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DOMINANCE BEHAVIOR AND WINTER HABITAT DISTRIBUTION IN JUNCOS (*JUNCO HYEMALIS*)

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INTRODUCTION

In a region where a bird species is normally found, there are occupied and unoccupied habitats. Whether or not a particular habitat is occupied depends on whether or not any individuals of the species choose to reside there. The habitat selection of the individuals is (and has been) acted upon by natural selection so that birds which choose to reside in the habitat best suited to their needs become more frequent in the population. The habitat selection of present individuals is the result of a long history of evolution, and may be presumed to be well adapted to, and therefore largely determined by, the factors which give rise to selective pressures. Then the operation of these selective factors, known as ultimate factors, is the major determinant of habitat distribution. The purpose of this paper is to consider in theory and with supporting data the characteristics of the habitat distribution of wintering Junco populations and some of the ultimate factors that influence that distribution. For the most part, I shall be concerned with the role of dominance behavior and its interaction with food supply.

The report is divided into sections each of which represents a separate small study. The format of each section is that of the usual scientific report. The general procedure followed the hypothetico-deductive philosophy of science (Tricker, 1965; Ghiselin, 1966). Thus, the explanation of previous observations is used to formulate specific hypotheses or general assumptions from which specific hypotheses may be deduced. These specific hypotheses are used to direct further observations, and if possible, to make explicit, testable predictions. The new observations, and the results of the tests of the predictions are then used to develop new hypotheses, if necessary, or to refine old ones.

This approach is distinct from the enumerative or descriptive methods. The enumerative philosophy considers only hypotheses which assert the existence of some potentially observable phenomenon under study. In the hypothetico-deductive philosophy, any hypothesis can be studied, and direct evidence for the existence of the phenomena under study is neither required nor often obtained. This means that usually the hypotheses are never proven absolutely correct or incorrect. However, it can be shown (Tricker, 1965) that

repeated verification of the predictions of an hypothesis, even indirect predictions, is substantial evidence for the validity of the hypothesis. Hypothetico-deductive research has been extremely successful in those fields (genetics, physics) where the descriptive approach is impossible because the phenomenon involved cannot be directly observed. No one could see genes, or electrons; yet, a great deal was learned about them. This success is ample justification for using the approach in areas where direct observation is expensive, destructive, or even inconvenient.

Consistent with the tenets of the hypothetico-deductive philosophy I have made a careful distinction between results which verify a prediction and results which were not directly expected, but which can be explained.

Formulation of the Basic Hypothesis

The basic hypothesis has two parts: (1) Habitat densities in winter populations of flocked sparrows in temperate regions are limited by food supply in such a way that many individuals are forced to reside in habitats unsuitable for feeding. (2) The mechanism restricting these densities involves dominance.

The first part of the hypothesis is derived from the assumption that sparrow populations are limited by winter food supply (no distinction is made between artificial and natural food sources). This assumption has been developed earlier in order to explain some observations on breeding finches at Raleigh, North Carolina (Fretwell, 1967 and unpublished). From this assumption, it follows that there is not sufficient food for all the members of a species to survive the winter, and mortality is directly related to a lack of available food. The available food supply of winter sparrow populations is fixed, however, by the seed production of the preceding summer and fall. If all the birds in the populations are permitted to eat, the food will be exhausted before the winter ends and all will die. Thus some birds must be forced away from the food at the beginning of the winter so that enough remains later on for the surviving population. This might be accomplished by limiting the density in the habitats where food is available, so that the excess population is forced to reside in unsuitable feeding areas. This argument does not apply to regions (e.g. tropical) where production of food is continuous. It does apply in temperate regions however, and so we have the first part of the basic hypothesis.

The second part of the hypothesis was derived from considering the results of a study (Fretwell, 1969) on habitat variation in nesting success in Field Sparrows (*Spizella pusilla*). In this study it was found that most of the Field Sparrows bred in a habitat where breeding success was lower than elsewhere. This habitat however also maintained a winter population of Field Sparrows while other breeding habitats did not. It was thought that the increased experience which accrued from breeding in the preferred winter habitat type gave individuals a dominance advantage (Nice, 1943; Sabine, 1959) which might be useful in the density-limiting process hypothesized above. If so, then Field Sparrows which, during the

summer, bred in the winter habitat would have, in the winter, more experience, high dominance status, and a higher non-breeding season survival rate which would compensate for their reduced breeding success.

There is evidence that winter sparrow populations are limited in the way postulated. Mewaldt (1964) found that removal of resident individuals in an area resulted in an influx of new individuals which presumably had been held away by the presence of the residents. Sabine (1955) found that junco (*Junco sp.*) flocks had mutually exclusive ranges. She also found (1949, 1955, 1959) that juncos had extensive dominance interactions which may serve to hold flocks apart (1959). Finally (1955), she noted that juncos which bred in the winter habitat were dominant.

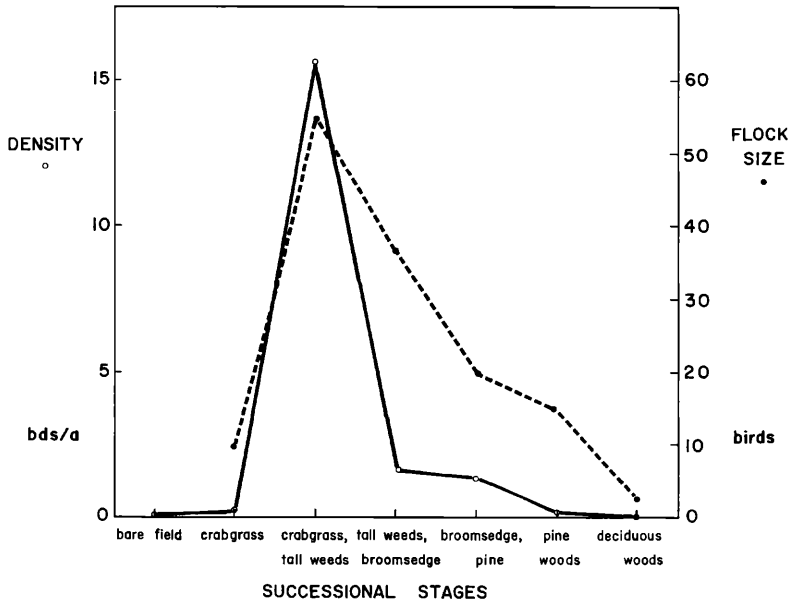
The basic hypothesis is equivalent to the density-limiting territorial hypothesis discussed in a previous theoretical paper on breeding habitat distribution (Fretwell and Lucas, 1969). The theoretical developments of that paper can easily be generalized to include winter bird habitat distributions. An ideal free distribution is identically defined. Also, the mathematical statement of the ideal territorial distribution defines an ideal dominance distribution as hypothesized to exist above. However, predictions which result from this theory are untestable in the winter populations, and so a more direct approach must be used. This approach, stated in the terminology of the theory, is to show directly the existence of a density-dependent t function which expresses the difference between the average suitability in a habitat and the suitability to the most sub-dominant individual. This earlier-developed theory is compared to the present development so that the hypothesis and approach may be well defined. However, the problem will be considered independently of this theory so that this paper will be self-contained.

Studies of this hypothesis on Field Sparrows have not been successful, but an opportunity to conduct studies on Juncos arose during the winter of 1964-65, and again in 1966-67. The population structure of Juncos is similar to Field Sparrows in the winter in this area (Quay, 1940; 1947). Before describing the circumstances of these studies, let us consider the distribution of Juncos around Raleigh, North Carolina.

The winter distribution of Juncos around Raleigh, North Carolina

The distribution of Juncos around Raleigh, N. C. in the winter with respect to plant communities is shown in Figure 1; also plotted is flock size (data from Quay, 1940). This figure describes in quantitative detail the major characteristics of the Junco population. In particular, the species is most abundant in open weed fields and less abundant elsewhere. Juncos are quite scarce in mature woods—both deciduous and coniferous. Also, flock size decreases as overall abundance decreases. Thus, in the extremes there are two spatially separated parts of the local Junco population which will be called *flocked* and *dispersed*. The *flocked* birds are found in large flocks in weed fields. The *dispersed* birds are found in small groups or alone

Figure 1. Density and flock size of Junco over plant successional stages at Raleigh, N. C. (after Quay, 1940).

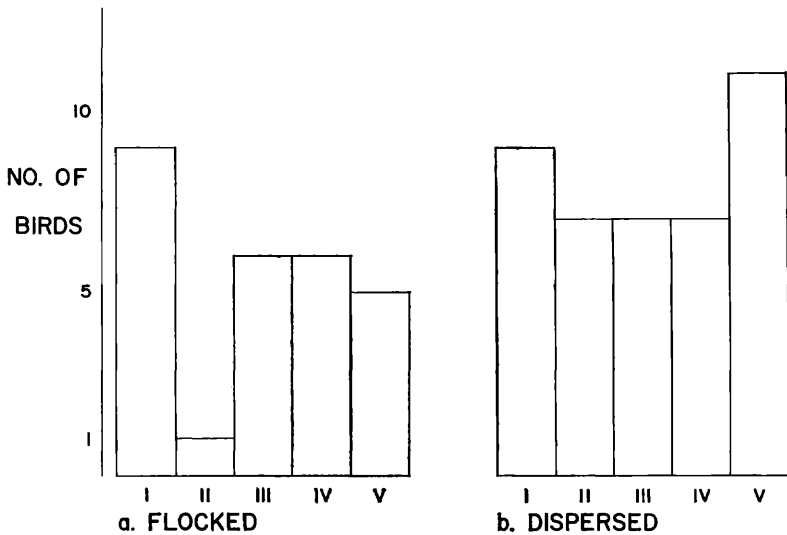


in mature woods. Of course, intermediates to these extremes occur. As an extension of the basic hypothesis, we will explicitly postulate that the Junco flocks in the evidently-preferred field habitats are using dominance behavior to limit the density there, forcing individuals into the less suitable woodlands.

Circumstances of the study

The opportunity to study Juncos arose by accident. A feeding station (mixed commercial bird seed scattered on the ground) was established at my home in an open wooded area in late fall of 1964. This station attracted Juncos slowly, and the birds usually came to the feeder alone or in small disorganized groups of 2-5 individuals. By mid-January however, there were about 40 regular visitors to this station, as determined by color banding. Another feeding station (similar to the first) was established in early February in an open clover field which was bordered by wooded areas on three sides and by a weed field on the fourth. This feeder quickly attracted a large (more than 40 individuals) flock of Juncos which always traveled in a tight group. In noting the marked difference in the way in which Juncos used the two feeding stations, I concluded that I had accidentally isolated individuals from two extreme parts of the local Junco population. Evidently the birds coming to these two feeders presented a good opportunity for examining the basic hypothesis as it applied to Juncos.

Figure 2. Distribution of birds with respect to percent of fights won. Class I represents birds which won from 0 to 19.9% of their fights; II, 20 to 39.9%; III, 40 to 59.9%; IV, 60 to 79.9%; V, 80 to 100%.



Dominance relations in wintering Juncos

The first step was to describe a reasonable mechanism by which the Juncos could regulate density with dominance behavior in flocks. I began by describing the dominance relations in both flocked and dispersed birds.

Procedure

In obtaining dominance data, both groups of birds were marked with color bands and observed at the feeders with binoculars. With the flocked birds, there was continual fighting and motion. This meant that it was usually impossible to identify both the winner and the loser of a fight (a displacement). The only measurement which could be made in quantity for every individual was the proportion of dominance struggles won. To estimate this, I noted at the first observation of an individual in a contest the color band code of the individual followed by a plus (+) or a minus (-), depending on whether that individual had won or lost. If that individual was later seen winning or losing a dominance contest, another plus or minus was recorded by its code name. For every individual with five or more records, the percent of the total which were won was calculated. Five classes of twenty percentage units each were established, and each bird placed in its appropriate class. For both flocked and dispersed types, the number of individuals in

each class was tabulated. Sabine's study (1949) was conducted in a semi-wooded area, on loosely flocked individuals and so appeared to deal with dispersed Juncos. Therefore, her data is presented along with mine for this group.

Results

An outstanding difference between the flocked and dispersed birds lay in the frequency of fighting. Dispersed birds were observed for about 30 hours, with an average of about .2 observed fights per hour per individual. Flocked birds were observed for 6 hours and the observed rate of fighting in that group was more than 5 fights per hour per individual. Sabine (1949) recorded about .4 fights per hour per individual. The distribution of individuals with respect to the percentage of victories is given in Figure 2.

Discussion

In the flocked birds, it appears that there are two distinct groups. The first group consists of individuals which win less than 20 percent of their dominance struggles; the second group consists of individuals which win more than 40 percent of their dominance struggles. Sabine (1949) showed that relatively dispersed Juncos have a stable peck order with few reversals. If this is true of flocked Juncos as well, then a flocked bird will lose fights to only those above him on the peck order. Thus, individuals which lose most of their dominance struggles (i.e. the first group described above) must do most of their fighting with birds above them on the peck order. The reverse is true of individuals which win most of their struggles (i.e. the second group described above). This implies that the birds in the upper group are dominant over the birds in the lower group and that most of the fighting takes place between groups as opposed to within a group.

As an explanation for these results, suppose the birds were in a food patch fighting over feeding positions which were fewer in number than the size of the flock. The dominant individuals would occupy the feeding positions while subdominant individuals would be without such positions. The fights would take place between those without feeding positions and those with, i.e. between a group of subdominants and a group of dominants. Since the peck order is stable, the dominants do not trade places with the subdominants. Thus, we would have a group of perpetually subdominant individuals repeatedly fighting with and repeatedly losing to a group of perpetually dominant individuals. Birds in the first group would lose all of their fights while birds in the second group would lose none. A frequency plot of such a situation would have all of the first group in the 0-20 percent class and all of the second group in the 80-100 percent class. The distribution in Figure 2 is not so extreme as this given explanation would suggest, but it is bimodal.

To account for the spread in the modes, we can employ the concept of individual distance, supposing that the Juncos fight with one another when in close contact. In this case, the birds in the feeding

positions would fight together if the feeding positions were close together, and similarly, the birds without feeding positions would fight together if they got close to one another. In this particular study, the food was scattered on the ground over a roughly circular area. The birds occupying feeding positions would be inside the circle while those without feeding positions would be outside the circle. This means that the dominant group were close together in a confined circle while the subdominants were more widely separated around the outside of that circle. We shall expect then that the dominants would fight among themselves more than the subdominants. Without this intra-group fighting we have seen that the dominants would all win 100 percent of their fights and the subdominants would lose 100 percent. With the addition of intra-group fighting however, some dominant group individuals fight with individuals above them on the peck order and thus lose some of their fights. Also, some subdominant group individuals fight with individuals below them on the peck order and thus win some of their fights. This creates a spread in the separate modes of the distribution—the more intra-group fighting, the more spread. Because of their closeness in feedings we expect the dominant group to fight among themselves more than the subdominant group, and so we expect more spread in their mode. Figure 2 conforms to this expectation.

When we examine the frequency histogram of the dispersed birds, we find it fairly uniform in comparison with that of the flocked birds. This may be interpreted as an increase in spread which effectively (but not completely) obliterates the bimodality. In terms of the explanation given above for the flocked histogram, this means that in the dispersed birds, fights resulting from individual distance violations are much more frequent than fights over feeding positions. This is probably due to the fact that the dispersed birds travel in such small groups that the number of feeding positions in the food patch was usually greater than the number of *Juncos* present.

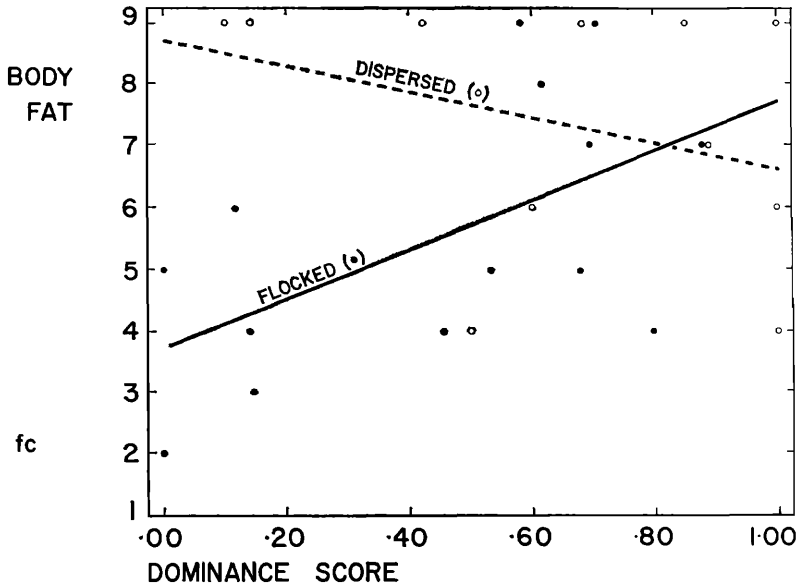
This explanation provides a tentative description of fighting in the flock. The importance of food is evident and there is an element of despotism whereby some individuals have good feeding positions at the expense of other individuals. This description provides a more explicit understanding of the basic hypothesis and leads to some testable predictions. We consider first the question of dominance and feeding positions.

Dominance and fat reserves

The idea to be considered is that dominant individuals in the flock have better feeding positions and therefore, more food than subdominant individuals. This is not expected to be true in dispersed birds since they travel in flocks which are small relative to the size of the food patch and have no need to fight over food.

In order to assess the food supply, it was assumed that birds which have better eating positions will have more visible fat re-

Figure 3. Body fat and dominance score. The lines are fitted by least squares to the plotted points.



serves. Then we can predict that if the above idea is correct, there will be a positive relation between fat reserves and dominance status in the flocked birds which despotically fight over feeding positions, but not in the dispersed birds, in which fighting is not so related to feeding positions. This prediction can be tested directly with flocked and dispersed birds for which both fat and dominance scores are available.

Procedure

When the birds were color-banded, they were placed in one of 9 ordinal classes based upon the amount of abdominal fat which could be seen through the skin. The procedure followed was modified from Helms and Drury (1960). In both groups, the majority of the birds were handled in a single morning (flocked) or afternoon (dispersed): only those birds were considered in the analysis. This was done to avoid the variation in fat class due to climatic factors or time of day (Helms and Drury, 1960; Helms, 1963). The model was formulated describing fat class as linearly dependent on dominance score in flocked, but not dispersed birds. Null hypotheses tested statistically were that the coefficients of dependence or proportionality relating fat class to dominance status were in both cases equal to zero, and were also equal to each other. The regression analysis followed Steel and Torrie (1960, pp. 191-180).

Results

Figure 3 shows a plot of the data points and the regression lines. As can be seen, all the requirements of the food hypothesis are met. The dependence of fat class on dominance is positive ($b = 4.014$) and significant ($t_b = 2.4$, 12 df) in the flocked Juncos but insignificant ($t_b = -1.2$, 9 df) in the unflocked birds. The coefficients of proportionality for the two groups are significantly different ($d = 6.144$, $t_d = 2.5$, 21 df).

Discussion

These results strengthen the reliability of the explanation given for the frequency plots and the implications of that explanation. The statistical tests of significance must be accepted with reservations, however, since they assume that errors are normal. As Hailman (1965) has pointed out, fat class data do not conform to this assumption.

Implicit in the basic hypothesis is the proposition that a major proportion of the mortality is directly related to a lack of available food. The above results suggest that this mortality would be restricted to the subdominant members of the population. This suggestion is considered in the next two studies.

Dominance and stress in flocked Juncos

Up to this point, we have evidence that Juncos in the flock fight over food, and the suggestion that this results in the subdominant individuals in the flock having a lower chance of surviving the winter. This suggestion is based essentially on the assumption that survival is related to food supply (fat reserves) which were shown to be lower in subdominant birds in the flock. If dominance is related to survival, we should expect low dominance to produce a stress reaction. It might be argued that low dominance would produce a stress reaction even if it is not related to survival, but it is hard to justify such a relation in terms of evolution. It is in fact hard to see why any factor not diminishing survival or reproduction would produce a stress reaction. The stress response is not considered to be a special adaptation to changes which occur normally in the environment of the species. Rather, it seems to be a general response of the organism to extreme and abnormal changes of all types. Such extreme changes may reasonably be considered to reduce the survival potential of the individuals exposed to them.

We may test the hypothesis that subdominance (by its effect on food supply) is related to survival by seeing whether subdominant individuals are under more stress than dominant individuals. An index of such stress is an increase in the size of the adrenal glands (Selye, 1950, p. 323). Therefore, this study was concerned with weighing the adrenal glands of some Juncos for which dominance scores were available, and then determining whether the gland size increased with decreasing dominance status.

Procedure

This experiment was conducted several weeks after the dominance scores had been obtained. It was conducted on the flocked birds only. Five birds were collected at 5:00 P. M., March 9, 1965, with a mist net. They were immediately weighed to .1 gram, and their color bands were removed. They were examined for fat, sacrificed, thoroughly wetted and placed in ice water. After a delay of about two hours, they were dissected and their adrenals examined, removed, and both weighed together on a Roller-Smith balance. In two cases, one of the adrenals could not be wholly removed. In one case, the unremoved gland was estimated to be about 2/3 the size of the unremoved gland. In the other, the glands appeared to be of equal size. In both cases, the single gland was weighed and an appropriate correction factor applied to make the weights comparable with the other weights of both glands. This was all done with no knowledge of the dominance status or weight of the bird being dissected. Therefore, it added only variability to the experiment and not any bias. Upon removal, the glands were placed on a piece of filter paper for about five seconds and then placed wet in the weighing cup.

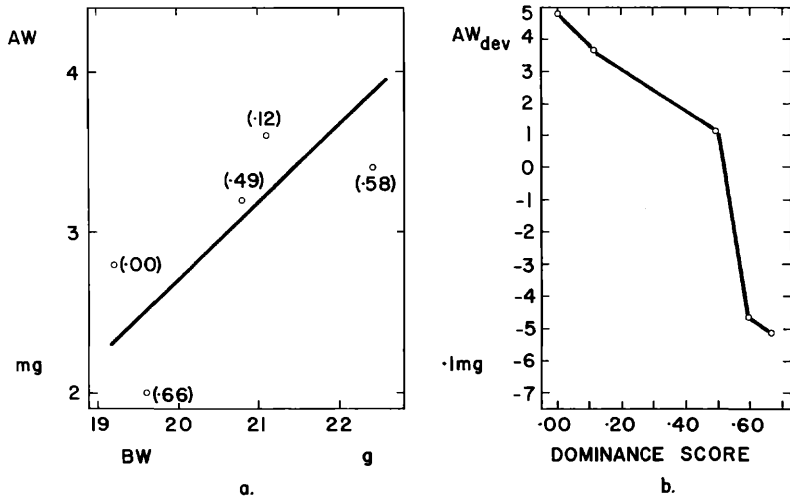
The data were analysed according to the principles of multiple regression in order to properly correct for body weight. The hypothesis was made that adrenal size was proportional to both both weight and dominance status. Using multiple regression, the available data is used to estimate both co-efficients of proportionality simultaneously. Each co-efficient is estimated as if the other variable were held constant. In this case, the estimate of the proportionality constant relating adrenal size to dominance status is as if all the birds in the sample were of the same weight. This is good for two reasons: (1) the variability of the adrenals weights due to body weight no longer disturbs the analysis, and (2) any correlation between adrenal weight and dominance status via their mutual dependence on body weight is automatically accounted for. The estimate of the proportionality constant relating adrenal size to dominance status can be tested for statistical significance (Steel and Torrie, 1960, chap. 14).

Results

In the results of the analysis, it was found that the corrected adrenal weights showed a significant negative relation with the percent of dominance contests won ($b = -1.47$, $F = 18.884$, 1, 2, d.f.): sub-dominant birds had large adrenals and thus appear to be under more stress. The range of percentages in the sample was 0-66; there is no reason to expect the dependence relation to hold outside this range. In view of the very small sample drawn (5 birds), the fact that a statistically significant relation was found indicates that the dependence of adrenal weight on both body weight and dominance is strong (i.e. has low variance). This result has also been found in mice (Welch and Klopfer, 1961).

The results are shown in Figure 4. In 4a., adrenal weight has been plotted versus body weight and a regression line drawn. The sample

Figure 4. Adrenal weight, body weight, and dominance score. In *a*, adrenal weight (AW) and body weight are plotted with the (multiple) regression line. Deviations (AW_{dev}) from the fitted line in *a* are plotted in *b* against dominance score.



points are also plotted with their respective dominance scores. The regression line can be considered as a running average of adrenal weights with an increase in body weight. We can see that the birds with low dominance scores are generally above the regression line, while those with higher scores are below the line, indicating that low dominance Juncos have heavier than average adrenals, while the high dominance Juncos have lighter than average adrenals. This relation can be clearly seen in 4b, where the distance each sample is from the regression line has been plotted versus the respective dominance status.

These results provide further evidence that dominance status is a factor affecting the survival of flocked Juncos.

Dominance and survival in flocked Juncos.

Another test of the hypothesis that dominance status, by its effect on food supply, also affects survival is based on the assumption that recapturability of banded individuals is directly related to their survival. Given this assumption we may compare the survival rates of dominant and sub-dominant birds through the winter season, by comparing their respective recapture rates. Thus, we are led to predict that if the dominance is positively related to food supply (or fat class), then dominance will also be positively related to recapturability. This prediction could not be tested in 1964-65 or 1965-66. In 1966-67 however, an ice storm (freezing rain, sleet) in late December permitted me to obtain 18 color banded

individuals which could be scored for dominance early in the winter. These birds provided an opportunity to test the prediction that dominance is positively related to recapturability.

The birds were winter residents in the area about my home, which in the two years since the earlier studies, had become considerably more open. Several fields and edges were available this year that were not in 1964-65. As might be expected then, the Juncos were less dispersed, traveling in flocks of from 5 to 15 birds. Some individuals were still solitary however, and the flock structure was not so tight as had been observed in the field Juncos in 1964-65.

Procedure

The ice storm occurred on December 24, 1966, and for the first time all winter, the flocks of Juncos in the immediate area about my yard came regularly to the baited area. There were about 30 birds present, and 23 were netted and color banded. Of these 23, 18 remained in the area. The 18 were observed for approximately 10 hours, and a rank order of dominance obtained.

The scoring method used earlier was not employed; instead the winner and loser of each fight was recorded whenever possible and the birds arranged in a linear order, so that if A dominated B, and B dominated C, then the order was A, B, C. Where the needed contests were not observed, individuals were given the same rank. The final ranking had ten classes, and on December 29, 1966, feeding at the baited area was discontinued. It was begun again January 15, 1967, and continued through January 19, 1967 to recover (by sight) the scored individuals. Fifteen of the 18 were recovered, and so the feeding was again discontinued until Feb. 9, 1967, when a six-inch snow fell. Only four birds were present at this time, and these were not regular at the feeding area. However, on Feb. 15, the snow had largely disappeared and eight of the other Juncos reappeared. On Feb. 19, the feeding was again discontinued until March 6, when the final batch of recoveries were made. From the time that dominance scores were obtained to the time of the last recovery, 68 days elapsed. On 14 (20 percent) of these days the Juncos were provided with artificial food. However, the birds used the bait regularly on only about seven days.

Most of the Juncos handled on December 24, 1966 were caught together in the morning. For all of these birds fat-class ranks were obtained. Twelve of these remained to be given dominance ranks and the fat class and dominance ranks were correlated in a Spearman's rank correlation test (Steel and Torrie, 1960; p. 409). The correlation coefficient was .68, with a significant *t* value (10 d.f.) of 2.8. Thus, this group of birds is subject to the prediction stated earlier. Since dominance is positively related to food supply or fat class, it is predicted to be positively related to recapturability.

Results

Eight of the 18 dominance-scored Juncos disappeared over the whole season. Figure 5 shows the relation between dominance and recapturability. Seven of the eight disappearing individuals were

below the median dominance level, a significantly high proportion ($t = 2.9$, 16 d.f.).

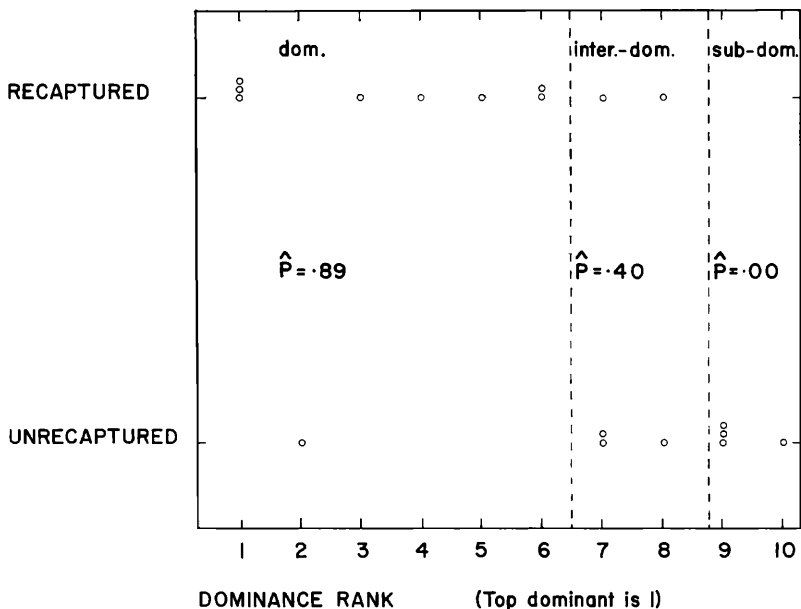
Discussion

The dominance—food supply—survival hypothesis is again verified; this time with data from an essentially natural (i.e. unbaited) population. Implied in the preceding development was the assumption that observations on semi-natural (i.e. baited) populations applied to natural populations as well. This assumption is substantiated in Figure 5, where all of the presumed mortality fell on an unbaited population.

Only one bird was reported as “disappeared” at one recapture attempt, but reappeared later, indicating that most of the disappearing birds were permanently absent. Also, there was no evident increase in the proportion of unmarked birds at any of the recapture efforts, indicating that little interchange of individuals with other, unbanded populations occurred. This agrees with the conclusion of Sabine (1955), that Junco populations are stable. Presumably all of the available suitable habitat for Juncos is filled with dominant individuals, and so the subdominants gain no advantage by dispersing. Thus, the disappearance probably reflects mortality.

On inspection of Figure 5, it appears that the points fall into three groups. There is a dominant group (ranks 1 to 6 containing 50 percent of the total) with survival rate 89 percent. There is a subdominant group (ranks 9 and 10, 22 percent of the total) with survival rate close to 00 percent. And there is an intermediate dominant group (ranks 7 and 8, 28 percent of the total) with survival rate 40 percent. This breakdown can be explained by further consideration of the food patch idea invoked in explaining Figure 2a. The bimodal distribution in Figure 2a. was explained by supposing that the flock fed on a food patch that contained fewer feeding positions than there were members of the flock. The dominant individuals occupied these feeding positions while some sub-dominants went without. This explanation was reasonable because the baited area where the dominance scores in Figure 2a. were obtained was in fact a food patch. For the explanation to apply in natural situations, we must postulate that the flock normally feeds on one or several natural food patches, each of which contains fewer feeding positions than members of the flock. If these natural food patches were all of a size, then they all would contain a certain number (N) of feeding positions. As the flock moved from patch to patch, the N top dominants in the flock would always have these feeding positions; and since most mortality is assumed to be related to a lack of food, these dominants would be expected to have a high survival rate. The rest of the flock would never have a feeding position and would all die or disperse. The breakdown of Figure 5 suggests that these two groups do in fact exist. But, besides the dominants and subdominants, there is a third group, intermediate dominants, with intermediate survival rate. This may be explained by supposing that there are several food patches, which vary some-

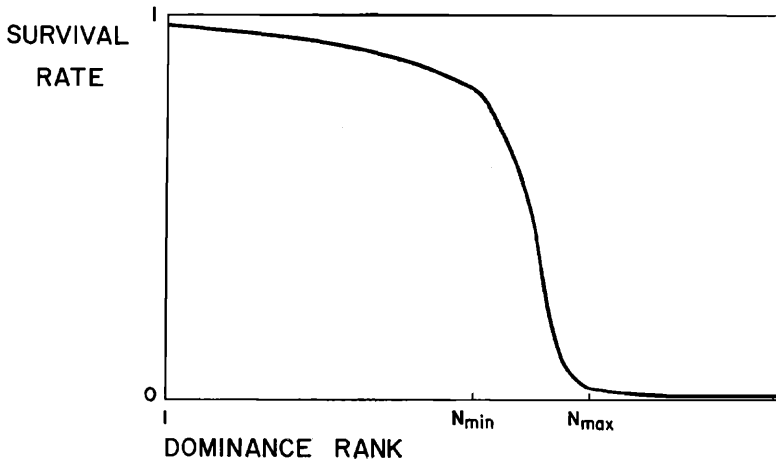
Figure 5. Dominance and recaptureability. The bird(s) of each observed dominance rank are plotted as recaptured (upper line) or unrecaptured (lower line). The birds are divided into three groups: dominant, intermediate dominant, and subdominant. This permits estimation of probabilities of recapture and the estimates (\hat{p}) are given.



what in size. Then there is a minimum and a maximum sized patch in the range of the flock, with other patches being of intermediate size. The number of feeding positions in the smallest patch (N_{\min}) would be less than the number in all other patches. The number in the largest patch (N_{\max}) would be greater than the number in all other patches. In this case only the N_{\min} top Juncos in the peck order will always have feeding positions, and the Juncos with dominance rank greater than N_{\max} will always be without a feeding position. The Juncos with dominance intermediate to N_{\min} and N_{\max} sometimes will have a feeding position, and sometimes will not depending on which patch the flock is feeding. These intermediate dominant Juncos may then be expected to have some intermediate survival rate, as seen in Figure 5.

This explanation may not be justified by the breakdown in Figure 5, which may have arisen by chance. However, it leads to a clear definition of this part of the basic hypothesis. This definition is described in Figure 6, where survival rate is related to dominance status. The survival rate is hypothesized to be highest for the top dominant, and at first decreases slowly for slightly less dominant individuals. It decreases rapidly for individuals with dominance

Figure 6. Dominance rank and survival. This theoretical graph summarises the data in Fig. 5. The dominance ranks N_{\max} and N_{\min} are respectively the number of feeding positions in the largest and smallest food patches in the flock's range.



rank greater than N_{\min} however, and approaches zero at rank N_{\max} . It is close to zero thereafter. The initial slow decrease is postulated since feeding positions within the patches are likely to vary slightly in their goodness, and the top dominant may have some advantage over other dominant class individuals.

Dominance behavior and the flock

Up to this point, evidence has been given that dominance behavior in the flock is partly motivated by hunger or related to food, and that it results in some individuals having more food than others. This has been interpreted as indicating that dominance behavior results in a stable survival differential in flocked birds whereby the dominant Juncos have a better chance of survival with respect to food than subdominant Juncos. Evidence has been obtained supporting this interpretation. We thus have evidence for a behavioral system that produces low-fitness individuals. We now need to see how this works to produce dispersal.

We have two states in which any given Junco can exist: flocked or dispersed. Let us first assume that there is some adaptive advantage to flocking. In particular, assume that the average survival of flocked birds is greater than the survival of dispersed birds. Let us further assume that, for a given density, that the survival rate of dispersed birds is a constant greater than zero. Now consider the survival rate of the least dominant member of the flock. If, as in the above analysis, the top dominant receives rank 1; the second dominant, 2, and so on, then it is clear that the rank of the bottom dominant equals the flock size. Accepting Figure 6 as a valid de-

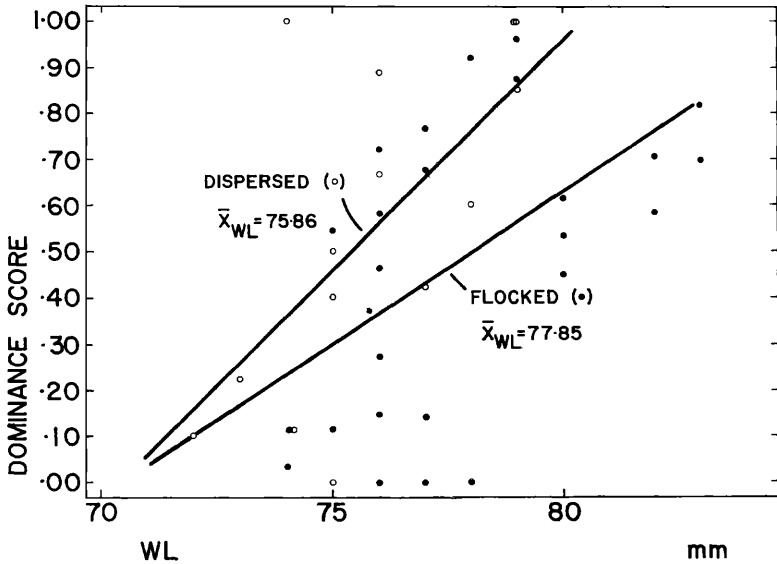
scription of the relationship between dominance rank and survival rate, it then follows that at a small flock size, the least dominant member of the flock has a lower rank, close to 1. It therefore has a survival rate not too different from the top dominant and therefore, very close to the flock average. Then its survival rate is higher than the survival rate of dispersed birds. As the flock size increases however, the most subdominant bird has a higher rank, and according to Figure 6, its survival rate eventually gets close to zero, below that of the dispersed birds. At some flock size (denoted fs_0), its survival rate is approximately equal to that of the dispersed birds. At larger flock sizes, the most subdominant bird in the flock is *less* likely to survive than a dispersed bird, and so its chances to survive would improve if it left the flock. If the individual birds are behaviorally adapted to respond to their position on the flock dominance order by either flocking or dispersing, whichever is advantageous, then at *any* flock size larger than fs_0 , the most subdominant bird will disperse. Then the largest permissible flock size is fs_0 . In this case, if there are more than fs_0 birds in the flock's range and just one flock, then only fs_0 of these will be flocked; the remainder will be dispersed, and the dispersed birds will be birds which would be least dominant if they were then to join the flock. The next sections will be concerned with finding evidence supporting this view.

Note that in the context of the theory of habitat distribution and territorial behavior referred to above (Fretwell and Lucas, 1969), Figure 6 is a direct demonstration of the t function, the existence of which is asserted by the basic hypothesis. Therefore, if that theory is accepted, the basic hypothesis is already completely verified, and further discussion is unnecessary. We will proceed because that general theory may not be wholly adequate. Further verification however supports both the basic hypothesis and the distribution theory.

Dominance and body size

The object of this study is to show that dispersed birds are subdominant to flocked birds. It was impossible for me to compare dominance relations between flocked and dispersed birds directly, and so an indirect approach was employed. The reasoning was as follows: Dominance is apt to depend on body size to some degree—larger individuals being in general more dominant. Therefore, we might expect a relationship between some index of size and dominance. If such an index can be found, we can then examine differences in the size index between dispersed and flocked birds. If dispersed birds are smaller, we may then predict that they would be subdominant. However, this inference would not be necessarily correct. Although we see a relationship between some index of size and dominance, individuals do exist which are contrary to the rule, e.g. small, dominant individuals. It is possible that for some reason the dispersed group of Juncos is composed entirely of these exceptions. We would then find that the dispersed birds were smaller

Figure 7. Dominance and wing length.



than the flocked birds, but our conclusion that they were also subdominant would be incorrect. The approach must be interpreted cautiously.

Procedure

The index of body size which was used was wing length. When each bird was banded, a measurement of the flattened wing was taken. In order to obtain the measurement, the bend of the wing and a millimeter rule were pressed together against the forefinger. The feathers of the wing were then pressed against the length of the rule. The distance from the bend in the wing to the end of the longest primary was the wing length measurement.

Results

The predictions are that wing length would be positively correlated with dominance status, and that dispersed birds would have shorter wings than flocked birds. To test the first hypothesis, regressions of dominance status on wing length were run within both the dispersed and flocked birds studied in 1964-1965. The results are given in Figure 7, where the data points are plotted as well as the regression lines. In both the dispersed and the flocked birds, the coefficients of proportionality were significantly greater than zero ($p < .01$), satisfying the first hypothesis. Wing length is a good index of dominance status in both groups of birds.

In order to test the second hypothesis measurements in both

dispersed and flocked birds were averaged. The means were then compared in a t-test. Given in Figure 7 are the means. The dispersed birds had significantly ($t = 2.38$, 38 d.f.) shorter wings, satisfying the second prediction. It is significant to note that the semi-flocked birds studied in 1966-1967 had an average wing length of 76.7 mm, intermediate to the two means given in Figure 7. We infer from these results that the dispersed Juncos would be subdominant to the flocked Juncos should the two groups ever come together. This is as predicted by the theoretical discussion preceding this section; we thus have further support for the hypothesis that dominance behavior in flocked Juncos results in a stable survival differential. More important, these results provide considerable insight into the effect of dominance behavior on the distribution of the species.

Dispersal and habitat distribution

We have already seen that when dominance behavior produces a survival differential in a typically flocking species, the population is apt to divide into two types of individuals; subdominant and dispersed, or relatively dominant and flocked. In essence, this division results because some individuals (the subdominants) are forced out of the flock by dominance behavior. We have evidence that this is so in wintering Juncos. In these Juncos, it has also been noted that the dispersed birds occupy habitats which are different from those occupied by flocked birds (woods vs. fields). Thus the dominance behavior in the flocked Juncos appears to force some individuals to leave not only the flock, but also the habitat occupied by the flock. In effect, the dominance behavior in the flock is apparently reducing and to some degree regulating the population density in the flock's range.

In order to understand just why dispersed birds would leave the flock's habitat as well as the flock itself, we might note that whatever is giving adaptive value to flocking must be operating in the flock's habitat while it may not be operating elsewhere. In particular, we note that both Field Sparrows and Juncos occupy similar open weed fields and have similar (tight) flock structures (Quay, 1940), suggesting that the weed field habitat selects for tight flocks in these small sparrows. But small sparrows in wooded areas are not generally so tightly flocked; they travel in loose mixed-species aggregations. Thus, it would seem that whatever is ultimately causing flocking is operating strongly in open weed fields and weakly in woods. So dispersed Juncos might be expected to evolve the response of moving to the woods because by so doing they avoid whatever is against dispersed small sparrows in the fields. This in spite of the fact that the woods may be less suitable in terms of food.

Another factor possibly affecting habitat selection is density of conspecific birds in each habitat (Fretwell and Lucas, 1969). The field habitats are densely occupied by Juncos while the woods are largely empty of this species. There is thus less non-dominance competition in the woods, and predators with density-dependent

activities would be less of a threat in woods. While dominance status seems to be involved in the habitat selection and distribution of *Juncos*, it does not operate alone but in interaction with other factors.

Wing length and population structure

We have assumed here that the *Juncos* in the fields and those in the woods are populations of competing individuals; that the small woods *Juncos* are nearly equivalent to and potentially freely interchanging with the small (subdominant) flocked field *Juncos*. We should like to test this assumption by following field *Juncos* into the woods or vice-versa. Dealing with the sparse, dispersed *Juncos* in the woods is difficult, however, and so an indirect test of this assumption was made by analyzing some wing length data on the field populations.

The hypothesis suggests that in the fields are flocks consisting of *Juncos* of various degrees of dominance. At the bottom of the dominance scale are generally small (shortwinged) individuals whose position in the flock is not stable. These individuals are prone to disperse or die. At the other end of the dominance order are generally large individuals whose position in the flock would be expected to be more stable. We have no reason to expect these individuals to leave the flock, or the flock's range.

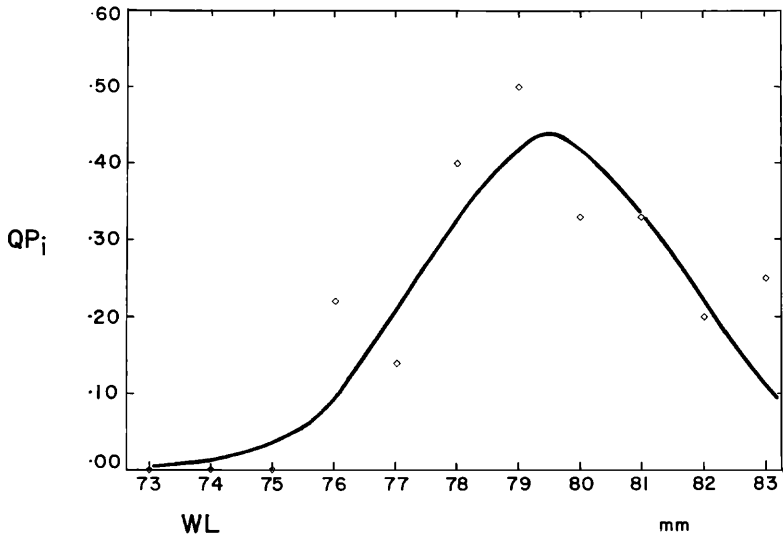
Procedure and results

During the winter, 14 mist-net samples of *Juncos* were made. Nine individuals were recaptured one or more times. These nine recaptured individuals are a sample of the more stable element of the population. Therefore, from the above discussion, we expect them to be in general larger than average. The average wing length of *Juncos* in the fields was 77.77 mm, while that of the recaptured birds was 78.88mm. The difference is not statistically significant, but is in the predicted direction.

The above test is statistically weak however, since the population average includes birds which stayed but were not recaptured, as well as birds which dispersed. A stronger test is achieved as follows; Divide the captured birds into wing length classes where class 1 contains all birds with wing length 72 mm, class 2 contains all birds with 73 mm wings, and so on. Let the probability that birds in class i will not disperse or die be denoted P_i ($i = 1, 2, \dots$). We expect this probability to increase with wing length, due to dominance-related stability of longer-winged birds. If the size of class i captured at first is N_i then $P_i N_i$ is the expected size available at time of recapture. Suppose Q is the proportion of the total recapturable birds which are recaptured. Assume Q is, on the average, constant for all classes. Then the expected number recaptured from each class in $QP_i N_i$. This number, divided by the total originally caught from class i , is $QP_i N_i / N_i = QP_i$, directly proportional to P_i . We can model our hypothesis with the linear equation:

$$(1) \quad P_i = B_0 + B_1 W L_i$$

Figure 8. Recaptureability and wing length. QP_i is the proportion of handled birds of wing length i later recaptured. WL is wing length. Curve is drawn by eye.



Where B_0 , B_1 are constants ($B_1 > 0$) and WL_i is the wing length of class i . Multiplying (1) by Q , we obtain

$$(2) \quad QP_i = QB_0 + QB_1WL_i$$

Since $0 < Q < 1$, QB_1 has the same sign as B_1 and in absolute value is less than B_1 . Thus, if QB_1 is greater than zero, B_1 also is greater than zero.

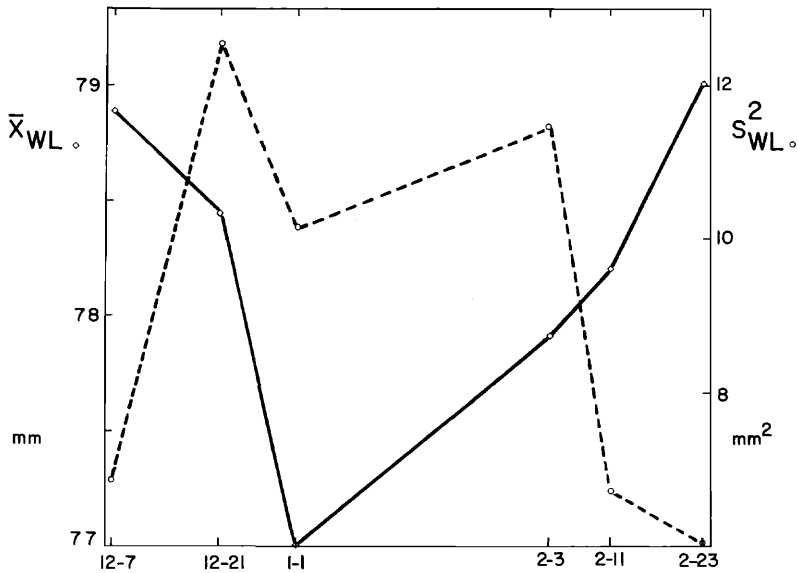
Applying this model is straightforward. QP_i for each WL_i is estimated, by definition, by the proportion of captured birds in the i^{th} class which were recaptured. (We will ignore classes with only one bird, and only birds captured before the population was baited were considered.) The plot of QP_i and WL_i is shown in Figure 8. QP_i evidently increases with increasing WL_i up to about 79.5 mm, when it begins to drop. The drop begins at a relatively long wing length however, and is less pronounced than the increase, so that the overall trend is positive. A linear regression analysis was applied to the data to fit the model (2). The analysis only approached significance ($p < .10$). QP_i was estimated at .0329. A curvilinear analysis following the model

$$(3) \quad QP_i = QB_0 + QB_1WL_i + QB_2WL_i^2$$

was highly significant ($p < .005$), indicating that the trends in Figure 8 are probably real. The decrease at high wing-length will be considered later.

We can make another testable prediction about the wing length

Figure 9. Wing length average and variance, winter 1964. Solid line is wing length average, broken line is variance. Abcissa is in days.



structure of the field population. Since the dispersing or dying segment has shorter wings, we expect the average wing length of the population to increase as the winter progresses. The average wing length over the winter of 1964-1965 is plotted in Figure 9. First arrival of Juncos is in late October. Figure 9 shows at the end of November a rather high average wing length. The wing length falls slowly, until after December 20, when it drops to a very low value around January 2. Measurements through January were not obtained, but by the first of February, the average wing length had again increased, but not to its original level. It continues to increase steadily through February into March. These trends were tested by an analysis of variance. The F value at 5 and 68 degrees of freedom was 4.885 and is highly significant.

The drop in average wing length in late December can be due to an exodus of long winged birds or an influx of short-winged birds. Since the recaptured birds were mostly long-winged, we can exclude the first possibility. Thus we are left with the explanation that the drop is due to an influx of short-winged birds. This influx could be due to a late migration of smaller birds, but considering the lateness of the season, that explanation seems unlikely. An alternative explanation is that some short-winged Juncos leave the woods or other unsuitable habitats as food there runs out, or as temperature or day length changes increase food requirements over that which the woods can provide.

From January 2 through the remainder of the winter, the average wing length increases. This could be due to an influx of long-winged birds or to a loss of short-winged birds. Both explanations are reasonable. Long-winged birds could arrive during this period as a result of weather movements from other, more northern regions. Short-winged birds could be lost due to dominance interactions, as we have predicted. These alternative explanations can be separated by looking at the variance in wing length. If the changes are due to gain and loss of only short-winged birds, then the variance should be negatively correlated with the mean. The addition of short-winged birds to a long-winged population simultaneously lowers the mean and makes the population less homogeneous, i.e. raises the variance. Conversely, if the changes are due to gain and loss of long-winged birds, then the variance should be positively correlated with the mean. In Figure 9, the variance is plotted above each mean. The trends are not clear, but it appears that the variance decreases with increasing wing length average, especially in February. The over-all correlation coefficient is estimated to $-.58$ but is not significantly different than zero.

Discussion

These observations on wing-length structure in the field population are generally consistent with the predictions of the hypothesis. They suggest however that the relation between dominance and distribution is complex and is affected by environmental factors. Whether subdominant birds die in the flock's range or disperse into other habitats to die is uncertain. It seems from Figure 9 that at least some go (back) to the fields to die, and that their death is not immediate. Thus, they probably consume some of the available field food before dying, and so the dominance system must not be totally efficient in protecting the winter food supply. This means that the maximum number of Juncos which could survive on the food available in the fields at the beginning of the winter do not survive, because some of that food is eaten by birds which are likely to die anyway.

If in fact short-winged Juncos are at a survival disadvantage, then the problem arises: why does the average wing length in the population remain stable generation after generation? In Figure 8 there is evidence that longer-winged Juncos are not as easily recaptured as Juncos with intermediate wing lengths, suggesting that they do not survive as well. Thus, there may be a selection against both extremes. Also, the average correlation between fat class and wing length in the total field data is $.00$ suggesting that although large birds are generally more dominant, they are not generally fatter. This means that large, subdominant birds have lower fat, as might be expected since larger birds must find more food than smaller ones in order to survive. Without a dominance advantage this might be difficult. Significant in this regard is the observation that the two intermediate dominant birds (Figure 6) which survived in 1967 had an average wing length of 71.0 mm (70, 72). The three intermediate dominant birds which did *not* survive had an average

wing length of 76.6 mm (77, 78, 75). The difference is statistically significant ($t = 4.148, 3 \text{ d.f.}$), and suggests further that long-winged, subdominant birds are at a disadvantage.

Finally, size differences might not reflect genotypic differences. Smaller Juncos may be smaller because of an inadequate food supply as nestlings, or because of age. Lack (1966) presents abundant evidence that lighter nestlings do not survive as well. If these lighter nestlings are also smaller as immatures and adults, then this survival disadvantage could be due to a dominance disadvantage. In this case, the size variation being selected against is not genotypic, and subsequent generations could reasonably show similar average wing lengths.

Field observations of dominance in Juncos

Special care was taken during the fall of 1965 to observe newly arriving Juncos to see whether or not dominance behavior could be observed in the field. The birds started to arrive in late October and continued to build up in numbers through mid-November. Aggression was extremely evident throughout this period, although not particularly food-oriented. Typically, whenever some Juncos were seen moving through the trees along the edge of the field, there were chases, displays and repeated displacements. Often a subdominant individual would be harassed for several minutes by a more dominant bird. The conflicts were usually observed in the trees, but this may be because the Juncos were not pressed to feed and when frightened by the observer, simply remained off the ground.

In the fall of 1966 when Juncos were more common, several undisturbed foraging groups were observed from my home. Dominance interactions were frequent, and some individuals were almost continually harassed. These observations are generally consistent with our interpretation of the role of dominance behavior, and provide direct evidence that the experimentally-observed mechanisms do in fact exist in natural situations.

Conclusions

At the beginning of this paper, a basic hypothesis was described which motivated the studies which followed. The essential elements of that hypothesis have been largely substantiated with certain reservations. It was hypothesized that habitat densities in Juncos would be limited by dominance behavior so that many individuals had to reside in habitats unsuitable for feeding. The results generally indicate that the use of food in the optimal habitats is to some degree limited by dominance interactions, and that density may or may not be limited depending on seasonal changes. This hypothesis has not been tested directly and so cannot be regarded as having been proved. Its predictions have been repeatedly verified however, and our confidence increased with respect to its validity. It certainly seems worthy of further test. Also, the basic hypothesis provides a common explanation for the results of a

diverse series of studies. We should note, however, that the hypothesis has been verified only in a single species, in a single geographic location. Its range of applicability remains to be established.

The hypothesis in its most explicit form is as follows: The winter food supply of Juncos is found in patches of somewhat variable size, in regions where there is selective pressure for flocking behavior. The Juncos have evolved flocking and concomitantly flock dominance behavior of such an intensity that some proportion of the population cannot find a feeding position which is in both the flock and a food patch. These individuals must leave the flock to feed. They must go either to patches in the flock's habitat where the flock is not feeding or to other habitats. In either case, they stand a very low chance of survival over the winter. It seems that most of these birds spend the early part of the winter in other habitats (especially mature woods), and the later part in the flock's habitats (fields). In any case, most die without seriously depleting the food supply of the flock. These subdominant individuals probably are the birds which most frequently utilize household feeding stations or baited trapping stations.

It should be stressed that these conclusions represent an oversimplified view of the situation. For example, flock size varies, flocks split up, and weather movements occur. How these phenomena fit in with the hypothesis is not known. I have kept the point of view simple in order to understand some of the interactions involved.

Summary

Studies by Quay (1940, 1947) on wintering Juncos showed that mature forests are infrequently occupied by unflocked birds while open weed-grown fields are usually occupied by large flocks. Dominance relations in flocked and unflocked birds were studied by attracting both types to feeding stations. Flocked Juncos at a feeding station in a field were found to be mainly of two types: Subdominants which lose more than 80 percent of their dominance struggles and dominants which lose less than 60 percent of their conflicts. Unflocked Juncos showed little such separation. In flocked, but not in unflocked, birds fat reserves are positively related to dominance. In flocked Juncos, adrenal weight and disappearance rate were inversely related to dominance status. Dominant birds also had longer wings and dispersed woods birds are shown to have, on the average, shorter wings than flocked birds. In the field, the long wing birds are more regularly recaptured. Analysis of field population wing length changes during the winter showed during the first part (Nov.-Dec.), long-wing birds predominate. Short-wing birds appear in the fields in numbers around January 1, and then decrease at a steady rate relative to long-wing birds through January and February. These results are shown to support the hypothesis that dominance behavior in the flock is a natural factor regulating food utilization, distribution, and mortality in Juncos.

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