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Received 13 July 1998, accepted 10 February 1999.
Associate Editor: J. Ekman

The Auk 116(4):1136–1141, 1999

Relationships Among Dominance, Foraging Proficiency, and Condition in Juvenile Dark-eyed Juncos

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Social dominance among flocking birds is well documented, and status within a group often varies with age, body size, sex, and prior residence (Piper 1997). The evolutionary significance of dominance relationships has been demonstrated in studies where dominant birds are either more likely to survive or less likely to disperse (Piper 1997). Although numerous studies of dominance in birds have been conducted with adults or with mixed flocks of adults and juveniles, few studies have focused on juveniles

(Arcese and Smith 1985, DeLaet 1985, Piper 1995). Dominance status during the juvenile stage may have important ramifications. For example, the ability of adult White-throated Sparrows (*Zonotrichia albicollis*) to dominate other adults may be determined during a crucial period in the juvenile stage (Piper 1995). Arcese and Smith (1985) found that dominant juvenile Song Sparrows (*Melospiza melodia*) had higher overwinter survivorship and an increased likelihood of becoming breeders the following spring, suggesting a potentially critical role for dominance interactions during the juvenile period.

High dominance status could mediate first-year survivorship in several ways. Dominant individuals may experience enhanced foraging success if they have greater access to preferred foraging areas and prey items or can exploit food resources located by subordinate flock members (Piper 1997). These in-

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dividuals may then be more likely to survive the juvenile period and enter the winter months in better physiological condition than more subordinate flock members. In addition, dominant flock members may incur lower risk of predation if they forage closer to cover (Schneider 1984, Koivula et al. 1994), or if they wait to resume activities after a predator has been detected (Hogstad 1986, Zanette and Ratcliffe 1994).

We conducted a field study of juvenile Dark-eyed Juncos (*Junco hyemalis caniceps*) to investigate potential proximate benefits of high dominance status in juveniles that could affect fitness. We predicted that dominant juveniles would have higher foraging success than subordinate flock members. Relative to females, male Dark-eyed Juncos tend to be larger and to attain higher ranks in winter flocks (Balph 1977, Baker and Fox 1978, Ketterson 1979). Therefore, we expected that, on average, juvenile males would attain higher dominance ranks than juvenile females. We also predicted that juveniles with relatively high dominance rank or high foraging success would be in better condition than other flock members. Physiological condition in small birds traditionally is measured by dividing body mass by an indicator of size such as wing chord or tarsus length, or by quantifying visible fat. Because free-ranging juvenile juncos have little visible fat, we did not quantify fat scores. We assessed condition using a variety of parameters including body mass divided by wing chord and hematological parameters such as hematocrit value and white blood cell differentials to look at immunological status. Very low hematocrit values may indicate anemia (Bush 1975). Studies on domestic fowl show that elevated counts of heterophils are indicative of infection (Dein 1982, Campbell 1988), and elevated ratios of heterophils to lymphocytes are indicative of stress (Gross and Siegel 1983). Eosinophilia, a high percentage of eosinophils, is a common consequence of parasite infections (Wilson and Wilson 1978, Roitt et al. 1993). We predicted that dominance rank and relative foraging success would be positively correlated with hematocrit value and negatively correlated with percent heterophils, ratio of heterophils to lymphocytes, and percent eosinophils.

Methods.—This study was conducted from 25 July to 16 September 1993 in the area surrounding Bridger Lake in the Uinta Mountains (3,500 m elevation) on the Utah/Wyoming border (40°57'N, 110°22'W). The gray-headed race of the Dark-eyed Junco is a common breeding species in this area. The study area was dominated by mixed aspen (*Populus tremuloides*) and conifer forest (lodgepole pine [*Pinus contorta*] and Douglas fir [*Pseudotsuga menziesii*]) interspersed with meadows and beaver ponds. Dark-eyed Juncos were chosen for this study because they are locally abundant, are relatively tolerant of human disturbance and thus easy to observe and capture, and form flocks as independent juveniles.

We used a feeding platform baited with millet

(*Panicum miliceum*), sunflower seeds (*Helianthus annuus*), and mealworms (*Tenebrio molitor*) to observe juncos. The feeding platform consisted of a 0.5-m² piece of painted sheet metal mounted on a wooden dowel (1.25 m long) and was designed to exclude chipmunks (*Eutamias* spp.). Cardboard was secured to the top of the metal to provide the birds with traction. Four petri dishes were taped to the cardboard 30 cm from each other. The petri dishes were filled with a mixture of soil, mealworms, and seeds. Although Dark-eyed Juncos are ground foragers (Ehrlich et al. 1988), preliminary observations in 1992 demonstrated that they will forage on platforms that are located near cover. Earlier attempts to provide juncos with food at ground level failed because chipmunks aggressively excluded juncos from feeding stations.

Independent juveniles were caught in mist nets and banded with a USFWS aluminum band and a unique combination of colored leg bands. Body mass and wing chord were measured at capture. Of 49 juveniles banded, 23 remained in the area after capture as members of a local flock. Nineteen of these 23 local birds were then used as focal animals for collection of behavioral data. The mean residence time for focal birds was 28 days (range 3 to 40 days). Foraging rates were based on 2 to 18 observations ($\bar{x} = 12.9$) and dominance rank on 3 to 88 observations ($\bar{x} = 30.8$). Sex was determined by wing-chord measurements based on measurements of adults of known sex in this population. Fourteen of 16 adult males (determined by cloacal protuberance) had wing chords at least 80 mm long, whereas 16 of 17 adult females (determined by incubation patch) had wing chords less than or equal to 78 mm in length.

Data on dominance status and feeding rate were collected for each of the 19 focal birds. All data were recorded using a hand-held tape recorder, a stop watch, and an event counter. The bird with the fewest previous observations was selected as the focal bird. Focal birds were observed until they left the platform (range 3 to 300 s).

Data on feeding rates were collected between 0630 to 1000 MST, with mealworms provided *ad libitum*. Feeding rate was defined as the number of mealworms consumed / time observed; these values were then converted into number of mealworms s⁻¹ for analysis. Prior to data analysis, we plotted seasonal progressions of feeding rate for each of the 19 focal birds. There were no consistent trends over time in this population, so mean values for each bird were used in all analyses.

Dominance status was determined by recording the winner and loser of each encounter on the feeding platform during observation periods (1 to 3.5 h) devoted exclusively to collecting dominance data. During these periods, both seeds and mealworms were provided. Birds won encounters either by directly attacking another bird and causing it to leave

TABLE 1. Associations of foraging rate and condition variables with dominance rank in juvenile Dark-eyed Juncos as measured by percent of encounters won (Hoeffding's d).

Variable	Predicted	Observed	d	P	n^a
Feeding rate					
Alone	+	+	-0.035	0.99	19
Social	+	+	0.142	0.005	16
Condition					
Mass divided by wing chord	+	+	-0.016	0.72	19
Hematocrit value	+	+	-0.035	0.96	15
% Heterophils	-	-	-0.015	0.60	15
Ratio of heterophils to lymphocytes	-	-	-0.023	0.78	15
% Eosinophils	-	-	-0.054	0.99	15

^a Number of birds sampled.

the platform or move away, or by the second bird moving away without direct aggression (Hinde 1952). We ranked birds by the percent of encounters they won.

Blood samples (100 μ L) were drawn from the brachial vein of 16 focal birds into heparinized microhematocrit capillary tubes. Each sample (75 to 100 μ L) was centrifuged for five minutes in a microhematocrit centrifuge at 1,500 rpm and then a hematocrit (% packed red blood cells per blood volume) value was determined using an International Equipment Company hematocrit reader. A drop of fresh blood from a second tube was used to make a blood smear to obtain total white blood cell differential for assessment of immunological status (Campbell 1988). All slides were stored in 100% ethanol until they were stained with Giemsa. Once the slides had been Giemsa-stained, leucocyte differentials (% heterophils, eosinophils, basophils, monocytes, and lymphocytes per 100 white blood cells) were determined by an avian hematologist with no knowledge of the birds' histories. The hematocrit value from one bird and the white blood cell smear from another bird were accidentally lost.

Nonparametric analyses were used because the data were not normally distributed. Hoeffding's d statistic, a nonparametric correlation procedure, was used for tests of association (Hoeffding 1948, SAS 1994). In this test, d -values range from -0.5 to 1.0, with 1.0 representing complete dependence. Because this was an exploratory study based on a small sample size, we were more concerned with making Type II errors (i.e. failing to identify relationships that could be the focus of future experimental studies) than with making Type I errors (i.e. identifying relationships that are later found to be the result of chance). Therefore, we did not correct for multiple comparisons. We report Z -values and d -values so that relative size of an effect can be assessed; P -values are based on two-tailed tests.

Results.—Juvenile juncos fed at higher rates when at least one other junco was present on the feeder than when they foraged alone (Wilcoxon signed-

rank test, $Z = -2.844$, $P < 0.01$). Consequently, for the remaining analyses we partitioned the data on feeding rates into observations collected when birds foraged alone and those collected when birds foraged socially. Individuals that were always observed foraging alone or were always in groups were dropped from some analyses.

Dominance status, as measured by percent wins, was not correlated with feeding rate when juveniles were alone but was strongly correlated with feeding rate when at least one other juvenile was present on the feeder (Table 1). This relationship was influenced by one individual that won all of its encounters and had an exceptionally high feeding rate, but the relationship persisted even when this "outlier" was removed from the analysis ($d = 0.120$, $P = 0.01$). These data suggest that all juveniles benefit from social foraging through increased feeding rate but that dominant individuals appear to derive greater benefits. We tested this explicitly by relating the change in feeding rate to dominance status. The magnitude of the change in feeding rate from foraging alone to foraging socially was strongly related to dominance status ($d = 0.093$, $P = 0.02$).

Birds with large wing chords won more encounters than smaller birds ($d = 0.05$, $P = 0.05$). Using wing chord, five juveniles were classified as males and nine as females, but sex could not be determined for the remaining five birds. Birds classified as males tended to win more encounters than those classified as females, although this relationship was not very strong (Mann-Whitney U -test, $Z = -1.667$, $P = 0.10$).

We predicted that dominant juveniles would be in better physiological condition than subordinate flock members but found little support for this prediction (Table 1). We found more support for our prediction that foraging success would be positively correlated with physiological condition (Table 2). Feeding rate in the presence of other juncos was correlated with the traditional measure of condition, mass divided by wing chord, and also with hematocrit value (Table 2). In addition, there was a weak relationship ($0.1 > P > 0.05$) among three condition variables (mass di-

TABLE 2. Relationship between condition in juvenile Dark-eyed Juncos and foraging rate when feeding alone or with other juncos (Hoeffding's *d*).

Variable	Predicted	Observed	<i>d</i>	<i>P</i>	<i>n</i> ^a
Feeding rate when alone					
Mass divided by wing chord	+	+	0.032	0.09	19
Hematocrit value	+	+	-0.040	0.99	15
% Heterophils	-	-	0.049	0.08	15
Ratio of heterophils to lymphocytes	-	-	0.002	0.07	15
% Eosinophils	-	-	-0.010	0.51	15
Feeding rate when social					
Mass divided by wing chord	+	+	0.061	0.05	16
Hematocrit value	+	+	0.109	0.02	13
% Heterophils	-	-	-0.003	0.39	14
Ratio of heterophils to lymphocytes	-	-	-0.008	0.47	14
% Eosinophils	-	-	-0.045	0.99	14

^a Number of birds sampled.

vided by wing chord, % heterophils, and ratio of heterophils to lymphocytes) and feeding rate when juncos foraged alone (Table 2).

The hematological parameters we measured fell within the ranges of values reported for other passerines (Bennett and Chisholm 1964, Farner 1982, Sturkie 1986). Hematocrit values ranged from 46 to 52% volume of packed red blood cells ($\bar{x} = 48.3 \pm \text{SD}$ of 1.8). Percent heterophils ranged from 2 to 19 ($\bar{x} = 8.9 \pm 5.2$), percent lymphocytes ranged from 64 to 90 ($\bar{x} = 77 \pm 7.6$), and percent eosinophils ranged from 0 to 9 ($\bar{x} = 5.2 \pm 3.1$). Our hematological measures of condition were related to the traditional measure of condition (mass divided by wing chord). Percent heterophils and ratio of heterophils to lymphocytes declined with increasing values of mass divided by wing by chord ($d = -0.10$, $P = 0.02$ and $d = 0.09$, $P = 0.03$, respectively). Hematocrit value was weakly correlated with mass divided by wing chord ($d = 0.04$, $P = 0.10$), and flock residence time was positively correlated with percent eosinophils ($d = 0.27$, $P < 0.01$).

Discussion.—Dominance status of juveniles was correlated with variation in social foraging behavior in this population of juncos; dominant juveniles had higher feeding rates than subordinates when other juncos were present on the feeder. In contrast, our failure to find a relationship between dominance status and feeding rate when juncos foraged alone suggests that dominant individuals do not have superior prey-handling skills. Our results add to the growing body of evidence reviewed by Piper (1997) that dominant individuals feed more efficiently than subordinates in social situations. All of the juncos in our study foraged at higher rates when a conspecific was present than when they foraged alone. Interestingly, the magnitude of this change was related to dominance rank. Therefore, although all birds gained from social foraging, dominant birds appeared to benefit the most.

We identified positive relationships between social foraging success in juvenile juncos and both the traditional measure of condition, mass divided by wing chord, and our measure of oxygen carrying capacity, hematocrit. In addition, weak relationships were present between feeding rate when alone and condition (mass divided by wing chord, % heterophils and ratio of heterophils to lymphocytes). The Dark-eyed Junco is a social species; juveniles spend much of their time in flocks, as do all age classes during the nonbreeding season. Juveniles that are relatively proficient foragers in the social milieu of a flock may have a higher probability of surviving to adulthood because of greater energy stores available for periods when adverse weather limits foraging time and greater resistance to disease.

Although foraging success was related to dominance and condition, we failed to find a relationship between dominance status and any of the condition variables that we measured. Piper (1997) points out that the relationship between fat storage (an index of condition) and dominance in small birds is not straightforward. Depending on the species and ecological conditions, dominant individuals may have higher, lower, or similar fat reserves relative to subordinates. The potential costs associated with acquiring and maintaining fat stores include decreased agility and increased exposure to predators while foraging (Pravosudov and Grubb 1997). In the late summer at our study site, insects and seeds were an abundant, predictable food, and the juncos we captured carried little if any visible fat. At this time of the year, dominant juveniles may pursue a strategy of minimizing the time they spend foraging to avoid predation rather than maximizing fat storage.

The paucity of data on hematological parameters in wild birds makes it difficult to interpret results based on these parameters. Hematocrit levels ranging from 33 to 55% are accepted as normal by avian clinical hematologists (Dein 1982). According to this

criterion, none of the juveniles in our study had abnormal hematocrit values, and too few data exist on normal values for wild passerines to determine if a difference of 1 to 5% in hematocrit value is clinically important. Even so, accumulating evidence suggests that relative differences in hematocrit level are related to important life-history parameters that include clutch size in Great Tits (*Parus major*; Dufva 1996) and parasite loads and growth rates in Cliff Swallow (*Petrochelidon pyrrhonota*) nestlings (Chapman and George 1991).

Similarly, because of the limited availability of normal differential white blood cell values for passerines, we are unable to say definitively whether any of the birds we studied were truly, rather than relatively, heterophilic. Ronald et al. (1968) documented mean percent heterophils of 28 for immature Red-winged Blackbirds (*Agelaius phoeniceus*). Because this value is nearly three times higher than the mean percent heterophils found in our study, counts of heterophils as well as lymphocytes may vary greatly among species (see Bennett and Chisholm 1964).

Eosinophil counts, an indicator of recent exposure to parasites (Roitt et al. 1993), were not related to dominance status or foraging success; instead, they varied with residence time in the juvenile flock. Birds that joined the flock early in the study had higher eosinophil counts at the end of the season than the presumably younger birds that joined the flock later in the study. Young juncos may acquire parasites when they forage on the ground in close proximity to conspecifics. The observed relationship between flock residence time and eosinophil count could arise if parasite challenge rates are a function of the amount of exposure to flock members, the number of intermediate hosts eaten in a particular area, or if a delay exists between exposure to parasites and eosinophil response. Wilson and Wilson (1978) documented a delay of three weeks between infection with a threadworm and hematological changes in Red Grouse (*Lagopus lagopus scoticus*).

The data presented here suggest a relationship among foraging behavior, social skills, and physiological condition in juvenile Dark-eyed Juncos. Short-term benefits may accrue to juveniles that attain high dominance status in this population because dominant individuals appear to derive greater benefits from social foraging than do subordinates. Our study is based on a small sample of birds, and these correlative results should be interpreted with caution. Nonetheless, our preliminary data point to the need for additional work that might link the short-term benefits suggested by our results with the long-term consequences for avian survivorship.

Acknowledgments.—We thank Sigma Xi, the United States Fish and Wildlife Service, and the United States Forest Service for financial support; Jian Fei Zhang for reading the white blood cell slides; and

Mark Elgar, Walter Piper, and an anonymous reviewer for insightful comments.

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Received 2 April 1998, accepted 27 January 1999.

Associate Editor: L. J. Petit

The Auk 116(4):1141–1144, 1999

Male House Sparrows Behave as if a Fertilization Window Exists

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Sperm competition can occur when a female copulates with more than one male during the period when her eggs can be fertilized (Parker 1970). In monogamous species, where the male typically contributes valuable parental care, intrasexual selection should act on males to produce traits that minimize sperm competition, thus helping ensure that the investing male's own sperm fertilizes most or all of his mate's eggs (Kempnaers et al. 1995). In birds, two of the main ways a male avoids cuckoldry are mate guarding and frequent copulation (Birkhead and Møller 1992, Briskie 1992). However, both of these behaviors may be very costly for males in terms of

energy expenditure and/or time (opportunity cost), so males can be expected to confine these behaviors to times when they would be most beneficial, if such times can be detected.

As laying commences, the presence of the first developing ovum in the oviduct apparently decreases the interval during which additional sperm can be introduced and have any chance of fertilizing the second ovum (Bakst and Bird 1987, Birkhead and Møller 1993, Bakst et al. 1994). This may reduce the hypothetical "fertilization window" ("insemination window" of Cheng et al. 1983) to as little as 10 to 60 min after the laying of the preceding egg, while the next ovum is in the infundibulum (Bobr et al. 1964). Thereafter, the second egg, fertilized or not, begins accumulating layers of albumen and membranes that trap sperm and act collectively as a barrier to fertilization of a third ovum (Bakst et al. 1994). Furthermore, the contractions that propel each egg through

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