

FLOCK SIZE AND POSITION EFFECTS ON VIGILANCE, AGGRESSION, AND PREY CAPTURE IN THE EUROPEAN STARLING¹

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Abstract. We studied autumn foraging flocks of European Starlings (*Sturnus vulgaris*) foraging on grass lawns to determine how flock size (up to ca. 250 individuals) and position within the flock (edge vs. center) affect the birds' foraging behavior. The birds fed exclusively by probing their bills into the ground, gaping, and extracting beetle larvae or earthworms, which were directly observed by us. Neither flock size nor position affected the rate of prey capture. Edge birds, however, spent more time vigilant and probed less than center birds. Rates of agonistic interactions did not differ between flock positions; therefore, the percentage of time actually spent foraging (i.e., walking, searching, and probing) was lower for edge birds due to their higher level of vigilance. The only behaviors affected by flock size were percentage of time spent vigilant and percentage of time spent foraging, but only for edge birds in flocks of ≤ 20 individuals. The rate of agonistic interactions did not increase with increasing flock size for edge or center birds. Probe rate was not correlated with prey capture rate, placing caution on indiscriminate use of probe (or peck) rate as an index of prey capture rate. The likely nature of the dispersion pattern of the starling's prey is discussed in relation to our results.

Key words: Foraging efficiency; group size; flock position; European Starling; *Sturnus vulgaris*; aggression; vigilance.

INTRODUCTION

Extensive theoretical and empirical work on flocking in nonbreeding birds points to two general hypotheses concerning its selective value. Flocking may serve to increase a group member's foraging efficiency or decrease vulnerability to predation, or both, compared to foraging alone (reviewed by Pulliam and Caraco 1984).

The energetic consequences of flocking are usually mediated through the effects of a forager's vigilance and aggressive interactions on its rate of prey capture (see Barnard and Thompson 1985 for a review). These relationships in turn can be influenced by other factors, such as temperature, flock size, and dominance status (e.g., Caraco 1979b, Barnard and Thompson 1985, Waite 1987). Though the relationship between various factors and prey capture rate has played a central role in understanding the costs and benefits of flocking, it is important to note that foraging success is usually not measured directly but rather is inferred from a bird's pecking rate. It is pos-

sible, however, that pecking rate is independent of, or nonlinearly correlated with, rate of foraging success. Indeed, Fleischer (1983) found an *inverse* relationship between pecking rate and foraging success in flocking Ruddy Turnstones (*Ar-enaria interpres*) when they were foraging on crabs, indicating that inferring simply an increased success rate from an increased peck rate may not always be valid.

We studied autumn foraging flocks of European Starlings (*Sturnus vulgaris*) to examine how a forager's prey capture rate, probe rate, vigilance, and aggression related to its flock size and position in the flock. We then used a multiple regression model to investigate the interrelationships between these variables. We chose the starling to study these relationships because, unlike most previous researchers, we were able to observe directly an individual's rate of prey capture and because we were able to study a wide range of flock sizes.

METHODS

We observed starlings foraging in flocks on grass lawns at the State University of New York Albany campus. Ten morning and 17 afternoon sessions were conducted on 19 days between 22 October and 20 November 1987. Each obser-

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vation session lasted 1–2 hr; the morning sessions usually started at 07:00–08:00 and the afternoon sessions usually began ca. 16:00. The lawns were <10 cm high and did not grow noticeably during the study period. There was no snowfall during the study period.

During a session, one observer (GCK) used a 20× spotting scope and spoke into a minicassette recorder while the other observer (LAD) recorded parts of the narration on paper, operated a stopwatch, and took data on flock information (see below). We used 15-sec focal sampling sessions (Altmann 1974). Birds were not individually recognizable.

FLOCK INFORMATION

We recorded the following data on starling flocks during each focal session:

Flock size. This was the number of birds on the lawn foraging with the focal bird. Flock size included the focal bird and was estimated in increments of five or 10 birds at sizes greater than 20. Flocks were usually discrete, roughly circular entities which tended to remain stationary as a whole, though the foragers were usually walking. Interneighbor distance was usually <1 m (not measured). The data presented were obtained from discrete flocks of <250 individuals and located under widely spaced trees or within 30 m of trees or shrubs. Small flocks (ca. <15) of foraging starlings usually occurred near a large number of conspecifics perched in adjacent trees.

Position in flock. “Edge” birds were picked from the periphery of the flock where no more than two birds separated them from open space. Data were not included in the analysis if an edge bird moved >2 m from the flock boundary (which happened rarely). “Center” birds were picked roughly in the center of the flock. Focal individuals were chosen at random within these definitions. All birds in groups ≤ 15 were counted as edge birds. In flocks containing >15 we alternated choosing focal individuals between edge and center birds to prevent biasing a flock position toward other variables (e.g., flock size, weather). Sample sizes, therefore, are similar for center and edge birds.

FORAGING BEHAVIOR

Starlings in our study fed exclusively by probing their bills in the ground, penetrating a depth of approximately a bill length (Lorenz 1949, Feare 1984, Stevens 1985). They captured either large

white beetle grubs (ca. 2 m × 0.75 cm, \bar{x} = 0.28 g, SD = 0.02, n = 11 grubs collected at study site) or red earthworms (unmeasured), each type conspicuously seen by the observer when captured. Starlings possibly fed on small insects or seeds, but we did not detect pecks (no soil penetration) oriented at the ground or grass blades as occurred frequently in other studies (Lorenz 1949, Feare 1984, Stevens 1985). In addition, nearly all unobserved swallowing motions revealed a grub or earthworm. We therefore regard ingestion of seeds or insects as negligible in our study.

The following foraging data were recorded for each focal bird:

Rapid probes. These were rapid single or sometimes double probes without an exaggerated gaping movement and were separated from other probes by the forager walking or turning to another piece of ground. Rapid probes lasted roughly 0.5 sec.

Intensive probes. These were counted as bouts of exaggerated probing, gaping, and/or digging motions at the same immediate piece of ground (thus beginning and ending by a change in the bird’s body position or location). Some bouts of intensive probes involved only one or two probes but were distinguished from rapid probes because intensive probes involve repeated digging and gaping motions whereas rapid probes do not. Intensive probes lasted roughly 1–3 sec.

Successful probes. A rapid or intensive probe was counted as successful if it ended in the acquisition of prey.

Vigilance. Vigilance was defined as the period of time a bird spent cocking its head above horizontal. Short periods of vigilance were assigned a duration of 0.5 sec and longer periods were timed when transcribing the tape.

Agonistic interaction. Agonistic interactions occurred whenever a focal bird was involved in a displacement, face-off (two birds erect and face to face at less than a body length), or kleptoparasitism. In escalated interactions the focal bird faced its opponent while hopping or fluttering (called “sky-dancing” by van der Mueren 1980). Escalated interactions occurred too infrequently to analyze separately and were pooled with agonistic interactions in all analyses except in calculation of foraging duration (below).

Foraging duration. Foraging duration represents the time a starling spent walking and searching the ground, probing, and handling prey.

It was calculated for each focal bird as $15 - V - A - 2(EA)$ where 15 is the length of each focal session in seconds, V is the focal bird's duration of vigilance (in seconds), A is its number of agonistic interactions (assumed to last 1 sec), and EA is its number of escalated interactions (assumed to last 2 sec).

DATA ANALYSIS

Rapid probes, intensive probes, agonistic interactions, and prey captures are reported as number of events per 15-sec focal session. Vigilance and foraging duration are reported as a percentage of 15 sec. Percentage of successful rapid probes is defined as the percentage of all rapid probes resulting in a prey capture; percentage of successful intensive probes is defined similarly. Small flocks are defined as flocks containing ≤ 20 foragers and large flocks as 21–250 foragers.

We used the SPSSX statistical package for all analyses (Nie et al. 1983). Regressions of foraging variables on flock size were done using first untransformed flock size and then \log_{10} flock size as the ordinate. If both of these ordinates produced a significant correlation for an independent variable, only the correlation generating the highest r^2 value is reported. For edge birds, regressions were run separately for small flocks (≤ 20), large flocks (21–250), and all flocks. Center birds occurred only in flock sizes of 16–250 (see above) and were therefore not divided into small and large flocks. Frequencies of flock sizes were more or less evenly distributed across the range of flock sizes.

Comparisons between edge and center birds for a foraging variable were made using chi-square or Mann-Whitney U -tests. When flock size was correlated with a foraging variable for small flocks (edge birds) but not large flocks, only large flocks were compared.

RESULTS

EFFECTS OF FLOCK SIZE

Neither the number of prey captures nor the number of agonistic interactions was significantly correlated with flock size for either edge or center birds. Only vigilance and foraging duration were affected by flock size; but this occurred only in edge birds foraging in small flocks (Fig. 1). For edge birds in small flocks, percentage of time spent vigilant was correlated negatively with the \log_{10} of flock size and percentage of time

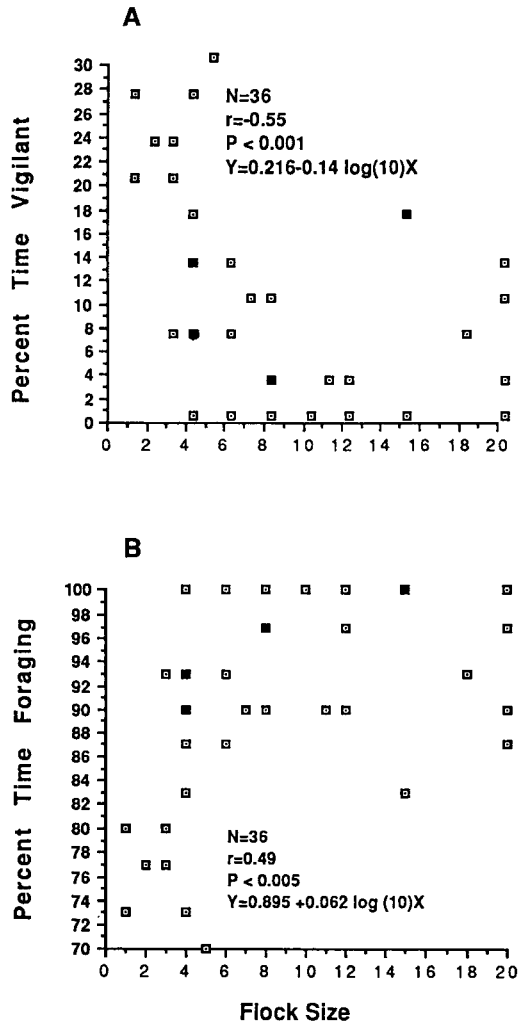


FIGURE 1. Effects of European Starling flock size on edge birds in flocks ≤ 20 . (A) Percentage of time spent vigilant. (B) Percentage of time spent foraging. These variables were not significantly correlated with flock size for edge birds in flocks of 21–250 or for center birds in flocks of 16–250. Darkened squares represent two data points.

spent foraging was positively correlated with the \log_{10} of flock size (Fig. 1). Number of intensive probes, number of rapid probes, percentage of successful rapid probes, and percentage of successful multiple probes were not correlated with flock size for edge or center birds (P 's > 0.10).

EFFECTS OF POSITION IN FLOCK

Number of prey captures did not differ between edge and center birds (Fig. 2). To corroborate the

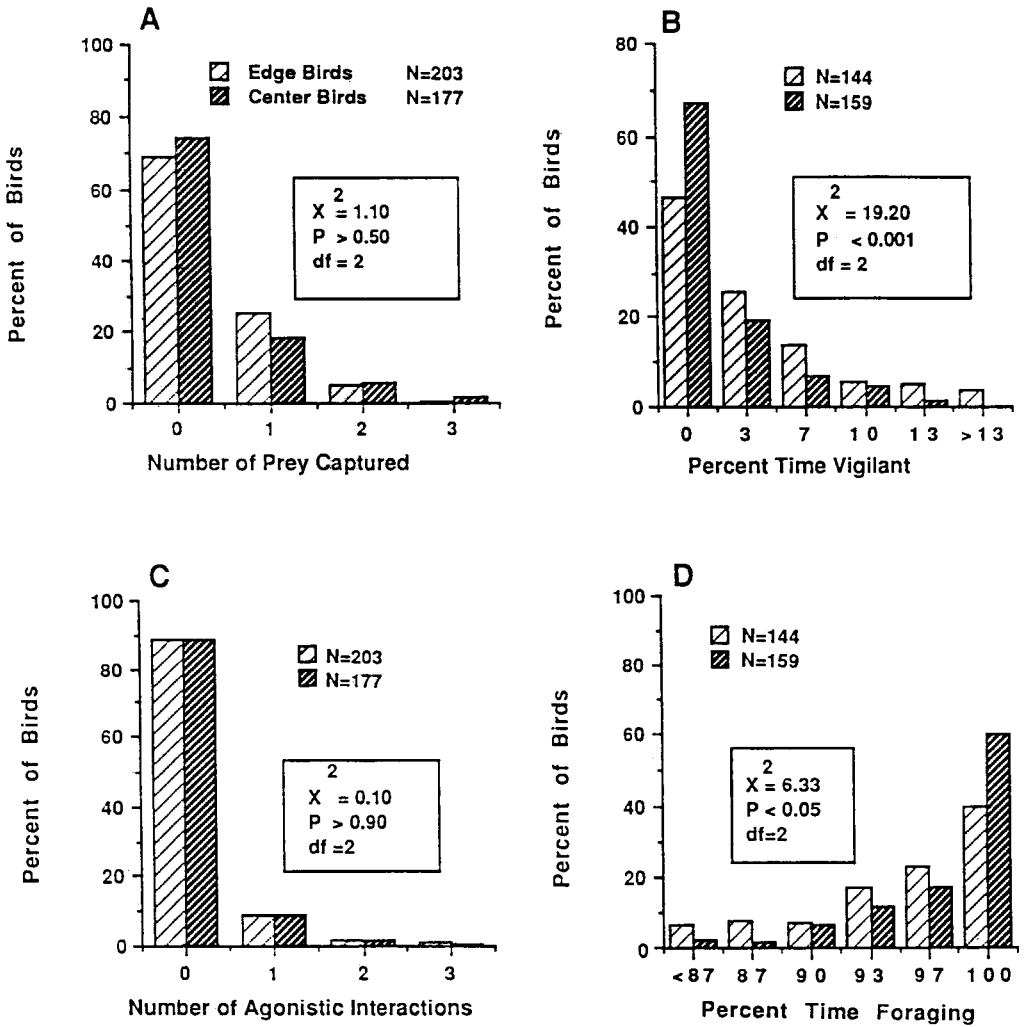


FIGURE 2. Frequency distributions in European Starlings for edge and center birds for (A) number of prey captures, (B) percentage of time spent vigilant, (C) number of agonistic interactions, and (D) percentage of time spent foraging. Frequencies are represented as percentages to standardize comparisons between unequal sample sizes. For variables correlated with flock size (Fig. 1), comparisons involve only edge birds in flocks of 21–250.

finding that number of prey captures was not influenced by flock size (above) or position in the flock, we ran a 2×2 ANOVA on prey captures with position (edge, center) and flock size (small, large; small = 1–20 for edge, 16–36 for center) as independent variables. There were no significant main effects or interaction (P 's > 0.10) thus reinforcing our finding. Altogether, a starling averaged approximately 1.5 prey items per minute regardless of its position in the flock or the size of the flock.

Though edge and center birds did not differ significantly in the number of prey captures, they did differ in other variables. Edge birds spent significantly more time vigilant than center birds (Fig. 2) and even more time vigilant when in small flocks (Fig. 1). Agonistic interactions were rare for both edge and center birds and did not differ between flock positions (Fig. 2); starlings were involved in an agonistic interaction approximately once every 1.7 min. The percentage of time actually spent foraging, therefore, was

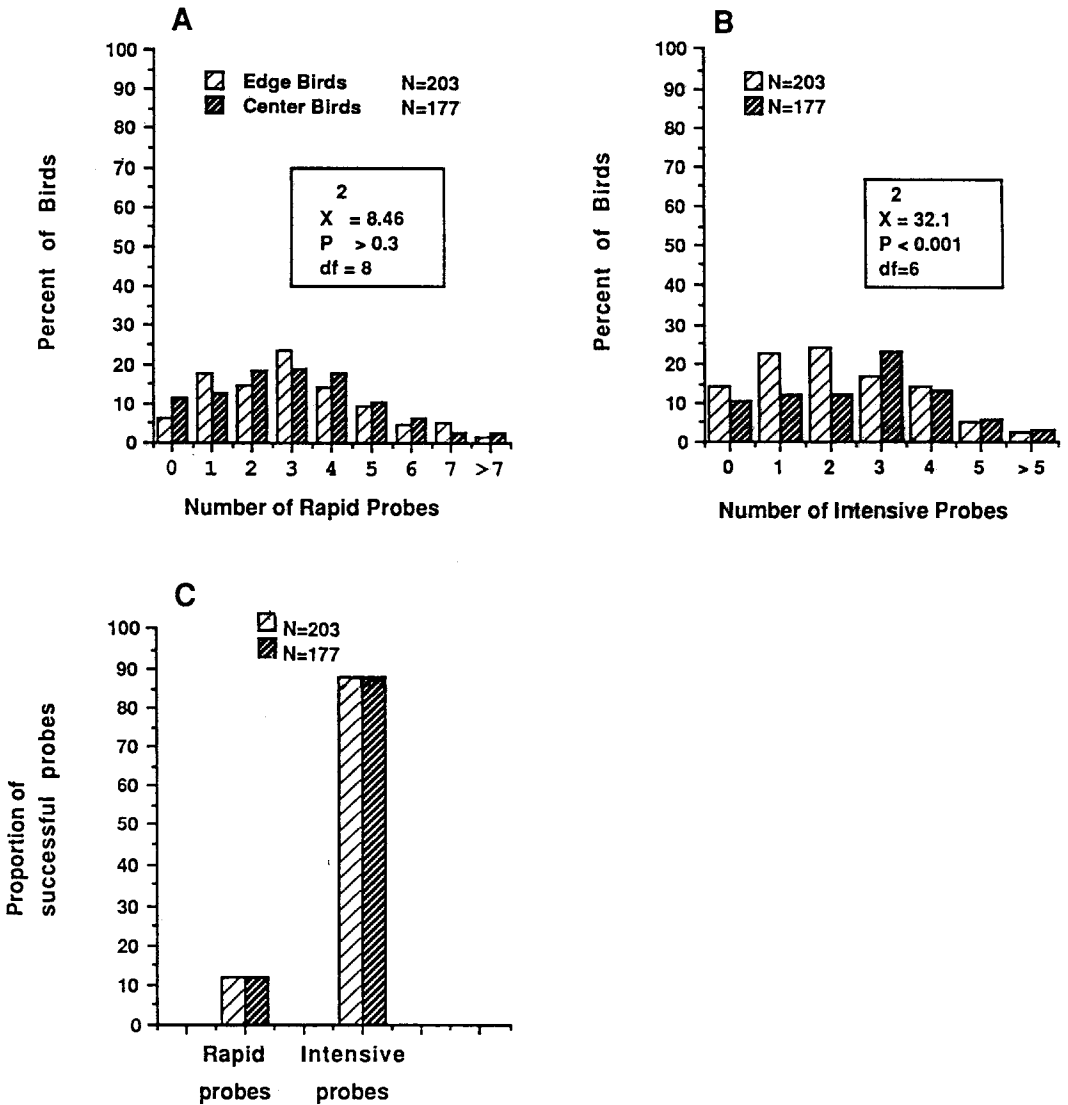


FIGURE 3. Frequency distributions in European Starlings for edge and center birds for (A) number of rapid probes, (B) number of intensive probes, and (C) percentage of successful or rapid probes out of all successful probes. Frequencies are represented as percentages to standardize comparisons between unequal sample sizes.

determined mostly by the time spent vigilant. Starlings spent most of their time under observation foraging (Fig. 2). Nevertheless, edge birds spent significantly less time foraging than center birds (Fig. 2) and this difference was even more pronounced when edge birds foraged in small flocks (Fig. 1). Over three-fourths of edge birds in large flocks spent $\geq 93\%$ of their time foraging whereas over three-fourths of center birds spent $\geq 97\%$ of their time foraging.

Edge birds averaged 3.5 rapid probes and center birds averaged 3.3 (Fig. 3). Most prey captures were the result of intensive probes, however (88%; Fig. 3); and edge birds in large flocks used significantly fewer intensive probes than center birds, averaging 2.2 and 3.0, respectively (Fig. 3). Approximately 19% of intensive probes were successful for edge birds and 11% were successful for center birds, though the difference was only close to significance (Mann-Whitney U -test, $U =$

TABLE 1. Stepwise regression of intensive probes and rapid probes for edge ($n = 180$) and center ($n = 159$) birds.^a

Flock position	Independent variable ^b	b	Partial df	F	P	R ²
Intensive probes						
Edge	Rapid probes	-0.26	177	23.7	<0.0001	11.7%
	Log ₁₀ flock size	-0.58	177	14.0	<0.0001	13.7%
	% time vigilant	-3.75	177	11.4	<0.0001	16.2%
Center	Rapid probes	-0.36	158	31.8	<0.0001	16.9%
Rapid probes						
Edge	Intensive probes	-0.47	177	23.7	<0.0001	11.7%
	Agonistic interactions	-0.97	177	16.5	<0.0001	15.7%
	% time vigilant	-4.14	177	12.7	<0.0001	17.8%
Center	Intensive probes	-0.47	157	31.8	<0.0001	16.9%
	Agonistic interactions	-0.71	157	18.0	<0.0001	18.7%

^a Independent variables are: percent time spent vigilant, number of agonistic interactions, flock size, and log₁₀ flock size for regressions on intensive probes and rapid probes, plus number of rapid probes for the former and number of intensive probes for the latter.

^b Variables are listed in the order they entered the model. Entry criterion is $P = 0.10$ and exit criterion is $P = 0.05$.

17,868.5, $P = 0.074$). Edge birds therefore used intensive probes less than center birds did, but were more successful per intensive probe.

INFLUENCES ON PROBE RATES

Since intensive probes were by far the most successful probe type, it is of interest to assess why edge birds used a lower number of these probes than center birds. We ran stepwise regressions on intensive probes separately for edge and center birds on the following independent variables: rapid probes, time spent vigilant, agonistic interactions, flock size, and log₁₀ flock size. The results are listed in Table 1.

For edge birds the model explained only 16.2% of the variation in intensive probes. Rapid probes contributed most to the variation though log₁₀ flock size and vigilance explained minor though significant amounts (Table 1). The model for center birds was similar ($R^2 = 16.9\%$) but only rapid probes entered. We were uncertain if there was a causal relationship between intensive and rapid probes so we ran similar regressions excluding rapid probes as an independent variable. The remaining variables behaved nearly the same as they did in the previous models.

In similar regressions on rapid probes (Table 1B) with intensive probes excluded as an independent variable, only agonistic interactions entered the model and only for edge birds, explaining 3.4% of the variation in rapid probes. Altogether, vigilance, agonistic interactions, and flock size played only minor roles if any in af-

fecting the number of rapid or intensive probes used by edge or center birds.

DISCUSSION

Our most striking result is that rate of prey capture was not affected by flock size or position in the flock. This is surprising in light of the fact that edge birds were more vigilant and used a lower number of intensive probes (the most successful probe type) than center birds; edge birds did not compensate by increasing their number of rapid probes. Agonistic interactions were rare for both edge and center birds in all flock sizes. As a result, time spent actually foraging was affected mostly by vigilance and edge birds spent less time actually foraging than center birds. Edge birds were more vigilant and foraged less when in small flocks. Flock size did not affect foraging behavior in edge or center starlings in flocks > 20 .

EFFECTS OF FLOCK SIZE

Because starlings did not suffer a decreased rate of prey intake or an increased rate of agonistic interactions when foraging in large compared to small flocks, it appears that starlings in our study should have benefitted by joining a larger flock if given the chance. Unless large flocks attract more predators, or enhance the predator's success, a starling joining a larger flock may benefit from a per capita reduction in the probability of being captured by a predator (the dilution effect, Hamilton 1971), though the magnitude of this benefit decreases with increasing group size.

Flocks with greater than 200 starlings were common in our study.

In contrast to our results, other studies have demonstrated costs to foraging in large flocks, and flock sizes in those studies were expectedly small. House Sparrows (*Passer domesticus*; Barnard 1980a, 1980b, 1980c) and Yellow-eyed Juncos (*Junco hyemalis*; Caraco 1979b; Caraco et al. 1980a, 1980b) became involved in an increasing number of agonistic interactions as flock size increased and their pecking rate (and presumably seed intake rate) consequently decreased. Birds in these studies foraged on patches of seeds and flocks were mostly restricted to the size of the patch. In our study, however, it is likely that the prey were not distributed in a few small rich patches but were more widely dispersed throughout the grass lawns, as occurred with starlings foraging on lawns in New Zealand (East and Pottinger 1975). Under these conditions, encounters between foragers would not be expected to increase with flock size and starling flocks would be expected to grow in number while remaining the same density. This may explain why in our study the rate of agonistic interactions per individual did not increase with flock size. It is interesting to note that starlings foraging in grain bins (Feare and Inglis 1979) faced a higher rate of agonistic interactions as flock size increased and consequently suffered a lower peck rate.

EFFECT OF POSITION IN FLOCK

Even though flock size had no effect on rate of prey capture in our study, it is still surprising that edge birds attained the same rate of prey intake as center birds who were less vigilant. Theoretical considerations of foraging flocks of birds frequently rest on a negative relationship between vigilance and rate of prey capture (e.g., Pulliam 1973, Caraco 1979a, Elgar and Catterall 1981). This relationship has been documented directly in some studies (Abramson 1979, Sullivan 1984) and indirectly in others (Caraco 1979b; Barnard 1980a, 1980b; Caraco et al. 1980a, 1980b; Jennings and Evans 1980) by using peck rate as an index of prey capture rate. In our study, prey abundance may have been lower in the center of flocks because of a greater overlap of search paths there than at the edge, an explanation that is likely since the flocks tended to remain stationary (Methods). If prey levels were in fact lower for

center birds, edge birds were foraging in a comparatively more profitable region and therefore may have traded off increased vigilance for a greater success rate per probe, as our data suggest. This trade-off appears to be the case in flocks of White Ibises (*Eudocimus albus*) foraging for crabs on mudflats (Petit and Bildstein 1987). Ibises on the edge of flocks were more vigilant and probed less than birds in the center yet still attained the same rate of prey intake. Edge birds were able to visually detect and chase crabs scurrying on the mudflat surface whereas center birds were forced to repeatedly probe holes for hidden crabs.

Both edge and center starlings in our study foraged on hidden prey, however, so one would still expect both types of foragers to be able to increase their rate of prey capture by increasing their probe rate. Although edge birds were more vigilant and used intensive probes less than center birds, vigilance was only weakly correlated with intensive probe rate for edge birds, explaining less than 3% of the variance. Unfortunately, why edge birds did not probe at the same rate as center birds and presumably increase their rate of prey capture cannot be addressed with our data. Edge birds, however, were noticeably more mobile than center birds. It may be that edge birds spent more time walking and visually searching for particularly profitable areas of turf (e.g., at the base of grass clumps or in sparsely probed regions) at the cost of intensive probe use, while these profitable patches were unavailable for center birds. It could be argued alternatively that profitable patches may have existed for center birds as well, but that center birds were too crowded and thus unable to search for them as much as edge birds could. If this latter explanation were correct we would expect greater numbers of agonistic interactions in center birds compared to edge birds, but our data do not reveal this.

OPTIMAL FORAGING

Our interpretations thus far rest on the assumption that starlings are striving to maximize their prey captures per unit time. This assumption may not be true. Starlings may possess digestive constraints which prevent them from processing greater than the 1.5 prey items per minute found in our study. Center and edge birds in various flock sizes therefore may be constrained to the same foraging efficiency by physiological and not

ecological factors. In a slightly different view, starlings may be able to obtain their daily food requirements in a relatively short period of time. A bird much closer to this requirement than flock members on average may forage at a submaximal rate because reaching the requirement level and leaving the flock may be more costly, perhaps owing to predation risk, than adjusting its foraging behavior and waiting for the rest of the flock to leave.

Our results as well as those of Fleischer (1983) and Petit and Bildstein (1987) fail to show a simple correspondence between peck (or probe) rate and prey capture rate. These studies thus indicate that peck rate should not be used indiscriminately as an index of prey capture rate. In a study similar to ours, Jennings and Evans (1980) determined that starlings feeding on the edge of flocks were more vigilant and correspondingly probed less than birds in the center. This might have been interpreted as indicating that edge birds capture fewer prey than center birds, but we have shown similar relationships between vigilance, probe rate, and flock position, yet no difference in the number of prey captured by edge and center birds. It seems reasonable that for birds feeding on visibly detectable seeds, pecking rate is a good index for prey capture rate. We suggest, however, that for birds which peck or probe to uncover hidden prey or which feed on prey that is difficult to handle, rate of pecking or probing is not *prima facie* a reliable measure of prey intake rate.

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