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Prior-residence and coat-tail effects in dominance relationships of male dark-eyed juncos, *Junco hyemalis*

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Abstract. Captive male dark-eyed juncos from two different aviaries were combined either in one group's original aviary (seven replicates) or in a third aviary (two replicates). These experiments controlled for effects of handling the subjects during transfers between aviaries and, in statistical analysis of the results, took into account constraints on the dominance relationships within combined groups. The results (1) confirmed the influence on dominance of prior residence in an aviary and (2) revealed a lack of independence in the dominance relationships between individuals from different original groups. This lack of independence probably resulted from an influence of dominant individuals on the relationships of their familiar subordinates, a 'coat-tail' effect. (3) The results further indicated that previous experience with dominance or recognition of previous opponents outweighed the effect of prior residence. Consequently, prior residence might represent a last resort in the settlement of contests in this species, as predicted on theoretical grounds for the use of conventional asymmetries in the settlement of contests. The coat-tail effect, if it applies in the field, would create an advantage for subordinates associating with familiar dominants.

Several decades of research have documented the complexity of behavioural, physiological and developmental mechanisms by which individuals attain their positions in dominance hierarchies of birds. Although there is considerable variation among species and conditions, competitive abilities can vary with sex, size and age, with genetic or hormonal differences, and also with experience in previous interactions (Collias 1943; Jackson 1988; Piper & Wiley 1989). Relationships in a dominance hierarchy can also depend on status signals, features of individuals that indicate their competitive abilities to potential opponents (Rohwer 1975; Balph et al. 1979; Ketterson 1979). These mechanisms all share one feature in common: they all generate a stable scaling of individuals' attributes that serves as a basis for social relationships.

The experiments reported here explore three mechanisms other than a stable scaling of individuals' attributes that might affect dominance relationships in wintering birds: (1) prior residence at the location of encounters, (2) effects of previous experience with opponents, and (3) effects of dominant individuals on the relationships of their familiar subordinates. Prior residence at the location of encounters or proximity to 'home' is known to provide an advantage in interactions with opponents in several permanently resident birds (Waser & Wiley 1980; Eden 1987; Desrochers et al. 1988; Zack & Rabenold 1989) and also in a migratory species that forms stable dominance relationships in its wintering range (Piper & Wiley 1989). In addition, prior residence affects dominance in laboratory studies of a variety of animals (Lerwell & Makings 1971; Figler et al. 1976; Zayan 1976).

Captive dark-eyed juncos have been frequent subjects for studies of prior residence in relation to dominance, since Balph's (1977, 1979) description of the phenomenon in this species. Yasukawa & Bick (1983), Cristol et al. (1990) and Holberton et al. (1990) controlled possible effects of handling birds during transfers between aviaries by catching residents as well as newcomers and then releasing them all simultaneously into the residents' aviary. They have all confirmed that prior residence can affect dominance relationships in this species. These studies have also considered whether or not any intrinsic differences in competitive ability might outweigh the influence of prior residence. Based on predictions of game theory (Maynard Smith & Parker 1976), Yasukawa & Bick (1983) argued that prior residence should determine relationships only among individuals that did not differ markedly in intrinsic abilities.

Yasukawa & Bick (1983) raised the additional issue of whether or not dominance relationships in combined groups in neutral aviaries were settled

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independently. Lack of independence in dominance relationships would affect the statistical treatment of experiments in which groups of birds were combined. In addition, if all birds from one original group tended to outrank the other in a neutral aviary, it would suggest an influence of dominant individuals on familiar subordinates' interactions with strange opponents, a 'coat-tail' effect.

The present series of experiments provides, first, a replication of Yasukawa & Bick's (1983) experiments on prior residence in dark-eyed juncos. For reasons explained below, questions about statistical interpretation make confidence in the original results uncertain. Second, the present experiments examine the question of whether previous experience with dominance or recognition of former opponents can outweigh the effects of prior residence. Third, separate experiments provide evidence for the possibility of a coat-tail effect. This result stands in contrast to Yasukawa & Bick's conclusions, although reanalysis of their data suggests no disagreement with results reported here.

Table I. Design of experiment I for twelve birds (two original groups of six) in different combinations in two aviaries

Birds in aviary A	Birds in aviary B
Stage 1 (birds in original aviaries)	
A,B,C,D,E,F	a,b,c,d,e,f
Stage 2 (high-ranking birds in one aviary, low-ranking birds in the other)	
A,B,C,a,b,c	d,e,f,D,E,F
Stage 3 (all birds returned to their original aviaries)	
A,B,C,D,E,F	a,b,c,d,e,f
Stage 4 (high-ranking and low-ranking birds separated but aviaries reversed in comparison to Stage 2)	
d,e,f,D,E,F	A,B,C,a,b,c

Different individuals are represented by letters, either A, B, C, D, E and F or a, b, c, d, e and f, indicating their ranks in their original aviaries. The rankings in this table represent the expected results under the hypotheses of an effect of prior residence (stage 2) and of previous experience with dominance or recognition of opponents (stage 4). This design was replicated seven times.

METHODS

Subjects and Aviaries

Dark-eyed juncos were trapped at four locations 1·5–8 km apart near Chapel Hill, North Carolina, during December and January 1977–1980. To distinguish the sexes, I used a combination of wing length, extent of brown in the plumage, and presence of inconspicuous dark streaks along the shafts of the feathers on the forecrown (Ketterson & Nolan 1976). Only males, i.e. birds with relatively long wings, little brown, and an absence of streaks on the crown, were used in the experiments. In six groups, birds were also matched for length of wing chord within 3 mm. This matching was not attempted in the remaining eight groups, but this difference had no noticeable effect on the results. Each bird was individually marked with coloured bands.

Subjects were held in captivity in individual, visually isolated cages for 1 to 15 days before they were placed in groups of four to six in large outdoor aviaries (2·5 × 2·5 × 2·5 m). An observation chamber with one-way glass on each aviary permitted close observation of the birds without disturbance. Birds caught in the same location within 1 week were placed in different aviaries; otherwise they were allocated to aviaries at random. Each of the eight aviaries used in these experiments had similar orientations and arrangements of perches, food and water. Food (mixed varieties of millet) was provided ad libitum in two trays measuring 20 cm in diameter. In practice, this arrangement allowed all birds to feed but not simultaneously. One subject died in the course of the experiments from unknown causes.

Experiment I

As Yasukawa & Bick (1983) have described, these experiments to investigate effects of prior residence consisted of a preliminary stage of observations followed by rearrangement of the birds between two aviaries and subsequent observations. Experiment I then continued for two additional rearrangements, to test for effects of recognition of opponents or previous experience with dominance. Experiment I thus had four stages in all (Table I).

To equalize any effects of handling the birds during transfers between aviaries, I captured all birds in two aviaries within a period of 10 min and held them in large cloth bags for 15–30 min before I released the new combinations simultaneously from the bags into the aviaries. Thus, even those birds replaced in their original aviaries had the same handling as those transferred to different aviaries.

Experiment I extended over three winters, December–April 1977–1980, and involved 14 groups of six birds each, making a total of seven sets of two aviaries between which birds were interchanged. Each of the seven sets of aviaries was treated identically (Table I). Stage 1, which began when the birds were first introduced to the aviaries, lasted 3–9 weeks to allow the birds to become fully acquainted with their aviaries and each other. In stage 2, the birds in a pair of aviaries were rearranged, so that the three highest-ranking birds from each aviary were placed in one of the original aviaries, and the three lowest-ranking birds from each aviary were placed in the other.

After 1–3 days in stage 2, the birds were again captured and rearranged so that each bird was once again in its original aviary with its original opponents. Thus, in stage 3, all birds were in the same locations as in stage 1. Following a further 1–3 days in stage 3, the birds in the two aviaries were again rearranged for stage 4. Once again the high-ranking birds from both aviaries were combined in one aviary and the low-ranking birds combined, but with the aviaries reversed from those in stage 2. Thus, in stage 4 the groups of opponents were the same as in stage 2, but the birds in their home aviary in stage 2 were now in a strange aviary and vice versa.

This protocol provided (1) a test for prior residence in stage 2, (2) a test for resumption of original rankings after separation in stage 3, and (3) a test for an effect either of recognition of opponents or of an influence of previous experience with dominance versus prior residence in stage 4.

Experiment II

To test for a coat-tail effect, a lack of independence in the formation of relationships between individuals from two original groups, groups of male juncos from two original aviaries were combined in a third aviary. I completed two replicates of this experiment in late February 1980. In the first instance two groups of five birds each were combined, in the second two groups of three and four birds each. In each case the members of each of the original groups had been caged together for 4 and 8 weeks respectively and the two groups had never interacted with each other.

Observations of Dominance Relationships

During each stage of these experiments, the groups were observed at least twice to establish dominance relationships. Before each observation period, birds were deprived of food for 30–45 min to increase the frequency of interactions. Behaviour indicating dominance relationships included supplantings, attacks and fights, all of which involved one individual initiating action that resulted in its taking the place occupied by another bird (see Balph 1977). During stages 2, 3 and 4, observations began the day following the transfers of birds. In some aviaries, some pairs of individuals had not interacted or had interacted only once even after two observation sessions.

Statistical Analysis

In analysing the statistical significance of the results of these and similar experiments, two related problems arise: (1) the number of possible different hierarchies under the null hypothesis, and (2) the independence of the dyadic relationships in each aviary. Since the present experiments and those of Yasukawa & Bick (1983) both involved groups of six birds and interchanges of subsets of three birds, the issues of statistical treatment are similar.

With respect to the first issue, Yasukawa & Bick (1983) argued that the six birds, three from each of two asymmetric groups, could form 6! different hierarchies, under the null hypothesis of no influence of prior residence. Consequently, the unique result of all three birds in one original aviary outranking all three from another aviary would have $P=1/(6!)$

More realistic assumptions, however, lead to a much reduced number of possibilities under the null hypothesis of no effect of prior residence. Recall that transfers among aviaries always involved groups of three birds (the highest- or lowest-ranking three) treated as units. The dominance relationships within these groups of three remained constant regardless of the transfers (see below), so it is not reasonable to include changes in their dominance relationships as possibilities. The more appropriate procedure is to focus on the nine relationships between the two sets of three birds from different original aviaries and to consider how many ways these relationships can be settled.

As Yasukawa & Bick (1983) noted, there are just 20 different hierarchies that can result under the constraint that groups of birds treated as units retain their relationships (Table II). Note that the 20 cases represent two reciprocal sets of 10, which would be equivalent if there were no reason to expect the birds from one original aviary to outrank

Table II. Twenty possible hierarchies of six individuals (three from each of two original groups, A, B, C and a, b, c, respectively) under the constraint that relationships of individuals from the same original group do not change

1. A,a,b,c,B,C
2. A,a,b,B,c,C
3. A,a,b,B,C,c
4. A,a,B,b,c,C
5. A,a,B,b,C,c
6. A,a,B,C,b,c
7. A,B,a,b,c,C
8. A,B,a,b,C,c
9. A,B,a,C,b,c
10. A,B,C,a,b,c

11–20. An analogous 10 hierarchies with A, B, C and a, b, c switched

those from the other. Therefore, in stage 2 of experiment I, in which we predict an effect of prior residence, there are 20 possible outcomes. If all were equally likely under the null hypothesis, the unique result that all birds in their home aviary would outrank those from the other would occur with probability of 0·05.

In fact, the 20 possible outcomes are probably not equally likely. If the birds with high rank in each group of three are more likely than the ones with low rank to have some intrinsic advantage, complete dominance of one group over the other would have a probability of less than 0·05, by an amount that would depend on how strongly intrinsic features correlated with dominance. Yasukawa & Bick (1983) found that one out of two groups of individuals in their original aviary showed complete dominance over a group from another aviary, a result that is suggestive but not conclusive as a demonstration of an effect of prior residence.

The issue of the independence of dyadic relationships is also important. Even when we focus attention on the nine dyadic encounters between the two groups of three birds from different original aviaries, the question arises as to whether these nine dyadic relationships are all settled independently. Imagine an extreme case in which the highest-ranking birds in each group settled their relationship without reference to prior residence and then the winner allowed its familiar subordinates to approach closer than the strangers. This behaviour might indirectly provide protection for these subordinates in their encounters with strange birds from the other original aviary, a coat-tail effect. In this case, we would expect that all three birds from one original aviary would always outrank all from the other.

By placing groups of birds from two original aviaries in a third, neutral aviary, one can determine whether the dominance relationships of birds from different aviaries are interdependent. In this case, for groups of six birds (two groups of three), there are only 10 possible outcomes for the relationships between birds from different aviaries, because there is no reason to expect that birds in either group should outrank those in the other in a neutral aviary.

These 10 outcomes differ in the degree to which birds from the same original group occupy adjacent ranks in the combined group. If the six birds from two original groups are labelled respectively A, B and C and a, b and c, then the hierarchy ABCabc has four adjacent pairs from the original groups (AB, BC, ab and bc). It is the only one of the 10 outcomes (not counting the reciprocal hierarchies obtained by exchanging A, B and C with a, b and c) that has such an interdependence score equal to 4. Two of the 10 possibilities have a score of 3, four have a score of 2, two have a score of 1, and one has a score of 0 (AaBbCc, see Table II). Thus, the population median of these scores under the null hypothesis of no interdependence would be 2.

Once again note that any influence of intrinsic attributes on dominance would make birds of similar rank in the original groups also tend to have similar ranks in the combined group and thus would tend to promote complete mixing of the two original groups. In other words, low interdependence scores would become more likely than high scores.

When Yasukawa & Bick (1983) combined groups of three birds from different aviaries in a third aviary, in four replicates they obtained hierarchies with interdependence scores of 4, 3, 3 and 2. Although these cases are too few for definite conclusions, there is a tendency for the distribution of observed scores to be skewed toward high scores in comparison with the expected distribution described above under the null hypothesis of independence of relationships. Contrary to their original conclusions, based on an assumption that all 6! possible arrangements of relationships in groups of six were equally likely, their results suggest that birds from different original groups might not settle their relationships completely independently. If so, these results would suggest a coat-tail effect, a possibility examined further in experiment II of the present study.

Since it is not yet proven that birds from different original groups settle their dominance relationships with strangers independently of each other, I have adopted the conservative assumption in experiment I that each combination of six birds represents only one independent trial. Thus in stage 2, if prior residence influences dominance relationships, significantly more trials should show that, for a majority of the dyadic relationships between birds from different original aviaries, the birds in their home aviary should dominate those in a strange aviary. Alternatively, one could consider only one dyadic relationship in each combined group, for instance that between the highest-ranking birds from the two original groups. Either hypothesis can be examined with a binomial test.

RESULTS

Experiment I

In stage 1, before any transfers between aviaries, all but one of the 14 groups had linear hierarchies. In the group with a non-transitive relationship, the rankings were assigned in the way that minimized the numbers of interactions below the diagonal in the interaction matrix. During observations in the last week of stage 1, reversals (interactions in which a bird supplanted a higher-ranked opponent) represented less than 2% of all interactions. Table III presents results for a typical pair of aviaries through all four stages of the experiment.

In one of these 14 groups, single birds dropped in rank during the course of the experiment. Otherwise, the relationships established in stage 1 persisted throughout the four stages of the experiment. The bird that changed rank was kept with the same group of three birds during all transfers between stages.

During stage 2, dominance relationships between the two sets of three birds from different original aviaries were less clearly defined than those observed toward the end of stage 1. Reversals constituted 0–15% of interactions. Non-transitive triads (triangles) occurred in more groups as well. As a result of the brief duration of stage 2, in some groups, some of the pairs of birds from different original aviaries did not interact during observation periods; overall 13 of 102 possible dyads did not interact during observations.

The results from stage 2 demonstrated a clear effect of prior residence (Table IV). In 11 of the 14 groups, the majority of the dyadic relationships between birds from different original aviaries showed this effect, in the sense that most of the birds 'at home' dominated those from 'away'. In two groups, the majority of dyadic relationships showed the opposite effect, and in the remaining aviary the numbers of observed dyadic relationships were equal (one-tailed binomial test, $P=0{\cdot}01$; the test was one-tailed because antecedent considerations predicted that deviation from random should occur in the direction of an effect of prior residence). In 7 of the 11 groups, all observed dyadic relationships conformed to an effect of prior residence. If one considers only highest-ranking birds from each original group, the individual that was in its home aviary dominated its counterpart from another aviary in 11 of the 14 combined groups (Table IV, one-tailed binomial test, $P=0{\cdot}03$).

In stage 3, in which all birds were returned to the same aviaries occupied during stage 1, with the same opponents, dominance relationships fit the same pattern observed in stage 1 (see Table III for examples). Just as in stage 2, the short duration of this stage resulted in some dyads not interacting during observations.

During stage 4, in which birds that had an advantage of prior residence in stage 2 now found themselves in a strange aviary, and vice versa, the effects of previous experience during stage 2 were opposed to any effects of prior residence. In this case, only five of the 14 groups showed a predominant effect of prior residence, in the sense that a majority of observed dyadic relationships fitted an effect of prior residence; in two of these cases, the relationships in stage 4 matched those in stage 2 (Table IV). In nine groups the majority of relationships failed to fit an effect of prior residence; instead, all (in seven cases) or most (in two cases) of the relationships matched those in stage 2. Overall, in 11 of the 14 groups the majority of relationships in stage 4 matched those in stage 2 (two-tailed binomial test, $P<0{\cdot}06$). Significantly fewer groups fitted an effect of prior residence in stage 4 than in stage 2 ($\chi^2=4{\cdot}81$, $df=1$, $P<0{\cdot}05$, contingency table test, corrected for continuity).

If we focus on the 11 groups that showed an effect of prior residence in stage 2 for a majority of the observed relationships, eight failed to show the same effect in stage 4 (a majority of relationships fitted those established in stage 2 instead; $\chi^2=9{\cdot}75$, $df=1$, $P<0{\cdot}01$, goodness-of-fit test, corrected for continuity).

Table III. A typical example of interaction matrices for birds in two aviaries during experiment I

Aviary A							Aviary B						
Stage 1 (birds in their original aviaries)													
	A	B	C	D	E	F		a	b	c	d	e	f
A	—	10	9	6	6	5	a	—	5	6	9	13	6
B	1	—	6	5	10	6	b		—	12	9	15	10
C			—	9	10	12	c			—	15	22	19
D				—	15	6	d				—	6	8
E					—	31	e					—	19
F						—	f					2	—
Stage 2 (high-ranking birds in one aviary, low-ranking birds in the other)													
	A	B	C	a	b	c		d	e	f	D	E	F
A	—	6	2	2		2	d	—	3	2	1	6	2
B		—	4	5	8	8	e		—	9	5		
C			—	7	3	2	f			—			
a				—	1	7	D	2	1	1	—	4	3
b					—	4	E	1	8	10		—	10
c						—	F		8	8	1		—
Stage 3 (all birds returned to their original aviaries)													
	A	B	C	D	E	F		a	b	c	d	e	f
A	—	5	3	2	1	4	a	—	1	1	3	2	
B		—	1	2	1	3	b		—	6	4		
C			—			4	c			—	9	3	
D				—	2	4	d				—	5	
E					—	3	e					—	2
F						—	f						—
Stage 4 (high-ranking and low-ranking birds separated but aviaries reversed in comparison to stage 2)													
	d	e	f	D	E	F		A	B	C	a	b	c
d	—	2	1		2	1	A	—	5	7	4	2	1
e		—	1	3			B		—	7	3	5	
f			—				C			—	7	4	5
D			1	—	1	4	a			1	—	3	3
E	1	1	1		—	4	b					—	8
F		6	3			—	c						—

Each matrix presents frequencies of interactions in which the individual in the left margin dominated the individual at the top. In stage 2, individuals are listed in accordance with the hypothesis that birds in their home aviary dominate those from a different aviary; in stage 4, they are listed in accordance with the hypothesis that dominance relationships are the same as in stage 2. Note that interactions occurred more often in some groups than in others; a few dyads interacted infrequently or not at all during observations. In stage 2, one group fitted predictions for an effect of prior residence (aviary A, eight of eight observed dyadic relationships between individuals from different original groups); the other did not (aviary B, three of nine dyadic relationships); in stage 4, all observed relationships matched those in stage 2.

Experiment II

There was a total of 35 dyadic relationships between birds from different original groups, 25 from the combination of two groups of five birds and 11 (of a possible 12) from the combination of groups of three and four birds. One pair of birds never interacted during observations.

In each neutral aviary, contrary to expectations, all birds from one original group dominated all those from the other. Not a single dyadic relationship departed from this pattern (two-tailed binomial test, $P<0{\cdot}01$).

DISCUSSION

The dominance relationships in stage 2 of experiment I showed a significant, but not invariable, effect of prior residence. The relationships in stage

Table IV. Dominance relationships obtained in seven replicates (14 groups of birds) of Experiment I during stages 2 and 4

	Stage 2			Stage 4		
Replicate (year)	Hierarchy*	Dyad score†	Result‡	Hierarchy	Dyad score	Result
1 (1978)	A, B, C, a, b, c	4:0	+	A, B, C, a, b, c	8:0	+
	d, e, D, c, E, F	5:2	+	d, e, D, f, E, F	7:0	+
2 (1979)	A, B, C, a, b, c	8:0	+	A, B, C, a, b, c	8:0	+
	D, d, E, F, *e*, f	3:6	−	*D*, d, E, F, *e*, f	8:0	+
3 (1979)	A, B, C, a, b, c	9:0	+	*a*, b, *c*, A, *B*, C	3:5	−
	d, e, f, D, E, F	6:0	+	d, e, f, D, E, F	8:0	+
4 (1979)	a, b, c, A, B	0:6	−	*a*, b, c, *A*, B	4:1	+
	d, e, f, D, E, F	9:0	+	d, e, f, D, E, F	8:0	+
5 (1979)	A, B, a, b, c=C	6:2	+	*a*, b, *c*, A, *B*, C	4:5	−
	D, d, e, E, F	4:1	+	d, e, E, D, F	3:0	+
6 (1980)	A, B, a, b, C	4:2	+	a, b=A, B, C	2:4	−
	c, D, E, F, d	3:3	0	c, D, E, d, F	5:1	+
7 (1980)	A, B, a, b	4:0	+	A, a, b	2:0	+
	c, d, e, C, D	6:0	+	c, d, e, C, D	6:0	+
Combined		71:22	11:2:1		76:16	11:3

*Each experiment involved two groups of birds, designated according to their ranks in stage 1 as A, B, C . . . and a, b, c . . ., respectively. The entries in the table list the birds according to their ranks in stages 2 and 4, during which half of the birds from each of the two original groups were combined. Italics indicate individuals involved in non-transitive relationships within groups.

†Number of dyads in agreement with the hypothesis:number of dyads contrary to the hypothesis. Overall, 13 dyads failed to interact during observations in stage 2.

‡Symbols indicate whether the dyad score supports the relevant hypothesis (+), is tied (0), or fails to support the hypothesis (−). The hypothesis in stage 2 is that birds in their home aviary dominate those from a different aviary; the hypothesis in stage 4 is that dominance relationships are the same as in stage 2.

4, on the other hand, showed a significant tendency to match relationships established previously with the same opponents in stage 2, despite asymmetries in prior residence. In analysing these results, I have adopted the conservative position that each group of birds, rather than each dyadic relationship, is a single independent trial. By replicating Yasukawa & Bick's (1983) experiments, so that each group of birds could be treated as a single independent trial, the present experiments thus established the statistical significance of this result. Experiment II, combined with the trends obtained by Yasukawa & Bick (1983), suggested that dominance relationships between birds from different groups were not in fact established independently of each other.

One important result in experiment I was the variation among groups. In a previous study of dominance interactions in many replicates of groups of dark-eyed juncos, it was also apparent that social organization varies among small groups (Wiley & Hartnett 1980). A lesson to be learned is that studies of dominance hierarchies, at least in small groups of captive birds, must be adequately replicated for general conclusions to be drawn.

The results of the present experiments suggest that three factors influence dominance relationships: prior residence, a coat-tail effect and experience in previous interactions. The following sections consider each of these factors in turn.

Prior Residence

In stage 2 of experiment I opponents were matched for dominance in their original groups, as well as for sex and in some cases for age. The only major systematic difference between opponents was their previous experience in the aviary occupied. In a significant majority of cases, this asymmetry influenced most of the dominance relationships in the combined groups.

The mechanism by which this effect occurs is not clear. Although it is evident that some aspect of 'familiarity' with the location of encounters or proximity to 'home' influences opponents' relationships, further experiments are necessary to establish both the features of an aviary or its surroundings that contribute to this effect and the time course over which these effects develop. It is noteworthy that this effect was clear despite the standardized arrangements of perches and food in the aviaries. My study examined effects of prior residence for periods of 3 or more weeks. These effects apparently also occur after periods of only 1 week (Cristol et al. 1990; Holberton et al. 1990).

The influence of this asymmetry on dominance relationships raises two questions about the interactions of birds in natural circumstances. Does this effect operate in the field, and, if so, does it represent the use of an uncorrelated asymmetry in the settlement of disputes? There is no direct evidence on these points for dark-eyed juncos during winter. In another emberizine, the white-throated sparrow, *Zonotrichia albicollis*, recent studies have demonstrated that birds dominate a higher proportion of opponents near the centres of their home ranges (Piper & Wiley 1989), an indication that prior residence or proximity to 'home' might influence dominance in the field for this species. In this case, dominance influences fat storage and annual survival (Piper & Wiley, in press) and exposure to predators, at least during competitive feeding (Schneider 1984; Piper, in press). There is no direct evidence on whether these consequences of dominance depend on an individual's location in its range. It is plausible, however, that a bird would realize more of an advantage from dominance in familiar locations. If so, pay-offs in contests between resident and intruder would differ, and this example would not represent use of an uncorrelated asymmetry in settlement of disputes.

Coat-tail Effect

In experiment 2, groups of individuals that had not met previously established dominance hierarchies on neutral ground in which all members of one group outranked those of the other. This interdependence in the relationships between birds from different original groups could result from a coat-tail effect. Since the relationships of birds within each original group remained stable, the highest-ranking individual in the combined group had to be the top-ranking bird from one of the two original groups. If this bird then allowed its familiar subordinates to approach closer than strangers when feeding, the former could have an advantage over the latter in the settlement of their dominance relationships. To borrow a political phrase, the top-ranking bird's subordinates could ride to high rank on his coat-tails. As a result birds from the same original aviary would form a coherent block in the combined hierarchy.

This result might depend on how long individuals had interacted before they were combined. In the present experiment, birds had been together in their original groups for 4 to 8 weeks. In Yasukawa & Bick's (1983) experiment, birds were together 1 week before transfer, a difference that might explain why their combinations of birds in neutral aviaries showed less evidence of a coat-tail effect.

If this effect operates in natural circumstances, it has important consequences for Rohwer & Ewald's (1981) suggestion that high- and low-ranking birds in dominance hierarchies might have mutualistic relationships. They proposed that high-ranking birds made use of food found by subordinates, while protecting the latter from attacks of other high-ranking birds. This argument would be particularly coherent if high-ranking birds protected their familiar subordinates by creating advantages for them in competition for food with strangers. The coat-tail effect thus provides a mechanism that could compensate low-ranking birds, at least in part, for the food lost to their familiar dominants. It could then pay for low-ranking birds to become close followers of a high-ranking bird.

Competing Influences on Dominance

In their second experiment, Yasukawa & Bick (1983) combined birds from different original groups to create a conflict between prior residence and any effect of prior dominance in the original groups. The high-ranking birds from one aviary were combined with low-ranking birds in the latter's original aviary. Birds high-ranking in their original aviaries would (1) tend to rank higher in intrinsic attributes influencing dominance and (2) also have the advantage of any influence of previous experience with dominance on subsequent interactions. This experiment thus determined whether prior residence outweighed such intrinsic attributes or previous experience. Their results indicated that it did not.

In the present experiment, birds combined in stage 4 differed in their prior residence in the aviary and also in their experience with the same opponents in stage 2. Thus, one group of three birds had previously dominated the other group of three, but now the combined group met in the latter's aviary. In this case, prior experience with the same opponents usually outweighed the effect of prior residence.

As in Yasukawa & Bick's experiment, there are two possible explanations for this result. In this case, either (1) the experience with dominance in stage 2 predisposed birds to achieving higher dominance in later stages in general (regardless of their particular opponents) or (2) the birds recognized their opponents from stage 2 and retained their relationships with them. The first possibility is somewhat weakened by the results in stage 3, when the experience of dominance in stage 2 had no influence on the relationships previously established in stage 1, even when low-ranking birds in stage 1 achieved dominance in stage 2. Thus, prior residence was outweighed by recognition of previous opponents or by previous experience with dominance. Zayan (1975, 1976) also found that recognition of opponents outweighed residence in determining dominance relationships in platyfish, *Xiphophorus helleri*.

Theoretical arguments predict that conventional settlement of disputes, for instance by recourse to prior residence, should only occur when asymmetries of competitive abilities or pay-offs in contests are not too great (Maynard Smith & Parker 1976; Hammerstein 1981). In agreement with this prediction, the present experiments, in combination with those of Yasukawa & Bick, suggest that prior residence in juncos is a last resort in settlement of disputes. Other influences on dominance, including possibly status signals, individual differences in competitiveness, previous experience with dominance and recognition of opponents, outweighed prior residence. On the other hand, both Cristol et al. (1990) and Holberton et al. (1990) have shown that prior residence can outweigh effects of age on dominance. The effects of age could depend either on age-related differences in competitive ability or on age-related status signals. When age-related status signals are controlled by plumage manipulations, any age-related differences in competitive ability appear to have little influence on dominance relationships, although age-related differences in success in interactions persist (Holberton et al. 1990). In the absence of plumage manipulations, older birds usually dominate first-year birds, at least among males (Cristol et al. 1990). It thus remains uncertain whether age might confer some competitive advantage aside from age-related status signals. Any such advantage would call into question an interpretation of the effects of prior residence as an example of conventional settlement of disputes under conditions of minimal asymmetries in competitiveness.

The possibilities of asymmetries in pay-offs have also not been excluded. As mentioned above, it is not known whether birds on familiar ground incur fewer risks or greater returns from contests. If such asymmetries actually applied to contests in natural populations of wintering juncos then the effects of prior residence on dominance in aviaries might reflect behavioural adaptations to these conditions in the field.

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