INFLUENCE OF SOCIAL STATUS, DISTANCE FROM COVER, AND GROUP SIZE ON FEEDING AND VIGILANCE IN WHITE-CROWNED SPARROWS

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ABSTRACT.—The trade-off of food return against predation risk by foraging White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) was assessed using focal sampling. Pecking and vigilance rates were compared among different social classes, bird densities, and distances from cover. Contrary to expectations from previous studies and from theory, pecking rate was significantly higher in subordinate than in dominant individuals. Pecking rate increased with distance from cover and was not affected by density. The only significant trend for vigilance rate was a decrease with distance from cover, which was counter to expectations. Increased vigilance towards conspecifics may have balanced any decrease in vigilance for predators as group size increased, or as distance from cover decreased. *Received 6 September 1994, accepted 26 July 1995.*

A MIGRATORY INDIVIDUAL's probability of survival over winter will be affected by its foraging and predator avoidance behavior. As foraging frequently increases predation risk, survival often will entail a trade-off between food acquisition and predation risk (Caraco 1979a). Flocking while foraging is one mechanism whereby individuals may decrease their predation risk (Hamilton 1971, Powell 1974) and, concomitantly, increase their food intake (Caraco 1979b). However, a consequence of flocking is increased competition, with foraging time lost to social interaction (Caraco 1979a, 1979b) and exclusion of subordinates from preferred feeding locations (Schneider 1984, Slotow and Rothstein 1995).

The importance of predation risk, food intake, and social interference will vary depending on an individual's perception of its current state, which is an expression of a number of proximate variables (e.g. satiation level, social status, displacement probability, experience, recent predation events, and weather). Differences in these variables should result in variation in several aspects of feeding behavior, such as feeding location and frequency, the length of foraging bouts, and the rates of pecking and vigilance for predators (i.e. all variables that

constitute an individual's foraging strategy; Caraco 1982). As an individual can not peck for food at the same time that it raises its head to watch for predators, feeding and vigilance for predators should be traded off, with vigilance increasing with relative predation risk. Therefore, pecking rate may be higher closer to cover or when foraging in larger groups (e.g. Barnard 1980, Caraco et al. 1980a), situations in which predation risk is reduced. In addition, as higher social status allows greater access to resources or to safer feeding locations, dominant individuals may have higher pecking rates and lower vigilance rates than subordinates.

We describe foraging behavior of individual White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) with respect to food intake (pecking rate) and predation risk (vigilance rate). We estimated pecking and vigilance rates by sampling different focal individuals and determined how these two behaviors varied with social class, distance from cover, number of individuals present, time of day, and duration of focal session. Specifically, we tested the following predictions: (1) Pecking rate is positively correlated with group size and negatively correlated with distance from cover. (2) Pecking rate is negatively correlated with social status because dominants feed closer to cover than subordinates (Slotow and Rothstein 1995). (3) Vigilance rate is positively correlated with distance from cover and negatively correlated with group size.

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METHODS

This study was carried out during the winter of 1989–1990 on the West Campus of the University of California at Santa Barbara, Santa Barbara County. Wintering White-crowned Sparrows at our study site form variably-sized foraging groups ranging from 2 to 35 or more individuals, while the total number of individuals using a feeding site over a period of two to three days can exceed 400 individuals (Slotow and Rothstein 1995). A social-dominance hierarchy exists among age-sex classes as follows (from most to least dominant): adult male, adult female, immature male, immature female (Fugle et al. 1984, Keys and Rothstein 1991).

We observed birds feeding on a 2 m × 6 m concrete slab in a mowed field. The slab was about 20 m south of an established feeding site, where food (millet seed) was provided the winter of 1988–1989 as well as during 1989–1990. The established feeding site was situated at the base of a row of dense shrubs and trees, and there was a parallel row of vegetation at the south end of the field, about 70 m from the slab. Individuals were captured and color banded at the established feeding site throughout the study, and there was always a small amount of seed present there.

We constructed an artificial shrub (2.5 m high × 1.2 m × 1.2 m) from cut conifer branches and placed this at one end of the concrete slab. Extensive observations showed that the sparrows used the "shrub" as a source of cover in that they usually first flew to it before feeding and dashed into it when they flushed while feeding. Furthermore, experiments with a structure that provided perches but no protective cover showed that the birds used the shrub as a source of cover and not simply as a convenient perch (Slotow and Rothstein 1995). We provided three feeding stations, consisting of transparent hard-plastic bowls (diameter 30 cm, depth 5 cm). These bowls were large enough to permit up to 15 individuals to feed at once, thus allowing a clear group size effect to manifest itself. Bowls were placed 0.3, 0.8, and 1.3 m from the outer branches of the shrub (bowls 1, 2, and 3, respectively). These distances were chosen as they span the usual feeding distances from cover for White-crowned Sparrows in coastal California (e.g. on average 87.5% of all individuals feeding were on bowls 1 or 2; Slotow and Rothstein 1995), and White-crowned Sparrows do trade off food return against predation risk over this distance (Slotow 1993). We placed abundant millet seed into each bowl the day before and at the beginning of every observation period, and replenished this if it was depleted. Therefore, there always was abundant food at each bowl, and the search cost at each bowl was zero.

We made observations from a motor vehicle approximately 4 m south of the bowls in the morning between 0730 and 0930 PST and in the afternoon between 1500 and 1645. We collected time-budget data on nine days spread between 26 January and 26 February 1990. The first individual whose color-band combination could be read was designated as the first subject, with the following subject as the next identified. Focal samples ended when the bird left the array of feeding bowls, or after 5 min. We recorded an individual's color-band combination, bowl location, number of feeding movements, number of vigilance movements, and duration of focal sample, as well as the number of other birds on that bowl (average number at start and end of focal session) and the time of day. Feeding was defined as a bird pecking at seeds, and vigilance as a bird raising its head up from feeding, and cocking its head in a clear act of scanning (a bird's long axis was horizontal to or pointed away from ground). Both behaviors were easily distinguished. We did not record other behaviors such as moving, but birds spent little time in this activity (moves usually lasted less than 2 s and almost always involved moving to new feeding bowl or off entire feeding site, which constituted a termination of the feeding bout and of the focal sample). We sometimes weighted our sampling towards birds on the bowls farther from the cover to increase sample sizes for those bowls with few focal birds. Feeding rate and vigilance rate were calculated by dividing the number of occurences of each behavior by the duration of the focal sample (in seconds).

In addition to these data collected by "direct" observation, we also video taped events on 29 and 31 December 1989. This allowed us simultaneously to observe individuals on different bowls. Data from these "video observations" were collected by a different observer than were those from direct observations. In analyzing these tapes, we followed an individual bird until it left the feeding array (or for 5 min), then rewound the tape to the start of the focal sample and observed the next bird identified on a different bowl (color bands were read onto video tape at time of recording). This allowed us to control for factors other than distance from cover (i.e. different times of day or days, and total number of birds present), and with the same observer following both birds.

Statistical analyses.—We performed multivariate analyses of the data. Initially, with either pecking rate or vigilance rate as the dependent variable, we ran stepwise multiple-regression models with all the other variables as independent variables (see Table 1 for list of independent variables), which allowed us to assess which independent variables were most important in influencing feeding and vigilance. We then ran an analysis of covariance (ANCOVA) with vigilance rate as the dependent variable, pecking rate as the covariate, and the important variables from the stepwise models as the independent variables. In a standard multiple-regression model with pecking rate as the dependent variable, the vigilance × bowl location × class interaction term had a significant effect on the model, thus violating the assumption for ho-

TABLE 1. Results for stepwise (forward selection, F-to-enter = 4.0) multiple regression of pecking rate (R^2 = 0.231, df = 173), and subsequent MANOVA (n = 178).[a] Class and bowl location are independent variables related to predictions.

	Stepwise multiple regression					MANOVA		
Variables in model	Beta coeffi- cient	F-to- remove	Variables not in model	Partial correla- tion	F-to- enter	Variable	F	P
Class	0.062	9.15	Date	0.002	0.01	Class	5.53	0.001
Bowl location	0.083	8.41	Log(duration)	0.014	0.03	Bowl location	2.38	0.10
Time of day	0.111	6.30				Time of day	12.08	0.001
Vigilance rate	0.759	21.86						

[a] Slopes of pecking rate and vigilance rate not homogeneous in multiple-regression model; therefore, ANCOVA could not be used.

mogeneity of slopes (Steel and Torrie 1980). There-fore, we could not use an ANCOVA with pecking rate as the dependent variable. Instead, we ran a multiple analysis of variance (MANOVA) with pecking rate as the dependent variable and the important variables from the stepwise models as the independent vari-ables. For comparison within variables, we used the Scheffe test for multiple comparisons, with a proba-bility value of 0.05. In each case, we controlled for the other variables by first performing a multiple re-gression of other independent variables against each behavior, and then performing a Scheffe test using residuals from these regressions as dependent vari-ables.

The data collected in the field involved 87 individ-uals, some of which were sampled more than once (median 2, range 1–6), but never sequentially. As re-peat observations occurred in separate observation sessions, at different times of the day, or at different bowls, or with different numbers of birds present, pseudoreplication (Hurlbert 1984) is not a problem with this data set. In addition, all analyses, except those dealing with social-class comparisons, include 35 focal samples of unbanded individuals. It is likely that few if any of 35 samples involve the same birds given the large number of individuals (>400 indi-viduals over three days; Slotow and Rothstein 1995) known to be using the site.

RESULTS

Social status. —We predicted that high ranking birds (i.e. adult males) would have the highest pecking rates and the lowest vigilance rate. Age-sex class did have a significant effect on the pecking model (Table 1). However, counter to our prediction, the most subordinate age-sex class (immature females) had significantly high-er pecking rates than the more dominant im-mature males (Scheffe test, P < 0.05; P > 0.05 for all other comparisons; Fig. 1A). Most im-portantly, dominant adult males did not have higher pecking rates than subordinates.

Vigilance rate did not vary among social classes (Fig. 1B), nor did class have a significant effect on the vigilance model (Table 2). There-fore, our predictions were not met for either pecking or vigilance rate. In the case of feeding, the results were the opposite of what we pre-dicted, with subordinate birds having higher pecking rates than dominant birds.

Distance from cover. —Distance from cover (i.e. bowl location) had no influence on pecking rate (Table 1, Fig. 2A), but did significantly influ-ence vigilance rate (Table 2). Note that vigilance

TABLE 2. Results for stepwise (forward selection, F-to-enter = 4) multiple regression of vigilance rate (R^2 = 0.217, df = 174), and subsequent ANCOVA (n = 214). Class and bowl location are independent variables related to our predictions.

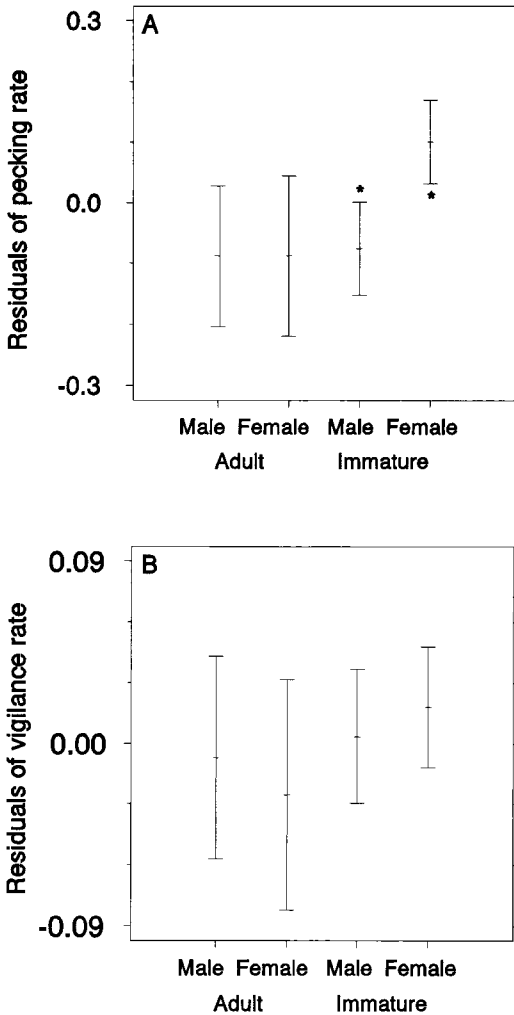|	Stepwise multiple regression					ANCOVA		
Variables in model	Beta coefficient	F-to- remove	Variables not in model	Partial correla- tion	F-to- enter	Variable	F	P
Bowl location	−0.03	6.04	Class	0.011	0.02	Bowl location	3.66	0.028
Date	0.004	16.71	Log(duration)	0.115	2.93	Date	2.65	0.008
Pecking rate	0.147	26.3	Time of day	0.129	2.93	Pecking rate	32.7	<0.001

Fig. 1. Pecking and vigilance rates of White-crowned Sparrows. (A) Pecking rate of different social classes, while controlling for distance from cover and time of day. (B) Vigilance rate of different social classes, while controlling for distance from cover and date. Mean residuals from multiple regression of each of controlled variables against given behavior, with Scheffe 95% confidence limits (whiskers). Sample sizes (from left to right for each group) were 26, 20, 59, and 73. Shared symbols indicate groups that were significantly different from each other ($P < 0.05$).
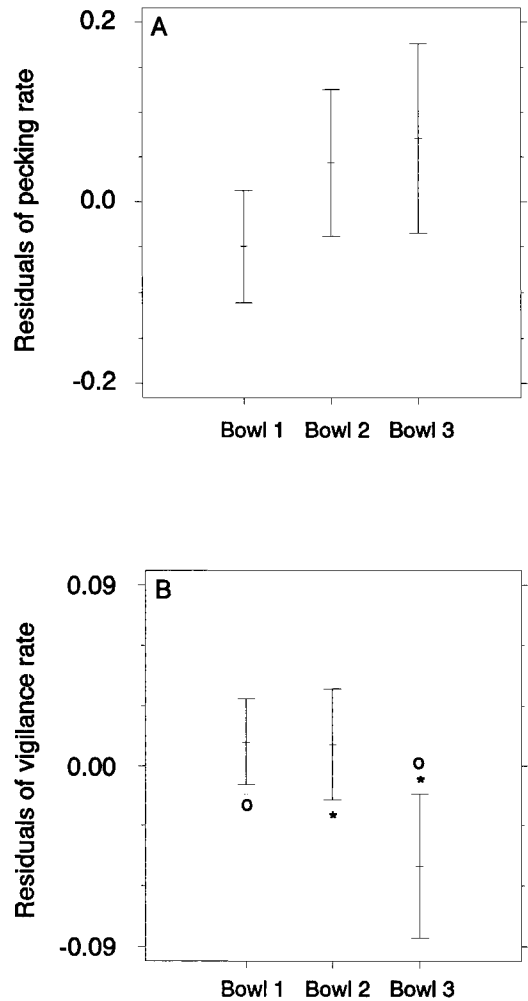
Fig. 2. Pecking and vigilance rates of White-crowned Sparrows. (A) Pecking rate at different distances from cover, while controlling for social class and time of day. (B) Vigilance rate at different distances from cover, while controlling for date and pecking rate. Mean residuals from multiple regression of each of controlled variables against the given behavior, with Scheffe 95% confidence limits (whiskers). Sample sizes (from left to right for each distance) were 93, 53, and 32. Shared symbols indicate groups that were significantly different from each other ($P < 0.05$).

was significantly lower at bowl 3 (furthest from cover) than at bowl 1 (Fig. 2B), which was the opposite to our predictions.

Our simultaneous video data of individuals on different bowls (i.e. at different distances from cover) showed no significant differences in either pecking (Table 3), or vigilance (Table

4) rates at different distances from cover. Distance from cover, therefore, was not as important as we predicted, and trends were contrary to our predictions.

Time of day, date, and duration of focal session. — We included time of day and date in the step-

TABLE 3. Comparison of simultaneous pecking rates (pecks/s; median with range in parentheses) at two bowls placed different distances from cover.

Comparison of bowls	First-listed bowl	Second-listed bowl	n^a	Z^b
1 vs. 2	1.10 (0.47–2.04)	1.11 (0.42–2.03)	19	0.141
2 vs. 3	0.96 (0.45–2.24)	1.03 (0.25–1.79)	17	0.852
1 vs. 3	1.08 (0.44–1.87)	1.20 (0.83–1.79)	13	0.629

[a] n differs given unique observations that comprised particular comparisons.
[b] Wilcoxon paired signed rank test. All $P > 0.05$.

wise models as they contributed to explaining variation. We do not discuss the implications of any differences because there are no clear *a priori* predictions as to when pecking or vigilance rates should be higher. Time of day had an important effect on the pecking model (Table 1), with pecking rate significantly higher in the afternoon than in the morning (Scheffe test, $P < 0.05$). Time of day did not have a significant effect on the vigilance model (Table 2). Date had no effect on the pecking model (Table 1), but a significant effect on the vigilance model (Table 2). However, there was no pattern for vigilance rate to either increase or decrease consistently through the study. Duration of focal session did not significantly influence either the pecking or vigilance models (Tables 1 and 2).

Number of birds on bowl.—As we could not normalize the group-size variable through transformation, group size was not incorporated into the stepwise regression model. Instead we performed nonparametric correlations on these data. There was no correlation between the number of individuals (group size) on the focal bird's bowl and either pecking rate (Kendall correlation, $T = 0.027$, $n = 169$, $P = 0.629$) or vigilance rate ($T = -0.072$, $n = 169$, $P = 0.196$). Because these two rates might be related causally, we also analyzed the importance of bird number with Kendall partial-correlation tests (Siegel and Castellan 1988). Holding vigilance rate constant, group size was not significantly

correlated with pecking rate (Table 5). Holding pecking rate constant, group size was not significantly correlated with vigilance rate (Table 5). We performed the same partial correlations separately for each bowl. None of the correlations were significant (all $P > 0.05$), except for a significant positive partial correlation between group size on Bowl 3 with vigilance rate (pecking rate held constant, $T_{xy,z} = 0.287$, $Z = 2.502$, $P < 0.05$).

Vigilance rates on bowls 1 and 3 my be similar because higher vigilance for other feeding conspecifics on bowl 1 (which had the largest group sizes) was countered by higher vigilance for predators on bowl 3. By holding group size on a bowl constant, we found that pecking rate was significantly positively correlated with distance from cover and vigilance rate was significantly negatively correlated with distance from cover (Kendall rank correlation; Table 5); that is, birds farther from cover had the highest pecking rates and the lowest vigilance rates. When we held distance from cover constant, there was no significant partial correlation between group size and pecking or vigilance rate (Table 5). Therefore, with the confounding influence of group size removed, pecking rate increased and vigilance rate decreased with increasing distance from cover.

In addition, we divided the data into two groups: one to four birds present; and five or more birds present. We made age-sex class comparisons, and overall comparisons (all classes

TABLE 4. Comparison of simultaneous vigilance rates (vigilance movements/s; median with range in parentheses) at two bowls placed at different distances from cover.

Comparison of bowls	First-listed bowl	Second-listed bowl	n^a	Z^b
1 vs. 2	0.20 (0.13–0.46)	0.21 (0.09–0.36)	19	0.131
2 vs. 3	0.22 (0.00–0.36)	0.18 (0.09–0.46)	17	0.710
1 vs. 3	0.19 (0.13–0.33)	0.18 (0.14–0.40)	13	0.275

[a] n differs given unique observations that comprised particular comparisons.
[b] Wilcoxon paired signed rank test. All $P > 0.05$.

TABLE 5. Effect of number of individuals on a bowl (group size) on pecking and vigilance rates. Procedure involves: (1) holding pecking or vigilance rate constant and evaluating effect of group size on other behavioral rate; (2) holding group size constant and evaluating effect of location on pecking and vigilance rates; and (3) holding location constant and evaluating effect of group size on pecking and vigilance rates.

Variable		Constant			
x	y	(z)	$T^a_{xy\cdot z}$	n	Z^b
Group size	Pecking	Vigilance	0.067	169	1.29
Group size	Vigilance	Pecking	0.008	169	0.15
Location[c]	Pecking	Group size	0.103	202	2.19*
Location[c]	Vigilance	Group size	−0.111	202	−2.35*
Group size	Pecking	Location	−0.024	202	−0.50
Group size	Vigilance	Location	0.020	202	0.42

[a] Kendall partial correlation (Siegel and Castellan 1988), which has effect of holding one variable (z) constant while correlating x against y.
[b] Test statistic related to normal distribution. *, $P < 0.05$.
[c] Bowl 1 was closer to cover.

combined), of both pecking and vigilance rates and found no significant differences between the rates in groups of one to four birds versus groups of five or more (Mann-Whitney U-tests, $Z < 0.881$, all $P > 0.1$).

DISCUSSION

We found little evidence supporting a trade-off of pecking rate against vigilance rate. There was no decrease in vigilance rate with increasing group size. There was no increase in vigilance rate with increasing distance from cover. Further, pecking rate neither increased with group size, nor decreased with increasing distance from cover. Dominant individuals did not have higher pecking rates than subordinate individuals, and the trend was for subordinates to have higher pecking rates than dominants.

Pecking rate.—Pecking rate did not decrease with distance from cover. Barnard (1980), working with foraging flocks of House Sparrows (*Passer domesticus*) similar in size to the birds we studied, found a suggestion of a slight increase in pecking rate with increasing distance from cover, although, as with our data, this was not statistically significant. As found in Great-tailed Grackles (*Cassidix mexicanus*; Smith 1977), pecking rate in our study did not increase with increasing bird density, although many other studies have found such a relationship (Barnard 1980, Caraco et al. 1980a, b, Jennings and Evans 1980, Lima 1987, 1988). Elgar (1987) noted that pecking rate of House Sparrows at a large feeder (1 m × 1 m) increased with increasing numbers at the feeder, while at a small feeder (15 cm × 15 cm), more comparable in size to the bowls

in our study, pecking rate decreased with increasing number.

Higher status gives dominant individuals access to the best feeding locations (e.g. Schneider 1984, Slotow 1993, Slotow and Rothstein 1995) and, presumably, to higher food intake with less risk of predation (e.g. Poysa 1988). Our results seem to contradict this tenet in that dominant individuals did not have the highest pecking rates. In another study of White-crowned Sparrows, Fugle (1983) found no differences in pecking rates among social classes in small groups (<5 birds), although adults had higher pecking rates than immatures in groups larger than five birds. In congeneric Harris' Sparrows (*Z. querula*), food capture rate was negatively correlated with dominance status when seeds were dispersed (Rohwer and Ewald 1981), the same result as we found when seeds were concentrated. Also, in Black-capped Chickadees (*Parus atricapillus*), dominant males and subordinate females had equal feeding rates (Desrochers 1989).

Vigilance rate.—Our technique may not accurately reflect subtle changes in vigilance behavior because we measured only the number of vigilance movements, and not the duration of each movement. However, nearly all vigilance movements were rapid and lasted the time of a pecking movement, although a small proportion lasted longer (for commentry on influence of vigilance duration, see Elgar and Catterall 1981). Handling time did not affect vigilance duration or rate in our study in that birds were feeding on small millet seed (see Popp 1988). In other species, the mean duration of a scanning movement was not correlated with

flock size (Elgar and Catterall 1981, Elcavage and Caraco 1983, Catterall et al. 1992, but see Studd et al. 1983), indicating that variance in vigilance duration may not bias results in any one direction.

Modification in vigilance rate may be a proximate reaction to immediate predation risk (Caraco et al. 1980a), and several studies have shown vigilance rate to be inversely correlated with group size (Lima and Dill 1990 and references therein), although other studies have found no influence of group size on vigilance rate (Smith 1977, Studd et al. 1983, Catterall et al. 1992, this study). Moreover, we found no change in vigilance rate with increasing distance from cover (i.e. with increasing predation risk). Barnard (1980) found vigilance rate was weakly and positively correlated with distance from cover, but that flock size and seed density had stronger effects. Several workers have found vigilance rate to increase with distance from cover (Caraco et al. 1980b, Ekman 1987, Hogstad 1988a) or with location in the flock (Jennings and Evans 1980, Keys and Dugatkin 1990), while others showed no change in vigilance with distance from cover (Elgar 1986, Lima 1988, Catterall et al. 1992, this study), or showed a decrease (Lima 1987). Some aspects of predation risk, therefore, do not have an overriding influence on an individual's vigilance behavior, especially at higher feeding densities.

At high densities, subordinates may spend more time attempting to anticipate the aggressive actions of other individuals, and give way more readily so as to avoid complete displacement from the feeding site. Thus, the lack of a decrease in vigilance rate with increasing density may be a consequence of increased wariness for conspecifics at higher densities (i.e. although vigilance for predation may decrease with density, vigilance for conspecifics increases). There is some corroborating evidence for this view from other studies: (1) House Sparrow vigilance rates were more strongly positively correlated with the number of birds in their immediate vicinity than with the total number of birds in the flock (Elgar et al. 1984). (2) Yellow-eyed Juncos (*Junco phaeonotus*) changed the amount of time spent watching other group members, and this varied with dominance status (Caraco 1979b). (3) Subordinate tits (*Parus* spp.) spend time looking out for both predators and dominant individuals (Hogstad 1988b, Poysa 1988). Barnard (1980) and Elgar and Catterall

(1981) found vigilance rate to decrease with group size up to a point, after which vigilance rate increased with group size. This latter increase may have been a result of increased scanning for conspecifics at higher densities (Caraco 1979b). Therefore, paying attention to feeding conspecifics may be advantageous because it allows subordinates to anticipate and avoid displacements by nearby dominants, and dominants to assess the relative richness of other feeding spots.

Conclusion.—Our data emphasize two points: (1) Dominant individuals do not have higher pecking rates than subordinates. (2) Vigilance does not increase with predation risk (distance from cover). We suggest that this pattern is mediated by increased wariness for conspecifics at higher densities.

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