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The coat-tail effect in merged flocks of dark-eyed juncos: social status depends on familiarity

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Abstract. When two groups of social animals combine to form a larger group, new social relationships must be formed. Among dark-eyed juncos, *Junco hyemalis hyemalis*, it has been reported that most members of one flock attain higher ranks than those of another flock when two groups are combined. A possible mechanism for this effect involves differential treatment of familiar and unfamiliar individuals by the most highly ranked bird in the combined flock: a so-called 'coat-tail effect' (Wiley 1990, *Anim. Behav.*, **40,** 587–596). To demonstrate this effect, 34 small flocks of wild-caught juncos were established, and then combined to form 17 flocks in which each bird's social status was determined. In the combined flocks, members of the highest-ranking bird's original flock attained adjacent, and higher, ranks than members of the other flock. In a second experiment, small flocks from which either the highest- or lowest-ranking bird had been removed were combined. In combined flocks lacking the highest-ranked bird from each flock there was no tendency for birds from one group to rank higher than those of the other. In contrast, when low-ranked birds were removed, members of one flock again attained adjacent, and higher, ranks than members of the other, indicating that the presence of the highest-ranked bird was necessary for a coat-tail effect to occur. There is evidence that juncos behaved differentially towards familiar and unfamiliar birds, and that flock members could have assessed the relative ranks of the highest-ranked members of the small flocks, suggesting a probable behavioural mechanism for the coat-tail effect.

Many bird species form flocks with stable dominance hierarchies during the non-breeding season. Subordinate individuals may experience reduced access to food (Ekman & Askenmo 1984), increased levels of physiological stress (Fretwell 1969), and lower overwinter survival (Hogstad 1989). Why do individuals endure low social status, rather than join another flock where their status might be higher? One possible explanation for the continued association of low-ranking birds with very highly-ranked individuals is that when a flock of birds encounters an unfamiliar flock, the 'top-ranking bird's subordinates could ride to high rank on his coattails' (Wiley 1990, page 594). Such an effect could provide an important benefit to subordinates in groups with a highest-ranked bird of above-average resource-holding potential, and could offset the disadvantages of low social status in these groups.

The proposal that members of a familiar flock do not attain ranks independently when combined with an unfamiliar flock was based on a study of captive flocks of dark-eyed juncos, *Junco hyemalis hyemalis* (Wiley 1990). In that experiment, four small junco flocks were combined to form two larger flocks, with the result that all members of one original flock ranked higher than all members of the other in both of the combined flocks. Wiley (1990) also found suggestive evidence for a coat-tail effect by reanalysing an earlier experiment in which small flocks of juncos had been combined (Yasukawa & Bick 1983). My first goal in the present study was to examine a larger number of flocks for evidence of inter-dependence in the determination of status. My second objective was to distinguish between two possible mechanisms for such an effect: (1) a mechanism in which subordinates benefit directly from familiarity with

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the top-ranked bird during initial encounters with unfamiliar birds, hereafter the 'coat-tail' hypothesis (Wiley 1990), or (2) a mechanism in which behavioural or physiological changes differentially affect individuals housed with the bird of greatest competitive ability, hereafter the 'training' hypothesis, in reference to the competitive advantage an athlete might gain from training with a champion. If the coat-tail hypothesis is correct, then the highest-ranked bird in the small flock must be present in the combined flock in order for other flock members to realize higher rank. If a training mechanism is operating, then the differences between members of the small flocks should persist even when the highest-ranked bird is not present.

METHODS

Experiment 1

Capture and housing of subjects

Dark-eyed juncos were captured using mist nets at eight locations near Bloomington, Indiana, from 26 October 1990 to 10 February 1991. Birds were fitted with an aluminium U.S. Fish and Wildlife Service ring and three plastic rings of a single colour (black, red, orange, white, green, lavender, yellow, or striped blue, A. C. Hughes, London). I classified birds as yearling or older based on skull ossification, eye colour, and rectrix shape (Pyle et al. 1987). Sex was determined by wing length and plumage colour (Ketterson & Nolan 1976). I established a small flock by selecting four birds of the same age and sex and placing them into a small cage (1 × 2 × 2 m). A second four-bird flock was assembled at the same time, using birds from other capture sites that were matched for age and sex with those in the first flock. Twenty-four of these matched pairs of four-bird flocks (hereafter 'sub-flocks') were housed in visual isolation from one another for 14–55 days ($\bar{X}$=19 days). Birds were provided with millet, corn, turkey mash, sunflower seeds, vitamins and water ad libitum. Birds were housed and tested in outdoor cages subject to natural photoperiod and temperature.

Type and number of flocks

I formed 12 combined flocks (hereafter 'intact flocks') by placing all members of a matched pair of sub-flocks into a larger test cage (6·8 × 2·3 × 2·0 m). These flocks were established at 1500 hours EST, thereby giving birds several hours of daylight in which to locate the food source and become familiar with one another before I began observations at 1000 hours the following day. Behavioural observations continued for an average of 5 days (range 3–7 days) until dominance hierarchies could be determined (see below). Each morning, 100 g of mixed seed was placed in a small depression (hereafter 'bowl') at the centre of a circular wooden tray (50 cm diameter, hereafter 'food disc') located at the centre of the test cage. The food disc was at the centre of two concentric circles, with radii of 0·6 and 1·2 m, respectively, that were marked with flagging tape on the floor of the cage (Fig. 1).

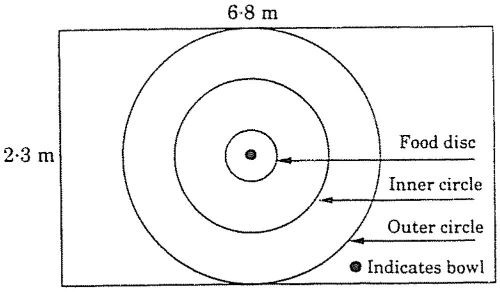

Figure 1. Schematic diagram of the test cage used in experiment 1 showing the bowl, food disc, and inner and outer circles. In experiment 2 food was scattered throughout the cage.

I also established six control flocks in experiment 1. In the intact flocks, described above, each bird was familiar with three of its seven flockmates because they had been housed together for several weeks, and may have come from the same capture location. Familiarity with flockmates was the variable of interest, so as a control I assembled flocks of eight juncos which had not been housed together and were from eight different capture locations. Each of the control juncos had been housed in a four-bird sub-flock under conditions identical to those of sub-flocks combined for intact flocks. By using only one bird from each of eight sub-flocks I established control flocks in which there were no familiar flockmates. For the purpose of comparison with intact flocks I randomly assigned each member of a control flock to one of two nominal sub-flocks. Husbandry, data gathering and analyses proceeded as with intact flocks (see below).

Table I. Numbers of eight-bird junco flocks of each age–sex class used for each treatment in experiments 1 and 2

	Female		Male	
	Yearling	Adult	Yearling	Adult
Experiment 1				
Intact flocks	4	1	5	2
Control flocks	1	0	3	2
Experiment 2				
Intact flocks	1	0	1	3
No high-ranked bird	3	0	2	3
No low-ranked bird	1	0	6	1

Experiment 1 was carried out from 3 December 1990 to 5 March 1991, and experiment 2 from 8 December 1992 to 28 February 1993. In experiment 2 all 'yearling' female sub-flocks consisted of three yearlings and one adult.

Dates of testing and details of age–sex classes used for each treatment are shown in Table I. All birds in experiments 1 and 2 (below) were released at the sites of capture following testing, and no bird was used more than once.

Behavioural data

Behavioural data were gathered both to assess the dominance hierarchies in each flock, and to determine the spatial and temporal proximity of familiar and unfamiliar flockmates during feeding. Two people in a blind adjacent to the test cage observed the flocks for 2–4 h each morning. Three types of data were gathered. (1) One observer recorded aggressive interactions between flock members. An individual that displaced a flockmate was classified as the winner of that encounter. After all flock members had interacted at least five times, win–loss data were used to construct dominance hierarchies (Brown 1975) for each flock. A bird was classified as higher ranking than an opponent if it won significantly more interactions than expected by chance, based on a binomial distribution ($P<0{\cdot}05$). (2) The same observer recorded the time, and order, of all arrivals to and departures from the food disc. (3) The second observer recorded the identities of every bird within the outer circle every 30 s. Birds were classified as being (1) in the bowl, (2) elsewhere on the food disc, (3) within the inner circle but not on the food disc, or (4) between the inner and outer circles.

Experiment 2

Capture and housing of subjects

Juncos were captured from 7 November 1992 to 12 February 1993 at seven of the locations used to capture birds for experiment 1. Pairs of sub-flocks were housed in small cages for 13–26 days ($\bar{X}=17$ days). All cages and other details of husbandry were identical to those in experiment 1, with the exception that some sub-flocks initially contained five juncos, as described below.

Type and number of flocks

There were two types of experimental flocks in experiment 2: 'removal' and intact. In removal flocks a single individual, either the highest-ranked bird or lowest-ranked bird, was removed from each of two five-bird sub-flocks immediately before an eight-bird test flock was established. In half ($N=8$) of the removal flocks the highest-ranked bird (HRB) was removed from each sub-flock before they were combined (hereafter 'No-HRB' flocks). In the other ($N=8$) removal flocks the lowest-ranked bird (LRB) was removed from each sub-flock before they were combined (hereafter 'No-LRB' flocks). Intact flocks ($N=5$) were replicates of the intact flocks in experiment 1, and were included to increase the sample size and to confirm that the coat-tail effect was robust to the protocol changes of experiment 2.

Experiment 2 differed somewhat from experiment 1, in that sub-flocks were observed separately, before being combined, in order to predetermine dominance relationships. This took place on 'day 1' for 2–3 h beginning at 0930 or 1230 hours. After day 1 observations, sub-flocks were returned to their isolated smaller cages. On the following morning at 0930 hours ('day 2') the sub-flocks were combined to form a flock in a cage different from the one used on day 1. In No-HRB flocks, the highest-ranked birds were combined separately as a dyad in a test cage at 1200 hours on day 2 to determine which of them was higher ranked.

Behavioural data

Dominance hierarchies were determined as in experiment 1, except that, because observations were begun as soon as sub-flocks were formed, rather than on the following morning, the first encounters within many dyads could be observed. When juncos first encountered one another they sometimes exhibited a prolonged agonistic display that has been called 'head-dance' display (Figure 2 in Balph et al. 1979), in which opponents face each other, with bills pointed straight up, for 10 s to several minutes. As no winner could be assigned during head-dance displays, the duration and dyads involved in all occurrences were recorded.

In an attempt to mimic more closely a natural foraging situation, food was sprinkled haphazardly on the earthen floor of the test cage, rather than being concentrated in the bowl as in experiment 1. Thus, data on feeding sequences and proximity to the food disc could not be gathered in experiment 2 because there was no point source of food.

Statistical Analysis

Inter-dependence score is a measure of how often birds from each original sub-flock attain ranks adjacent to other members of their sub-flock in the combined flocks. Inter-dependence scores were determined for each dominance hierarchy following Wiley (1990), with one point being assigned to each flock in each case where a pair of birds from the same original sub-flock obtained adjacent ranks in the combined flock. Inter-dependence scores range from zero to six for flocks of eight birds, and a flock in which all members of one sub-flock rank higher than all members of the other would have a score of six. The presence of non-transitive relationships in some of the dominance hierarchies potentially complicates the interpretation of inter-dependence scores because two different hierarchical arrangements can be constructed in cases where the birds involved in the non-transitive relationship are separated by only one position in the hierarchy. In such cases ($N=4$ flocks) the mean of the two possible inter-dependence scores was assigned. Given the constraint that, in this species, ranks within sub-flocks remain stable after combining flocks, there are only 35 different possible hierarchies for combined eight-bird flocks (see Wiley 1990). If no assumption is made about the order in which hierarchy positions were determined, then each possible hierarchy would be equally likely. The inter-dependence scores of the combined flocks were compared with the scores for all possible hierarchies using a Mann–Whitney U-test.

While inter-dependence scores indicate the degree to which members of sub-flocks obtain adjacent ranks in the combined flocks, it is also important to determine whether members of the sub-flock containing the overall top-ranked bird in the combined flock (hereafter the 'OTB') obtained higher ranks than members of the other sub-flock. To do this I calculated a 'difference-in-rank' score for each flock by subtracting the mean rank of the members of the OTB's sub-flock (excluding the OTB) from the mean rank of members of the other sub-flock (excluding the top-ranked member of that sub-flock). Difference-in-rank scores in eight-bird flocks can assume values between $-3{\cdot}0$ and $4{\cdot}0$, with a higher score indicating a greater status advantage for members of the OTB's sub-flock. As with inter-dependence scores, the difference-in-rank scores were compared with the scores of all 35 possible hierarchies using a Mann–Whitney U-test.

To calculate the inter-dependence and difference-in-rank scores for control flocks, birds were randomly assigned to either the OTB's sub-flock, or the other sub-flock, prior to testing, and then calculations were carried out in the same manner as for experimental flocks. An α-level of 0·05 was used for all statistical comparisons, except when multiple tests were done, in which case a sequential Bonferroni adjustment was applied (Rice 1989). Means and standard errors are shown in the figures for visual comparison.

RESULTS

Inter-dependence Scores

The inter-dependence scores of the intact flocks in experiment 1 were significantly higher than the scores of the hierarchies expected under the null hypothesis (Mann–Whitney $U=101$, $U'=319$, $N_1=35$, $N_2=12$, $P<0{\cdot}01$; significant at Bonferroni adjusted $\alpha=0{\cdot}025$; Fig. 2a). The inter-dependence scores of the five intact flocks in experiment 2 were also significantly higher than those of the expected hierarchies (Mann–Whitney $U=20$, $U'=155$, $N_1=35$, $N_2=5$, $P<0{\cdot}01$). The inter-dependence scores of the control flocks in experiment 1 were significantly lower than the scores of intact flocks of experiment 1 (Mann–Whitney $U=8$, $U'=64$, $N_1=12$, $N_2=6$, $P<0{\cdot}01$; significant at Bonferroni adjusted $\alpha=0{\cdot}017$).

The inter-dependence scores of the No-HRB flocks in experiment 2 were significantly lower

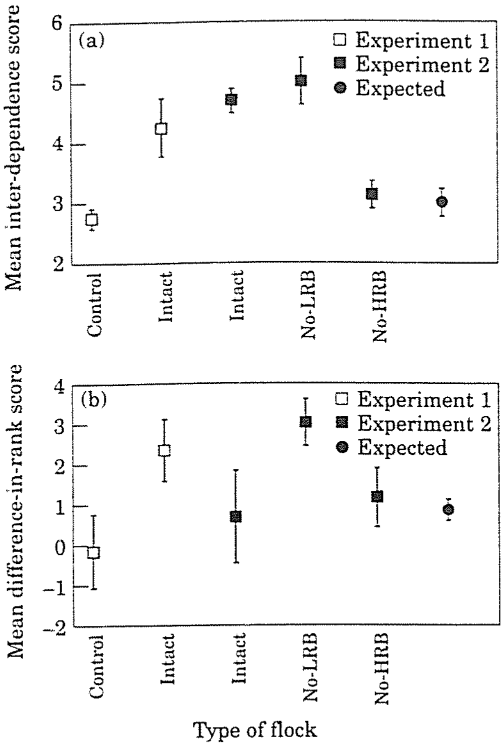

Figure 2. (a) Inter-dependence scores ($\bar{X}\pm$ SE) indicating the tendency for juncos to establish adjacent ranks in combined flocks in experiments 1 and 2. (b) Difference-in-rank scores ($\bar{X}\pm$ SE) indicating the tendency for juncos from the highest-ranking bird's subgroup to attain higher ranks in the combined flock than members of the other subgroup in experiments 1 and 2. Control flocks were those in which no birds were familiar with any flockmates (N=6). Intact flocks were those in which all sub-flockmates were familiar with one another and all birds were present in the combined flock (N_1=12, N_2=5). No-LRB flocks were those in which the subordinate junco had been removed from each sub-flock (N=8). No-HRB flocks were those in which the highest-ranking bird had been removed from each sub-flock (N=8). The expected values were calculated from all possible hierarchies under the null hypothesis of independent determination of ranks for members of each sub-flock. See text for statistical analysis.

than those of intact flocks in experiment 2 (Mann–Whitney U=1, U'=39, N_1=8, N_2=5, $P<0\cdot01$; significant at Bonferroni adjusted $\alpha=0\cdot025$; Fig. 2a). The inter-dependence scores for the No-LRB flocks were significantly higher than those of No-HRB flocks (Mann–Whitney U=4, U'=60, N_1=8, N_2=8, $P<0\cdot01$; significant at Bonferroni adjusted $\alpha=0\cdot017$).

Difference-in-rank Scores

Analysing these same flocks on the basis of the difference in average ranks between the three lower-ranking birds from each original sub-flock indicates that experiment 1 intact flocks had significantly higher difference scores than the hierarchies expected under the null hypothesis (Mann–Whitney U=118, U'=302, N_1=35, N_2=8, $P<0\cdot05$; Fig. 2b). Thus within intact flocks, members of the sub-flock containing the OTB attained higher ranks than members of the other sub-flock. The difference-in-rank scores of the control flocks in experiment 1 tended to be lower than the scores of intact flocks of experiment 1, but this difference was not significant (Mann–Whitney U=16, U'=56, N_1=12, N_2=6, $P=0\cdot06$). In the five intact flocks of experiment 2 difference-in-rank scores did not differ from those of the expected hierarchies (Mann–Whitney U=85, U'=90, N_1=35, N_2=5, $P>0\cdot9$).

In flocks from which the lowest-ranked birds had been removed difference-in-rank scores were significantly higher than those of the expected hierarchies (Mann–Whitney U=42, U'=238, N_1=35, N_2=8, $P<0\cdot01$). In flocks from which the highest-ranked birds had been removed the difference-in-rank scores did not differ significantly from those of hierarchies expected under the null hypothesis (Mann–Whitney U=118, U'=162, N_1=35, N_2=8, $P>0\cdot5$).

Dominance Hierarchies

Within each eight-bird flock there were 28 possible dyads. In experiment 1 I was able to determine dominance status in 98% (493/504) of potential dyads. The mean number of interactions observed for each dyad was 17. Dominance hierarchies were essentially linear, but 4% (19) of the dyads in which ranks could be determined did not fit into linear hierarchies.

In experiment 2 I was able to assign status to the birds in 90% (341/380) of the dyads possible in the 42 sub-flocks on day 1. An average of 4·3 interactions was recorded for each dyad. Less than 2% (5) of the dyads had non-transitive relationships. On day 2, I determined the status in 96% (563/588) of the dyads possible in the 21 combined flocks. The mean number of interactions between members of each dyad was 5·5. Less than 1% (5) of dyads had non-transitive relationships.

Occupation of Food Disc in Experiment 1

When one bird left the food disc, the next bird to feed could have been either a member of its own sub-flock ($P=3/7$), or a member of the other sub-flock ($P=4/7$). In intact flocks, transitions between members of the same sub-flock occurred more frequently than expected by chance (1713/3735 transitions, $G=6.682$, $df=1$, $P=0.02$). In control flocks, where birds were randomly assigned to each nominal sub-flock, the occurrence of within-sub-flock transitions was not greater than expected by chance (663/1494 transitions, $G=0.72$, $df=1$, $P=0.2$). These data included only transitions in which less than 30 s passed between one bird leaving the food disc and the next one arriving, but if longer intervals are included the conclusions do not change.

Feeding Near Highest-ranked Bird in Experiment 1

I examined the data on the locations of every bird within the outer circle for all instances in which the OTB occupied the food bowl while another bird fed near it on the food disc. Juncos do not normally feed within a few centimetres of one another without one bird quickly displacing the other. During over 30 h of observations I observed only 58 instances of this while the OTB occupied the food bowl. The bird feeding close to the OTB was a member of its original sub-flock in 85% (41/48) of the cases. Since there were only three birds (43%) familiar with the OTB in any flock, as opposed to four unfamiliar birds (57%), the occurrence of familiar birds on the food disc while OTBs were on the bowl was significantly more frequent than expected by chance ($G=9.13$, $df=1$, $P<0.001$). In control flocks there was no tendency for birds feeding close to the OTB to be familiar, as only 22% (4/18) of cases involved birds from the same sub-flock ($G=0.625$, $df=1$, $P>0.2$).

Head-dance Displays in Experiment 2

The head-dance display occurred exclusively during the first 2 h of observations. I observed 38 dyads engaging in the head-dance display, and in 87% (33) of these cases dyads participating in the display consisted of birds from different sub-flocks encountering each other for the first time. Considering only those flocks in which the highest-ranked birds of the original subgroups were still present (i.e. intact and No-LRB flocks), one or the other of the highest-ranked birds was a member of 42% (13/31) of the dyads involved in head-dance displays. This differs little from the proportion expected by chance, given that 46% (13) of the possible dyads in each flock include one of the original highest-ranked birds ($G=0.047$, $df=1$, $P>0.8$). In 26% (8) of these cases the dyad consisted of the highest-ranked bird from both of the sub-flocks. Since only 4% (1/28) of the possible dyads in each flock contained both of the original highest-ranked birds, this is a significantly greater proportion than expected by chance (Fisher's exact $P=0.027$). Head-dance displays were observed in all three types of flocks, but three of the four flocks in which they were absent were No-HRB flocks. The head-dance display was never observed in the eight cases where a pair of unfamiliar highest-ranked birds was tested in the absence of flockmates (after having been removed from No-HRB flocks). These tests were carried out on day 2 in the same test cages used for flocks, but birds were observed for only 10–20 min, so a direct comparison cannot be made with the results from flocks.

DISCUSSION

In the intact flocks of both experiments 1 and 2 members of each original sub-flock obtained ranks adjacent to familiar birds in the combined flocks. In experiment 1 members of the sub-flock familiar with the bird ranked highest in the combined flock benefited by obtaining higher ranks in the new flock. This did not occur in experiment 2, but the discrepancy between experiments 1 and 2 might be explained by the greater number of intact flocks tested in experiment 1 ($N=12$, as opposed to $N=5$). These results suggest that, at least in captivity, when two sub-flocks of juncos merge, ranks are not determined independently of other members of the same sub-flock. In addition, the results of intact flocks in experiment 1 suggest that when flocks merge, lower-ranking members can benefit from familiarity with higher-ranked members of their original sub-flock.

Wiley (1990) suggested that familiarity with the highest-ranked bird in the combined flock somehow increases dominance status when facing unfamiliar opponents. The coat-tail hypothesis would involve differential behaviour on the part of the highest-ranked bird towards familiar and unfamiliar flockmates. Another possible mechanism is the training hypothesis in which previous exposure to the highest-ranked bird, rather than its presence in the combined flock, enables members of the highest-ranked bird's sub-flock to outrank unfamiliar birds independently. While it has been shown in other species that exposure to a highly ranked individual can lead to lowered social status (Drummond & Osorno 1992; and see citations in Beacham & Newman 1987), it seems plausible that, under certain circumstances, a physiological change resulting from exposure to a highly ranked bird might lead to higher dominance status (e.g. hunger or decreased fat reserves, Cristol 1992). These two hypotheses are fundamentally different because the latter does not suggest flock organization, individual recognition, or emergent properties of familiar groups.

The No-HRB flocks allowed for a test of the training hypothesis, as they indicated whether the highest-ranked bird must be present for a coat-tail effect to occur. In the No-HRB flocks, unlike the intact flocks of experiment 1, there was no evidence of inter-dependence in ranks of birds from the same original sub-flock, or of higher ranks for birds from the highest-ranked bird's original sub-flock. This indicates that the highest-ranked bird's presence was required when sub-flocks were combined in order for members of its sub-flock to have a social-status advantage. Thus it falsifies the critical prediction generated by the training hypothesis, since, under that hypothesis, physiological or behavioural advantages should have been apparent whether the highest-ranked bird was present or not.

The No-LRB flocks served as a control for the removal of birds in the No-HRB flocks. No-LRB flocks exhibited inter-dependence scores significantly higher than No-HRB flocks, and difference-in-rank scores significantly higher than expected under the null hypothesis. Thus, the removal of lowest-ranked birds appeared to have no effect on the attainment of adjacent ranks by birds from the same original sub-flocks, or higher ranks by members of the OTB's sub-flock. This indicates that in the No-HRB flocks the lower inter-dependence scores, and the lack of an advantage of familiarity with the OTB, were due to the absence of one or both highest-ranked birds, rather than simply the disruption of the sub-flocks caused by the removal of one of its members. It appears that the social status advantage of being a member of the OTB's sub-flock was facilitated by the presence of one or both highest-ranked birds. It remains to be explained why the second-ranked individuals did not function as new highest-ranked birds in the No-HRB flocks.

What is the Mechanism of the Coat-tail Effect?

One suggested mechanism for the coat-tail effect is that the highest-ranked birds allow closer approaches by familiar birds while feeding (Wiley 1990), which could then translate into increased social status for familiar birds through the development of site-dependent dominance around the food source. Three of the behavioural observations from this study indicate that some of the necessary conditions for such a mechanism were present. (1) In the intact flocks I found that when a bird left the food disc there was a greater-than-expected chance that the next bird to occupy the disc would be a member of the same original sub-flock. This could indicate that sub-flock members were able to identify each other as such. There are alternative explanations for this pattern, however, such as that only a few birds in each flock tended to follow one another while feeding. (2) In cases when a bird was present on the food disc while the OTB occupied the bowl only a few centimetres away, the bird on the disc was significantly more likely to be from the OTB's original sub-flock. This suggests that, at least while feeding at a point source, OTBs tolerated closer approaches by familiar individuals, enhancing the possibility of increased site-dependent dominance by familiar flockmates. (3) Finally, the dyads that engaged in head-dance displays included the highest-ranked members of both sub-flocks more often than expected. These prolonged displays could have provided information to members of each sub-flock about the relative status of each highest-ranked bird. Given these conditions, the coat-tail hypothesis is plausible. The occurrence of the coat-tail effect in experiment 2, where food was available throughout the cage, however, means that a mechanism involving site-dependent dominance is unlikely.

Although other mechanisms are conceivable, such as formation of alliances among mid-ranked members of sub-flocks, or differences between sub-flocks in housing or capture sites, the finding that a hierarchy undisturbed at the top is required for the coat-tail effect to occur narrows considerably the range of possible mechanisms. Explanations based on pre-test differences in physiological condition or other factors are ruled out by the disappearance of the phenomenon when highest-ranked birds were removed before sub-flocks were combined. The coat-tail hypothesis is consistent with the available data. Further detailed observations, including videotaping of initial encounters, will be necessary to describe unequivocally the precise behavioural mechanism for this surprising phenomenon.

Ecological Significance of the Coat-tail Effect

Gaining a better understanding of the social dynamics that occur when groups of unfamiliar animals interact will facilitate more realistic modelling of dispersal, migration and territoriality among gregarious species. For example, the occurrence of a coat-tail effect among free-living dark-eyed juncos could have important implications for our understanding of their migratory behaviour. In autumn, female juncos generally migrate further than males (Ketterson & Nolan 1976, 1983). Several hypotheses have been advanced to explain the winter population segregation that results from differential migration in juncos and other species, including the dominance hypothesis, which states that low-ranking birds migrate further to avoid competition from more highly ranked birds (Gauthreaux 1978). If the coat-tail effect occurs among free-living birds, then a migrating low-ranking bird would have the option of increasing its status either by gaining familiarity with a high-ranking bird, or by migrating to an area populated by individuals of lower rank. Such behavioural variability would add complexity to any attempt to predict the outcome of dominance-driven migration patterns.

The coat-tail effect may be ecologically relevant for any species in which low-ranking individuals have the option to choose social groups, and inter-group conflicts over resources occur. The importance of the coat-tail effect would depend on the frequency of inter-group interactions, being especially likely where stable groups compete for patchily distributed resources with unfamilar groups. Wintering juncos would seem to be likely candidates to experience coat-tail effects in the field as they are migratory, have relatively large home ranges, live in dominance-structured flocks (Sabine 1949), and concentrate on exposed patches of food (personal observation). Unfortunately, I am aware of no study describing the degree to which discrete flocks of juncos mix. Besides migratory birds that are gregarious in winter, other species likely to experience coat-tail effects might include: songbirds in the genus *Parus*, in which stable flocks defend large group territories in winter; waders and waterfowl that feed in small flocks and then compete with other groups for limited space at communal roosts; communally breeding birds that defend large territories against unfamiliar neighbouring groups; and other mobile, gregarious animals, such as some social mammals. Even if groups rarely come into contact under normal circumstances, the coat-tail effect could still be important during rare times of environmental stress, such as severe snowstorms, when resources are extremely limited and unfamiliar groups are most likely to interact.

For the coat-tail effect to be important in shaping behaviour, any social-status advantage gained by joining a flock with a highest-ranked bird of above-average resource-holding potential must outweigh the costs of joining and living in this flock, which might include below-average priority of access to food and other resources. It will not be possible to calculate these costs and benefits until we have a better understanding of three additional facets of life in a flock. First, what is the cost to an individual of joining a flock, or gaining familiarity with a dominant bird? Since joining flocks may be costly in terms of energy, stress, or time, the advantage of joining would have to offset these costs. Second, is it more costly to live as a subordinate under some dominant birds than under others? Perhaps it is no more or less costly to be a subordinate in the flock of a highest-ranked bird with 'big coat-tails' than in the flock of a less competitive highest-ranked bird. Finally, do the costs of subordination vary linearly with status? It could be that being the second-ranked bird in a flock of eight is functionally equivalent to being eighth-ranked. If these questions can be answered with careful studies of captive flocks, and the coat-tail effect can be verified in free-living groups, we should gain a better understanding of why and how subordinates join groups of dominant individuals.

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