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Effect of prior residence on dominance status of dark-eyed juncos, *Junco hyemalis*

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Abstract. Both prior residence and age have been reported to influence rank in avian dominance hierarchies. The aim of this study was to determine the relative effects of these two factors on dominance status of dark-eyed juncos. Twenty-one mixed-age flocks of recently captured juncos (192 individuals) were observed in two similar aviary experiments, one conducted during autumn migration and the other after autumn migration had ended. In the experimental treatment, a group of adult juncos was held in a cage for 1 week and then introduced to an observation cage in which a group of young juncos had already been housed for 1 week, thereby giving the young birds a prior-residence advantage. In the control treatment, groups of each age were held in separate cages for 1 week and were then introduced simultaneously to a neutral observation cage. Dominance ranks of all individuals were determined through observation of aggressive interactions. When given prior residence, young birds clearly dominated adults. Because adults tended to dominate young in control flocks, these results demonstrate that prior residence can reverse age-related dominance among flocks of juncos under semi-natural conditions. If these results apply to wild populations, they indicate that young juncos might gain in dominance status during winter if they timed their autumn migration so as to arrive on the wintering grounds before adults.

Prior residence has been recognized as a determinant of dominance rank in birds since the pioneering research of Schjelderup-Ebbe (1922) on pecking orders in chickens, *Gallus gallus*. The prior-residence effect, whereby residents tend to dominate intruders, has since been demonstrated in many wild species: invertebrates (Dingle 1969; Davies 1978), bony fish (e.g. Braddock 1949; de Boer & Heuts 1973; Figler et al. 1976), amphibians (e.g. Boice & Witter 1969), reptiles (e.g. Evans 1936), mammals (e.g. Lerwill & Makings 1971), and birds (e.g. Balph 1977, 1979; Yasukawa & Bick 1983).

Because of its effect on dominance status, prior residence should be considered in all natural systems characterized by strong social dominance interactions. Dark-eyed juncos exhibit a differential autumn migration in which the age and sex classes of the population tend to migrate different distances into the winter range (Ketterson & Nolan 1976, 1983, 1985). Social dominance has been proposed as a mechanism producing differential migration in this and other species (Ketterson & Nolan 1976; Gauthreaux 1978, but see Ketterson & Nolan 1982, 1983). The dominance hypothesis, which predicts that subordinate individuals will migrate further than dominant ones to avoid competition with them, has been supported by research on some bird species (Nichols & Haramis 1980; Byrkjedal & Langhelle 1986; Kerlinger & Lein 1986). However, the winter age distribution of juncos is inconsistent with dominance as a sole mechanism for differential migration because, despite a tendency for adults to dominate young (Ketterson 1979; Zink & Watt 1987; Rogers et al. 1989), adults tend to migrate further south into the winter range than young of the same sex (Ketterson & Nolan 1983).

Our aim in this study was to compare the relative magnitudes of the effects of prior residence and age on dominance, when the two effects were measured in opposition. Early arrival on the wintering ground could lead to a prior-residence advantage in juncos. If prior residence enables young juncos to dominate adults, and if young juncos arrive at wintering sites before adults, the dominance hypothesis would not be inconsistent with the junco's winter distribution. We report here the results of two aviary experiments. In experiment I, we tested the prior-residence effect using only male juncos caught in Indiana during winter. In experiment II, we tested juncos during the autumn migration, employed birds of both sexes, and included birds from Michigan as well as Indiana, in an attempt to verify the findings of experiment I using a broader range of subjects.

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METHODS

General Methods

Juncos were captured using mist nets baited with millet and cracked corn at 11 widely scattered sites near Bloomington, Indiana, and were housed in outdoor aviaries. Young birds were distinguished from adults on the basis of skull ossification (Ketterson & Nolan 1982) and iris colour (Yunick 1977). Sex determination was based on wing length (flattened) and on crown and body coloration (Ketterson & Nolan 1976, 1982). Birds were colour-banded upon capture to habituate them to wearing colour bands, and were then given new, randomly chosen colour bands on the evening prior to the first dominance observations. After initial capture, all weighing, colour-banding and handling took place after dark.

Outdoor enclosures, constructed of hardware cloth and measuring $7 \times 4 \times 3$ m, were used for all housing and testing. Subjects were provided with heated water baths, several cut evergreen-tree roosts, and an unlimited supply of cracked corn, millet, sunflower hearts and turkey mash. Food was scattered so that all birds could feed simultaneously. Birds were held at low densities ($0{\cdot}10/m^2$), and all appeared to be in good health throughout the experiments.

Flock Establishment

After capture, adults and young were held separately in large, visually isolated enclosures for several days until our capture efforts produced sufficient numbers to form several groups. We then simultaneously introduced groups of five or six birds of the same age and sex into new enclosures where they were held in visual isolation from other such groups for 7–8 days. After this period (the 'pre-flock' period), we created amalgamated flocks by combining a group of young juncos with an adult group of the same sex and number of individuals. To avoid the possibility that adult and young subjects had already established dominance relationships before capture, birds of different ages from the same capture sites were never placed in groups that were destined to be combined.

Flocks that were established by introducing an adult group to the enclosure already occupied by a young group (so that the young birds had 7–8 days of prior residence) are referred to as experimental flocks. Control flocks were formed by introducing both a group of young and a group of adult birds into a neutral test enclosure. The purpose of the pre-flock period of 7–8 days was to allow some groups to gain prior residence in an enclosure that would ultimately serve as their test enclosure, while also controlling for time in captivity in all groups. Groups were assigned to each treatment at random, and control and experimental flocks were established and observed either simultaneously or during alternate weeks to avoid any confounding effects of season. To equalize handling effects, all groups, including groups of young birds that were destined to remain in their home enclosures for testing, were removed from their cages for weighing and colour-banding at the time the amalgamated flocks were formed.

Experiment I was carried out from 3 January to 3 March 1988, after the end of the autumn migration of juncos (Ketterson & Nolan 1976, 1985). Experiment II was performed during the following autumn migration, from 6 November to 3 December 1988. The designs of the two experiments were identical, but there were some differences in methods that will be described below.

Experiment I: Prior Residence in Wintering Juncos

All subjects in this experiment were males. There were 12 replicate flocks with a total of 112 individuals. In each flock there were potentially $N(N-1)/2$ interacting pairs of birds (total: 472 pairs). Subjects were held for 1–13 days before group formation. Prior to flock establishment, birds with missing tail feathers or possible wing sprains were removed. To keep group sizes equal, we then removed a randomly chosen member of the corresponding group. We removed one or two birds from each group, resulting in amalgamated flocks of 8 or 10 birds.

Experiment II: Prior-residence Effect in Migrating Juncos

The purpose of the second experiment was to assess the magnitude of the prior-residence advantage during the autumn migration of juncos. We assumed that most juncos were still migrating when captured, but some had probably already terminated their migrations. Five subjects had almost certainly terminated their migrations, because they were caught at locations where they had wintered in the previous year.

Unlike experiment I, subjects of both sexes were used in this experiment. There were nine replicate

flocks with a total of 80 individuals (320 potentially interacting pairs of flockmates). Separate flocks of males ($N=5$) and females ($N=4$) were tested. One flock of males and one flock of females consisted of birds captured in Kalamazoo, Michigan, 1 day prior to group formation and transported to Bloomington by car. All subjects were captured 1–5 days before the formation of groups. Individuals with missing tail feathers or injuries were removed from groups before flock establishment, as were randomly chosen members of corresponding groups, but no removals were necessary in three replicates. All amalgamated flocks contained 8 or 10 individuals as in experiment I.

Behavioural Observations

All birds were uniquely identified by three plastic bands of a single colour in addition to an aluminium U.S. Fish and Wildlife band. Observations were made from a blind 2–3 m away while birds fed at a single source of food. To increase feeding activity, all food was removed from the cage for 0·5–2·5 h before the beginning of the observation period, at which time, a single dish of seed was provided. Observers recorded all interactions occurring at the food dish, as well as occasional interactions occurring nearby. All interactions were classified as: (1) active displacement (one bird drove away another that was less than 0·3 m away); (2) passive displacement (one bird's approach caused another to move away, but departure occurred while the approaching bird was more than 0·3 m away); or (3) standoff (escalated interaction in which neither bird retreated). Observation periods lasted several hours and were repeated daily until each bird in a flock had interacted with every other bird at least five times.

Analysis of Dominance

Dominance hierarchies were constructed by combining active and passive displacements and creating a win–loss matrix (Brown 1975). An individual was classified as dominant over another only if its ratio of wins to losses was greater than expected by chance alone (binomial distribution, $P<0·10$). Despite using a cut-off of $P<0·10$, this criterion is considerably more stringent than that used in most published dominance studies. For example, if one bird displaced another bird five times and never yielded ($P<0·10$), it was classified as dominant. Alternatively, if it displaced another five times but yielded to it once ($P>0·10$), the pair was classified as tied. A dominance score was calculated for each bird as the number of its flockmates dominated divided by the total number of its flockmates. In the case of ties, 0·5 was added to the dominance score of each member of the tied pair. Dominance scores were normalized using an arcsine transformation and compared using two-factor (experiment I: treatment age) or three-factor (experiment II: treatment, age, sex; we randomly omitted four young and four adult males from this data set to meet requirements of equal cell sizes) ANOVA.

RESULTS

Dominance Hierarchies

The dominance hierarchies in all flocks were nearly linear, with intransitivity occurring in only 3% of the pairs in experiment I ($N=472$ pairs) and 5% of the pairs in experiment II ($N=320$ pairs). Ties occurred in 5% of the pairs in experiment I and 10% of the pairs in experiment II. The mean number of interactions per pair of flockmates was 16 in both experiments I and II.

Experiment I

The dominance scores of adult juncos were higher than those of young in control flocks, whereas they were lower than those of young when young were given prior residence (Fig. 1a). Analysis of variance indicated a significant interaction between treatment and age ($F_{\text{interaction}}=27·08$, $df=1$, $P<0·0001$). As a result of the experimental design, the treatment effect was not free to vary because low dominance scores within a dominance hierarchy are always balanced by high dominance scores. The age effect was not significant across treatments because adult dominance scores were lower in experimental flocks while young dominance scores were lower in control flocks ($F=1·51$, $df=1$, $P>0·20$).

An alternative analysis compared the dominance scores of groups, rather than considering each individual's score as an independent data point (see Discussion). In control trials groups of adults had higher dominance scores than groups of young, while the reverse was true in experimental trials. As above, the only significant effect was the interaction

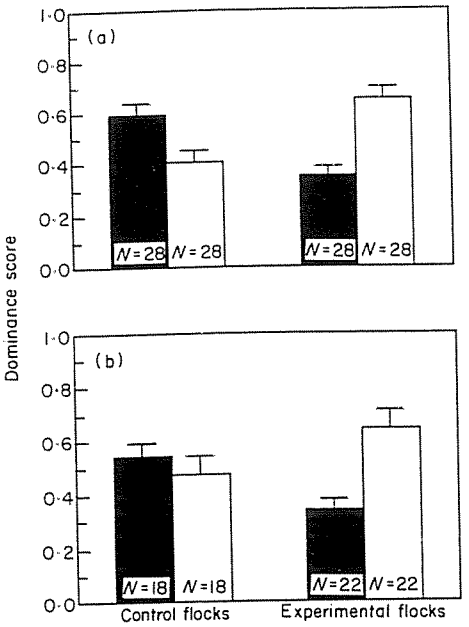

Figure 1. Comparison of dominance scores ($\bar{X}+$SE) of adult (■) and young (□) dark-eyed juncos in control and experimental (i.e. young given prior residence) flocks. (a) Experiment I, winter 1988; (b) experiment II, autumn 1988.

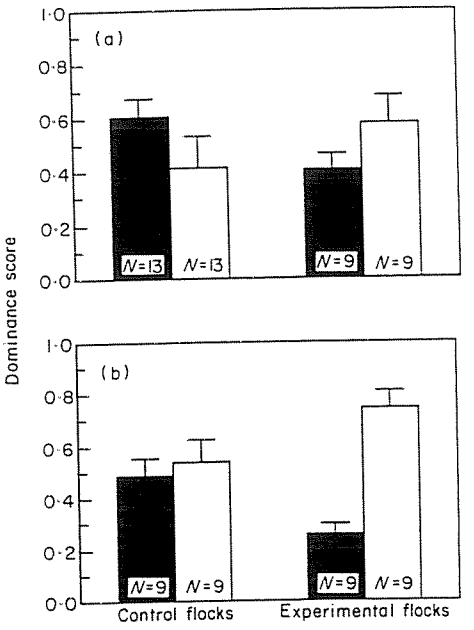

Figure 2. Comparison of dominance scores ($\bar{X}+$SE) of adult (■) and young (□) dark-eyed juncos from experiment II control and experimental (i.e. young given prior residence) flocks. (a) Males; (b) females.

of treatment and age ($F_{\text{interaction}}=29{\cdot}51$, $df=1$, $P<0{\cdot}0001$; control flocks: adult $\bar{X}=0{\cdot}89$, $N=6$; young $\bar{X}=0{\cdot}67$, $N=6$; experimental flocks: adult $\bar{X}=0{\cdot}63$, $N=6$; young $\bar{X}=0{\cdot}97$, $N=6$).

Experiment II

The dominance scores of adults were higher than those of young in control flocks and lower than those of young in experimental flocks ($F_{\text{interaction}}=8{\cdot}64$, $df=1$, $P<0{\cdot}005$; Fig. 1b). Several factors (treatment, sex, treatment–sex interaction) of the ANOVA are not free to vary because dominance scores were generated from hierarchies (see above) and sexes were tested in separate flocks. There was a significant interaction of sex and age ($F_{\text{interaction}}=5{\cdot}23$, $df=1$, $P<0{\cdot}03$), which indicates that the patterns of dominance across treatments differed between flocks of males and flocks of females. The mean dominance score for adult males was higher than that for young males in control flocks, and lower than that of young males in experimental flocks (Fig. 2a). In flocks of females, mean dominance scores of adults and young did not differ in control flocks, while dominance scores of adult females were much lower than those of young females in experimental flocks (Fig. 2b).

In the alternative analysis using group dominance scores, female trials were omitted owing to small sample size. Mean dominance scores of adult groups tended to be higher than those of young groups in control trials, while the reverse was true in experimental trials, but this difference was not significant ($F_{\text{interaction}}=3{\cdot}55$, $df=1$, $P>0{\cdot}10$; control flocks: adult $\bar{X}=0{\cdot}92$, $N=2$; young $\bar{X}=0{\cdot}64$, $N=2$; experimental flocks: adult $\bar{X}=0{\cdot}67$, $N=3$; young $\bar{X}=0{\cdot}88$, $N=3$).

DISCUSSION

Prior Residence and Age-related Dominance

Both during and after autumn migration, prior residence in a large outdoor aviary increased the dominance status of young dark-eyed juncos relative to that of adults of the same sex. These results are only partially consistent with the findings of Yasukawa & Bick (1983) for this species. In their experiment I, juncos with 1 week of prior residence tended to dominate non-residents in four small

flocks of males matched for age. However, in their experiment II low-ranking residents did not defeat high-ranking non-residents. Our experimental treatment was more similar to their experiment II because adult non-residents were pitted against young residents. Yet, we found that the prior-residence effect elevated the dominance status of young juncos so that they tended to dominate adults. In males, the prior-residence advantage overcame the age-related dominance that adults demonstrated in the control flocks. Among females prior residence clearly elevated the status of young in the experimental flocks. However, because no age-related dominance was found in the female control treatment, the magnitude of the prior-residence advantage relative to the effect of age on dominance is unknown for that sex.

Our results are consistent with those of two other recent studies on dark-eyed juncos. We showed that a prior-residence advantage overcame the usual dominance advantage of adults over young. Holberton et al. (1990) have shown that although resident young can dominate intruding adults, resident adults dominate intruding adults by a greater margin, indicating that prior residence and age can be considered additive components of dominance status. Wiley (1990) also demonstrated that resident juncos dominate non-residents, but found that the magnitude of the prior-residence advantage was not great enough to overcome previously established dominance relationships (Wiley 1990).

Wiley (1990) presents suggestive evidence that when two established junco groups are joined, the rank achieved by some members of the original groups may influence the ranks achieved by other members (i.e. the 'coat-tail' effect). We found no evidence for a coat-tail effect in our 10 control flocks (unpublished data), possibly owing to the short tenures of our flocks (7–8 days) relative to those of Wiley (4–8 weeks). However, because the existence of such an effect could affect the interpretation of our results, we presented an alternative analysis in which we considered each group as a single data point. The purpose of the alternative analysis was to control for the possibility of non-independent dominance scores among members of the same groups. In the face of this more conservative analysis, our results still showed that groups of young had higher mean dominance scores than groups of adults in experimental flocks, while the reverse was true in control flocks.

Adult juncos dominate young in both field and laboratory studies (Ketterson 1979; Zink & Watt 1987; Rogers et al. 1989), and this phenomenon has been reported for other species as well (e.g. Harris' sparrow, *Zonotrichia querula*, Rowher et al. 1981; white-crowned sparrow, *Zonotrichia leucophrys*, Zink & Watt 1987). Young birds dominate adults in several other bird species (e.g. Barken et al. 1986; Komers 1989), and at least one study of juncos indicates that neither age class tends to dominate in caged pairs (Holberton et al. 1990). Thus, our finding that young female juncos were not subordinate to adult females in the control flocks of experiment II is not without precedent. This result may indicate a sex-specific difference in the age-related dominance of male and female juncos, but our small sample sizes of each sex necessitate caution in drawing further inferences. An additional consideration is the demographic difference between our winter and autumn samples. If dominance status influences which adults settle at each wintering site and which migrate further, then the winter sample would tend to be biased towards those adults dominant enough to settle at the capture site. The autumn sample may have included more subordinate adults, which might have continued migrating had they not been captured. This explanation is consistent with our finding that adult dominance over young in the control flocks was more pronounced in winter (experiment I) trials.

Prior Residence and Junco Migration

Laboratory evidence has suggested that young captive juncos begin migratory activity about 1 week earlier than similarly treated adults (Ketterson & Nolan 1985). Furthermore, banding data have shown that young individuals that return to Bloomington as adults in later winters tend to be recaptured slightly later in the second year, whereas returning adults show no change in median capture date between years (Ketterson & Nolan 1985). These observations are consistent with the hypothesis that a prior-residence advantage might elevate the dominance status of early-arriving young juncos, enabling them to dominate at least some adults. However, Nolan & Ketterson (in press) have recently shown that juncos that became resident at Bloomington tended to arrive later than transient juncos. Further, the mean arrival date of young residents was later than that of adult residents of the same sex. This seems to argue against

a role for prior residence as a determinant of migration distance in wintering juncos. Thus, despite our finding of a strong prior-residence effect in captive dark-eyed juncos, it appears unlikely that selection for early arrival on the wintering grounds has been an important mechanism in the evolution of differential migration in this species.

The finding that prior residence was a determinant of dominance in aviary flocks, and overcame the effect of age on dominance, raises the question of why young juncos do not arrive on the wintering grounds before adults. Young that are produced early in the breeding season are independent long before their parents terminate breeding if their parents attempt to breed for a second time. Unlike adults, young juncos do not undergo a complete pre-basic moult prior to autumn migration (Pyle et al. 1987). Both of these considerations suggest that young juncos might be capable of initiating migration sooner than their parents. Several explanations for the apparent later arrival of young juncos in Bloomington seem plausible. (1) The prior-residence advantage demonstrated under semi-natural aviary conditions may not exist in the field, in which case the hypothesized selection pressure for early autumn arrival would not exist. (2) Dominance may not function as a mechanism in determining where juncos terminate their autumn migration, which would uncouple the social advantages of prior residence from migration. (3) Birds making their first migration may have much longer travel times or less direct routes than adults and so face constraints arising from inexperience. (4) There may be strong selection pressure on young to delay departure from their natal sites in the autumn so as to gain experience on potential breeding sites that might give them a prior-residence advantage the following spring.

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