

Department of Zoology, University of North Carolina, Chapel Hill

Effects of Hunger on Aggression, Approach, and Avoidance by Juncos (*Junco hyemalis*)

By R. HAVEN WILEY and SUE A. HARTNETT

With 7 figures

Received: April 2, 1979

Accepted: June 9, 1979

Abstract

The aggressive tendencies of male dark-eyed juncos *Junco hyemalis* did not differ significantly following deprivation from food for 20 and 60 min. Tendencies to approach opponents at food, in contrast, increased with longer deprivation. Acute hunger and aggression are thus not competing behavioral systems. Nor do differences in rates of approach by subordinates affect aggressive tendencies of dominant birds.

Introduction

Aggression in many animals serves to defend a supply of food (MARLER and HAMILTON 1966). Individuals often adjust their patterns of aggression to the availability or density of food. For instance, territory size in some birds varies inversely with the density or nutritional quality of food (STENGER 1958; LANCE 1978; MILLER and WATSON 1978). One explanation of this finding is that individuals become more aggressive when they are hungry or when they determine in some other way that food is scarce. Another explanation is that hungry individuals wander over larger areas but have no greater aggressive tendencies in comparable situations (WASER and WILEY 1979).

Several experimental studies of animals in standardized situations have failed to demonstrate an effect of food deprivation on aggressive tendencies. Instead, rates of aggressive interactions increase among hungry individuals because locomotory activity, and consequently encounters between individuals, increase with food deprivation (ANDREW 1956; ROHLES and WILSON 1974). MARLER (1956) used his technique of movable feeders to study aggressive tendencies of captive male chaffinches *Fringilla coelebs* during winter. He found that two feeders 20 cm apart were simultaneously occupied much more frequently after birds were deprived of food, but two birds simultaneously on the feeders were no more likely to engage in aggression than during control periods.

Because ambient temperature influences metabolic demands, effects of temperature on aggressiveness might match effects of food deprivation. Yet SABINE (1959) noted that on winter days with low temperatures dark-eyed juncos *Junco hyemalis* tended to show more tolerance of nearby juncos than on warmer days. Recently, PULLIAM et al. (1974) confirmed this finding among wintering juncos. The percentage of encounters that resulted in aggression at a separation of 35 cm between individuals correlated positively with temperature. In one interpretation of these results, the increased metabolic demands at lower temperatures increase hunger, and hungrier birds become less aggressive toward nearby opponents. In this view, hunger and aggression are competing behavioral systems. The nature of hunger induced by low temperatures might well differ from that induced by acute deprivation from food. At any rate, the effects of low temperature and the effects of acute food deprivation on aggressiveness appear to differ.

In another explanation for the effects of low temperatures on aggression, SABINE (1959) suggested that subordinate birds approach dominant juncos at feeding stations more frequently in cold weather, with the result that dominant birds tend to habituate to close proximity of subordinates. In this view, aggressiveness decreases in cold weather as a secondary consequence of increased rates of encounter among hungry birds.

In the course of a study of aggression in dark-eyed juncos, we repeated MARLER's experiments on effects of food deprivation. Since we had devised techniques for measuring individuals' tendencies to approach and withdraw from opponents, in addition to their tendencies to engage in aggression, we could evaluate changes in all of these tendencies as a consequence of food deprivation (WILEY and HARTNETT, in press). Our results confirmed MARLER's conclusions that acutely induced hunger changes individuals' tendencies to approach opponents but not their aggressive tendencies.

Methods

For our experiments we used 4 groups of 6 male juncos, each housed in an 2.5 m cube outdoor aviary with a special observation chamber. Two groups were studied in March 1976 and two in March 1977 and again in April 1977, so that altogether we completed 6 series of experiments. Results from the two series on each of two groups in 1978 were no more similar in their trends than results from series with different groups of birds; consequently we have considered that each of the 6 series is an independent experiment.

Two feeders in each aviary were suspended from wires and remained at least 1 m apart except during experiments. For the experiments reported here, the feeders were moved to a separation of 15 cm. Further details of our procedures are presented elsewhere (WILEY and HARTNETT in press).

For each series of observations in these experiments, we studied a group of juncos on two days following 20-min deprivations of food and on two days following 60-min deprivations. The four experiments in a series were conducted on different days within one week; observation periods began between 8.00 and 9.30 h in the morning.

Each series involved a balanced design of two durations of deprivation with replication under approximately similar weather conditions. Temperatures during the observation periods within any one series were within 5 °C. No observations were conducted during precipitation or high winds. Within any one series, we alternated deprivations of 20 and 60 min. Half of the series began with 20-min deprivations and half with 60-min deprivations.

Procedures for recording behaviour at our feeders (WILEY and HARTNETT in press) focused on two social states: encounters, birds on both feeders simultaneously; and alone periods, a bird on one feeder while the other remained vacant. Encounters could terminate in four ways: the dominant bird could supplant the subordinate; the dominant or the subordinate could leave; or a third bird could supplant one of the two participants. Alone periods could also terminate in three ways: the subject could leave; another bird could join the subject by occupying the other feeder and thus initiating an encounter; or another bird

could supplant the subject. The terminations of both encounters and alone periods constitute exhaustive, mutually exclusive classifications. Our observation periods lasted 15 min. They began after carefully timed deprivations of 20 or 60 min during which the feeders were removed from the aviaries.

The best measure of an individual's behavioral tendencies is its probability of performing particular actions per s of opportunity. We have shown previously that these rates (actions/s of opportunity) are available from temporal analysis of the terminations of social states, such as the encounters and alone periods observed in this study (WILEY and HARTNETT in press). Such analyses are greatly simplified if the rates of termination of social states remain constant with time after the initiation of the state. In this case, an individual's tendency to perform an action A is simply the proportion of action A in terminations of the state divided by the mean duration of the state (WILEY and HARTNETT in press). When the mean durations of a social state are the same in two situations, such as following two durations of deprivation, then differences in proportions of an action A in terminating the state in the two situations reflect differences in individuals' tendencies to perform action A. In this paper, as in our previous one, we show that encounters and alone periods tend to terminate with approximately constant rates following their initiations and to have approximately equal durations under both conditions of deprivation. Thus for each of the two kinds of social states, the proportions of each kind of termination reflect individuals' behavioral tendencies in that state.

To test the significances of differences in behavioral tendencies under the two conditions of deprivation, we used t-tests for paired data. The two durations of deprivation in each series were paired ($N = 6$ series). These tests employed angular transformations of the proportions of each kind of termination of encounters or alone periods. To evaluate the consistency of differences between 20- and 60-min deprivations across the 6 series, we employed sign tests.

Results

Our results revealed no significant differences in tendencies of individuals to perform aggression toward nearby opponents following 20 and 60 min of deprivation from food. Although the proportions of encounters that involved supplantation of one opponent by the other or aggression (either supplantation or threat by at least one participant) were higher after longer deprivation, these differences were not statistically significant (Fig. 1). On the other hand, the numbers of encounters in 15-min observation periods increased by a factor of approximately 2.5 after 60 min in comparison to 20 min of deprivation (Fig. 2). As MARLER (1956) reported, tendencies to perform aggression toward nearby opponents were not affected by deprivation, but rates of encounters between individuals increased markedly when the duration of deprivation increased.

Closer examination of the terminations of encounters can provide information about individuals' tendencies to withdraw from opponents, while examination of the terminations of alone periods can provide information about individuals' tendencies to approach opponents. Both encounters and alone periods tended to terminate at approximately constant rates following initiation (Fig. 3). Because the durations of encounters under the two conditions of deprivation were the same (Fig. 2), differences in the proportions of the different kinds of terminations of encounters reflect changes in individuals' behavioral tendencies.

Following the longer period of deprivation, a greater proportion of encounters was terminated by a third bird supplanting one of the participants (Fig. 4). Thus although opponents were no more likely to engage in aggression once an encounter had begun after longer periods of deprivation, they were more likely to supplant another individual from a distance in order to obtain access to food. When we consider the terminations of alone periods (below), we can show that this difference results from an increased tendency to approach food after longer deprivation rather than an increased tendency to engage in aggression.

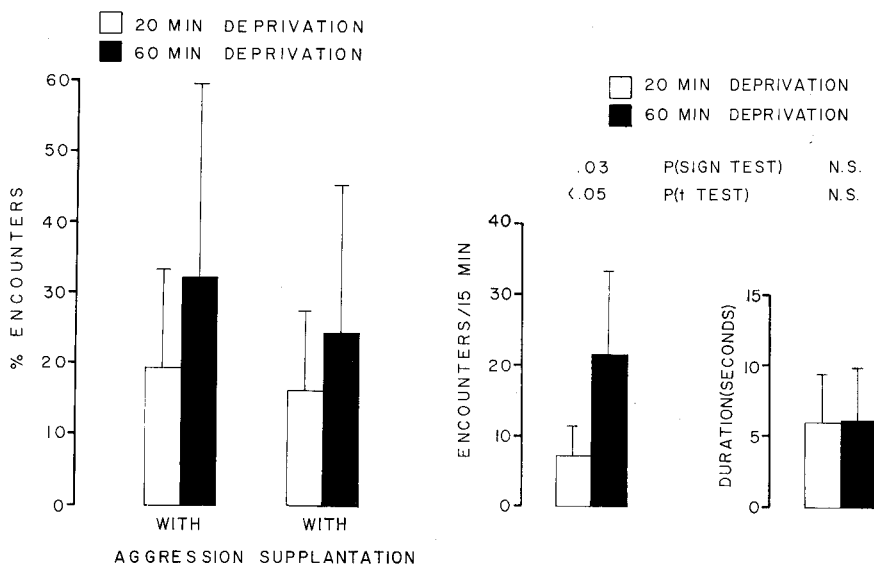


Fig. 1 (left): Mean percentage of encounters that included aggression (one bird supplanted or threatened the other) or supplantation by one of the participants. Open bars, following 20 min deprivation; dark bars, following 60 min deprivation. Each bar shows the mean for $N = 6$ series of observations; the vertical line above each bar represents one standard deviation around the mean. No significant differences ($p > 0.4$, 2-tailed, in both cases)

Fig. 2 (right): Mean rates (left) and durations (right) of encounters after 20 and 60 min deprivation. At the top are significance probabilities (2-tailed) for differences between the two levels of deprivation according to a sign test and a t-test for paired data (calculated from angular transformations of the proportions). See Fig. 1 for further expl.

Although both the dominant and subordinate participants in an encounter were less likely to terminate the encounter by leaving after 60 min rather than 20 min of deprivation, neither of these trends was statistically significant. Evidently deprivation from food had no reliable effect on individuals' tendencies to withdraw from encounters at food.

Alone periods had virtually identical durations following the two durations of deprivation (Fig. 5) and furthermore occurred at approximately the same rate (Fig. 3). Again the constant rates of terminations after the initiation of alone periods and the equal durations of alone periods under the two levels of deprivation mean that differences in the proportions of kinds of terminations of alone periods reflect differences in individuals' behavioral tendencies in this situation.

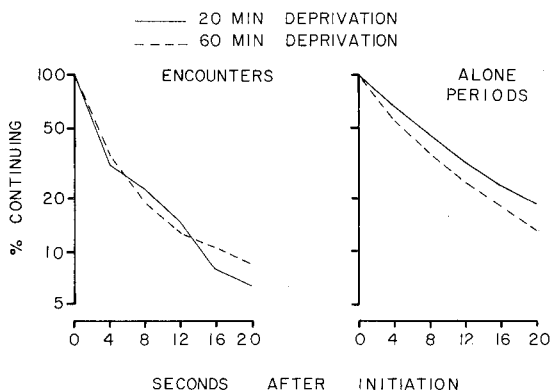


Fig. 3: "Survivorship" plots for encounters and alone periods following two durations of deprivation

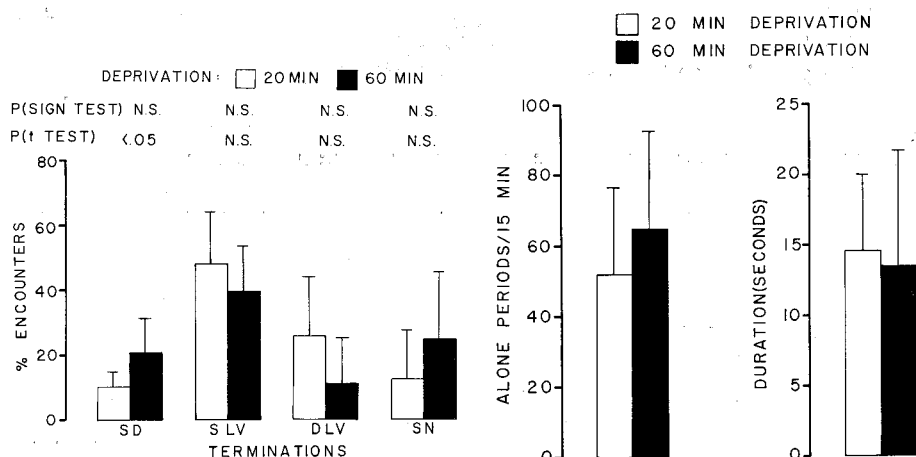


Fig. 4 (left): Terminations of encounters following 20 and 60 min deprivation. Encounters terminated when a bird supplanted one of the participants (SD), the subordinate participant left (SLV), the dominant participant left (DLV), or the dominant supplanted the subordinate (SN). Nonsignificant differences (N.S.) have $p > 0.2$, 2-tailed, in each case.

Fig. 5 (right): Mean rates (left) and durations (right) of alone periods following 20 and 60 min deprivation. See Fig. 2 for expl. No significant differences ($p > 0.3$, 2-tailed, in both cases).

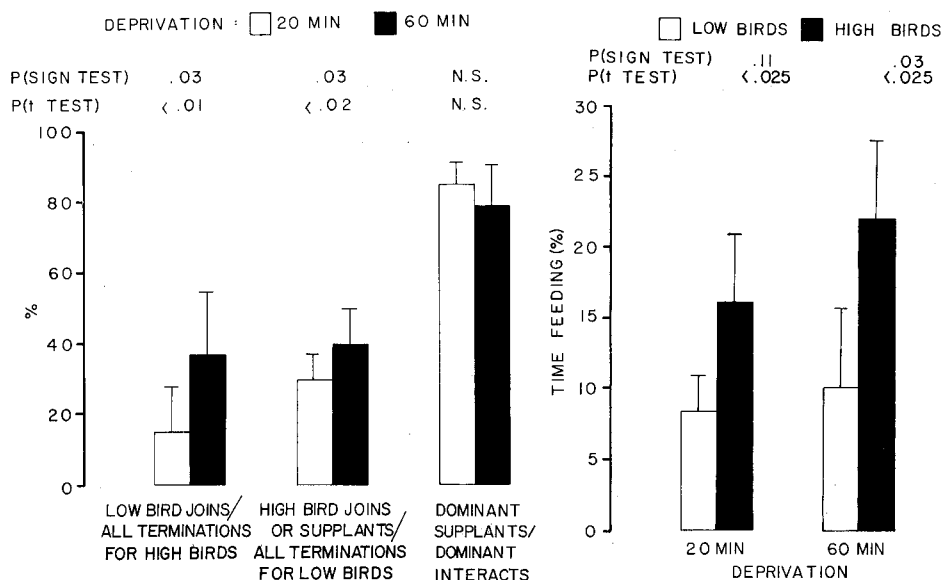


Fig. 6 (left): Terminations of alone periods of high-ranking and low-ranking birds following 20 and 60 min deprivation. Left: tendencies of the three lowest-ranking birds to join one of the three highest-ranking birds (mean percentages of alone periods of high birds terminated by a low bird joining). Center: tendencies of high-ranking birds to interact with (either join or supplant) low-ranking birds (mean percentages of alone periods of low birds terminated by interaction with a high bird). Right: tendencies of high-ranking birds to join rather than supplant solitary low-ranking birds (mean percentages of joins among those alone periods of low birds terminated by high birds). See Fig. 2 for expl.

Fig. 7 (right): Mean percentage of time spent feeding by the three highest-ranking birds and the three lowest-ranking birds following 20 and 60 min deprivation. See Fig. 2 for expl.

Following 60 min of deprivation, in comparison to 20 min, alone periods were far less likely to terminate by the subject leaving the feeder (60 min, $.40 \pm .10$; 20 min, $.60 \pm .08$; $t = 7.30$, $p < .01$). As we should expect, hungry birds were reluctant to leave food. Hungry birds were also much more likely to interact with opponents at close range in order to obtain access to food. Thus if we consider the alone periods of the three highest-ranking birds in each series, the three lowest-ranking birds were more likely to join them after 60 min of deprivation than after 20 min. Similarly the high-ranking birds were more likely to interact with (either join or supplant) low-ranking solitary opponents after the longer period of deprivation. Yet after longer deprivation, a bird was no more likely to supplant than join a solitary subordinate opponent (Fig. 6). Birds clearly had greater tendencies to approach food after longer deprivation, even when this involved interacting at close range with opponents. Nevertheless, a bird's tendency to behave aggressively toward subordinates as opposed to taking an empty feeder nearby did not change.

Our observations confirmed the advantage of dominance in obtaining access to limited food (FRETWELL 1972; BAKER and FOX 1979). After both levels of deprivation, the three highest-ranking birds in a group spent more time feeding than the three lowest-ranking birds. After greater deprivation, both groups of birds increased their time feeding, but the high-ranking birds increased their time feeding proportionately more than did the low-ranking birds (Fig. 7).

Discussion

Our results confirm that acute deprivation from food increases individuals' tendencies to approach other individuals at food but not their tendencies to perform aggression under conditions of comparable proximity to opponents (MARLER 1956). After longer deprivation, an individual is more likely to supplant a subordinate opponent at a feeder when both feeders are occupied, yet deprivation has no effect on an individual's tendency to supplant rather than join a solitary subordinate.

Deprivation has no reliable effect on an individual's tendency to supplant an opponent once an encounter has begun. The large difference between the two levels of deprivation in proportions of encounters with supplantation suggests that further work might reveal a reliable increase in aggressiveness with increased hunger. Certainly there is no suggestion in our results that acute hunger and aggressiveness constitute competing behavioral systems, so that increased hunger would reduce the tendency of an individual to perform aggression. Nor is there any indication, within the short periods of our observations, that the increased rates of encounters between nearby individuals tend to habituate dominant individuals to proximity of subordinates. Of course, such habituation might develop over longer periods than the 15 min we permitted for observations. Clearly the mechanisms by which low temperatures reduce aggressiveness in juncos require more than the acute effects of hunger on aggression or short-term effects of increased rates of approach by subordinates.

Summary

By using two feeders 15 cm apart, we investigated the tendencies of male dark-eyed juncos *Junco hyemalis* (Fringillidae) to perform aggression, to

approach and to withdraw from opponents under standardized conditions following deprivation from food for 20 or 60 min. Our results revealed no reliable differences in the aggressive tendencies of male juncos after these two levels of deprivation. Tendencies to approach and interact with opponents at food increased with longer deprivation, but duration of deprivation had no effect on the tendencies of individuals to supplant rather than approach solitary subordinate opponents or to supplant opponents once an encounter had begun. Acute hunger and aggression are thus not competing behavioral systems, in the sense that increased hunger reduces tendencies for aggression. Nor within short periods of time do differences in rates of approach by subordinates influence aggressive tendencies of dominant birds.

Zusammenfassung

Aggressionsverhalten, Annäherung und Ausweichen gegenüber Artgenossen beim Winter-Junco (Scharr-Ammer) wurden an zwei 15 cm voneinander entfernten Futterplätzen untersucht. Die Tiere hatten jeweils entweder 20 oder 60 min nichts gefressen. In der aggressiven Tendenz zeigten sich keine signifikanten Unterschiede zwischen beiden Bedingungen. Längere Hungerzeit förderte die Annäherung an fressende Artgenossen, ließ aber die individuelle Entscheidung, Rangtiefer zu verdrängen, unbeeinflusst. Kurzzeitiger Hunger wirkt der Aggression nicht entgegen.

Acknowledgments

We thank A. DAVIS and M. ANDREWS for assistance in observing the birds and H. MUELLER for help with the manuscript. This study, a contribution from the Behavior Research Station in the North Carolina Botanical Garden, was supported by grants from the University Research Council of the University of North Carolina, Chapel Hill, and the National Institute of Mental Health (MH 22316).

Literature cited

- ANDREW, R. J. (1956): Influence of hunger on aggressive behaviour in certain buntings of the genus *Emberiza*. *Physiol. Zool.* 30, 177—185.
- BAKER, M. C., and S. F. FOX (1979): Dominance, survival, and enzyme polymorphism in dark-eyed juncos, *Junco hyemalis*. *Evolution* 32, 697—711.
- FRETWELL, S. D. (1972): *Populations in a Seasonal Environment*. Princeton Univ. Press, Princeton.
- LANCE, A. N. (1978): Territories and the food plant of individual red grouse. II. Territory size compared with an index of nutrient supply in heather. *J. Anim. Ecol.* 47, 307—313.
- MARLER, P. (1956): Studies of fighting in chaffinches. 3) Proximity as a cause of aggression. *Brit. J. Anim. Behav.* 4, 23—30 • MARLER, P., and W. J. HAMILTON III (1966): *Mechanisms of Animal Behavior*. Wiley, New York • MILLER, G. R., and A. WATSON (1978): Territories and the food plant of individual red grouse. I. Territory size, number of mates and brood size compared with the abundance, production and diversity of heather. *J. Anim. Ecol.* 47, 293—305.
- PULLIAM, H. R., K. A. ANDERSON, A. MISZTAL and N. MOORE (1974): Temperature-dependent social behaviour in juncos. *Ibis* 116, 360—364.
- ROHLES, F. H., Jr., and L. M. WILSON (1974): Hunger as a catalyst in aggression. *Behaviour* 48, 123—130.
- SABINE, W. S. (1959): The winter society of the Oregon junco: intolerance, dominance, and the pecking order. *Condor* 61, 110—135 • STENGER, J. (1958): Food habits and available food of ovenbirds in relation to territory size. *Auk* 75, 335—346.

WASER, P. M., and R. H. WILEY (1979): Mechanisms and evolution of spacing behavior. In: *Handbook of Behavioral Biology: Social Behavior and Communication*. (MARLER, P., and J. VANDENBERG, eds.) Plenum Press, New York • WILEY, R. H., and S. A. HARTNETT (in press): Mechanisms of spacing in groups of juncos: measurement of behavioral tendencies in social situations. *Anim. Behav.*

Authors' address: R. H. WILEY and S. A. HARTNETT, Department of Zoology, University of North Carolina, Chapel Hill, N. C. 27514, U.S.A.