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Food deprivation influences dominance status in dark-eyed juncos, *Junco hyemalis*

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Abstract. Among gregarious birds, an individual's dominance status may influence its access to limited food resources and, consequently, its fat reserves during the non-breeding season. This study investigated whether food deprivation affected an individual's dominance status during encounters with conspecifics. In 45 dyads of dark-eyed juncos, one member was deprived of food for 4 h to reduce its stored fat level, thereby increasing its motivation to feed. Deprived juncos were dominant to their opponents significantly more often than were birds that had fed normally prior to the tests. When there was a measurable difference in fat reserves before food deprivation (16 dyads), the leaner individual was always dominant. Most dominance relationships remained unchanged for at least 24 h after food deprivation, but many dyads eventually reversed ranks when birds were introduced into a flock situation after 48 h. Dominance ranks in juncos may be established on the basis of an asymmetry in the value of a contested resource. Motivational asymmetries may be important determinants of dominance in the absence of large asymmetries in resource holding potential, and could have important ecological implications.

Dominance hierarchies are important components of the social organization of many animals. Among birds that associate in flocks during the non-breeding season, an individual's dominance status may influence its access to food (e.g. Ekman & Askenmo 1984), probability of survival (e.g. Hogstad 1989) and dispersal distance (e.g. Gauthreaux 1978; but see Rogers et al. 1989). Because of the potential significance of dominance in the behavioural ecology of many avian species, the factors that make one individual dominant to another have been the focus of a great deal of research. Studies of several bird species have established that aspects of an individual's fighting ability, or resource holding potential (Parker 1974), can contribute to its dominance status, including age (Rohwer et al. 1981), sex (Balph 1977), body size (Ketterson 1979), plumage coloration (Holberton et al. 1989), hormone levels (Searcy & Wingfield 1980), genetic heterozygosity (Baker & Fox 1978), heritable aggressiveness (Moss et al. 1982) and previous fighting experience (Popp 1988).

Asymmetries in resource holding potential have been the subject of many studies of social dominance (e.g. Richner 1989), but only a few have focused on asymmetries between contestants in the value of the contested resource (e.g. Ewald 1985; Hansen 1986). Deprivation is an easy way to increase the value of a resource experimentally. Food deprivation can increase rates of approach to opponents at feeders (Wiley & Harnett 1979) and displacement of opponents of previously superior rank (Popp 1987). Data on several mammals also indicate that food-deprived individuals tend to be more aggressive (e.g. Lore et al. 1986) and tend to win more aggressive interactions (e.g. Bruce 1941) than individuals that have fed normally. Nearly all of these studies have tested the effects of food deprivation on individuals with pre-existing dominance relationships. This confounding factor, and the presence of asymmetries in size, age, sex and other components of resource holding potential, may have diminished the effect of deprivation in many such studies. Here, I report a test of the hypothesis that dominance status in dark-eyed juncos can be determined on the basis of an asymmetry in the value of a food resource. Juncos with no previous contact were matched for important components of fighting ability, and then one of the contestants was deprived of food before testing. In this way the most important asymmetry between contestants was the value of the food resource to each individual.

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METHODS

Study Area, Capture and Housing

I captured dark-eyed juncos from 27 October 1989 to 5 January 1990 at four locations near Bloomington, Indiana, using mist nets baited with cracked corn. Both migrating and overwintering individuals were included in the study (Ketterson & Nolan 1976, 1982). I classified subjects as either young (less than 1 year old) or adult (older than 1 year) by skull pneumatization (Ketterson & Nolan 1982), iris colour (Yunick 1977) and outer rectrix shape (Pyle et al. 1987). Sex was determined by head and body plumage and wing length (Ketterson & Nolan 1976).

Upon capture all birds were fitted with coloured rings for individual identification. Subjects were housed with previously captured juncos for 10–30 days in one of six large holding enclosures measuring 3 × 3 × 3 m. Birds were housed outdoors and were subject to natural temperature and light regimes. Subjects were fed a mixture of cracked corn, sunflower hearts, millet and turkey starter mash ad libitum.

Dyad Establishment

On the night prior to the first behavioural observations, I removed two matched juncos from different holding enclosures and placed them in separate small flight cages measuring 0·9 × 0·8 × 0·4 m. Members of each dyad were matched for mass at capture (within 1·5 g), fat at capture (within one fat score, see below), wing length (flattened, within 1 mm), age class (young or adult), sex and capture date (within 10 days). I then randomly assigned one member of each dyad to the experimental or control treatment. Birds in the experimental treatment (hereafter 'deprived') were given no food until the observation period at 1200–1300 hours on the following day. Control subjects were provided with mixed seed ad libitum in their flight cages. Thus, on the first day of behavioural observations, one member of each pair had not eaten for 4–4·5 h following normal night fasting, while the other member had experienced no such deprivation.

I always established groups of three dyads concurrently. A total of 15 such groups were established ($N=45$ dyads), and each junco ($N=90$) was used only once. Members of each dyad had never seen each other before testing, with the possible exception of a few dyads (less than 10%) in which both members were captured at the same field site, and thus could have had previous contact in the wild.

Establishing Dominance Ranks: Stage I

To determine relative dominance ranks, I removed subjects from their flight cages and introduced them simultaneously into a test cage. Each test cage had identical dimensions and contained a suspended perch (0·4 m long) and single dishes of food and water placed centrally on the cage floor. From a blind, an observer simultaneously watched three dyads in adjacent test cages. An observation period was terminated after 3 h, or as soon as the subjects in each of the three test cages had interacted at least five times. After the first hour of observation, the perch was removed to increase activity by forcing both birds to perch nearer to each other on the floor.

A subject was classified as dominant if it displaced its partner more than expected by chance (an arbitrary rule based on the binomial distribution, see Holberton et al. 1989). If neither bird displaced the other more than expected by chance, neither was classified as dominant.

Following the first observation period, each of the three dyads was housed in a separate large enclosure measuring 7 × 4 × 3 m, and provided with two feeders, a water bath and several evergreen-tree roosts. In this way, the two members of each dyad were housed together continuously after their first exposure to one another, but not under conditions in which aggressive encounters were frequent. Subjects that died ($N=3$) during any stage of the experiment were replaced immediately to standardize conditions, but data from affected dyads were not included in the analysis.

Retesting Dominance Ranks

Stage II: dyad tests after 24 h

Between 1200 and 1300 hours on the day following the first behavioural observations, I began retesting the dominance relationships within each dyad as in stage I. In this stage, however, neither member of a dyad had been deprived of food since the initial treatment, and members were not encountering each other for the first time.

Stage III: flock tests after 48 h

After the subjects' ranks were retested (stage II), the members of the three dyads were combined simultaneously in a large enclosure to create a flock of six birds. Dominance relationships within each flock were observed for several hours daily for 3 days. None of the subjects had ever been in the large flock enclosure, but its dimensions were identical to the enclosures used for housing between stages I and II. Only 84 of the original subjects were placed into flocks for stage III ($N = 14$ flocks). Dyads were retested in stage III for the dominance relationships of stage II, but in the context of a flock. The members of each dyad had been in continuous contact since stage I, but had undergone no further food deprivation.

Fat Score and Mass

Subcutaneous fat levels and masses were recorded at the following times: 0800–1100 hours on the morning of capture, 1900–2100 hours on the night before the first behavioural observations, 1400–1600 hours immediately following the first and second behavioural observations (ends of stages I and II), and 1300–1500 hours on the third day after flock formation (end of stage III). Subjects were weighed using a 50-g Pesola spring balance. Fat level was scored using a modification of the method described by Helms & Drury (1960) on a continuous scale from 0–4 as follows: 0, no fat or traces of fat present at the bottom of the furcula; 1, layer of fat present but filling less than $\frac{1}{3}$ of the furcula; 2, fat filling $\frac{1}{3}-\frac{2}{3}$ of furcula; 3, fat filling $\frac{2}{3}-\frac{3}{3}$ of furcula; and 4, furcula filled with fat above level of pectoralis muscle. I assumed that these fat scores reflected overall fat reserves.

Changes in fat scores between measurements were significantly correlated with changes in masses for every time interval (unpublished data). This is consistent with the findings of more comprehensive studies on the relationship between mass and visible subcutaneous fat scores (Helms & Drury 1960). Therefore, I will report only fat scores, as variation in stored fat would seem to be a more direct measure of stored energy reserves than changes in overall body mass, and fat measurements are not sensitive to the presence of undigested food in the bird's crop. Fat scores were compared with the Mann–Whitney *U*-test, using the Bonferroni method to adjust significance levels to correct for the effect of multiple tests (Miller 1981).

RESULTS

Effects of Treatment on Dominance

Of the 44 dyads observed during stage I, deprived birds were dominant to controls in 24 dyads, while control birds were dominant in 11 dyads (Fig. 1). Deprived birds thus dominated their opponents in 67% of the dyads in which ranks could be determined (sign test: $z=2\cdot56$, $N=35$, $P<0\cdot05$). The remaining dyads could not be classified because neither bird met the strict criterion for rank classification ($N=7$ dyads), or the subjects failed to interact ($N=2$ dyads). In those dyads that could not be classified, there was no tendency for deprived birds to win more interactions than control birds, or vice versa. In four of these unclassified dyads, however, the deprived bird won the first three interactions before losing to the control bird, whereas in no case did the control subject win the first three interactions.

In stage II, 16 formerly deprived subjects and 14 control subjects dominated their opponents, as compared with 24 and 11, respectively, in stage I. This reduction in the number of dominant birds from the deprived treatment was not primarily the result of reversals of rank within the dyads, which occurred only once (see below). Rather, three dyads that were originally dominated by deprived birds were not retested in stage II, three failed to meet the criterion for rank classification during stage II, and two did not interact. The increase in the number of dominant control birds resulted from the single case of rank reversal combined with two cases in which subjects could not be classified during stage I.

Formerly deprived birds showed no tendency to dominate control birds in the flocks (stage III). Ranks could be determined during stage III for 35 of the dyads from stages I and II. Deprived birds dominated in 18 cases and control birds dominated in 17.

Stability of Dominance Ranks

In stage II, ranks could be classified in only 15 of the 24 dyads in which deprived birds had been dominant during stage I. Of the 15 dyads, 14 were again dominated by the deprived subjects and rank was reversed in one dyad. Ranks remained unchanged in stage II for all of the 11 dyads that were originally dominated by control birds.

Among the 14 dyads dominated by deprived birds in stage II, nine remained unchanged in stage

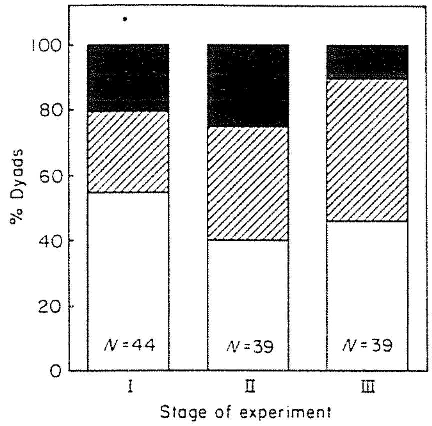

Figure 1. Percentage of dyads dominated by deprived subjects (□), dominated by control subjects (▨), or not dominated by either (■) immediately following food deprivation (stage I), after 24 h (stage II) and after being placed in a flock for three days (stage III). *Deprived birds were dominant significantly more than control birds only during stage I ($P<0.05$).

III, while five exhibited rank reversals. Of the 12 dyads dominated by control birds in stage II, seven remained unchanged in stage III, while five reversed ranks. Thus, 10 dyads (39%) reversed rank between stages II and III. This is a significantly higher rate of rank reversals than that between stages I and II, when only one dyad (4%) reversed ranks ($\chi^2=8.43$, $df=1$, $P<0.005$).

Effects of Fat Reserves on Dominance

Changes in fat levels

Fat scores of the treatment groups were similar at capture (Fig. 2a). The fat scores of deprived subjects were significantly lower than those of control subjects only after the food deprivation ($z=2.7$, $N=77$, $P<0.01$). There were no significant differences between the fat scores of the treatments during stages II or III (all $P>0.05$, Fig. 2a).

Both treatment groups tended to lose fat when placed in the small flight cages prior to stage I. Deprived birds lost more fat than control birds during this deprivation period ($z=2.4$, $N=77$, $P=0.015$; Fig. 2b), but the difference was not significant at the $\alpha=0.01$ level required by the Bonferonni correction. The change in fat scores of the treatment groups did not differ significantly between any other successive stages of the experiment (all $P>0.05$), despite the fact that deprived birds gained fat between stages I and II, while the fat scores of control birds decreased slightly (Fig. 2b).

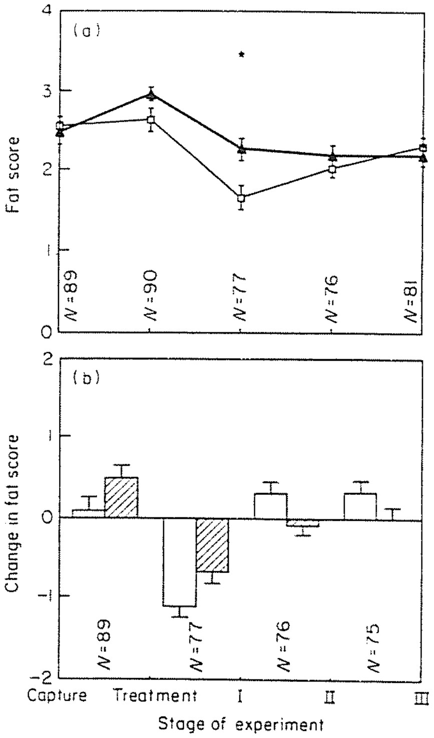

Figure 2. (a) Fat scores (mean ± SE) of deprived (□) and control subjects (▲) at capture, at the onset of the treatment and after stages I, II and III. (b) Changes in fat scores (mean ± SE) for deprived (□) and control subjects (▨) between each of the measurements shown in (a). The treatment caused a significant drop in fat reserves, but deprived birds quickly regained lost fat. See text for explanation of fat scoring technique. *$P<0.01$ between treatment groups.

Fat reserves as predictors of dominance

Subjects were matched for fat at capture, but birds in some dyads were no longer matched for fat on the night prior to food deprivation. This was probably a result of variable responses to captivity by individual subjects, differing lengths of time in captivity and different social conditions within the six holding enclosures (e.g. variable numbers, ages or social ranks of occupants). Since the food deprivation reduced fat levels by only one fat score, on average, some deprived birds actually had higher fat scores than their control opponents during establishment of dominance ranks. To determine whether pre-deprivation fat score was a better predictor of dominance than treatment group per se,

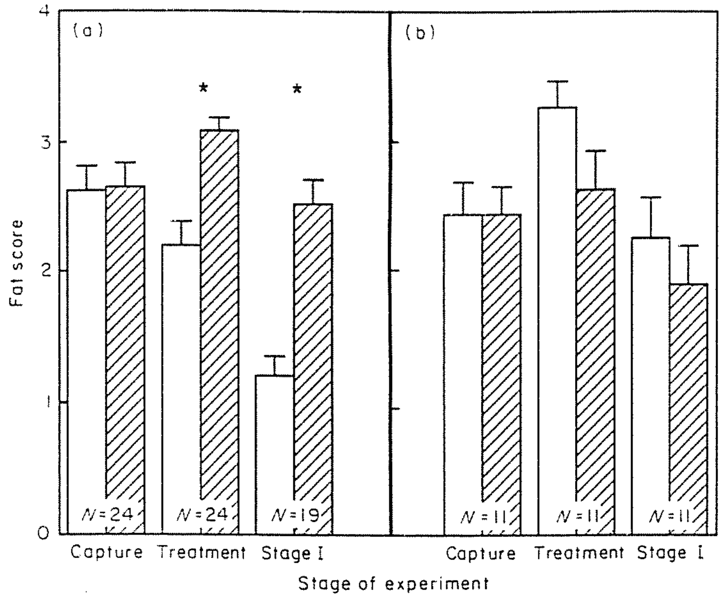

Figure 3. Fat scores (mean + SE) of deprived (□) and control subjects (▨) at capture, at the onset of the treatment and after stage I. (a) Dyads dominated by deprived birds during stage I. (b) Dyads dominated by control birds during stage I. Asymmetries in fat reserves prior to treatment predicted dominance status. $^*P<0{\cdot}001$ between treatment groups.

I divided the deprived members of all dyads into three categories in which their fat scores were either higher than ($N=6$), lower than ($N=10$) or equal to ($N=15$) that of their opponent. In dyads where contestants exhibited an asymmetry in stored fat levels ($N=16$), the subject with less fat was always dominant to its cagemate, regardless of treatment group. In contrast, the deprived bird won in only 10 (67%) of the cases ($N=15$) where there was no fat asymmetry. Because of low expected values in some of the cells, a contingency test cannot be performed. However, the amount of stored fat before the deprivation, rather than the food deprivation per se, is a better predictor of dominance rank.

Another method of comparing the effects of fat level and treatment is to compare fat asymmetries within dyads that were dominated by deprived birds with those within dyads dominated by control birds. Dominant deprived birds had significantly lower fat scores than their opponents on the night prior to deprivation ($z=3{\cdot}74$, $P<0{\cdot}0001$, Fig. 3), and on the day of rank establishment ($z=4{\cdot}27$, $P<0{\cdot}0001$). In contrast, subordinate deprived subjects had higher fat scores than their dominant opponents on the night prior to deprivation ($z=2{\cdot}11$, $P=0{\cdot}034$), and their fat scores remained higher following deprivation.

Change in fat reserves and stability of ranks

To investigate the relationship between change in fat level and dyad stability, I compared the change in fat scores of deprived and control subjects in both stable and unstable dyads. Deprived birds in stable dyads did not differ significantly from their control opponents in change of fat level after the food deprivation ($P>0{\cdot}6$, Fig. 4). In contrast, deprived birds in unstable dyads lost significantly more fat than control birds during the food deprivation ($z=2{\cdot}26$, $P=0{\cdot}01$). Thus, rank reversals occurred in those dyads in which deprived subjects had lost significantly more fat than their opponents during the food deprivation. All but one of the reversals occurred between stages II and III, when many deprived birds increased their fat levels to that of their opponents.

DISCUSSION

Resource value and fighting ability are the most important variables in contests between animals (Enquist & Leimar 1987). In my experiment the value of a food resource was increased, through deprivation, for only one member of a dyad of

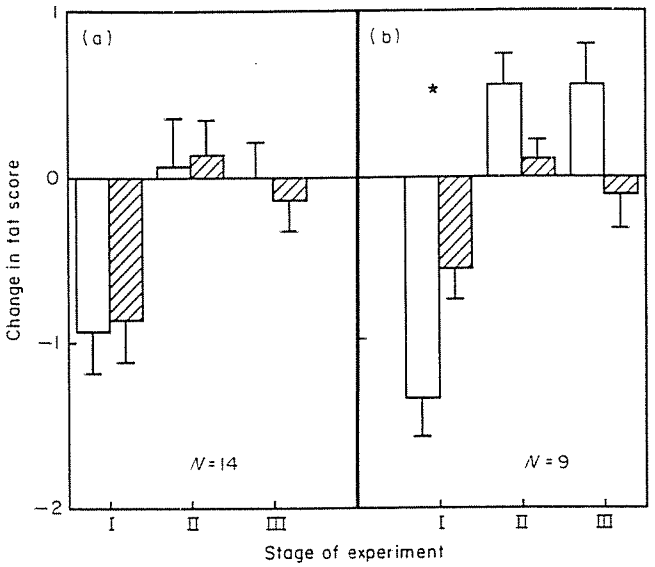

Figure 4. Change in fat score (mean ± SE) of deprived (□) and control subjects (▨) between the onset of the treatment and stage I, between stages I and II, and between stages II and III. (a) Dyads that did not reverse ranks at any point in the experiment. (b) Dyads in which subjects reversed ranks during stage III. Food deprivation resulted in much greater fat asymmetries in those dyads in which ranks eventually reversed. *P < 0·05 between treatment groups.

juncos. The individuals in each dyad had no preexisting dominance relationship, and were matched for age, size and sex, important components of fighting ability in this species. The dyads were dominated by food-deprived subjects significantly more than expected by chance. Assuming that the food-deprived birds were more motivated to feed than their opponents, this result supports the hypothesis that dominance contests can be settled on the basis of a resource value asymmetry. In those dyads where deprived subjects still had higher levels of stored fat than their opponents, despite the food deprivation, the leaner individual was always dominant. This suggests that it was an individual's stored fat reserves, rather than acute hunger, that determined the perceived value of the food resource, and best predicted dominance status.

Motivation to feed can be important in determining the outcomes of initial encounters between two individuals, but it is critical to determine if ranks settled in this way are stable once the resource value asymmetry disappears. All but one of the dominance relationships that were established during stage I remained stable during stage II (more than 95% of classifiable dyads) but, in 15% of the retested dyads, the subjects failed to interact or did so too infrequently to determine ranks. Thus, most dominance relationships remained stable for at least 24 h after food deprivation, but some relationships may have changed in the unclassifiable dyads. Deprived subjects had increased their fat reserves between stages I and II, so that no statistically significant asymmetry remained. This suggests that relationships influenced by a motivational asymmetry can be stable after the disappearance of such an asymmetry. By this interpretation, the increase in rank reversals that occurred between stages II and III could have been a result of the fact that subjects entered a flock in stage III, and chance occurrences in the new social environment caused relationships to become unstable.

An alternative interpretation for the apparent stability of dominance ranks for at least 24 h after deprivation, and the subsequent reversal of many of these ranks in stage III, is that the fat asymmetry that occurred following deprivation may have persisted into stage II, but was no longer great enough to be detected statistically. Subjects could have repeatedy reestablished ranks based on this lingering asymmetry, and then reversed ranks once the asymmetry disappeared. By this explanation, the rank reversals seen during stage III were the result of the disappearance of any fat asymmetry, rather than the effects of a new social environment. If this explanation is correct, then approximately half of the dyads should have undergone rank reversals by stage III, when differences in stored fat reserves between the treatment groups finally disappeared completely. In fact 39% of dyads reversed ranks during stage III, which does not differ significantly from the expected rate of 50% ($\chi^2=0{\cdot}69$, $df=1$, $P>0{\cdot}4$).

This second explanation for instability of ranks would also be supported if those dyads undergoing rank reversals were the dyads in which motivational asymmetries had been great enough to overcome some other asymmetry, such as resource holding potential, that later regained importance as a determinant of dominance in the absence of such a motivational asymmetry. An examination of which dyads reversed rank during stage III is consistent with the latter interpretation. Deprived members of unstable dyads lost more fat than their control opponents after the deprivation (stage I, see Fig. 3). In striking contrast, deprived members of stable dyads did not differ from their opponents in change of fat score at any phase of the experiment. Thus, dyads that were unstable tended to be those in which the food deprivation had created a large motivational asymmetry between opponents, suggesting that relationships influenced by an asymmetry in resource value eventually reverted back to what they would have been in the absence of such an asymmetry. Further study will be necessary to assess the stability of social ranks established after food deprivation because motivation to feed and social environment were varied simultaneously during stage III of this experiment.

Resource value asymmetries could be important ecologically even if the social relationships they influence are stable for only 24 h as suggested by this study. There are instances in which the results of initial interactions can have profound effects on an individual's chances of survival. Piper (1990) recently reported that subordinate, but not dominant, white-throated sparrows, *Zonotrichia albicollis*, leave familiar home ranges during a period of food shortage. This illustrates a situation in which individuals without previously established ranks might settle dominance contests based on a motivational asymmetry. Lindström et al. (1990) has shown that in post-breeding bluethroats, *Luscinia svecica*, dominance status was correlated with fat reserves at a moulting site where food supplies were limited and unpredictable. Autumn migration is another situation in which birds interact without prior relationships and with asymmetries in motivation to feed. Late migrants probably arrive at stop-over sites with little stored fat and compete with residents or earlier migrants that have greater reserves. Motivational asymmetries such as hunger may be important determinants of dominance, which in turn may influence many aspects of avian population dynamics.

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REFERENCES

Baker, M. C. & Fox, S. F. 1978. Dominance, survival, and enzyme polymorphism in dark-eyed juncos, *Junco hyemalis*. *Evolution*, **32**, 697–711.

Balph, M. H. 1977. Winter social behaviour of dark-eyed juncos: communication, social organization, and ecological implications. *Anim. Behav.*, **25**, 859–884.

Bruce, R. H. 1941. An experimental analysis of social factors affecting the behavior of white rats III: dominance and cooperation motivated by water and food deprivation. *J. comp. Psychol.*, **31**, 395–412.

Ekman, J. B. & Askenmo, C. E. H. 1984. Social rank and habitat use in willow tit groups. *Anim. Behav.*, **32**, 508–514.

Enquist, M. & Leimar, O. 1987. Evolution of fighting behaviour: the effect of variation in resource value. *J. theor. Biol.*, **127**, 187–205.

Ewald, P. W. 1985. Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Anim. Behav.*, **33**, 705–719.

Gauthreaux, S. A., Jr. 1978. The ecological significance of behavioral dominance. In: *Perspectives in Ethology. Vol. 3* (Ed. by P. P. G. Bateson & D. S. Farner), pp. 93–168. New York: Plenum Press.

Hansen, A. J. 1986. Fighting behavior in bald eagles: a test of game theory. *Ecology*, **67**, 787–797.

Helms, C. W. & Drury, W. H. 1960. Winter and migratory weight and fat: field studies on some North American buntings. *Bird-Banding*, **31**, 1–40.

Hogstad, O. 1989. Social organization and dominance behavior in some *Parus* species. *Wilson Bull.*, **101**, 254–262.

Holberton, R. L., Able, K. P. & Wingfield, J. C. 1989. Status signalling in dark-eyed juncos, *Junco hyemalis*: plumage manipulations and hormonal correlates of dominance. *Anim. Behav.*, **37**, 681–689.

Ketterson, E. D. 1979. Aggressive behavior in wintering dark-eyed juncos: determinants of dominance and their possible relation to geographic variation in sex ratio. *Wilson Bull.*, **91**, 371–383.

Ketterson, E. D. & Nolan, V., Jr. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos, *Junco hyemalis hyemalis*. *Ecology*, **57**, 679–693.

Ketterson, E. D. & Nolan, V., Jr. 1982. The role of migration and winter mortality in the life history of a temperate zone migrant, the dark-eyed junco, as determined from demographic analyses of winter populations. *Auk*, **99**, 243–259.

Lindström, A., Hasselquist, D., Bensch, S. & Grahn, M. 1990. Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. *Anim. Behav.*, **40**, 453–461.

Lore, R., Gottdiener, C. & Delahunty, M. J. 1986. Lean and mean rats: some effects of acute changes in the food supply upon territorial aggression. *Aggress. Behav.*, **12**, 409–415.

Miller, R. G., Jr. 1981. *Simultaneous Statistical Inference*. New York: Springer-Verlag.

Moss, R., Watson, A., Rothery, P. & Glennie, W. 1982. Inheritance of dominance and aggressiveness in captive red grouse *Lagopus lagopus scoticus*. *Aggress. Behav.*, **8**, 1–18.

Parker, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *J. theor. Biol.*, **47**, 223–243.

Piper, W. H. 1990. Site tenacity and dominance in wintering white-throated sparrows *Zonotrichia albicollis*. *Ethology*, **85**, 114–122.

Popp, J. W. 1987. Resource value and dominance among American goldfinches. *Bird Behav.*, **7**, 73–77.

Popp, J. W. 1988. Effects of experience on agonistic behavior among American goldfinches. *Behav. Proc.*, **16**, 11–19.

Pyle, P., Howell, S. N. G., Yunick, R. P. & Desante, D. F. 1987. *Identification Guide to North American Passerines*. Bolinas, California: Slate Creek Press.

Richner, H. 1989. Phenotypic correlates of dominance in carrion crows and their effects on access to food. *Anim. Behav.*, **38**, 606–612.

Rogers, C. M., Theimer, T. L., Nolan, V., Jr & Ketterson, E. D. 1989. Does dominance determine how far dark-eyed juncos, *Junco hyemalis*, migrate into their winter range? *Anim. Behav.*, **37**, 498–506.

Rohwer, S., Ewald, P. W. & Rohwer, F. C. 1981. Variation in size, appearance, and dominance within and among the sex and age classes of Harris' sparrows. *J. Field Ornithol.*, **52**, 291–303.

Searcy, W. A. & Wingfield, J. C. 1980. The effects of androgen and antiandrogen on dominance and aggressiveness in male red-winged blackbirds. *Horm. Behav.*, **14**, 126–135.

Wiley, R. H. & Hartnett, S. 1979. Effects of hunger on aggression, approach, and avoidance by juncos (*Junco hyemalis*). *Z. Tierpsychol.*, **51**, 77–84.

Yunick, R. P. 1977. Eye color changes in the dark-eyed junco and white-throated sparrow. *N. Am. Bird Bander*, **2**, 155–156.