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## TIME BUDGETING AND GROUP SIZE: A TEST OF THEORY<sup>1</sup>

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**Abstract.** Foraging flocks of granivorous Yellow-eyed Juncos (*Junco phaeonotus*) were studied for two winters to test hypothesized relationships between group size and time budgets. Required feeding time is so large that it constrains aggression. At low temperatures (high foraging requirements) a large flock forms in the area of maximal food availability. Group size decreases at warmer temperatures, since the constraints on aggression are reduced. Group size variance responds similarly.

As group size increases, individuals scan less often for approaching predators. The time saved is employed to increase feeding rates, unless aggression levels are extremely high. Rates of aggressive interaction increase with group size, and with both ambient temperature and food density.

Dominants apparently forage more efficiently than subordinates because of differences in habitat utilization and time allocation. These differences are consistent with the hypothesized correlation between increasing dominance and greater overwinter survivorship.

**Key words:** dominance; flocking; foraging efficiency; group size; *Junco phaeonotus*; time budget.

In a companion paper (Caraco 1979), I assume that members of avian winter flocks attempt to maximize their probability of surviving to the next breeding season. Sociality is viewed as an interactive response to the survivorship provided by different levels of predator avoidance and foraging efficiency. The decision to join a flock or forage alone incorporates time budget comparisons. In species sensitive to flock alarm signals, social foraging should allow an individual to decrease the time spent scanning for predators and increase its feeding time (Pulliam 1973). However, time lost in aggressive interactions will also increase with group size, particularly if dominants try to reduce resource depletion by aggressively driving others from the group (Fretwell 1972).

Temperature and food density should also govern time budgets. Temperature determines energy requirements, while food density influences the time needed to fulfill these requirements. Decreases in either temperature or food density demand greater foraging efforts. Individuals must then reduce their initiation of aggressive interactions in a time-constrained system. As time lost to aggression increases, the foraging time gained in a group by reducing predator scanning will increase the flock's attractiveness to a solitary. Larger groups then form, and flocks will occupy a habitat's more profitable areas.

A field study of winter-flocking Yellow-eyed Juncos (*Junco phaeonotus*) allowed tests of these predictions. The results are presented here.

### INTRODUCTION TO THE FIELD STUDY

I observed Yellow-eyed Juncos from January to April 1975 (1st yr) and from September 1975 to April 1976 (2nd yr). The study population resides in Upper Bear Canyon, near Tucson, Arizona (see Pulliam et al. 1974). From September–April the juncos forage on the ground, consuming grass seeds. Seeds are produced after the summer rains and all are shed by January, so that resources are nonrenewing during winter's coldest months.

I colorbanded 37 juncos during the study. A few other previously banded birds also frequented the area. The population's daily turnover was small. The juncos are probably quite familiar with resource availabilities and with each other.

In addition to food limitation, predators impose mortality during the winter. Cooper's Hawks (*Accipiter cooperi*) were observed regularly in the study area; a pair nested there in March 1975. Juncos previously have been reported as prey of Cooper's Hawks (Storer 1966, Davis 1973).

### METHODS

#### *Habitat variables*

**Distance to cover.**—I partitioned the study site into five areas, each  $\approx 1$  ha. Changes in vegetation determined the boundaries. During the 2nd yr I collected little data in area 1, since juncos rarely foraged there.

Distance to cover can influence the probability of avoiding predation. When flushed, juncos usually fly to thick bushes  $\geq 1$  m high. Cover was sufficiently available across the study site so that it did not limit the utilization of any area. However, the spatial distribution of seeds could force the birds to forage so that the realized distance to cover varies among areas.

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For every group observed during a census, I estimated distance from the group's center to nearest cover. Variances were homogeneous within each year's data (Cochran's test). A one-way fixed effects analysis of variance tested each year's observations for differences among areas.

*Food density, soil samples.*—I sorted grass seeds from 10 cm × 10 cm × 0.5 cm surface soil volumes, counted and weighed them. I collected the soil samples near the close of winter (March 1975). In each of the five areas, I randomly generated six sampling coordinates: three replicates in the 10 m nearest the canyon wash and three in the 2nd 10 m (apparently drier soil). I converted seed weights to an estimate of available food per square meter, a scale at which the birds presumably can respond to differences. Cochran's test indicated homogeneous variances, so I conducted a two-way fixed effects analysis of variance. Spatial variation in food density should decrease through the winter, since the birds are likely to exploit better patches (Tullock 1971). If March samples show significant differences in seed density, the model's assumption that food availability varies across foraging sites must hold.

*Food density, seed traps.*—I also used seed traps (Pulliam and Brand 1975) to sample resources from October–December 1975, when seedfall terminated. Four traps (10 cm × 10 cm) were placed randomly in areas 2–5. I estimated seed production in grams per square meter per week for each area. The data required a  $\log_{10}(x + 1)$  transform to achieve homogeneity of variances, and I then performed a two-way (area × month) fixed effects analysis of variance.

#### *Food perturbation*

Increased seed density reduces search time and should affect group size, since the birds can allocate time released from foraging to increasing aggression, resting in cover secure from predation, etc. I used millet (*Panicum miliaceum*) to increase food availability. I randomly dispersed 22.7 kg of inviable millet over a 90 m × 40 m area in January 1976. An additional 4.54 kg were distributed weekly until April, to negate resource depression. Note that this spatial dispersion of food contrasts with experiments employing extremely high seed-density patches.

#### *Flock characteristics*

*Predator scanning rate.*—Foraging juncos scan for predators in two ways. An individual may cock its head about the vertebral axis so that the upper eye can detect movement. More often a bird raises its head straight up so that the bill breaks a plane parallel to the ground at eye level. The rate of these events determines the time an individual allocates to predator detection ( $T_D$ ).

After noting group size, I watched an individual junco through binoculars, counted scanning events, and measured elapsed time. An observation ended whenever group size changed or the bird engaged in an aggressive encounter. I recorded scanning rates over all foraging sites and regressed the mean individual scanning rate (events/min) against group size.

*Film analyses.*—Super-8 movies yielded estimates of the ratio of predator scanning time ( $T_D$ ), and interference (aggression and avoidance) time ( $T_I$ ), to total time ( $T_T$ ) for individual juncos. I filmed on several days during each month of the study, and confined filming to short-grass areas. This insured that entire groups could be viewed continually and that seed density differences would not obscure group size dependent variation. I regressed individual observations of  $T_D/(T_T - T_I)$  and  $T_I/T_T$  against group size.  $T_I$  was subtracted from  $T_T$  in the first analysis to allow comparison with predator scanning rates.

*Feeding rate.*—I estimated individual feeding rates by the number of pecks at the ground per minute; pecking rate is assumed proportional to feeding time ( $T_F = T_T - T_I - T_D$ ). Data were recorded and analyzed in the same manner as scanning rates. I excluded portions of the study site with low seed density when collecting these data to insure independence of group size and food density within this analysis.

*Displacement rate.*—I counted all aggressive displacements in a flock and timed observation periods. I recorded these data only in short-grass areas to minimize variation due to seed density differences (before the perturbation) and to assure that all group members were continually visible. Using a linear model, I multiply regressed displacements per minute against group size, ambient temperature and hour of the day, 0800–1700. I treated pre- and post-perturbation data separately to demonstrate the relation between food availability and aggression.

#### *Time budgets*

I divided pre-perturbation time budget data into three temperature ( $t$ ) regimes:  $t \leq 9^\circ\text{C}$ ,  $10^\circ\text{C} \leq t \leq 18^\circ\text{C}$ , and  $t \geq 19^\circ\text{C}$ . Late-winter temperatures restricted post-perturbation time budgets to the two colder temperature intervals. Following the perturbation, I collected separate data for the three most dominant birds. Sampling involved focal animal (J. Altmann 1974), fixed interval time point (Chow 1975) observations. Individuals were randomly selected, except for the dominants, and followed until either lost from sight or 5 min had elapsed. I recorded the animal's behavioral state every 15 s. Sampling was allocated equally to each hour of the day from 0800–1600. For each sequence I recorded ambient temperature, foraging area and group size.

Each observation classified the individual's behavior into one of eight behavioral states:

- F Capture and consumption of food.  
 S Search for food, a slow walk with head lowered.  
 R Perching in cover.  
 W Time on the ground not expended in foraging or aggression: predator detection, watching other birds and avoiding a more dominant individual (quickly walking away from a dominant without gazing at the ground) are included. Dominants occasionally watch other group members for a moment just prior to displacing a subordinate; W also includes this behavior.  
 A Aerial chasing. An aggressor's behavior was recorded as A+; an entry of A- identified a bird being chased. Both male and female Yellow-eyed Juncos aerially chase conspecifics.  
 D An aggressive displacement in a foraging group. Field notes show D+ for a winner, D- for a loser.  
 P All nonforaging maintenance behaviors (preening, bathing, etc.).  
 Fly Flying, other than aerial chasing.

Note that some predator detection also occurred during F; a bird sometimes looked up while husking a seed. To avoid subjectivity, W includes important behaviors not easily differentiated without binoculars. For each temperature-food density combination I calculated the proportion of observations spent in each behavioral state, totaled over the day.

#### *Dominance and social organization*

The model assumes a linear dominance hierarchy. During the 2nd yr I recorded 436 aggressive interactions involving color-banded birds. I used these data to construct a dominance matrix for 19 birds.

The hierarchy allowed comparison of social rank with an index of short-term foraging efficiency. The index is simply the product of relative food availability and the square root of group size. I arbitrarily assigned the area of lowest food availability a value of 1; seed production in the best area was 2.04 times this value. The square root of group size reflects the concave relation of pecking rate to the size of a flock (see Results). I collected 1000 observations of the 19 ranked birds where each observation noted foraging area and group size. I calculated a mean foraging index for each bird and then rank correlated social status with the indices. The foraging index is conservative, since it lacks sensitivity to the advantage of dominance under conditions of extremely low resource availability.

Subordinate juncos move quickly to avoid dominants and spend time watching other flock members after being displaced, perhaps looking for a safe place to feed. Time budget sequences indicated dominance or subordination when the bird won or lost its encounter(s). Each of these sequences provides a ratio  $W/(W + F + S)$ , an approximate index of time lost to avoidance and watching (see *Time budgets*). The important

comparison of this ratio is the difference between dominants and subordinates before the food manipulation, since required foraging time was greater.

#### *Group size*

Foraging group sizes were usually censused between 1100 and 1200. I recorded only feeding group sizes, and observed from 25-35 birds/census. Each census provides an 0-truncated frequency distribution of group sizes. For this analysis, censuses are characterized by group size mean and variance. Census temperature is the average of ambient temperatures recorded before and after data collection.

## RESULTS

### *Habitat variables*

*Distance from cover.*—Observations of 323 feeding groups of all sizes (data from all foraging areas combined) recorded the 1st yr reveal that the proportion of groups feeding  $d$  metres (a discrete variate) from cover,  $f(d)$ , follows a geometric distribution:

$$f(d) = .257 (.743)^d \quad d = 0, 1, 2, \dots$$

The expected distance equals 2.891 m, but 15% of all groups feed  $>5$  m from cover.

The probability function describing a group's distance to cover assumes that observations in all foraging areas were samples from the same discrete distribution. Analysis of variance of each year's distance-to-cover data reveals no significant differences among foraging areas (1st yr:  $F_{4,215} = 1.331$ ; 2nd yr:  $F_{4,289} = 1.345$ ). Therefore proximity to cover constrains the juncos' use of space equally in each area. Any differential attraction among the areas should be due only to variation in food density and group size.

*Food distribution.*—The model assumes a patchy food distribution. The analysis of variance conducted on estimates of milligrams of seeds per square m (soil samples) showed significant variation among foraging areas along the canyon wash ( $F_{4,20} = 4.2$ ,  $P < .05$ ). Distance from the wash did not reveal a significant difference in food availability ( $F_{1,20} = 1.28$ ). Because late winter samples indicate heterogeneous food availability among areas, the assumption of a patchy food distribution holds in this system.

*Seed production.*—Table 1 displays the analysis of variance of the transformed estimates of seed production (seed trap data). Highly significant differences exist among areas and months; December's seed production was very low. Paired comparisons show that no foraging area has a greater mean seed production than area 3 (Scheffe's test).

Habitat results suggest a simple test of one of the model's predictions. At lower temperatures the largest group should form in area 3, since the food resources will attract subordinates when temperature constrains

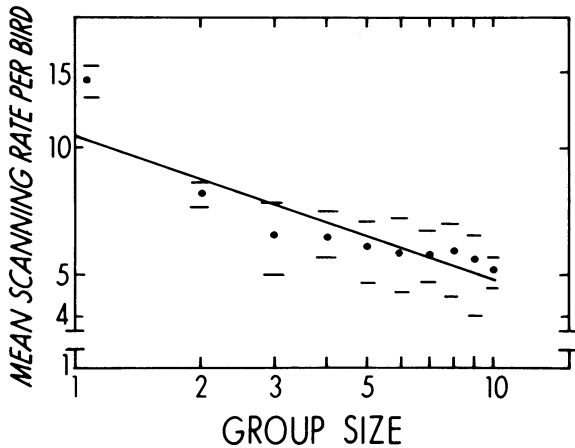


FIG. 1. Mean predator scanning rates, in scanning events per individual per minute, ( $Y$ ), vs. group size ( $G$ ). The regression equation for the line in the figure is:  $\log_{10} Y = 1.047 - .399 \log_{10} G$ ,  $r = -.92$ . The slope indicates that the probability of detecting a predator's approach should increase with group size. This has been initially confirmed by regressing flushing distance from a group's periphery ( $z$ ) to an approaching observer. These data were regressed against group size:  $\log_{10} Z = .81 + .22 \log_{10} G$ ,  $r = .88$ .

aggression. As temperature rises, dominants will increase their aggression (see time budget results) and the group(s) in area 3 will be smaller.

The probability that the largest group in a census occurred in area 3 shows the predicted relation. If a census produced no single largest group, the calculation assumes such a group was observed outside of area 3. I combined data from both winters, but excluded censuses following the food perturbation, since the experiment reduced constraints on aggression. If  $Y$  = the probability that the largest group fed in area 3, then:  $Y = .99 - .027t$ , where  $t$  is the temperature in  $^{\circ}\text{C}$ . For this regression equation,  $r = -.89$ . The slope differs significantly from zero ( $\alpha = .05$  in all regressions). Subordinates exploit the most profitable area at low temperature, but their ability to do so decreases at higher temperatures, when dominants allocate more time to aggression.

#### Flock characteristics

Figure 1 gives the estimated mean individual predator scanning rate (events/min),  $Y$ , as a function of group size,  $G$ . The linear equation is  $\log_{10} Y = 1.047 - .399 \log_{10} G$ ,  $r = -.92$ ,  $df = 8$ .  $t$ -tests, adjusted for sequential hypotheses (Hamilton 1965), reveal that the slope is both significantly  $<0$  and significantly  $>-1$ . Scanning is reduced as flock size increases, providing time the individual can use to increase its energy acquisition rate (Pulliam 1973). If the probability of detecting a predator's approach remains constant with group size, assuming independently scanning group members, the regression slope would not significantly

TABLE 1. Two-way fixed effects analysis of variance of seed production estimates ( $x$ ) transformed to  $\log_{10}(x + 1)$ , with  $x$  measured in grams per square meter per week

Source	df	Sum of squares	Mean square	F
Total	48	3.6327		
Mean	1	2.2292		
Foraging areas	3	.2976	.0989	7.099**
Months	2	.3134	.1567	11.249**
Interaction	6	.282	.047	3.374*
Error	36	.5015	.0139	

\* Significant variation ( $P < .05$ ).

\*\* Highly significant variation ( $P < .01$ ).

differ from  $-1$ . Statistical analysis of the slope, however, indicates that the probability of the group detecting a predator's approach increases with group size (see Fig. 1 legend), even though  $T_D$  decreases for each individual. Flock alarm signals (calls, display of white tail feathers) are presumably the mechanisms by which the individual benefits from the group's detection of predators.

Film analysis also indicates that the mean proportion of time ( $T_T - T_D$ ) in a group spent scanning for predators is a function of group size,  $G$ . The regression was calculated using all (97) observations.  $T_D/(T_T - T_D) = .322 - .041G$ ,  $r = -.6$ . The slope differs significantly from zero, confirming the hypothesis that the birds devote a significantly decreasing proportion of time to predator detection as group size increases.

Figure 2 provides mean individual rates of pecking for food as a function of group size (averaged over all temperatures). Both years' data are given, though neither the intercepts nor the slopes differ significantly between regressions. Let  $Y$  = the mean individual pecking rate (pecks/min); the linear regressions are:

$$(I) \text{ 1st yr: } \log_{10} Y = 1.22 + .42 \log_{10} G, \quad r = .89$$

$$(II) \text{ 2nd yr: } \log_{10} Y = 1.25 + .56 \log_{10} G, \quad r = .87$$

Both regression slopes differ significantly from zero. Pecking increases with group size; the juncos employ at least part of the time gained from decreased  $T_D$  for feeding.

The films reveal that the birds respond to the social environment and peck more often between scanning events as group size increases. They do not merely peck faster, stimulated by an increasing number of feeders; they actually shift their time allocation between behavioral categories.

Using the film analysis and time budgets (see below), I compared the feeding times of a solitary and a member of a group of five birds over a 10-h day at low temperatures ( $<9^{\circ}\text{C}$ ), before the food perturbation. The solitary spends more time scanning, but the group member loses time to aggression and avoidance. Calculations indicate that the group member has an

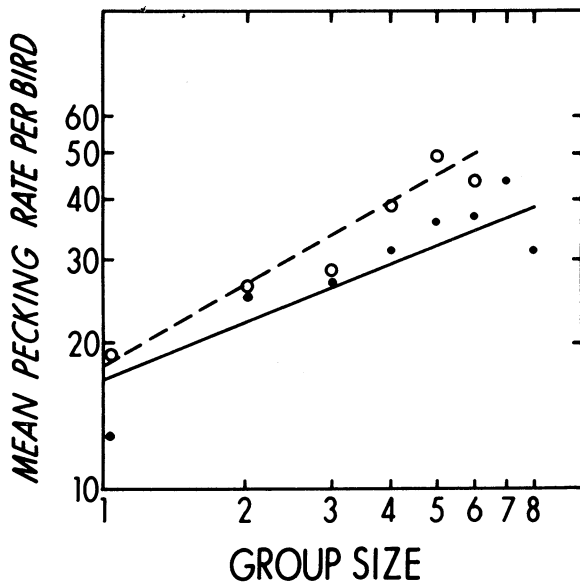


FIG. 2. Mean pecking rates, as a function of group size ( $G$ ). Dots are winter 1975 (1st yr) data; circles are the means of fall 1975 (2nd yr) observations. With  $Y$  equal to the mean pecking rate in pecks per bird, per minute, the regressions are:  $\log_{10}Y = 1.22 + .42 \log_{10}G$ ,  $r = .89$  (solid line), and  $\log_{10}Y = 1.25 + .56 \log_{10}G$ ,  $r = .87$  (broken line). Neither the intercepts nor the slopes of the two regressions differ statistically.

extra 28 min of foraging time per day under these conditions, a substantial increment over solitary feeding. At higher temperatures increasing aggression will reduce this difference.

The model assumes that time spent in aggression and avoidance increases with group size. Figure 3 shows that the mean  $T_I/T_T$ , averaged over all temperatures, increases as expected. The regression line was calculated using all (126) observations:  $T_I/T_T = .007 + .021G$ ,  $r = .44$ . The slope differs significantly from zero. Prevailing environmental conditions will determine the extent of the increase in aggression with group size, and whether or not these losses exceed the gains from decreases in predator detection time.

The model predicts that aggression will increase not only with group size, but with increases in either temperature or food density. I multiply regressed displacements per min for entire groups ( $Y$ ) against group size ( $G$ ), temperature ( $t$ ) and hour of the day ( $H$ ), where  $H$  is expressed in the 24-h system. The following equation explains the greatest amount of variation in the pre-perturbation data:  $Y = -.103 + .27G + .11t - .063H$ ;  $N = 480$ ,  $R^2 = .66$ . Each variable contributes significantly in explaining the total variation (group size 37%, temperature 25% and hour of the day 4%).

Similar data were collected after the food perturbation. The following regression explains the greatest

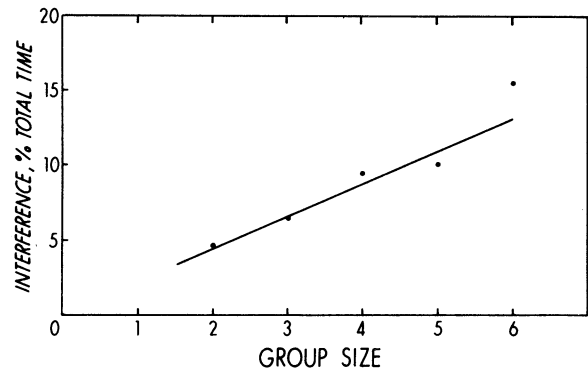


FIG. 3. Film analysis: mean percentage of total time ( $T_T$ ) spent in aggression and avoidance ( $T_I$ ) as a function of group size ( $G$ ). The regression line was calculated using the 126 filmed observations:  $T_I/T_T = .007 + .021G$ ,  $r = .44$ .

percentage of the total variation:  $Y = -.027 + .46G + .28t - .24H$ ;  $N = 280$ ,  $R^2 = .68$ .

Each variable again explains a significant percentage of the total variation (group size 29%, temperature 27%, and hour of the day 12%). The group size response was expected, since juncos defend an individual distance and the probability of encounter between any two individuals increases with group size. In addition, dominants should aggressively try to reduce the size of large groups, since the seed depletion rate then decreases.

Both the group size and temperature effects vary little between regressions in explaining variation in displacement rate. However, the two response surfaces differ considerably. Regression coefficients for group size and temperature approximately double after the food perturbation. The economics of aggression strongly depend on resource levels (Gill and Wolf 1975).

Hour-of-the-day effects can be attributed to time budget changes through the day. Within temperature and food density levels, time allocated to aggression is nearly constant through the course of a day. However, at higher temperatures the ratio of aerial chasing to displacement time ( $A/D$ ) increases in the afternoon. For temperatures  $>9^\circ\text{C}$  before the perturbation, this ratio averages .75 in the morning, and increases to 1.17 in the afternoon. If a dominant has acquired energy sufficient to meet all 24-h costs, it should increase aerial chasing, since this type of aggression more effectively disperses subordinates. Displacement rates decrease slightly through the day, but the energy expended in aggression increases, since aerial chasing costs more energy.

#### Time budgets

Table 2 lists the daily proportional time allocations for seven circumstances. Vectors 1 through 3 are randomly selected (average) birds prior to the perturba-

TABLE 2. Time budgets. Each entry is proportion of time spent in that behavioral state. *N* is number of observations; standard errors of estimates appear in parentheses. Vectors 1 through 5 refer to 'average' birds. Vectors 6 and 7 are time budgets of the three most dominant birds. Food availability and temperature (*t*) conditions for the different vectors are as follows. Pre-perturbation: (1)  $t \leq 9^{\circ}\text{C}$ ; (2)  $10^{\circ}\text{C} \leq t \leq 18^{\circ}\text{C}$ ; (3)  $t \geq 19^{\circ}\text{C}$ . Post-perturbation: (4) and (6)  $t \leq 9^{\circ}\text{C}$ ; (5) and (7)  $10^{\circ}\text{C} \leq t \leq 18^{\circ}\text{C}$

Behavioral state*	1	2	3	4	5	6	7
F	.459 (.009)	.404 (.009)	.366 (.011)	.407 (.01)	.309 (.013)	.269 (.032)	.246 (.025)
S	.294 (.008)	.244 (.008)	.174 (.009)	.1 (.006)	.097 (.008)	.051 (.016)	.1 (.017)
R	.07 (.005)	.159 (.007)	.219 (.01)	.2 (.008)	.274 (.013)	.284 (.032)	.262 (.025)
W	.058 (.004)	.068 (.004)	.087 (.007)	.109 (.006)	.08 (.008)	.132 (.024)	.113 (.018)
A	.008 (.002)	.021 (.003)	.039 (.005)	.029 (.003)	.045 (.006)	.066 (.018)	.063 (.014)
D	.03 (.003)	.02 (.003)	.032 (.004)	.058 (.005)	.068 (.007)	.081 (.019)	.06 (.014)
P	.009 (.002)	.02 (.003)	.004 (.002)	.031 (.003)	.02 (.004)	.02 (.01)	.063 (.014)
Fly	.068 (.005)	.067 (.004)	.079 (.006)	.067 (.005)	.107 (.009)	.096 (.021)	.093 (.01)
<i>N</i>	2981	3112	1757	2486	1273	197	301

\* See METHODS for explanation of behavioral state codes.

tion, in the temperature (*t*) ranges: (1)  $t \leq 9^{\circ}\text{C}$ , (2)  $10^{\circ}\text{C} \leq t \leq 18^{\circ}\text{C}$ , and (3)  $t \geq 19^{\circ}\text{C}$ . Vectors 4 and 5 are average birds after the experimental manipulation, in temperature ranges (4)  $t \leq 9^{\circ}\text{C}$  and (5)  $10^{\circ}\text{C} \leq t \leq 18^{\circ}\text{C}$ . Vectors 6 and 7 provide the time budgets of the three most dominant birds after the perturbation, in temperature ranges (6)  $t \leq 9^{\circ}\text{C}$  and (7)  $10^{\circ}\text{C} \leq t \leq 18^{\circ}\text{C}$ .

Temperature and food density increments should result in decreased foraging time (F + S) and increased aggression (A + D). Vectors 1 through 3 show this inverse relation between temperature and foraging time. As temperatures increase from (1)  $t \leq 9^{\circ}\text{C}$  to (3)  $t \geq 19^{\circ}\text{C}$ , a junco shifts one-fifth of its day (28% of F + S) from foraging to other activities. Vectors 4 and 5 reveal a similar temperature dependence. While rising temperature reduces homeothermy requirements, increased food density reduces search time. Within any temperature range, the food perturbation should also result in decreased foraging time. Comparing vector 1 with 4 and 2 with 5 shows that the perturbation allowed a junco to reduce foraging an average of 24.4% of its entire day.

Reduced foraging time should result in dominants increasing their expenditures for aggression, so that all birds spend more time in aggression. Vectors 1 through 3 demonstrate a near doubling of aggression as temperature increases; aerial chasing increases five-fold. Surprisingly, these data do not reflect the temperature response noted in the displacement rate regressions. Vectors 4 and 5 also show more aggression at the higher temperature. Within temperature range, increased food availability results in an average increase in aggression of 6.1% of a bird's day (compare vector 1 with 4 and 2 with 5). Aggression more than doubled in both temperature ranges after the perturbation.

Time released by a reduction in either energetic re-

quirements or search time can also be used to enhance survivorship if a bird spends some of this time hiding in cover. Time budgeted to this behavioral category (R) triples with increasing temperature before the perturbation (vectors 1 through 3). Vectors 4 and 5 display a similar shift. Within a temperature range, increased food availability allows an individual more time in cover. Preening and related maintenance behaviors increase similarly.

A post-perturbation comparison (vector 4 vs. 6) reveals that the proportion of time dominants spend in aggression is significantly > the same proportion for subordinates ( $P < .005$ , likelihood ratio test). However, this statistical discrimination cannot be found when comparing vectors 5 and 7 ( $.25 < P < .5$ ).

Time budget sequences also indicate that dominants allocate a significantly increasing proportion of their total time to aggression as group size increases:  $(A + D)/T_T = .1 + .02G$ ;  $r = .9$ ,  $df = 4$ . The slope of this equation, compared to Figure 3, again indicates that avoiding dominants, not just aggression itself, is very important in determining the group size dependent variation in  $T_T$ .

#### Dominance and social organization

The model's assumption of a linear hierarchy proved appropriate for this system, since the dominance matrix required that only 7% of the observed interactions be classified as reversals.

The model predicts that dominants should forage more efficiently than subordinates, at least when energetic demands are high. Therefore, I computed a rank correlation of the short-term foraging index (see Methods) with hierarchy position. The rank correlation is significant ( $r_s = .63$ ,  $N = 19$ ), primarily because dominants spend more time than subordinates in high seed-density patches. The proportions of observations of the four highest ranking birds recorded

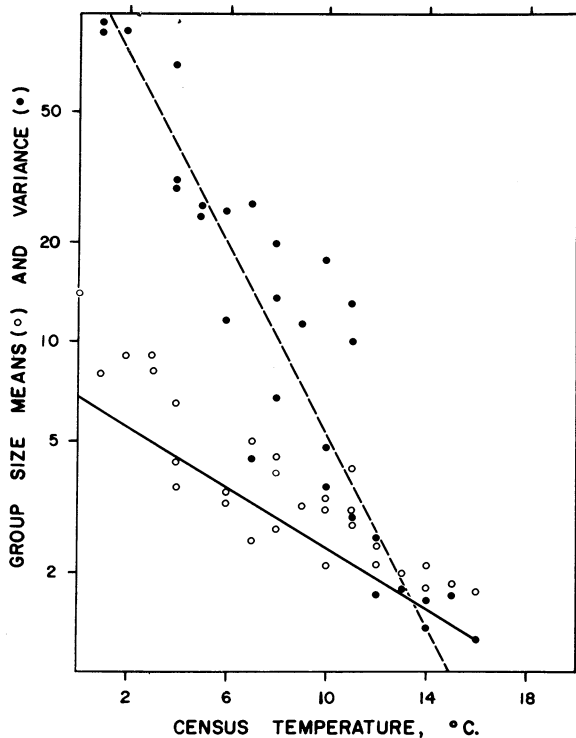


FIG. 4. First year census means and variances as functions of ambient temperature ( $t$ ). Open circles are group size means ( $\bar{G}$ ); closed circles are group size variances ( $s^2$ ). The regression lines are:  $\log_{10}\bar{G} = .84 - .05t$ ,  $r = -.79$ , and  $\log_{10}s^2 = 2.24 - .151t$ ,  $r = -.89$ .

in the area with the greatest food density ranged from .79-.89 (significantly  $>.25$ , the null value), and decreased at lower ranks.

Dominants' and subordinates' time budgets were also predicted to differ since avoidance costs should be greater for subordinates. The ratios ( $W/W + F + S$ ) from pre-perturbation time budgets differ markedly.

For dominants the value is  $63/879 = .0717$ , while for subordinates the ratio is  $149/877 = .1699$ . The proportions differ significantly ( $P < .005$ , likelihood ratio test). This result is consistent with the finding that peripheral group members, usually subordinates (Moore 1972), do not scan for predators significantly more often than central birds, which are usually dominants ( $F_{1,4} = .231$ , analysis of variance blocked along group size). However, prior to the perturbation, central birds pecked for food more often than peripheral birds ( $t = 2.14$ ,  $df = 54$ ,  $P < .05$ ), indicating that dominants' and subordinates' energy acquisition rates differ when energetic requirements are greatest.

Note that after the perturbation, dominants allocated more time to behavioral category W than did subordinates. Subordinates still avoided the more aggressive individuals, but dominants increased the time spent watching other group members, especially be-

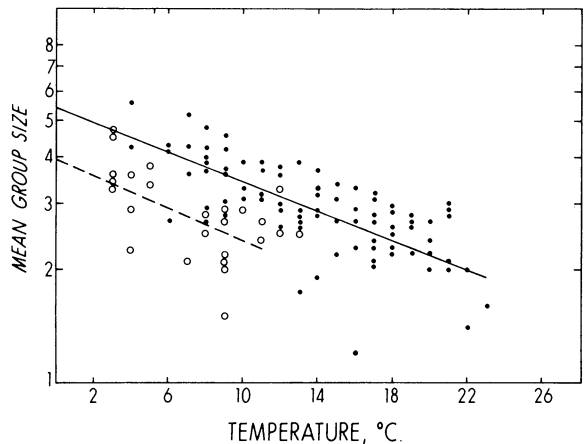


FIG. 5. Mean group size ( $\bar{G}$ ) for 2nd-yr censuses as a function of ambient temperature ( $t$ ). Unbroken line (dots) is the pre-perturbation regression. Broken line (open circles) is the post-perturbation regression. The equations are as follows: Pre-perturbation:  $\log_{10}\bar{G} = .73 - .019t$ ,  $r = -.67$ ; post-perturbation:  $\log_{10}\bar{G} = .6 - .021t$ ,  $r = -.53$ .

fore initiating aggressive chases. In addition, dominants seldom tolerated large groups around them after the perturbation; the time budget comparison thus also reflects predator detection differences.

#### Group size

Results to this point (1) indicate that the model's assumptions concerning habitat and social organization apply to the junco system, and (2) confirm the hypotheses relating both temperature and food density to time budgeting. The model integrates these relations to predict that the means and variances of group size censuses should vary inversely with temperature and food density, since aggression is constrained by these two environmental variables.

Figure 4 provides the temperature relations for the 1st yr, during which no perturbation was performed. Both regression slopes are significant:

$$\log_{10}\bar{G} = .84 - .05t, \quad r = -.79.$$

$$\log_{10}s^2 = 2.24 - .151t, \quad r = -.89.$$

Both moments decrease with temperature, as predicted.

Figure 5 shows mean group sizes for all 2nd-yr censuses as a function of temperature. Pre-perturbation data are described by the regression:  $\log_{10}\bar{G} = .74 - .019t$ ,  $r = -.67$ . The post-perturbation regression is:  $\log_{10}\bar{G} = .6 - .021t$ ,  $r = -.53$ . Both regression slopes differ significantly from zero. Moreover, group size for a given temperature decreases after the food perturbation, since the regression adjusted means differ significantly (analysis of covariance,  $F_{1,106} = 9.7$ ,  $P < .01$ ).



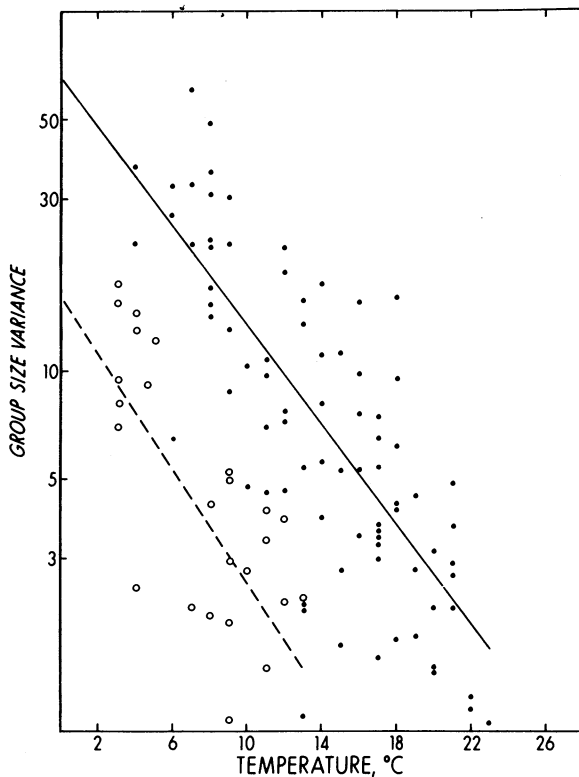


FIG. 6. Group size variance ( $s^2$ ) for 2nd-yr censuses as a function of ambient temperature ( $t$ ). The solid line (dots) is the pre-perturbation regression. The broken line (open circles) is the post-perturbation regression. The equations are as follows: Pre-perturbation:  $\log_{10}s^2 = 1.82 - .07t$ ,  $r = -.77$ ; post-perturbation:  $\log_{10}s^2 = 1.21 - .08t$ ,  $r = -.66$ .

Figure 6 gives both pre- and post-perturbation census variances regressed against temperature. The equation for the pre-perturbation data is:  $\log_{10}s^2 = 1.82 - .07t$ ,  $r = -.77$ . Following the increase in food density, the equation becomes:  $\log_{10}s^2 = 1.21 - .08t$ ,  $r = -.66$ . Both regression slopes differ significantly from zero. Within temperature, increased food density decreases the group size variance, since the adjusted means differ significantly (analysis of covariance  $F_{1,106} = 8.9$ ,  $P < .01$ ). Increased temperature and the addition of food, both of which reduced energetic constraints on time budgeted to aggression, bring about a decrease in both the mean group size and census variance.

## DISCUSSION

### Time budgets

Yellow-eyed Junco time budgets mediate relations between the environment, individual requirements and the resulting sociality. Temperature and food density are especially important environmental factors influencing junco groups, since foraging time requirements

so strongly constrain aggression. The time budgeting trade-off between predator detection and foraging time requires a response to the number of other birds in a group; juncos possess a keen awareness of their social environment.

### Social foraging

A variety of suggestions have been proposed to explain the evolution of social foraging. Many authors cite predator avoidance as the original function of flocking; feeding as a group is then incidental. Groups may reduce predation per individual by concealment (Paloheimo 1971, Vine 1971), or by detecting predator approaches more efficiently than solitaires do (Siegfried and Underhill 1975, Treisman 1975). Group formation may reduce the area or volume where an individual member is most vulnerable to predation (Williams 1964, Hamilton 1971), and sometimes allows active defense against predation (DeVore 1963, Kruuk 1964).

Another approach attributes sociality to enhanced feeding efficiency. Hypothesized mechanisms include avoiding areas previously gleaned of resources (Cody 1971), using other group members as information sources (Horn 1968, Krebs 1974), increased hunting efficiency for groups (Kuhme 1965, Caraco and Wolf 1975), and enhanced prey availability due to group movements (Bartholomew 1942).

The origins of sociality may be as diverse as its manifestations. The relative evolutionary contributions of these and other causes probably are not duplicated in any two social systems.

Yellow-eyed Juncos respond to both potential predation and differential energy acquisition rates. For the juncos, neither predator avoidance nor foraging efficiency can be maximized without decreasing survivorship. Therefore, I view social behavior as a multivariate optimization, rather than the result of a single ultimate cause.

Several authors have taken an integrated approach. Pulliam (1973) suggested that predator detection decreases and feeding increases with group size increments. Powell (1974) reached the same conclusion after experiments with captive starlings (*Sturnus vulgaris*); the starlings' trade-off between predator detection and feeding resembled the juncos' group size dependent behavior.

Krebs (1974) documents that Great Blue Herons (*Ardea herodias*) reduce scanning rate and increase feeding rate as group size increases. Krebs feels that scanning in herons functions primarily to detect movements of conspecifics, since the birds acquire information from each other on locations of ephemeral patches of high food density. He believes heron foraging group size reflects local availability of indefensible resources and that social feeding offers no time budgeting advantage independent of food density.

The herons' resource predictability contrasts sharply with the junco population. The juncos' resources show much less short-term variation, an important aspect of the economics of aggression. Food location does not vary, but subordinates' access to food changes with environmental factors.

#### Optimization

Group size may be an optimal response to the environment. Kummer (1968) showed that Hamadryas baboon (*Papio hamadryas*) groups change size during the day as the critical resource changes. Ecological factors appear to influence mean group size in a number of primates (Denham 1971, Crook 1972), and in the African antelopes (Jarman 1974). Perhaps, as S. Altmann (1974) suggests, these models are overly deterministic in viewing only "average" animals behaving in the same optimal manner. This study indicates that individual juncos differ in their ability to dominate others; these differences govern important time and energy expenditures. Dominants and subordinates apparently adopt different survivorship strategies and the optimal group sizes advancing these strategies probably also differ (Caraco 1979).

Dominant birds may survive winter better because they acquire preferred resources (Fretwell 1972, Swingland 1975) or because subordinates lose foraging time avoiding dominants (Murton and Isaacson 1962). Yellow-eyed Junco dominants maintain preferential access to sites of high seed density, and subordinates cannot use foraging time as efficiently as dominants when energetic constraints are most severe. Apparently, aggression allows dominants to insure their dietary requirements will be met. Subordinates cannot be so sure of finding adequate food and probably suffer lower overwinter survivorship.

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