control birds and found that there was no correlation between the fat score prior to flock establishment and the percent change in metabolic rate ($r^2 = 0.10$, $F = 1.82$, $P = 0.20$).

Corticosterone

On day 1, when control and experimental subjects received identical treatment, corticosterone among high-ranking subjects ($n = 18$) averaged 10.4 ± 6.2 ng/ml, while the mean for low-ranking subjects ($n = 12$) was 12.3 ± 6.1 ng/ml ($t = 0.5$, $P = 0.4$). Among experimental subjects, high-ranking birds tended to exhibit a small increase in corticosterone between day 1 and day 2 while subordinates tended to exhibit little change (Fig. 1A). Among control subjects, both high- and low-ranking individuals tended to exhibit a small increase in corticosterone between day 1 and day 2 (Fig. 1B, see Table 4 for mean values on day 1). Despite these possible trends there were no significant main effects, interactions, or covariation of treatment, dominance rank, or temperature for change in corticosterone between days 1 and 2 (all $F < 3.8$, $P > 0.05$).

Access to food

Nearly all subjects exhibited a slight decline in mass between day 1 and day 2. High-ranking experimental subjects and low-ranking controls tended to lose more mass than low-ranking experimentals or high-ranking controls (experimentals: dominants $-2.5 \pm 2.9\%$; subordinates $-0.4 \pm 1.5\%$; controls: dominants $-0.8 \pm 2.5\%$; subordinates $-2.9 \pm 2.8\%$; see Table 4 for day 1 values), but absolute losses were slight and differences were non-significant (treatment: $F = 1.5$, $P = 0.22$; dominance rank $F < 0.2$, $P = 0.6$; all interactions $P > 0.1$, temperature $F = 0.7$, $P = 0.4$).

on the food disc and in the surrounding circle. Pecking rate data are for day 2 only. Sample sizes in parentheses

On day 1, before flock switching, dominant subjects tended to spend more time on the food disc than subordinates, but this difference was not quite significant ($F = 2.8$, $P = 0.055$); temperature was not a significant covariate ($F = 0.4$, $P = 0.5$; see Table 4 for mean values). Subordinate subjects spent more time than dominants in the surrounding circle ($F = 6.8$, $P = 0.014$), while temperature again, was not a significant covariate ($F < 3.5$, $P = 0.7$).

On day 2 there were no significant effects of treatment or dominance rank on time spent at the food disc (all $F < 0.1$; $P > 0.1$; mean values given in Table 4). There was no effect of dominance rank ($F = 2.1$, $P = 0.16$), or treatment ($F = 0.03$, $P = 0.86$), but there was a significant interaction of treatment, dominance rank, and temperature ($F = 4.8$, $P = 0.04$), on time spent in the surrounding circle on day 2. Experimental subordinate subjects tended to spend more time in the surrounding circle than other birds (Table 4), but this multiple interaction term is difficult to interpret and will not be considered further. There was no detectable difference in pecking rate regardless of treatment or status (all $F < 3.1$, all $P > 0.09$; see Table 4 for mean values), and there was no significant covariation with temperature.

Discussion

Dominance rank and aggressive interactions

Among experimental birds, a subject's change in dominance rank upon arrival in a new flock depended on its initial rank: dominant birds dropped an average of two positions in the hierarchy, whereas subordinates remained lowest-ranked. This result was not surprising, given that experimental subjects were joining birds that had prior residence, which has been shown to increase dominance rank in this species (Cristol et al. 1990). The number of aggressive interactions that birds engaged in was unaffected by the treatment, regardless of dominance rank. Thus, even experimental dominants, while losing more and winning fewer interactions in the unfamiliar flock, were involved in aggressive encounters at nearly the same rate in familiar and unfamiliar flocks.

Metabolic rate

In experimental flocks, dominant subjects, on average, increased metabolic rates on day 2, while subordinates declined. Control subjects, which remained with familiar flocks, exhibited the opposite pattern, with dominants having decreased metabolic rates and subordinates experiencing a slight increase on day 2. The changes found in controls indicate the cumulative

effects of handling, cage-switching or other experimental factors, and can be considered the expectation for the experimental birds had they not been placed in unfamiliar flocks. Although I had not anticipated that the response of controls would differ according to initial dominance rank, it is consistent with the findings of other studies that show differential physiological responses to experimentally induced stress among high- and low-ranking individuals (e.g., Sapolsky and Sare 1994). A speculative explanation for the drop in metabolic rate by control dominants is that on day 1, when control flocks were first inhabiting the greatly increased space of the test cages, there may have been some degree of social instability. Perhaps the drop in metabolic rates among dominants on day 2 reflects a return to social stability as groups adjusted to the larger living quarters. The same explanation could apply to the tendency for control subordinates to have increased metabolic rates on day 2 if low-ranking birds benefited from temporary loss of despotic control by dominants on day 1. Admittedly, this explanation would be more convincing if aggression or corticosterone levels had undergone significant changes between days 1 and 2.

Although there were detectable differences between dominant and subordinate birds in the metabolic response to joining a new group of juncos, my results differ from those of previous workers in showing no evidence of a metabolic cost of maintaining high dominance rank in a familiar flock. On day 1, before experimental manipulations, the mean metabolic rates of dominant and subordinate individuals did not differ significantly. Other studies of non-breeding season metabolic rates among birds have indicated that dominants had higher metabolic rates than subordinates (Roskaft et al. 1986; Hogstad 1987; Bryant and Newton 1994). Two of these studies were on songbirds in the genus *Parus*, which winter in small flocks, while the third was on dippers (*Cinclus cinclus*), which exhibit some degree of winter territoriality. Given the relatively large sample size of the present study, the absence of detectable rank-related differences in metabolic rate may reflect a real difference between juncos and previously studied species. This discrepancy could reflect ecological or behavioral differences, such as the relatively large social group size of wintering juncos, which could result in less rigidly hierarchical flock organization. Further studies are needed to determine whether the metabolic cost of high dominance rank is a widespread phenomenon in other wintering birds. The present finding, that dominants do not have higher resting metabolic rates than subordinates, must also be validated with free-living juncos.

Corticosterone

Corticosterone increases have been reported in response to many forms of stress, such as changes in

social group membership (Satterlee et al. 1983), in wild and domestic birds, including juncos (Harvey et al. 1984; Rogers et al. 1993). Under the conditions of this experiment I was unable to detect the predicted increase in corticosterone among high-ranking experimental subjects, despite a possible trend in the predicted direction. This may indicate that joining a new social group is not a highly stressful experience for juncos, regardless of social status. However, repeated sampling might have revealed rank-related differences in response to capture stress among experimental birds, as baseline levels do not always parallel differences in response to repeated sampling (see references in Wingfield et al. 1992). Alternatively, corticosterone levels may have risen immediately after flock switching, but declined by the time I sampled blood 22 h later.

The mean corticosterone of the captive subjects in this study was approximately half of that reported for non-captive juncos trapped from the same locations (Rogers et al. 1993), but was very similar to levels reported for captive juncos in two other studies (isolates, Holberton et al. 1989; unstressed flocks, Ramenofsky et al. 1992). These lower values among captives might reflect the more rapid capture and blood sampling that are possible when working in aviaries. The lack of a significant difference between dominants and subordinates in baseline corticosterone levels in the present study is also in agreement with these earlier studies of captive juncos.

Access to food

Nearly all subjects declined slightly in mass between days 1 and 2, possibly due to lost feeding time during oxygen consumption measurements on day 1, but there were no significant effects of dominance rank or treatment on change in mass. I measured mass, rather than stored fat reserves, because mass can be rapidly quantified with high precision and accuracy. The drawback to this is that mass changes probably reflect change in both stored fat reserves and recently ingested food, and thus are more difficult to interpret. Without reliable measurements of stored fat reserves it is difficult to conclude much from these data except that none of the birds appeared to be undergoing marked weight loss.

Dominants tended to spend more time on the food disc than subordinates, and spent significantly less time in the area surrounding it, on day 1. There were no clear differences in preferred feeding area or feeding rate on day 2, regardless of rank or treatment, although there may still have been a tendency for subordinates to spend more time in the area surrounding the food disc. Thus, although I detected rank-related differences in feeding behavior before the treatment, reduced access to the concentrated food source was not one of the costs of switching into a new flock under the condi-

tions of this experiment. The data gathered were intended only to test the relative effects of flock switching on access to food among dominants and subordinates, and are not sufficient to fully explore the relationship between dominance rank and energy reserves. That relationship is a complex one, as subordinates maintain greater energy stores than dominants under some conditions (e.g., Ekman and Lilliendahl 1993).

Conclusions

I found that dominant juncos experienced increased metabolic rates when joining a new social group, while subordinates did not, despite the fact that joining a new flock did not differentially affect amount of aggression, weight loss, feeding behavior, or corticosterone levels in dominants and subordinates. I suggest that the cost of establishing relationships with unfamiliar individuals may be substantial in terms of energy, but only for birds experiencing a drop or change in social status. Further investigation is needed to determine the precise behavioral or physiological mechanism responsible for the socially-mediated increase in metabolic rate in the absence of food shortage, increased rates of aggression, or other factors.

Based on these results it is tempting to predict that dominant individuals are less likely than subordinates to leave a familiar flock. For an ecologically similar sparrow species, *Zonotrichia albicollis*, it has been stated that "dominance in a particular location leads to residence there" (Dearborn and Wiley 1993, p. 43), with the effect that only subordinates left familiar areas during a period of reduced food availability (Piper 1990). Unfortunately, as with most bird species, little is known about the dynamics of junco groups in the wild. One problem is that it is difficult to distinguish flock switching from mortality in most study populations. Another shortcoming of most studies is that individual dominance ranks are rarely known in free-living birds. The little evidence that exists on wintering juncos is equivocal. Several laboratory experiments and limited field studies suggest that subordinate juncos are more likely to die or to attempt dispersal than dominants (Fretwell 1969; Baker and Fox 1978; Terrill 1987), but a larger study indicates that there were no differences in within-season recapture rates among juncos of different sex/age classes, which tend to be correlated with social status (Ketterson and Nolan 1982).

In other flocking systems where flock fidelity has been studied, an individual's choice of its non-breeding flock has been related, in part, to territory inheritance (e.g., sparrows, Smith 1978; magpies, Eden 1987) or future mating success (e.g., tits and chickadees, Ekman 1990; Smith 1991). In contrast, juncos in the population used for this study are not paired while on their winter range (as males and females migrate

different distances), and winter hundreds to thousands of kilometers from their breeding range, with the result that they may face fewer constraints on inter-flock movement than many other species. Differential metabolic costs of joining a new social group could be a proximate determinant of flock-switching behavior in juncos. Juncos may be more likely to make flock-switching decisions based on direct costs and benefits, rather than on territorial or mating benefits accrued later. However, even in this species, in which territory inheritance and mate retention are not factors during the non-breeding season, there are numerous other possible explanations for greater flock fidelity among dominant than subordinate birds. For example, dominant individuals might be older birds with greater site familiarity from previous years, or subordinate birds might run out of accessible food more quickly during periods of severe weather, and therefore wander more widely in search of alternate food sources. This study demonstrates that there are detectable physiological differences between birds of varying social status in their response to joining new social groups. If the results of this study are confirmed in free-living flocks, and are augmented by studies of other potential measures of cost (e.g., pathogen resistance) it will be possible to make more informed predictions about the degree of group fidelity exhibited by various individuals in a population.

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