

MECHANISMS OF SPACING IN GROUPS OF JUNCOS: MEASUREMENT OF BEHAVIOURAL TENDENCIES IN SOCIAL SITUATIONS

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Abstract. To investigate behavioural mechanisms that regulate the spacing of individuals, we studied aggression, approach, and avoidance of captive male juncos (*Junco hyemalis*) in relation to the distance between individuals. We measured behavioural tendencies by analysing the terminations of social states so as to determine the instantaneous probability rates of terminal actions. These rates permit accurate comparisons of behavioural tendencies in different social situations. An individual's tendencies to supplant, approach, or withdraw from an opponent depended on the dominance relationship of the two birds and on the distance between them. Interactions did not vary with the magnitude of the difference between opponents' ranks. The dependence of aggression, approach, and avoidance on the distance between opponents controls the spacing of individuals.

Introduction

The spatial relationships of individuals are a fundamental feature of any social structure. They result from individuals' tendencies to approach and avoid each other as a function of the distance separating them. While it is widely recognized that the effects of many social interactions include adjustments in the distances between individuals (Tinbergen 1959; Marler 1968; Wiley 1976), discussions of the mechanisms of spacing in animal societies have not in general focused on approach and avoidance, in part because of the difficulty of studying these actions quantitatively. Instead, discussions of spacing usually centre on aggression (actions of attack and threat).

It is true that different forms of aggression, determined by the circumstances in which individuals attack or threaten others, generate different spatial relationships of individuals. The various forms of dominance hierarchies, territoriality, defence of an individual distance, and defence of mates or progeny (see Marler & Hamilton 1966; Waser & Wiley 1979) are all associated with distinctive patterns of spacing. Nevertheless, aggression between individuals controls spatial relationships only through its effects on approach and avoidance. To understand the behavioural mechanisms that regulate spacing we need to examine aggression, approach and avoidance at controlled distances between individuals.

Aggressive tendencies (an individual's probabilities of attacking or threatening opponents in specified situations) and approach and avoidance tendencies probably have reciprocal effects on each other. On the one hand, the outcome of aggression between opponents is likely to influ-

ence each individual's subsequent tendencies to approach and avoid opponents. On the other hand, approach and avoidance tendencies influence the rates of aggressive encounters. In addition, approach and avoidance tendencies are likely to influence the outcomes of encounters. For instance, if individuals differed in their tendencies to approach and avoid opponents, those that tended to approach more closely and not to avoid opponents would tend to supplant those that approached less closely and avoided more. Supplantation, a common form of aggression in which one individual takes another's place, is a form of approach and avoidance.

The relationship between aggression and spacing became clear for the first time in Marler's (1956) classic demonstration that chaffinches *Fringilla coelebs* are more likely to attack each other the closer they are together. As a measure of the relationship between aggression and proximity, Marler defined a '50% distance': that separation at which 50% of encounters resulted in overt aggression. Patterson (1965) subsequently reported that an intruder's distance from a territorial black-headed gull (*Larus ridibundus*) determined the probability of attack or threat by the resident.

On the other hand, there is little information on individuals' tendencies to approach and avoid each other as a function of their distance apart nor on the relationship of these tendencies to aggression (see Grubb 1974; Hazlett 1975). Marler did not apply his technique to approach and avoidance tendencies of chaffinches in winter dominance hierarchies.

This study examines approach, avoidance, and aggression between captive male dark-eyed

juncos (*Junco hyemalis*) at controlled distances from each other in small groups with dominance hierarchies. This species normally forms stable dominance hierarchies in flocks during the winter (Sabine, 1949, 1955, 1956, 1959; Balph 1977; Baker & Fox 1979). We adapted Marler's procedure for studying individuals at controlled distances from each other in order to investigate aggression, approach and avoidance in relation to the proximity and dominance relationships of opponents.

Any study of the behavioural mechanisms that regulate social structure encounters a fundamental problem. The goal is to assess the behavioural tendencies of individuals in specified social situations. Yet any determination of individuals' tendencies from observations of freely interacting individuals, even when opportunities for interactions are constrained by the experimenter, presents problems never completely resolved. Previously proposed measures of individuals' tendencies have been based on the frequencies or proportions of their actions (see for example Hinde & Atkinson 1970; Hinde 1977). Yet the frequencies or proportions of different responses by an individual do not in general provide accurate measures of its tendencies, since the proportion of any one kind of action depends on the tendencies of each individual to perform each of its possible actions.

An individual's behavioural tendencies in a specified social situation are best defined as instantaneous probability rates (probabilities per unit time) of performing each possible action. We present some simple methods for obtaining estimates of these probability rates from temporal analyses of the terminations of social states. Only in special circumstances are these rates accurately reflected in the proportions of different responses.

Methods

Subjects and Observation Procedures

Eight aviaries used for observations each consisted of wire mesh on a wooden frame in a 2.5-m cube. On one side an enclosed observation chamber permitted close study of the birds through a window of one-way glass. Birds in such an aviary return to normal activity within a minute after an observer enters the observation chamber.

Each aviary was fitted with two feeders, each with a small perch that permitted only one bird to use the feeder at a time and encouraged the bird to perch facing the feeder (Fig. 1, Plate I).

Thus only two birds in an aviary could feed at the same time, one on each feeder, at a separation controlled by the observer.

Juncos captured at several locations near Chapel Hill, N. C., served as subjects for these studies. The results reported here are based on nine groups of six male juncos each, three groups studied during February 1975, four during February through April 1976, and two during February through April 1977. The observations for each aviary began in February within two weeks of the birds' introduction to the aviary.

Juncos can be sexed accurately without laparotomy. We have followed a procedure suggested by Ketterson & Nolan (1976) based on wing length and pattern of pigment on crown feathers. Of 24 birds that we sexed as males by these criteria, one proved on subsequent laparotomy to be a female.

After capture each bird was held in an individual cage indoors for 3 to 15 days. A group of six male juncos of similar size (wing length within 2 mm) were then introduced simultaneously to an observation aviary. Within 5 to 10 days, all individuals had begun to use the feeders. Frequent use of the feeders by the birds occurred only when no other sources of food were available in the aviary. It was important to clean all spilled food from the aviaries.

Except during scheduled observations, the two feeders were left at a separation of 1.5 m or greater, a distance at which interactions between birds on the feeders essentially never occurred. For systematic observations the feeders were positioned with the two perches either 15 or 60 cm apart, separations selected for clear differences in the birds' agonistic behaviour.

Because the birds' behaviour depended on their states of deprivation, the time of day, and the temperature (see Sabine 1959; Pulliam et al. 1974; Ketterson 1978), these variables were controlled during observations. One observer collected data from two aviaries each morning. In each aviary, the observation period lasted only 15 min in order to reduce changes in birds' behaviour with satiation. An aviary was deprived of food, by removing the hoppers from the feeders, for exactly 45 min before observations began. Observations began between 0830 and 1030 hours in the morning. On successive mornings the observer permuted the separation of the feeders and the order in which the two aviaries were observed. No observations were made on days with high winds or precipitation. Generally, observations could be scheduled so that tempera-

PLATE I

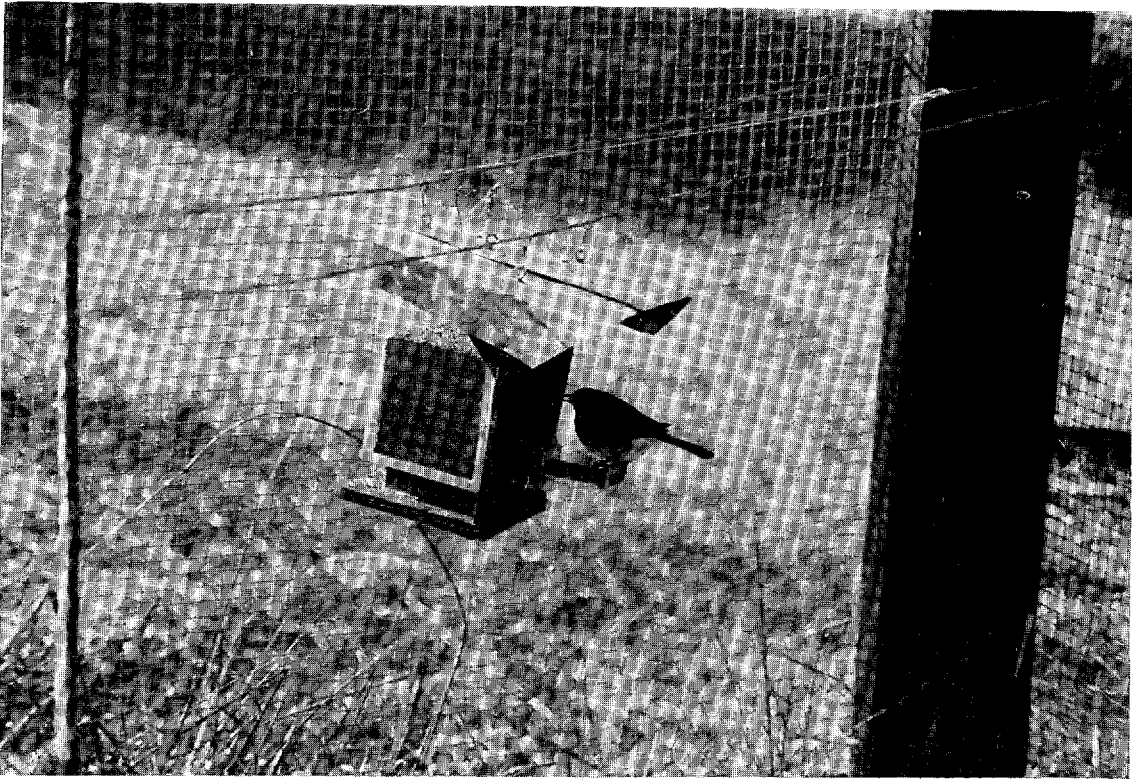


Fig. 1. A junco feeding from a movable feeder in one of our aviaries. Two such feeders slide along wires stretched diagonally across each aviary.

tures during observation times varied no more than 5°C from day to day within an observation series. Six to 10 days of observation of an aviary constituted one observation series. The following analysis includes 18 such series of observations on the nine groups.

Analysis Procedures

Because the feeders constrained the interactions between feeding birds, we could readily categorize the behaviour of individuals at the feeders into a few classes of events: start (ST, land on a feeder when both were empty), join (JN, land on an empty feeder when the other was occupied), leave (LV, leave a feeder regardless of whether or not the other was occupied), supplantation from a distance (SD, a bird not on a feeder displaces a bird on a feeder and lands on that feeder), supplantation with previous proximity (SP, when birds occupy both feeders, one bird displaces the other and takes its position), and threat (TH, when both feeders are occupied, one bird directs a threat toward the other). The last two categories in the preceding list constitute overt aggression between feeding birds. The observer recorded each of these six actions for each individual during an observation session.

These six behavioural events in turn initiate and terminate three categories of states: neither feeder occupied; one feeder occupied (an individual feeding alone, termed an Alone Period); and both feeders occupied (two individuals feeding simultaneously, termed an Encounter for those two individuals). We focused on the latter two states and the events that terminated them.

Observations were recorded with a Datamyte DAK-8 computer-compatible event recorder (Electro-General Corporation). Each action by each individual was entered as a coded statement on the Datamyte keyboard, which automatically recorded the time of each event. An observer with several days of training could record these observations on a Datamyte recorder with very few errors. The observer always had a cassette recorder available for dictating any typing errors at the time they occurred. The recording code was specifically designed with enough redundancy that isolated typing errors on the keyboard were readily detectable. The observer did not face difficulties in deciding into which category a given behavioural event fit, because the situation in the aviaries was designed to permit only a few clearly distinct kinds of actions. The small number of individuals in each aviary and their easily observed coloured bands made errors in identify-

ing individuals rare; since each individual's visit to a feeder in any social context always involved entering its identity twice, accidental errors in recording individuals' identities were easily detected. This information was then analysed at the University of North Carolina Computation Center.

To compare behaviour at 15- and 60-cm separations of the feeders, we calculated the angular transformations of the proportions of the various terminations of social states and then applied *t*-tests for differences in means of paired samples (the two distances were paired for each series). We applied sign tests to assess the consistency, across series, of differences between the two distances.

Behavioural Tendencies of Individuals in Social Situations

To understand the complexities in estimating behavioural tendencies, even in social interactions as constrained as those in our aviaries, consider the behaviour that regulates the duration of an Encounter at a given distance, an example of a specified social state (see Altmann 1974). Once two individuals have approached to a given distance by each occupying one feeder, the Encounter can terminate in four ways: the dominant participant supplants the other (SP); either the dominant or the subordinate participant leaves its feeder (DLV or SLV); or a third individual supplants one of the original two (SD) (the end of an observation period is a fifth possibility, no more than 1% of the total). As these possibilities constitute a mutually exclusive and exhaustive classification of terminations of Encounters, an increase in the proportion of any one kind of termination might result either from an increase in the rate of this kind of termination or a decrease in the rates of the other two kinds.

The different terminations of Encounters include each individual's possible actions in terminating this social state. As a consequence, the instantaneous probability rates of terminal actions (expressed as probabilities of terminal actions per unit of time) are appropriate measures of behavioural tendencies in this specified social state. Such rates might well change as a function of time after the initiation of the state.

Probability rates of terminal actions are particularly important for a comparison of behavioural tendencies in different situations. For such comparisons, investigators have previously relied on the proportions or frequencies of different kinds of terminations of social states

(see Hinde & Atkinson 1970; Hinde 1977). Marler's (1956) original studies of proximity and aggression employed such measures. Yet only when two conditions are satisfied do the proportions of each kind of termination of a social state reliably indicate termination rates and thus permit accurate comparisons of individuals' behavioural tendencies in different situations: (1) the rates must remain constant with time after the initiation of the state; and (2) the overall rate of termination of the social state must be the same in all situations compared.

To establish these two points, first consider the rates of terminal actions for a specified social state. To measure these rates we need a sample of instances of the specified state; for each instance, we need to know the duration of the state and the kind of termination. An estimate of the instantaneous probability rate of all terminations at time t after initiation of the state is then

$$\dot{T}/(N - T)$$

where N is the number of instances in the sample, T is the cumulative number of instances terminated by time t after the initiation of the specified state, and a dot over a symbol represents the derivative with respect to time. This rate, the number of instances that terminate at time t as a proportion of those that last to time t , is analogous to an 'age-specific mortality rate' in demography or a 'hazard rate' or 'failure rate' in other applications. A log-linear 'survivorship' graph, $\ln(N - T)/N$ versus t , provides a convenient way to investigate such rates, including the overall rate of terminations of a social state. We present such graphs below for Encounters and Alone Periods of juncos. If this graph is a straight line with slope $-c$, then the rate of termination, $\dot{T}/(N - T)$, is constant with time after initiation of the state and equal to c .

To measure behavioural tendencies we need estimates of the instantaneous probability rates of each separate kind of termination or

$$\dot{T}_i/(N - T)$$

where T_i is the cumulative number of terminations of type i by time t . When the kinds of terminations constitute an exhaustive, exclusive classification, the rates for each separate kind of termination sum to the overall rate of termination. These rates, based on a sample of a defined social state, provide estimators of behavioural tendencies in this social state.

The proportions of each kind of termination T_i/N when $T = N$, although easy to calculate, have no fixed relation to the rates of terminations and thus no fixed relation to behavioural tendencies. To see this problem, imagine a social state (for instance, encounters at a specified distance between feeding birds) for which all $\dot{T}_i/(N - T) = a_i$ constant with time after the initiation of the state, where the i are an exhaustive, exclusive classification of the terminations of encounters. Thus the overall rate of termination, $\dot{T}/(N - T)$, equals

$$\Sigma a_i = c.$$

At any time t after the initiation of the state, the proportion of all terminations that are of type i , T_i/T , equals

$$\frac{a_i}{c}$$

and the proportion of all encounters that have terminated in manner i , T_i/N , equals

$$\frac{a_i}{c} \left(\frac{T}{N} \right).$$

The proportion of each kind of termination in the entire sample, T_i/N when $T = N$, thus equals

$$\frac{a_i}{c}.$$

Imagine comparing two situations (for example, Encounters at two distances) for which only one of the a_i differ. A change in a_2 , for instance, will produce a change in c and consequently also in the proportion T_i/N , even though the rate a_1 remains constant. A change in the rate of one kind of termination will produce changes in the proportions of all other kinds of terminations. Thus the proportions of different kinds of terminations in two situations reflect the rates of terminations, and thus behavioural tendencies, only when the overall rate of termination is constant and the same in both situations.

A constant overall rate of termination, c , equals the reciprocal of the mean duration of the state, D . For constant c , the density function for durations is the negative exponential function

$$ce^{-ct}$$

and thus the mean duration is $1/c$. Consequently when termination rates are constant with time

after the initiation of a state, the rate of each kind of termination, a_1 , equals the proportion of each kind of termination in the entire sample divided by the mean duration of the state, D :

$$a_1 = \frac{T_1/N}{D} \text{ when } T = N$$

When termination rates are constant, the a_1 provide estimators of the behavioural tendencies of individuals in that social state.

In most cases in our results, the overall rates of termination of social states, either Encounters or Alone Periods, are approximately constant with time after the initiation of the state. After establishing this point, we can then use the mean duration for a social state in a defined situation to estimate the overall rate of termination of this state. Only when the overall termination rate of a state is the same in two situations, as indicated by the mean durations, can we then use the proportions of each kind of termination to compare the rates of these terminations and thus behavioural tendencies in the two situations.

Results

Dominance relationships in our aviaries were clearly defined by supplantations. In four of the nine groups, the birds maintained linear dominance hierarchies during the observations. In two aviaries one bird dropped one or two ranks. Three aviaries each included one triangular relationship.

The hierarchy in an aviary remained the same at feeder separations of 15 and 60 cm. However, in one instance, when the ranking of two adjacent individuals was unclear, preceding a reversal of their ranks, the polarity in their frequencies of supplanting each other was greater at 15 than at 60 cm.

Terminations of Encounters

An Encounter terminated in one of four ways: the subordinate participant could leave (SLV); the dominant could either leave (DLV) or supplant (SP) the subordinate participant; or a third bird could supplant one of the participants (SD), an action that terminated one Encounter and initiated a new one. The instantaneous rates of these terminations reflect the behavioural tendencies of opponents in Encounters, in particular their tendencies to leave or attack each other. Differences in the overall proportions of each kind of termination accurately indicate differences in these rates only if the overall rate of

termination is constant after the start of an Encounter and is the same at both separations of the feeders.

The overall termination rate of Encounters at each separation of perches was approximately constant. Survivorship plots reveal that the proportions of Encounters surviving fit a negative exponential function of time after the initiation of an Encounter (Fig. 2). Although the overall termination rate was nearly constant, a dominant was more likely to supplant than to leave its opponent in the first 4 s of the Encounter than later (Table I). At both distances in all five cages for which full temporal analyses were completed, dominant participants supplanted their opponents, rather than departed, proportionately more often in the first 4 s than later in an Encounter. Although the dominant participant's action in terminating an Encounter changed with time after the initiation of an Encounter, his overall tendency to terminate Encounters did not change with time. Nor did tendencies for a third bird or for the subordinate participant to terminate an encounter differ consistently between the first 4 s and later.

There were no consistent trends for the overall termination rate at one separation of the feeders to differ from that at another (Fig. 2). The mean

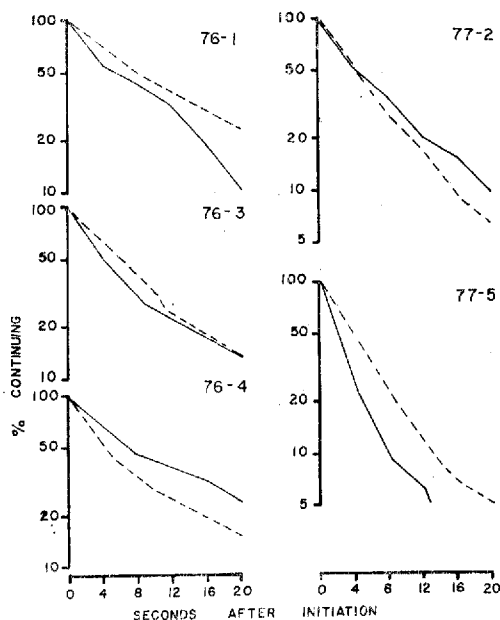


Fig. 2. Survivorship plots of Encounters in five aviaries. Solid lines, feeders 15 cm apart; dashed lines, feeders 60 cm apart.

Table I. Terminations of Encounters in First 4 s and Later

Kind of termination	Number of comparisons with proportion in first 4 s > proportion after first 4 s	<i>P</i> (sign test, two-tailed)
Third bird supplants a participant	6	NS*
Subordinate leaves	6	NS†
Dominant leaves	2	NS*
Dominant supplants subordinate	9	0.004†

Based on the proportions of each kind of termination among encounters that lasted 4 s or less and among encounters that lasted longer.

**N* = 10 (2 separations × 5 aviaries: 76-1, 76-3, 76-4, 77-2, 77-5).

†*N* = 9 (as a result of one tie in sample of 10).

durations of Encounters were nearly identical at 15 and 60 cm (Fig. 3). As described below, interruptions by a third bird occurred more frequently at 60 cm and thus compensated for reduced tendencies by the two participants to terminate an Encounter. Since the durations of Encounters at both separations of feeders approximates 10 s, the rate of each kind of termination approximates the overall proportion of that kind of termination divided by 10 s.

The proportion of encounters in which one participant supplanted the other was twice as

great on average at 15 as at 60 cm (means 16.8% and 8.1% respectively, Fig. 4). The proportions of encounters in which one participant showed aggression (either supplanted or threatened the other) differed even more between 15 and 60 cm (32.1% and 8.1% respectively, Fig. 4). The proportion of encounters with aggression was significantly greater at 15 cm than at 60 cm for each of the nine groups (χ^2 tests, $P < 0.01$ in 17 sessions, $P < 0.05$ in the remaining sessions). Thus Marler's (1956) conclusions about the

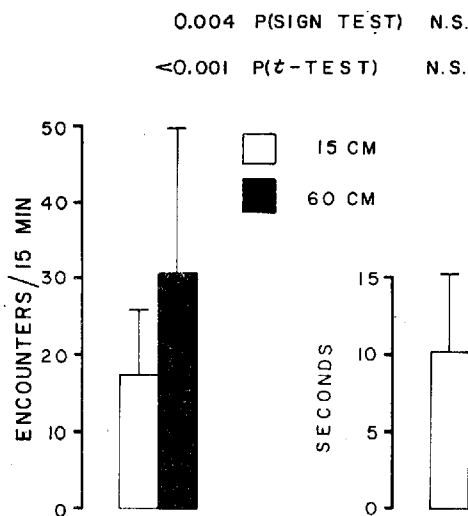


Fig. 3. Mean rates (left) and durations (right) of Encounters at 15- and 60-cm separations of the feeders. Dark bars, feeders 60 cm apart; open bars, feeders 15 cm apart. Each bar shows the mean for *N* = 18 series of observations; the vertical line above each bar represents 1 sd around the mean. At the top are levels of significance for differences between the two distances according to a sign test and a *t*-test for paired data (calculated from angular transformations of the proportions).

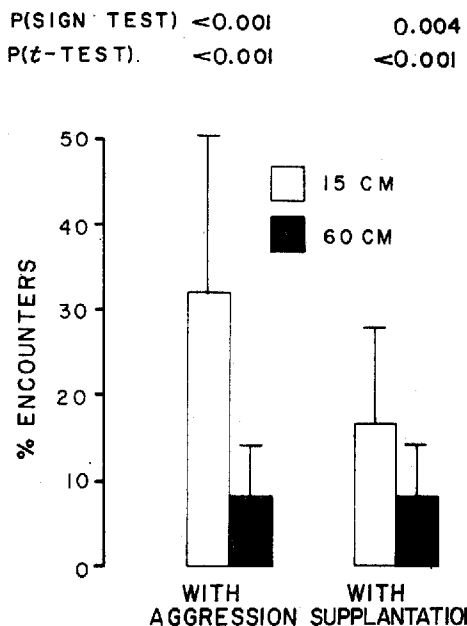


Fig. 4. Mean percentages of Encounters that included aggression (one bird supplanted or threatened the other) or supplantation by one of the participants. See Fig. 3 for conventions.

effects of proximity on the probability of aggression were clearly confirmed by our results.

No consistent seasonal trends occurred in the five aviaries observed for several series, although the proportions of Encounters with aggression (supplantation or threat) sometimes varied considerably between series (Table II). Both among the 9 initial series for each aviary and among the total of 18 series, aggression occurred about four times as often at 15 as at 60 cm, and supplantations occurred about twice as often.

Supplantations by a third bird were more likely when the participants in an encounter were 60 rather than 15 cm apart (Fig. 5). Birds were thus more likely to supplant a subordinate at a feeder when other opponents were farther away. Since subordinates were more likely to approach higher-ranking birds at 60 cm than at 15 cm (see below), a third bird with rank intermediate between the two feeding birds would be more likely to supplant the subordinate when the dominant was farther away.

The subordinate participant in an Encounter was more likely to leave at 15 than at 60 cm (Fig. 5). The dominant participant, on the other hand, was less likely to leave at 15 than at 60 cm (Fig. 5), although this result was not consistent across series. Thus when two birds were closer together, the subordinate individual had a greater tendency to leave the Encounter, while a dominant individual had a greater tendency to supplant the subordinate and perhaps less tendency to leave.

Terminations of Alone Periods

Encounters were nearly twice as frequent at 60 as at 15 cm (Fig. 3). This result indicates that tendencies to approach opponents, as well as tendencies to attack or leave, varied with the separation of feeding sites. Analysis of the terminations of Alone Periods can provide more information about tendencies to approach oppo-

nents. An Alone Period terminated in one of three ways: another bird joined the subject at the other feeder to initiate an Encounter; the subject left; or another bird supplanted the subject while the other feeder remained empty.

Neither the durations of Alone Periods nor the average numbers of Alone Periods per 15 min differed at the two distances (Fig. 6). At both distances, Alone Periods terminated at approximately constant rates after initiation (Fig. 7). There was no consistent tendency for the three lowest-ranking birds in an aviary to differ from the three highest-ranking birds in the number of Alone Periods at either distance. Nor did low- and high-ranking birds differ consistently in the durations of Alone Periods. Consequently, the rate of each kind of termination of Alone Periods approximately equals the overall proportion of that kind of termination divided by 10 s, the average duration of Alone Periods for both separations of feeders.

The proportion of Alone Periods that terminated by the subject leaving differed slightly at the two separations of the feeders: an individual's tendency to leave a feeder was influenced even by its proximity to a vacant feeder. The proportions of the other two kinds of terminations also differed at 15 and 60 cm separations of the feeders: joins were more likely at 60 cm and supplantations were more likely at 15.

These differences resulted in part from increased tendencies of birds to join, rather than supplant, solitary lower-ranking birds when the feeders were farther apart (Fig. 8). With an opportunity to feed at a sufficiently great distance from a subordinate, a dominant tended to take this opportunity rather than supplant the subordinate. This tendency, however, did not appear during the first observation series, when the birds in each aviary had been together less than three weeks.

Table II. Comparisons of Agonistic Behaviour at a Separation of 15 cm in Different Series (Aviaries 76-1, 76-3, 77-2, and 77-5)

	Encounters/ 15 min	% with aggression
Comparison of series 1 and series 2*		
Mean difference (SD)	4.8 (7.6)	10.2 (10.7)
<i>t</i> (<i>df</i> = 3)	1.25	1.91
Comparison of series 1 and series 3*		
Mean difference (SD)	1.9 (12.6)	2.8 (9.3)
<i>t</i> (<i>df</i> = 3)	0.31	0.61

*Series 1, February; series 2, March; series 3, March-April.

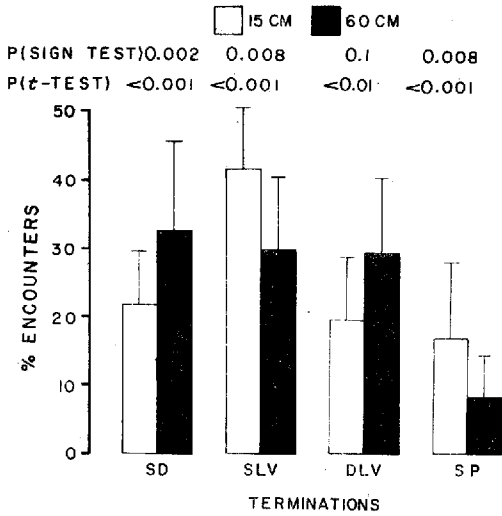


Fig. 5. Terminations of Encounters at 15- and 60-cm separations of feeders. Encounters terminated when a third bird supplanted one of the participants (SD), the subordinate participant left (SLV), the dominant participant left (DLV), or the dominant supplanted the subordinate (SP). See Fig. 3 for conventions.

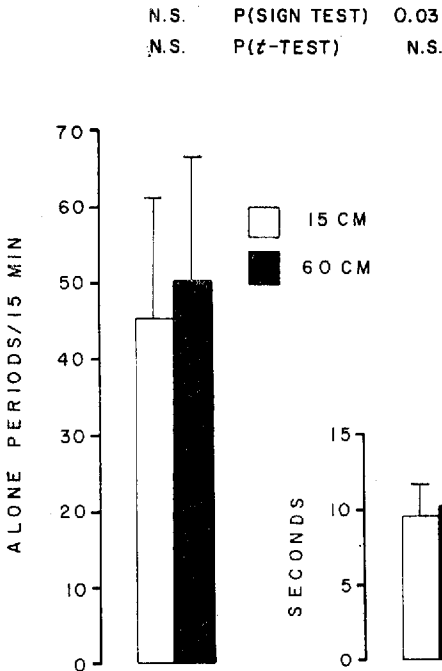


Fig. 6. Mean rates (left) and durations (right) of Alone Periods at 15- and 60-cm separations of the feeders. See Fig. 3 for conventions.

In addition, the bottom three birds were more likely to join the top three birds at a separation of 60 cm than at 15 (Fig. 8). In contrast, the top three birds were equally likely to interact with the bottom three birds at 15 and 60 cm (Fig. 8), but when they did interact, as just noted, they joined the subordinate opponent more often at 60 cm than at 15 and supplanted the subordinate more often at 15 cm.

A bird was thus more likely to approach a higher-ranking opponent at a separation of 60 cm than at 15 cm. A bird was equally likely to interact with a lower-ranking opponent at either distance, but at 60 cm, in comparison to 15, it was more likely to join than supplant its opponent. Thus when the situation required close approach, a high-ranking bird was more likely to supplant its low-ranking opponent straight away.

Reactions to Different Subordinate Opponents

Marler (1956) briefly considered whether or not aggressive tendencies were related to an opponent's rank in a dominance hierarchy. He found no clear evidence that interactions between chaffinches in dominance hierarchies varied with

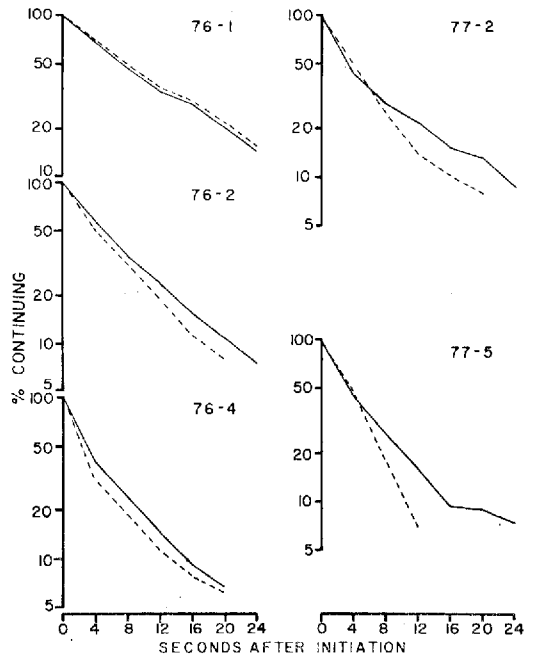


Fig. 7. Survivorship plots for Alone Periods in five aviaries. Solid lines, feeders 15 cm apart; dashed lines, feeders 60 cm apart.

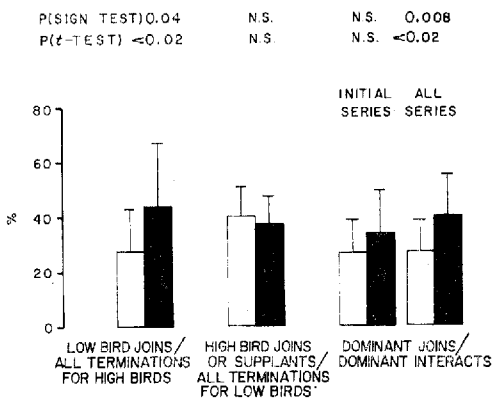


Fig. 8. Terminations of the Alone Periods of high-ranking and low-ranking birds at 15- and 60-cm separations of feeders. Left: tendencies of the three lowest-ranking birds to join one of the three highest-ranking birds (mean percentages of Alone Periods of high birds terminated by a low bird joining). Centre: 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). For the latter, means from the initial observation series ($N = 9$ series in February, the first series for each aviary) are separated from means based on all 18 observation series. See Fig. 3 for conventions.

the magnitude of the difference in rank between birds. Aggressive behaviour of one dominant bird toward individual subordinates varied but showed no obvious correlation with difference in rank.

In our studies also, the terminations of Encounters did not depend on the magnitude of differences in rank. We found no consistent differences in comparisons of Encounters between birds that differed in rank by at least 3 ($\Delta R \geq 3$) and those for which $\Delta R = 1$ (Table III). A bird was no more likely to supplant its immediate subordinate or avoid its immediate superior than opponents that differed considerably. Our studies also revealed that tendencies to supplant or join a solitary subordinate did not depend consistently on the magnitude of differences in rank (Table IV). Comparisons of Encounters between the top-ranking bird and each of the five lower-ranking birds showed that the proportion of Encounters in which the top bird supplanted its opponent did not vary with the latter's rank.

Further evidence along these lines comes from supplantations by a third bird when both feeders were occupied. When the third bird had intermediate rank between the two already on the feeders, the newcomer invariably supplanted the lower-ranking opponent. In many cases, how-

Table III. Terminations of Encounters for Participants with Large Differences in Rank ($\Delta R \geq 3$) and Small Differences in Rank ($\Delta R = 1$)

Kind of termination	Number of comparisons with proportion for large $\Delta R >$ proportion for small ΔR	P (sign test, two-tailed)†
Encounters terminating in 8 s or less/all encounters		
15 cm	3	
60 cm	4	NS
Third bird supplants a participant*		
15 cm	4	
60 cm	3	NS
Subordinate leaves*		
15 cm	1	
60 cm	2	NS
Dominant leaves*		
15 cm	3	
60 cm	2	NS
Dominant supplants subordinate*		
15 cm	4	
60 cm	2	NS

*Based on the proportions of each kind of termination for large ΔR and small ΔR among encounters that ended in 8 s or less.

† $N = 10$ (5, 15 cm; 5, 60 cm), Aviaries 76-1, 76-3, 76-4, 77-2, 77-5.

ever, the third bird out-ranked both birds on the feeders, so that it had a choice of which to supplant. Analyses of these choices revealed that birds had no systematic tendencies to supplant either the opponent closer in rank or the opponent farther in rank from the subject. This result applied regardless of whether the two opponents differed by one step in rank or by more.

In conclusion, birds in these hierarchies reacted distinctly differently to opponents with higher and lower ranks but did not react differently to opponents that were closer and farther in rank.

Discussion

Mechanisms Generating Stable Linear Hierarchies

Juncos form linear, stable hierarchies at feeding stations in winter (Sabine 1949, 1955, 1956, 1959) as well as in captive flocks (Balph 1977; Baker & Fox 1979). The hierarchies formed by our juncos were both linear and stable, with few exceptions, over periods of weeks or months. Our study provides some new information about the behavioural mechanisms that could generate such hierarchies.

Stable hierarchies could result from several different mechanisms. Each individual could recognize opponents and remember its dominance relationship with each. Alternatively, each individual could differ in some single dimension of its agonistic behaviour (either a single trait or a constellation of correlated traits). For instance, if each individual had a distinct distance at which it withdrew from opponents, those that withdrew at greater distances would be subordinate to those that withdrew at shorter distances. Individual differences in agonistic tendencies could arise through previous experience in agonistic encounters without regard to the identity of opponents or could come from intrinsic differences among individuals. Unidimensional variation in status signals could also produce stable hierarchies.

Table IV. Tendencies of Birds to Supplant (SD) or Join (JN) Solitary Subordinates at 15 cm Separation of Feeders for Large and Small ΔR (Aviaries 76-1, 76-2, 76-3, 76-4, 76-5; $N = 5$)

	Dominant JN/Dominant JN or SD mean (SD)
$\Delta R = 1$	0.617 (0.203)
$\Delta R \geq 3$	0.610 (0.204)
t	0.087
P (two-tailed)	NS

Infrequent triangles provide no clear evidence about the mechanisms of hierarchy formation. Although a small number of our juncos had triangular dominance relationships with opponents ($A > B$, $B > C$, $C > A$), these deviations from strictly linear hierarchies constituted a small fraction of the total number of dyadic relationships. They could indicate either recognition of special relationships with a few opponents or occasional importance of more than one dimension of opponents' agonistic tendencies and status signals in the determination of rankings.

The occurrence of occasional reverse supplantations (A usually supplants B but B sometimes supplants A) also admits of alternate interpretations. Either recognition of opponents or differences among opponents in a single dimension of agonistic behaviour could vary somewhat. The presence or absence of reverse supplantations in a hierarchy is the basis for the distinction between 'peck-right' and 'peck-dominance' hierarchies, but this distinction has no necessary connection with different mechanisms of hierarchy formation.

Clearer evidence concerning the mechanisms of stable, linear hierarchies comes from our comparisons of interactions between birds with small and large differences in rank. The hypothesis that rank depends on individual variation in a single dimension of agonistic behaviour or status signals predicts that, at any given separation, interactions between opponents farther apart in rank should be more polarized than those between opponents closer in rank. In fact we have not found any tendencies for juncos to behave differently to opponents, either higher-ranking or lower-ranking, in accordance with the magnitude of the difference in rank. Juncos must at least recognize opponents as members of two classes, those higher and those lower in rank.

When rank does not result from unidimensional variation in agonistic tendencies, the linearity of a dominance hierarchy requires higher order interactions between individuals (Chase 1974). For linear hierarchies, the interactions between any two individuals must depend on their interactions with other individuals. Our observations provide evidence that birds are sensitive to individuals other than their immediate opponents. For instance, individuals were more likely to supplant one of two opponents when the separation of the opponents was 60 rather than 15 cm, an indication

that the interactions between any two birds are affected by the proximity of a third.

Measurements of Individuals' Tendencies in Social Interactions

As measures of individuals' tendencies in social interactions, we have relied on the ways in which social states terminate. A social state is any situation in which individuals have some defined relationship with each other for a measurable duration (see Altmann 1974 for the distinction between behavioural events and states). The ways that individuals' interactions terminate a social state reflect their behavioural tendencies in that state. Such tendencies are thus accurately estimated by the instantaneous probability rates of terminal actions at any given instant after the initiation of the state. These measures amount to probabilities per unit duration of opportunity to perform the actions. They are analogous to instantaneous age-specific death rates, more specifically to instantaneous age-specific death rates for different mutually exclusive and exhaustively classified causes of death.

We have shown that these probabilities of actions per unit duration of opportunity can be estimated by means of a temporal analysis of the terminations of a social state, provided that the terminal actions constitute an exclusive, exhaustive classification. Furthermore, if the probability rates for each terminal act remain constant with time after the initiation of a social state, then the proportions of the different actions permit easy calculations of the estimated rates: (proportion of terminal action A)/(mean duration of the social state in seconds) = (probability of terminal action A) / second.

In only one case in our experiments did birds' tendencies change consistently with time after the initiation of an encounter. In particular, a dominant was more likely to supplant a subordinate opponent in the first few seconds after the initiation of an encounter in comparison to later. Otherwise, behavioural tendencies remained constant during encounters. Evidently the stimulus for overt aggression is greatest shortly after the appearance of an opponent at close range. This finding is in accord with suggestions that 'stimulus contrast' influences aggressive tendencies (Archer 1976).

As a result of the constant termination rates during both social states investigated here, the proportions of the different terminations of Alone Periods or Encounters are easily converted

to probabilities per second: divide the percentages in Figs. 5 and 8 by 100 (to convert to proportions) and then by 10 s (the mean duration of Encounters and Alone Periods at both separations of feeders). Only the double coincidence of essentially equal durations of both states at both separations of feeders makes it possible to compare the proportions of terminations without calculating the actual rates.

Seasonal and Long-Term Changes in Agonistic Behaviour

Comparisons of observations in February with those in March and April revealed only one significant difference. After a group had been together for several weeks, birds supplanted solitary subordinates less often when feeding sites were farther apart. No comparable changes occurred in subordinates' tendencies to avoid dominants. The change in the behaviour of individuals toward subordinates would tend to reduce overt aggression between individuals in stable flocks, provided sufficiently dispersed feeding sites were available.

Balph (1977) reported that juncos in aviaries engage in aggression more frequently and maintain greater separations during February and March than during December. Although one or two birds in the top half of the hierarchy in each of our aviaries began to sing in April, we observed no changes in the birds' agonistic behaviour at feeders. Possibly changes occur only in interactions away from food. Another possibility that might explain our failure to observe seasonal changes is the absence of females in our groups.

Agonistic Behaviour and Spacing

Our results show that tendencies to behave aggressively, to approach, and to avoid opponents vary with the distance between opponents and their dominance relationship. A bird is more likely to supplant a subordinate opponent in encounters at closer separations. Even when initiating an interaction with a solitary subordinate opponent, a bird is more likely to supplant the opponent when feeding sites are closer together and less likely to occupy a vacant feeding site.

Reactions to dominant opponents also vary with the distance between birds or available feeding sites. A bird is more likely to withdraw from a dominant opponent in Encounters at close range. In addition, when feeding sites are closer together, a bird is less likely to approach

a solitary dominant opponent. Reactions to dominant opponents thus suggest that a bird avoids situations in accordance with its chances of being supplanted.

Conditioned avoidance might explain why birds were more likely to leave a feeder when a vacant feeder was close by, even in the absence of any overt interaction with another bird. The tendency to supplant subordinates, rather than approach to close range, could lead to some avoidance of a nearby feeding site even when vacant.

Encounters were more frequent at greater separations for two reasons: birds were (1) more likely to join dominant opponents and (2) more likely to join, rather than supplant, solitary subordinates when feeding sites were farther apart. Yet Encounters lasted no longer at greater separations once they had begun. Although the participants were less likely to terminate an Encounter at a greater separation, a third bird was more likely to supplant one of the participants.

In conclusion, although juncos spent more time feeding simultaneously when feeders were farther apart, this effect of greater separation between feeding sites resulted entirely from more frequent, rather than longer, Encounters. The increased frequency of Encounters at a greater separation resulted in turn from changes in each bird's behaviour toward both dominant and subordinate opponents as the separation of feeding sites increased.

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