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Scanning-group-size effect in flocks of house sparrows: quantifying the contribution of competition and anti-predatory vigilance

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Of

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ABSTRACT

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Grégory Schmaltz

As social foraging groups increase in size, individual levels of scanning decrease while time spent feeding increases. Traditionally, anti-predatory considerations provide the preeminent explanation for this scanning-group-size effect, but contest and scramble competition could also account for the results. The anti-predatory hypothesis predicts that the reduced need of vigilance in groups allows subjects to decrease their scanning and consequently increase their feeding rate. Contest competition tends to decrease the group foraging benefits especially for subordinate individuals. However, the scramble competition hypothesis predicts that competition drives individuals to increase their feeding rate by decreasing their handling time per peck and, therefore, is consistent with an increased rate of feeding in the inter-scan intervals. I used this rationale to explore the contribution of each factor to the scanning-group-size effect of house sparrows (*Passer domesticus*) observed while they fed from an artificial seed patch during the winter. The inter-scan pecking rate of individuals, excluding scanning, increased with group size while handling time per peck decreased. Dominants pecked more quickly than subordinates at group sizes greater than 12, subordinates hopped more than dominants

and spent more time handling each seed for group sizes greater than 18. These results suggest a contribution of contest and scramble competition to the scanning-group-size effect. Dominants appeared to be more sensitive to changes in group size than subordinates and both competitive and anti-predatory considerations might help to explain this result.

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INTRODUCTION

Foraging animals often engage in scanning by lifting their heads and surveying their surroundings. This scanning is often termed vigilance when its presumed function is to provide early detection of approaching predators. However, not all scanning is necessarily vigilance because a number of studies have described scanning in situations with no predators (eg. islands: Catterall et al. 1992) or serving other functions such as detecting scrounging opportunities (Coolen et al. 2001), sampling food (Langen & Gibson 1998) or obtaining social information such as flock composition (Caine & Marra 1988; Pravosudov & Grubb 1999). Therefore, in the current study, the word "scanning", rather than vigilance, will refer to the behaviour associated with scrutinizing the environment with the head up.

A common observation in group foraging animals, especially in birds, is that as group size increases, individuals decrease their levels of scanning, freeing up time they can then devote to foraging (Pulliam 1973; Caraco 1979; Elgar 1989; Quenette 1990). This scanning-group-size effect is traditionally associated with anti-predatory considerations (McNamara & Houston 1992; Lima 1998; Bednekoff & Lima 1998). That is, the presence and vigilance of flock-mates dilute the risk of predation and increase the probability of detecting a predator in time to escape an attack (Pulliam 1973; Roberts 1996). Therefore, less vigilance is required per individual to maintain similar levels of safety and the time thus saved can be used to feed. Many studies have found a link between scanning rate and both group size and predation risk. For instance, the increases

in scanning observed either with an increased distance to cover (Schneider 1984; Lazarus & Symonds 1992) or the introduction of an aerial predator (Lendrem 1984; Caraco et al. 1980) leave little doubt concerning the causal relationship between predation danger and scanning (Roberts 1996; Lima 1998, Bednekoff & Lima 1998).

Unequivocal support for the anti-predatory explanation of the scanning-group-size effect, however, requires control of other confounding factors that might alter the relationship between group size, scanning, and pecking time (Elgar 1989; Beauchamp 1998). For instance, under conditions of scramble competition in large groups, the best foraging strategy may be to minimize handling time, maximize speed of search or ingestion, and increase feeding time at the expense of scanning in order to secure the greatest possible proportion of the food supply (Lendrem 1984; Clark ms; Clark and Mangel 1986; Cézilly & Brun 1989; Saino 1994). Since scramble competition intensity likely increases with increasing group size, it can also account for the scanning-group-size effect. Few studies have considered the possible contribution of scramble competition to the scanning-group-size effect (Clark ms; Clark & Mangel 1986; Yamamura & Tsuji 1987; Shaw at al. 1995), and even fewer have examined the problem empirically (Beauchamp & Livoreil 1997; Lima et al. 1999). So the direction of causation from scanning to feeding time could be reversed, with increased competitive pressure being the primary driving force behind the reduction of scanning with increasing group size (Clark & Mangel 1986; Shaw et al. 1995). In a manner consistent with the scramble competition hypothesis, spice finches (*Lonchura punctulata*) scanned less in a food-limited environment while they pecked and handled seeds at a faster rate with

increasing group size (Beauchamp & Livoreil 1997).

Pressures from competition and predation could have separate effects on different components of foraging behaviour. For instance, in house sparrows (*Passer domesticus*), there is no correlation between scanning rate and feeding bout length (Studd et al 1983; Elgar et al. 1986; but see Férrière et al. 1996), suggesting that the decision to scan is independent of inter-scan length. In addition, the inter-scan pecking rate of barbary doves (*Streptopelia risoria*) is independent of inter-scan length whether a bird is tested alone or with a conspecific (Cézilly & Brun 1989). The rate of pecking for solitary foragers during the inter-scan interval may correspond to an optimal solution that maximizes net energy gain between the number of seeds eaten, the efficiency of processing (husking and/or crushing), and swallowing (Clark ms; Zweers 1982). However, when in a group, pecking during the inter-scan interval could be increased to maximize a bird's share of the resource, possibly at the expense of processing efficiency (Kenward & Sibly 1977; Sibly 1981). This higher inter-scan pecking rate could, for instance, constitute a Nash solution to the competitive foraging game of maximizing each individual's share and hence qualify as an ESS (Clark & Mangel 1986; Giraldeau & Caraco 2000). That is, no individual could improve its payoff by reducing its foraging rate when the other players continue using their higher Nash equilibrium foraging rate strategy. Scan frequency and duration on the other hand could be based on predation risk alone.

It is also possible that competition and predation combine their effects; the influence of competition on the foraging variables would then be affected by predation pressures and vice versa. For instance, in *S. risoria*, inter-scan pecking rate increases as

competition intensifies but the rate of increase is lower in a high predation risk situation compared with a low risk situation (Lendrem 1984). Interestingly, even when predation risk is large, the effect of competition persists, indicating that predation risk does not override competition (but see Lima et al. 1999). Conversely, in the presence of a mirror that simulates competitor presence, juvenile coho salmon (*Oncorhynchus kisutch*) become less sensitive to predation risk, and travel a longer distance to consume a prey than when they are tested in visual isolation (Dill & Fraser 1984). However, in a recent experiment with the same species, Grand & Dill (1999) found that this risk-taking behaviour was affected by the number of competitors but not by the presence of a predator.

It is a demanding task to distinguish between the competitive and anti-predatory contributions to the scanning-group-size effect because manipulating the intensity of predation while holding competitive pressures constant or vice-versa is difficult. Furthermore, working at the individual level requires recognizable subjects. Fortunately, the two hypotheses do not always generate the same general predictions and the potential effects of group members on pecking rates can vary according to two different scenarios (Fig.1): the more time to feed scenario A and the faster pecking scenario B. In scenario A, reductions in scanning time lead to more feeding time and hence a higher pecking rate in groups than when alone. In A, the inter-scan pecking rate when foraging alone is equal to inter-scan rate when in groups because non-scanning handling time (the blocks in the figure) does not change with group size; the birds always feed at the same optimal rate. In A, group size has no effect on the inter-scan pecking rate but only on time available for

pecking. In B, scramble competition drives the individuals toward a higher feeding rate. The higher rate is achieved by increasing the inter-scan pecking rate by reducing the time spent in non-scanning handling. Scramble competition is consistent with increased inter-scan pecking rate and decreased non-scanning handling per peck with increasing group size.

Scramble competition is not the only type of competitive pressure that could contribute to the scanning-group-size effect. Aggressive or ritualized contest competition can also affect foraging (Cresswell 1998a) through competitor avoidance (Vines 1980; Pravosudov & Grubb 1999), resource defence within the patch (Monaghan & Metcalfe 1985; Van Schaik 1989; Grant 1993), time-constrained energy budgets (Caraco 1979) or daily unpredictability of food supplies (Caraco 1979; Giraldeau & Caraco 2000) that can, for instance, affect a bird's energy reserves (Cuthill & Houston 1997). Contest competition, often referred to as interference competition (Cresswell 1997; Cresswell 1998a), is especially relevant since it is a direct effect caused by the presence of competitors in the same patch (Lessells 1995) and therefore its intensity likely increases with group size (Tregenza et al. 1996 a, b; Cresswell 1998b) at least until intermediate population densities (Grant 1993; but see Sirot 2000). Blackbirds (*Turdus merula*) responded to such contest competition at larger group sizes by increasing conspecific surveillance at the expense of feeding rate (Cresswell 1997). An individual's dominance status likely influences the intensity of competition it experiences (Baker et al. 1981; Robichaud et al. 1996; Koenig 2000). Dominant individuals are expected to perform better than subordinates because they are less affected by contest competition. Each

individual might therefore adjust its inter-scan pecking rate, handling time, and hopping rate to flock size on the basis of its dominance rank.

The objective of this study is twofold: first to explore experimentally the distinct contributions of anti-predatory and competitive pressures to the scanning-group-size effect in flocks of house sparrows feeding in the field; second, to document the extent to which dominance rank affects an individual's response to group size for inter-scan pecking rate, handling time, and hopping rate.

METHODS

In order to recognize individual birds, over 350 house sparrows were mist-netted, sexed, aged, and colour-banded during the summer of 1998 at a convenient bird-gathering locality near the experimental site. Fifteen marked individuals were frequently observed at the field site during the test period, from mid-December 1998 through the end of February 1999. These 15 subjects were part of an estimated local population of 60 resident individuals within the Macdonald College farm of McGill University in St-Anne-de-Bellevue, Québec, on the west tip of the Island of Montréal. The subjects were at least one and a half year old adults with a 7:8 (M:F) sex-ratio. I observed the subjects as they foraged in a 4 m^2 area located under a 3.6 m high roof, 3.2 m away from a stone wall containing their nesting sites (Fig.2).

At the start of an observation day, I randomly selected one of four different millet seed densities: 125, 250, 500 or 1000 ml/m^2 to be used that day. I sat in a car 7 m from

the centre of the food patch and videotaped birds from 0900 to 1300, three times a week. Each trial consisted of videotaping one focal individual for at least 10 s until group size changed or the bird flew away. I repeated each trial with either the same individual, if it was still present in the flock, or with a different focal bird. A flock was defined as a group of individuals where each member was separated from its nearest neighbours by less than one meter. I only recorded single flocks foraging on the 4 m^2 area and discarded the few trials where individuals were split into subgroups separated by one meter or more. Seed handling, defined as the time necessary to remove the husk and ingest a seed, could occur with either the head up or down. Not all handling, therefore, involves scanning (head up), however all scanning occurred while handling and is referred to as "food-handling scanning" (sensu Lima et al. 1999; Fig.1). Other components of an individual's time budget include pecking, aggressive interference, and hopping. The hopping rate refers to the number of hops per individual per min in the feeding patch and thus gives an estimate of movement within the flock. No other behavioural component such as preening was observed during a trial.

During videotaping, I counted the number of individuals in a flock, calling any change in number into the videotape's audiotrack. From playbacks of the tapes, I also noted the colour code of the bird, the duration of a trial, and the number and duration of hops, pecks, seed handling, and scans defined roughly as when the line between a bird's eyes and nostrils was at or above the horizontal (Coolen et al. 2001). I also noted when the focal bird either chased another bird or was chased and recorded this as "aggressive interference". Observations were recorded when flock size was stable for at least 5 s

before videotaping. Behaviour was entered from video playbacks into a computer running "The Noldus Observer" as an event recording software (time schedule 0.1 s).

I recorded ad libitum aggressive dyadic interference encounters involving banded birds only when they occurred away from food patches while the birds were pecking at feeders, dust bathing or competing for perching sites visible from the car. Dominance ranks are calculated using methods described in Brown (1975).

I conducted observations only on sunny days without any major cloud cover and without any noticeable wind. I recorded the time of day of trials and the ambient temperature, using a thermometer placed on the ground 1 m away from the feeding patch.

All repeated measures analyses were performed as analyses of covariance (ANCOVAR) with dominance rank as covariate using the SPSS 10.0 Statistical Software. For the ANCOVARs and the stepwise regression analysis the statistical results are based on means. All subjects differ in the number of observations per group size per food density treatment. In order to avoid any effect of group size I also used means for the multivariate analysis of variance; especially since the two dependent variables are affected by group size. I calculated six means representing six classes of group sizes (1-5, 6-10, 11-15, 16-20, 21-25, and 26-30) for each subject, food density treatment, and dependent variable. Scanning, handling times per peck, and hopping were rank-transformed to meet the assumptions of parametric tests. For each ANCOVAR the sphericity assumption must be verified. However, Mauchly's test of sphericity performed in statistical packages is overly sensitive to departures from normality and therefore not recommended (Stevens 1986). Therefore, for each ANCOVAR, I will provide P values

when sphericity is assumed and then adjust the degrees of freedom with the Huynh-Feldt epsilon to provide a reasonable test that keeps the actual α close to the nominal α (Stevens 1986).

Pecking rate was calculated by dividing the number of pecks in a trial by the total trial duration. To calculate inter-scan pecking rate, I subtracted the time spent in aggressive interference and the time spent scanning from the total trial duration, and divided the number of pecks in a trial by the remaining time (Fig.1). I will refer to this pecking rate as the inter-scan pecking rate that gives an estimate of the speed upon which the birds are pecking during the inter-scan intervals.

RESULTS

My results are based on a total of 499 min of videotaped observations distributed over 21 d and 16 h of recordings. The temperature averaged -2.9°C (+5.2 to -10.1) at the feeding patch. The dominance ranks of the 15 subjects were based on 252 interference interactions between colour-banded birds.

The birds commonly formed a linear flock advancing along the same edge of the feeding patch. The birds moved toward the centre of the feeding patch but never occupied more than one fourth of the 4 m^2 area. After 30 min of cumulative foraging, patch depletion became apparent from the car in the lower food density treatment. The birds never fed for more than 50 cumulative min on any observation day and supplementary seeds were added to the patch once per day if the subjects had foraged for more than 30

cumulative min.

Food density had no detectable effect on pecking rate and scanning time per min (Table 1) so the data for all seed densities are combined for subsequent analyses. Neither temperature ($P > 0.2$) nor time of day ($P > 0.5$) significantly affected flock size (one-way ANOVAs).

A step-wise regression with inter-scan pecking rate as the dependent variable and group size, scanning time per min, and interference rate as independent variables revealed that only group size affected inter-scan pecking rate significantly (Table 2).

The birds spent less time scanning as group size increased (Table 3). The decline in scanning time was particularly pronounced at small group sizes, levelling off at group sizes beyond 12 (Fig.3). Dominance did not significantly affect scanning time per min (Table 3).

Both pecking rate (Table 4a; Fig.4a) and inter-scan pecking rate (Table 4b; Fig.4b) increased with group size. However, a significant interaction between group size and dominance indicated that the extent to which the pecking rate (Table 4a) and inter-scan pecking rate (Table 4b) were affected by group size depended on the individual's dominance rank. For the pecking rate, the interaction is only significant if sphericity is assumed (Table 4a). With the Huynh-Feldt correction there is still a trend however not significant. Dominant individuals appeared more sensitive to changes in group size than subordinates for both types of pecking rates (Fig.5). The dominant birds' pecking rates increased more rapidly with group size than the rates of subordinates. Moreover, at small group sizes, subordinates pecked faster than dominants but at large group sizes it is the

dominants that pecked faster (Fig.6a). Inter-scan pecking rate showed the same trend; dominants pecked at a faster rate than subordinates when group size increased beyond 12 individuals but the reverse holds for smaller group sizes (Fig.6b).

Birds spent less time handling seeds per peck as group size increased (Table 5). There was a significant group size by dominance status interaction on handling time per peck (Table 5). Subordinate birds spent more time handling seeds per peck than dominant individuals when group size increased beyond 18 individuals, the reverse holds for smaller group sizes (Fig.6c).

Hopping rate increased with increasing group size, and there was a significant group size by dominance interaction on hopping rate (Table 6). Subordinate birds hopped more per min than dominant individuals for all group sizes. However, the rate of increase in hopping was higher for dominant individuals (Fig.6d).

DISCUSSION

The current results confirm the existence of a scanning-group-size effect in flocks of house sparrows similar to what had been previously reported for this species (Barnard 1980; Elgar 1987). The birds spent less time scanning with increasing group size while their pecking rate increased. The study provides quantitative evidence suggesting a contribution of competitive pressures to the scanning-group-size effect in two ways: first, the inter-scan pecking rate of individuals increased with group size and second, handling time per peck decreased with group size. Moreover, the results show that the way an

individual responds to change in group size depends on its social rank. Dominants pecked at a faster rate between scanning events than subordinates at group sizes beyond 12. Subordinates hopped more than dominants and spent more time handling each seed for group sizes beyond 18. Dominants were more sensitive to changes in group size than subordinates and both competitive and anti-predatory considerations might help to explain the results.

Relevance of the inter-scan pecking rate variable

A number of empirical (Caraco et al. 1980; Beauchamp 1998; Pravosudov & Grubb 1999) and theoretical (McNamara & Houston 1992; but see Lima 1990) studies assume that foraging and vigilance are mutually exclusive activities. Because inter-scan pecking rate is the result of the subtraction of scanning behaviour from the trial's total duration, it is possible that effects attributed to inter-scan pecking rate reflect effects on scanning. Scanning in the present study, as is the case for all studies using millet seeds, was always concomitant with handling (Lima 1988). So when scanning was subtracted from trial duration it also included the handling that occurred while scanning, what Lima et al. (1999) call "food-handling scanning", potentially removing a handling component from the estimate of inter-scan pecking rate. However, this removal is unlikely to be a problem for two reasons. First, of all variables included in the step-wise regression analysis, only group size was a significant predictor of the inter-scan pecking rate and food-handling scanning was excluded from the model. Second, the high food density used in this study

reduces the need for search, making handling time the major limiting step in between two consecutive pecks. Because all scanning is done while handling, and because scanning increases at small group sizes, removing food-handling scanning would remove a larger percentage of the food-handling at small group sizes. This should result in higher inter-scan pecking rate for smaller groups, exactly the opposite of what was observed. So, food-handling scanning in itself is not likely to be a factor that was involved in altering a subject's inter-scan pecking rate. The birds increased their inter-scan pecking rates, a result that is consistent with the competition hypothesis.

To compute inter-scan pecking rate, it was also necessary to remove the time spent in aggressive interference to avoid any potential effect of increased aggressive interference with increasing group size. The results from the step-wise regression indicate that interference had no significant effect on inter-scan pecking rate, and thus its removal is unlikely to be a problem. Direct aggressive interactions were rare at the feeding patch and only represented a maximum of six percent of an individual's time budget at large group sizes. This lack of aggressiveness is attributable to two different factors. First, the 4 m^2 feeding patch was large enough so that the individuals could spread out. Even at group sizes of 30 individuals, a flock only occupied about one fourth of the feeding area. Second, house sparrows remain in the vicinity of their nesting sites even during winter (Summer-Smith 1967). The 60 resident birds are probably very familiar with each other, avoiding some of the costs associated with dominance maintenance, and explaining the small number of aggressive displays in this species in these conditions (Caraco & Bayham 1982; Elgar 1986; Solberg & Ringsby 1997).

Prediction about inter-scan pecking rate

The increase in inter-scan pecking rate with group size suggests a contribution of scramble competition to the scanning-group-size effect (scenario B, Fig.1). An increased food-processing rate with group size has been reported in different taxa including birds: yellow-eyed juncos (*Junco phaeonotus*; Caraco 1979), spice finches (Beauchamp & Livoreil 1997), barbary doves (Wright 1975, Lendrem 1984; Cézilly & Brun 1989), fish: juvenile coho salmon (Dill & Fraser 1984; Grand & Dill 1999), goldfish (*Carassius auratus* L.; Street et al. 1984), and mammals: common shrew (*Sorex araneus* L.; Barnard et al. 1983). The current results show that the increase in inter-scan pecking rate continues up to groups of 30 individuals, well beyond the small (2-6) group sizes used in earlier studies. Moreover, the current study is one of the first to document a link between dominance rank and the behavioural components of foraging that are adjusted with increased group size.

Inter-scan pecking rate increased with an individual's dominance status and intensification of competitive pressures with increasing group size provide the most parsimonious explanation for this inter-scan pecking rate increase. This interpretation is consistent with the absence of any effect of dominance on scanning (see also Hogstad 1988). Furthermore, the increased inter-scan pecking rate for dominants cannot be explained by the dominants monopolizing the central, safer flock positions where less scanning is necessary (Lazarus 1978; Yaber & Herrera 1994; Flynn & Giraldeau 2001)

precisely because the inter-scan pecking rate excluded scanning.

Prediction about handling time

The time spent handling per peck significantly decreased with increasing group size. Because in the present case a large component of handling also includes scanning (the food-handling scanning) both anti-predatory and competition hypotheses are consistent with this result. However, competition is more likely to explain the results for two reasons: 1- The anti-predatory hypothesis only accounts for an effect on food-handling scanning. Because the inter-scan pecking rate, which excludes food-handling scanning, increased with group size, it implies a reduction in the remaining non-scanning handling (head down) and hence less handling per seed (Fig 1). Furthermore, even when increased digestive costs associated with shorter handling times are taken into account, game theoretical models suggest that the best solution may still be to scramble for food (Shaw at al. 1995) and reduce handling times when group size increases (Clark & Mangel 1986; Lima et al. 1999). 2- The subjects varied their handling time per peck according to their dominance rank (Fig.6c) and differences in competitive pressures among ranks could account for this result. These individual differences in handling are not easily explained by anti-predatory considerations given that dominance did not significantly affect scanning time per min. Handling may, therefore, be a decision variable (Newman et al. 1988; Johnson et al. in press) that participates in the animal's response to competitive pressure. The effect of predation cannot be ruled out however and could at least partially

explain the results if the individuals can scan for predators while their head is down (Lima & Bednekoff 1999).

Differences among dominance ranks

Dominant individuals are expected to perform better than subordinates because they are less affected by contest competition and therefore should be the ones responding the least to changes in group size. High ranking individuals could perform better by chasing subordinates from good locations (Schneider 1984; Monaghan & Metcalfe 1985; Slotow & Rothstein 1995a), by forcing them to change their diet (Engen et al. 1988) or simply by feeding more efficiently (Caraco 1979; Ens & Goss-Custard 1984). The significantly higher hopping rates noted for subordinates support the idea of competitor avoidance within the foraging group. Concomitant with this increased hopping, subordinates spent more time handling each seed than dominants at group sizes beyond 18 individuals, and this is consistent with increased conspecific surveillance and avoidance in large groups (Slotow & Rothstein 1995b; Beauchamp & Livoreil 1997; Pravosudov & Grubb 1999; Johnson et al. in press). Competitor avoidance and conspecific surveillance tend to demonstrate the occurrence of ritualized contest competition within the foraging groups. However, the results show the opposite; dominants responded the most to changes in group size (Fig. 5-6). Further research is needed to understand the adaptative value of this group size response and an economic approach incorporating both the effect of predation and competition might explain these results (Ydenberg & Dill 1986). For instance,

Kenward & Sibly (1977) showed that pigeons feeding on brassicae seeds ingest them at a higher rate than the optimal digestion rate. Krebs (1979 p.226) assumes that feeding competes for time with other activities such as avoiding predators and this might explain why pigeons are found digesting their food in the safety of trees.

Effect of food density

The four different seed densities did not significantly affect the pecking rates of foragers. At 1000 ml/m^2 the feeding patch is completely covered by a single layer of seeds. One eighth of this density being the lowest food density in the experiment may still represent a super-abundant food resource for the birds. Interestingly, even in such a scenario, the birds behave in a competitive manner and both scramble and contest competition participate in this effect. The result suggests that a high food density should not be taken in itself as an indication of competition-free foraging (Shaw et al. 1995; but see Lima et al. 1999). In the present study, the roof above the feeding patch may lower the need for scanning and hence made it easier to detect the effect of competitive pressures. This may be especially true if the effects of competition and anti-predatory considerations complement each other.

Conclusion

The results suggest that competition contributes to the scanning-group-size effect but

does not rule out the effect of anti-predatory factors. Several studies on the scanning-group-size effect argue that a reduction in scanning and a concomitant increase in feeding time are sufficient to account for higher feeding benefits (Sullivan 1984; Elgar et al. 1986; Elgar 1989; Beauchamp 1998). The current results suggest that this might not be so. In fact, it is possible that the competitive pressures that induce individuals to increase their inter-scan pecking rate and alter their handling times also cause them to reduce their scanning. Future studies need to go beyond simple qualitative descriptions of the scanning-group-size effect, and focus on the influence of competition on foraging behaviour and particularly on its influence on the feeding rates of individuals. It is especially important to incorporate dominance status in the analysis since the dominant individuals explain most of the variations in foraging.

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Table 1. Multivariate analysis of variance evaluating the effect of food density on pecking rate and scanning time per min.

Effect	Wilks' Lambda value	Multivariate F	Hypothesis df	Error df	p
Food density	0.985	0.83	6	666	0.549

Table 2. Stepwise regression evaluating the effect of scanning, interference, and group size on the inter-scan pecking rate (Model summary: n = 30; $R^2 = 0.91$; df = 1, 28; $P < 0.001$).

Entered variable	**Coefficient**	**Partial r**	**t**	**p**
Group size	0.512	0.956	17.17	< 0.001
Constant	39.5			
Excluded variable	**Coefficient**	**Partial r**	**t**	**p**
Interference	-0.496	-0.265	-1.43	0.164
Scanning	-0.111	-0.206	-1.094	0.283

Table 3. Repeated measures analysis of covariance evaluating the effect of group size and dominance rank on scanning time per min.

Source of variation	Test	df	ms	f	p
Within-subjects Effect					
Group size	Sphericity assumed	29	23892.15	3.59	< 0.001
	Huynh-Feldt	17.43	39737.93	3.59	< 0.001
Group size * Dominance interaction					
	Sphericity assumed	29	3240.61	0.49	0.99
	Huynh-Feldt	17.43	5389.86	0.49	0.96
Error	Sphericity assumed	377	6660.62		
	Huynh-Feldt	226.67	11078.08		
Between-subjects Effect					
Dominance rank		1	16988.92	0.1	0.76
Error		13	171884.24		

Table 4. Repeated measures analysis of covariance evaluating the effect of group size and dominance rank on both types of pecking rate.

a) pecking rate

Source of variation	Test	df	ms	f	p
Within-subjects Effect					
Group size	Sphericity assumed	29	296.67	6.76	< 0.001
	Huynh-Feldt	14.71	584.88	6.76	< 0.001
Group size * Dominance interaction					
	Sphericity assumed	29	72.9	1.66	0.019
	Huynh-Feldt	14.71	143.72	1.66	0.063
Error	Sphericity assumed	377	43.88		
	Huynh-Feldt	191.22	86.5		
Between-subjects Effect					
Dominance rank		1	12.17	0.03	0.86
Error		13	402.91		

b) inter-scan pecking rate

Within-subjects Effect					
Group size	Sphericity assumed	29	218.62	5.02	< 0.001
	Huynh-Feldt	13.15	482.07	5.02	< 0.001
Group size * Dominance interaction					
	Sphericity assumed	29	82.41	1.89	0.004
	Huynh-Feldt	13.15	181.72	1.89	0.033
Error	Sphericity assumed	377	43.55		
	Huynh-Feldt	170.97	96.03		
Between-subjects Effect					
Dominance rank		1	142.18	0.141	0.71
Error		13	1009.21		

Table 5. Repeated measures analysis of covariance evaluating the effect of group size and dominance rank on handling time per peck.

Source of variation	Test	df	ms	f	p
Within-subjects Effect					
Group size	Sphericity assumed	29	65609.96	7.48	< 0.001
	Huynh-Feldt	17.68	107622.51	7.48	< 0.001
Group size * Dominance interaction					
	Sphericity assumed	29	20963.53	2.39	< 0.001
	Huynh-Feldt	17.68	34387.27	2.39	0.002
Error	Sphericity assumed	377	8767.18		
	Huynh-Feldt	229.83	14381.14		
Between-subjects Effect					
Dominance rank		1	286.57	0.004	0.95
Error		13	78320.52		

Table 6. Repeated measures analysis of covariance evaluating the effect of group size and dominance rank on hopping rate.

Source of variation	Test	df	ms	f	p
Within-subjects Effect					
Group size	Sphericity assumed	29	54444.68	7.07	< 0.001
	Huynh-Feldt	15.81	99871.19	7.07	< 0.001
Group size * Dominance interaction					
	Sphericity assumed	29	43671.67	5.67	< 0.001
	Huynh-Feldt	15.81	80109.6	5.67	< 0.001
Error	Sphericity assumed	377	7695.43		
	Huynh-Feldt	205.52	14116.19		
Between-subjects Effect					
Dominance rank		1	57396.64	0.255	0.62
Error		13	224930.35		

FIGURE LEGENDS

Figure 1. Potential effects of group members on pecking rates. Each block represents a peck (dot) and the associated handling with the head pointed down. The thin line gives scanning time (Sa scanning alone and Sg scanning in groups), which in this case is really food-handling scanning (sensu Lima et al. 1999). In reality this time would be interspersed between pecks but is cumulated into one single bout for ease of presentation. In scenario A, the usual account of the scanning-group-size effect where reduction in scanning time leads to more feeding time and hence a higher pecking rate in groups than when alone ($4/T > 3/T$). However in A, the inter-scan pecking rate alone is equal to inter-scan rate in groups $\{3/(T-Sa) = 4/(T-Sg)\}$. In scenario B, the presence of competition leads to an increase in inter-scan pecking for the group condition $\{3/(T-Sa) < 5/(T-Sg)\}$. The increased inter-scan rate implies a reduction of handling with the head down that follows each peck. Scenario B would be indicative of a contribution of competitive pressures to the scanning-group size effect.

Figure 2. Top view schemata of the field site in which the sparrow population was active during the 1998-1999 winter.

Figure 3. Mean scanning time of 15 house sparrows expressed in s spent scanning per individual per min decreases as a function of group size. Each point represents the mean scanning rate calculated from the 15 subject's individual means. Bars indicate standard

errors.

Figure 4. Mean pecking rates of 15 house sparrows expressed in number of pecks per individual per min. In A, the mean pecking rate increases as a function of group size. In B, the mean inter-scan pecking rate also increases with group size. Each point represents the mean pecking rate calculated from the 15 subject's individual means. Bars indicate standard errors.

Figure 5. Slopes of the linear regressions between pecking rate (a) and inter-scan pecking rate (b) versus group size plotted as a function of the dominance rank. Each point represents one individual with its associated sample size (above the point) and dominance rank. □ represent slopes not significantly different from 0. The least squares linear regression model is significant for (a) $Y = 1.142 - 0.053X$, $r^2 = 0.69$, $P = 0.0008$ and for (b) $Y = 1.012 - 0.06X$, $r^2 = 0.51$, $P = 0.003$. Bars indicate standard errors.

Figure 6. Effect of the group size by dominance rank interaction on four different foraging variables. In A, the mean pecking rate of the five most dominant birds (■) and the five most subordinate birds (□), in number of pecks per individual per min, increases as a function of group size. The least squares linear regression models are significant for dominants $Y = 30.22 + 0.9X$, $r^2 = 0.88$, $P < 0.0001$ and for subordinates $Y = 33.62 + 0.51X$, $r^2 = 0.85$, $P < 0.0001$. In B, the mean inter-scan pecking rate of the five most dominant birds (■) and the five most subordinate birds (□), in pecks per individual per

min, also increases as a function of group size. The least squares linear regression models are significant for dominants $Y = 37.23 + 0.69X$, $r^2 = 0.82$, $P < 0.0001$ and for subordinates $Y = 43.31 + 0.18X$, $r^2 = 0.28$, $P = 0.0025$. In C, the mean handling times per peck of the five most dominant birds (■) and the five most subordinate birds (□), in sec spent handling per individual per peck, decreases as a function of group size. The least squares linear regression models are significant for dominants $Y = 1.63 - 0.032X$, $r^2 = 0.85$, $P < 0.0001$ and for subordinates $Y = 1.2 - 0.008X$, $r^2 = 0.45$, $P < 0.0001$. In D, the mean hopping rate of the five most dominant birds (■) and the five most subordinate birds (□), in number of hops per individual per min, increases as a function of group size. The least squares linear regression models are significant for dominants $Y = 6.17 + 0.26X$, $r^2 = 0.64$, $P < 0.0001$ and for subordinates $Y = 14.21 + 0.10X$, $r^2 = 0.16$, $P = 0.028$. Bars indicate standard errors.

Figure 1

TWO SCENARIOS FOR THE SCANNING-GROUP-SIZE EFFECT

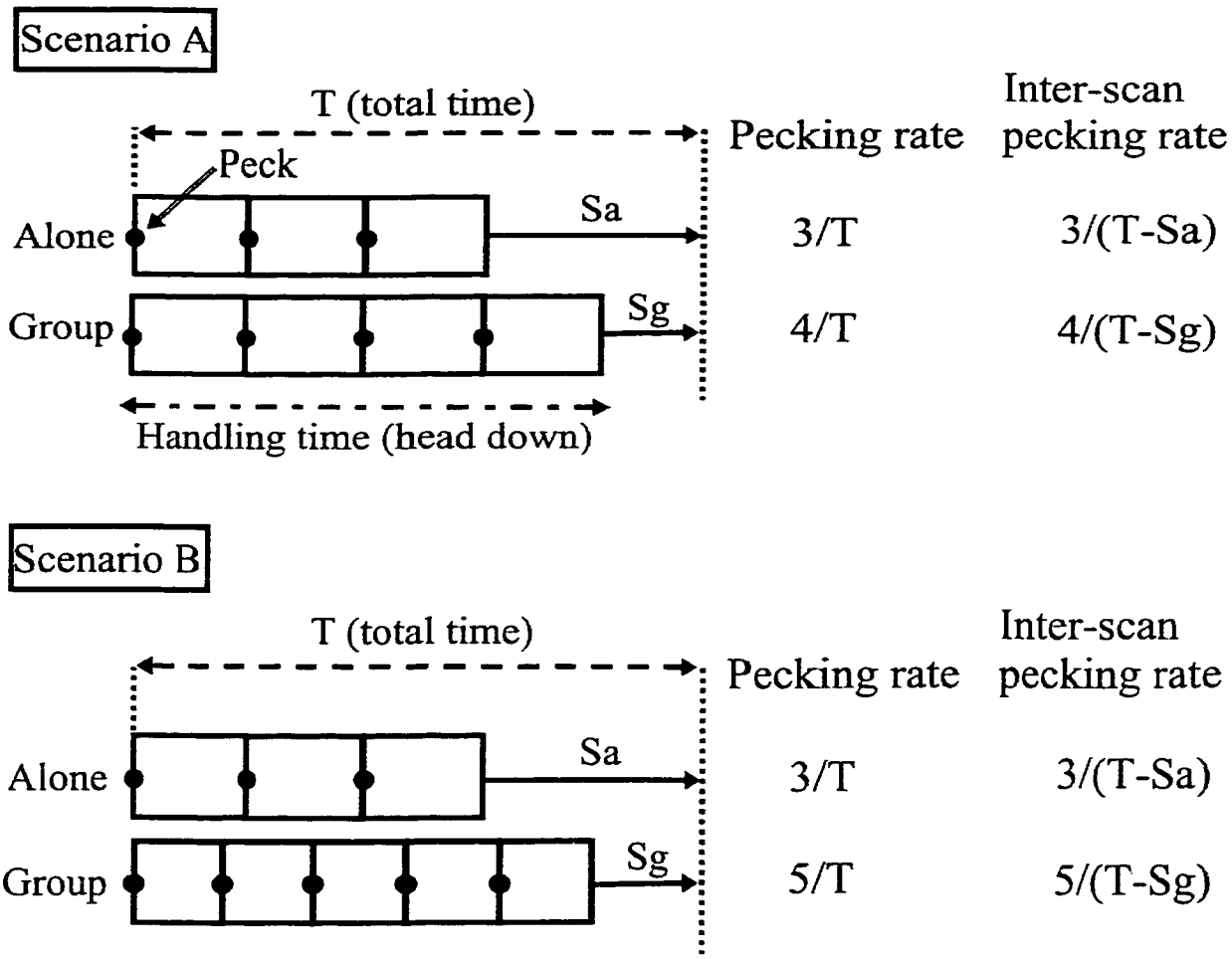


Figure 2

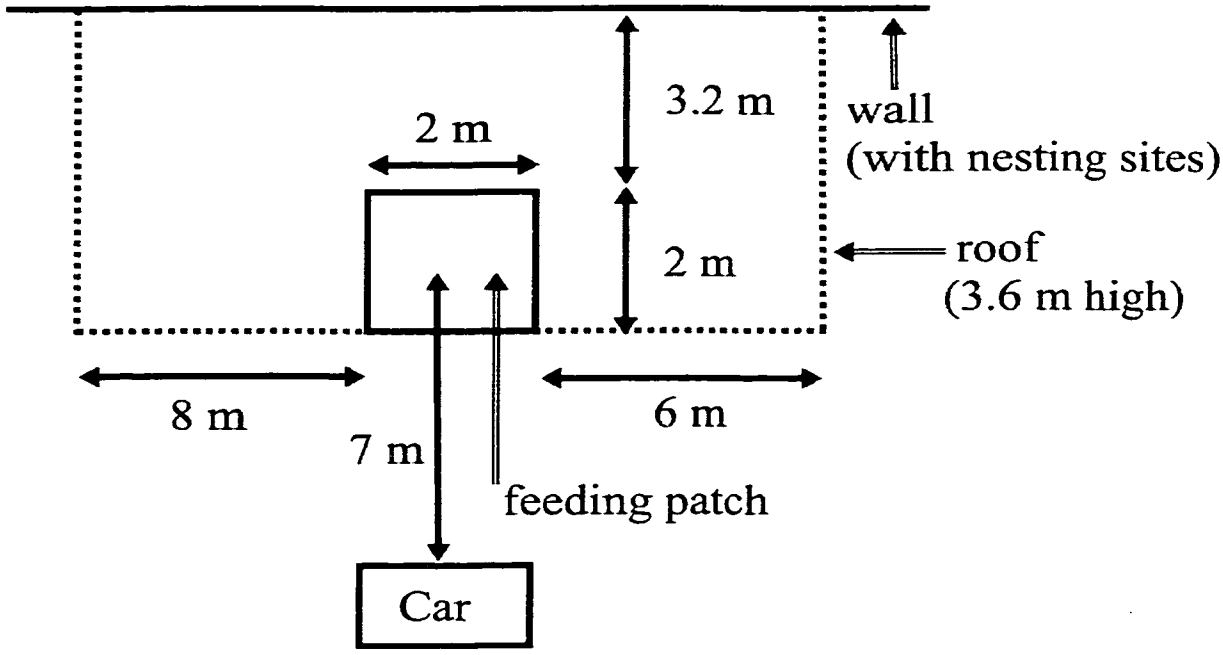

3.2 m
2 m
wall
(with nesting sites)
2 m
roof
(3.6 m high)
8 m
6 m
7 m
feeding patch
Car

Figure 3

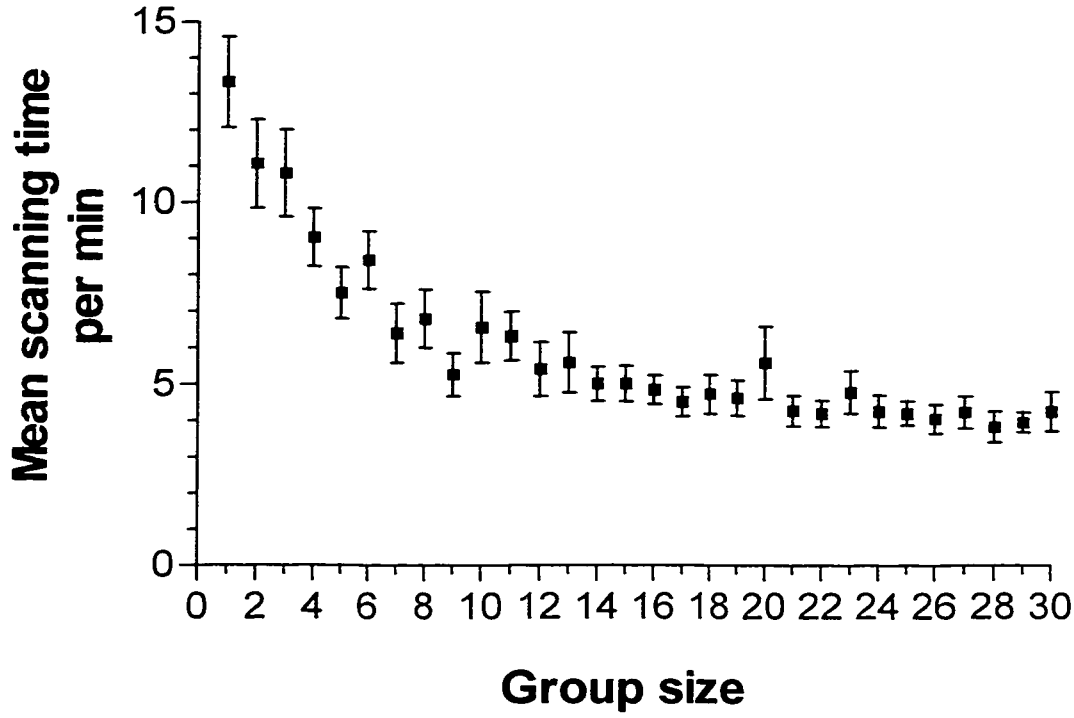

Mean scanning time per min
15
10
5
0
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
Group size

Figure 4

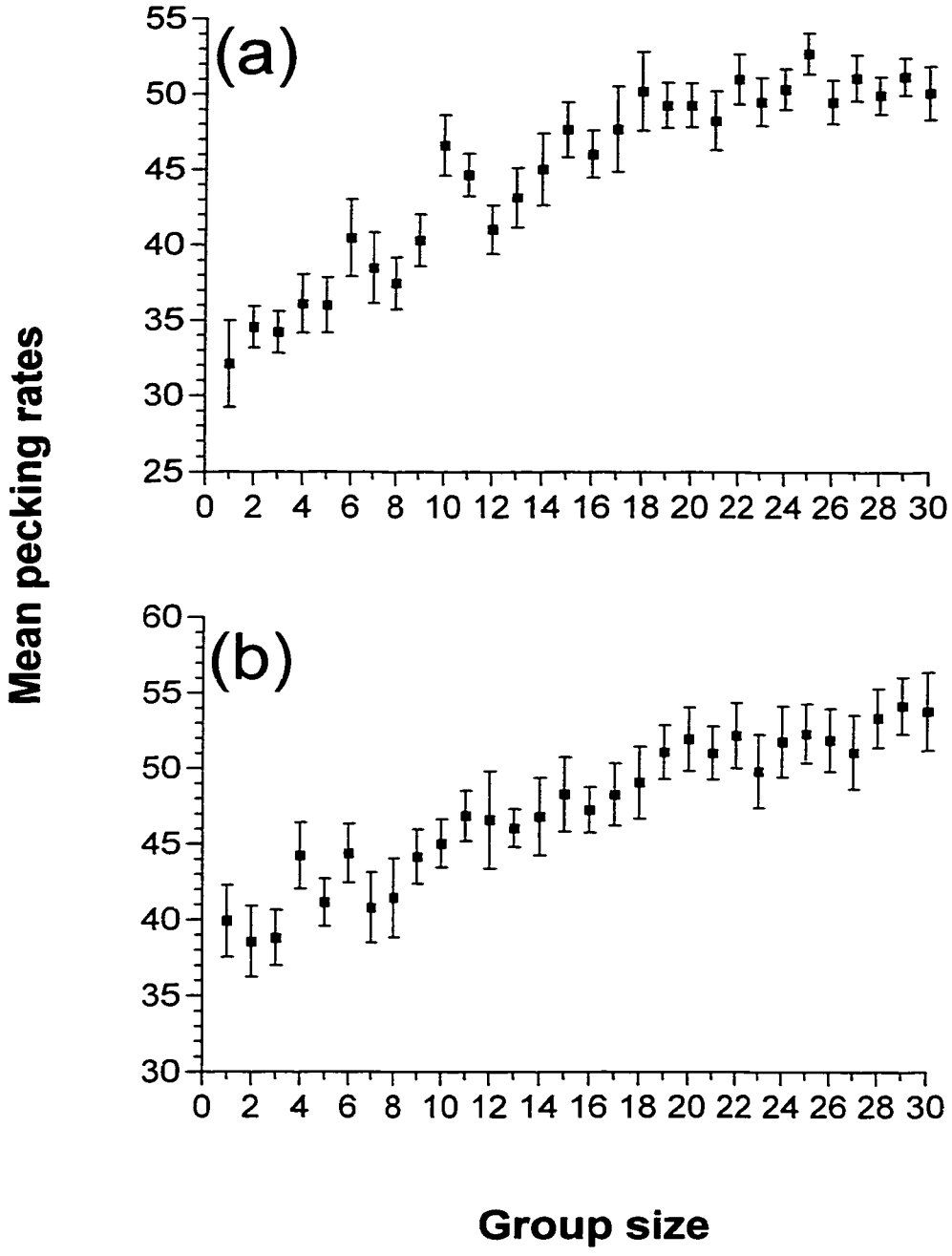

(a)
(b)
Mean pecking rates
Group size
55
50
45
40
35
30
25
60
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30

Figure 5

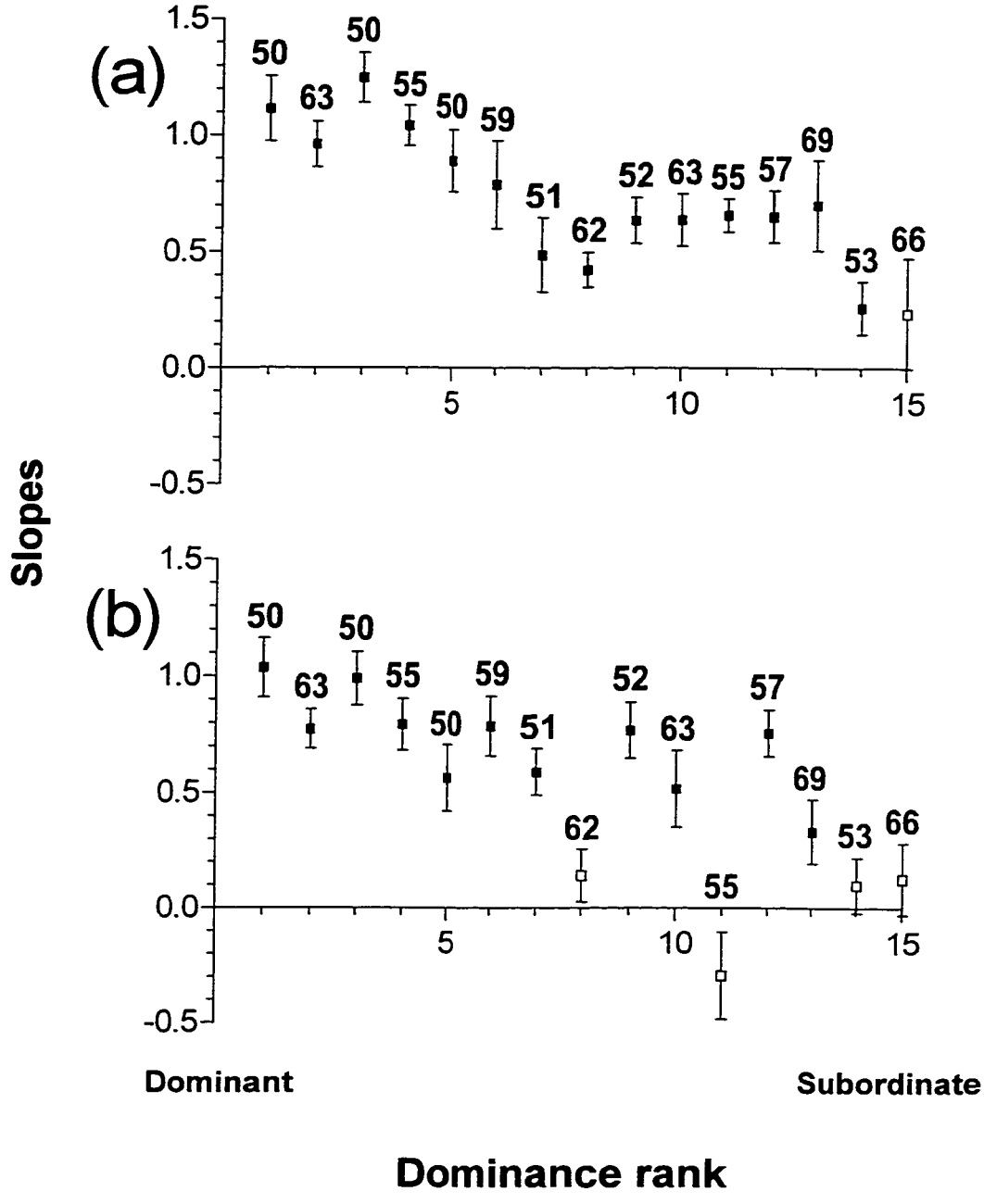
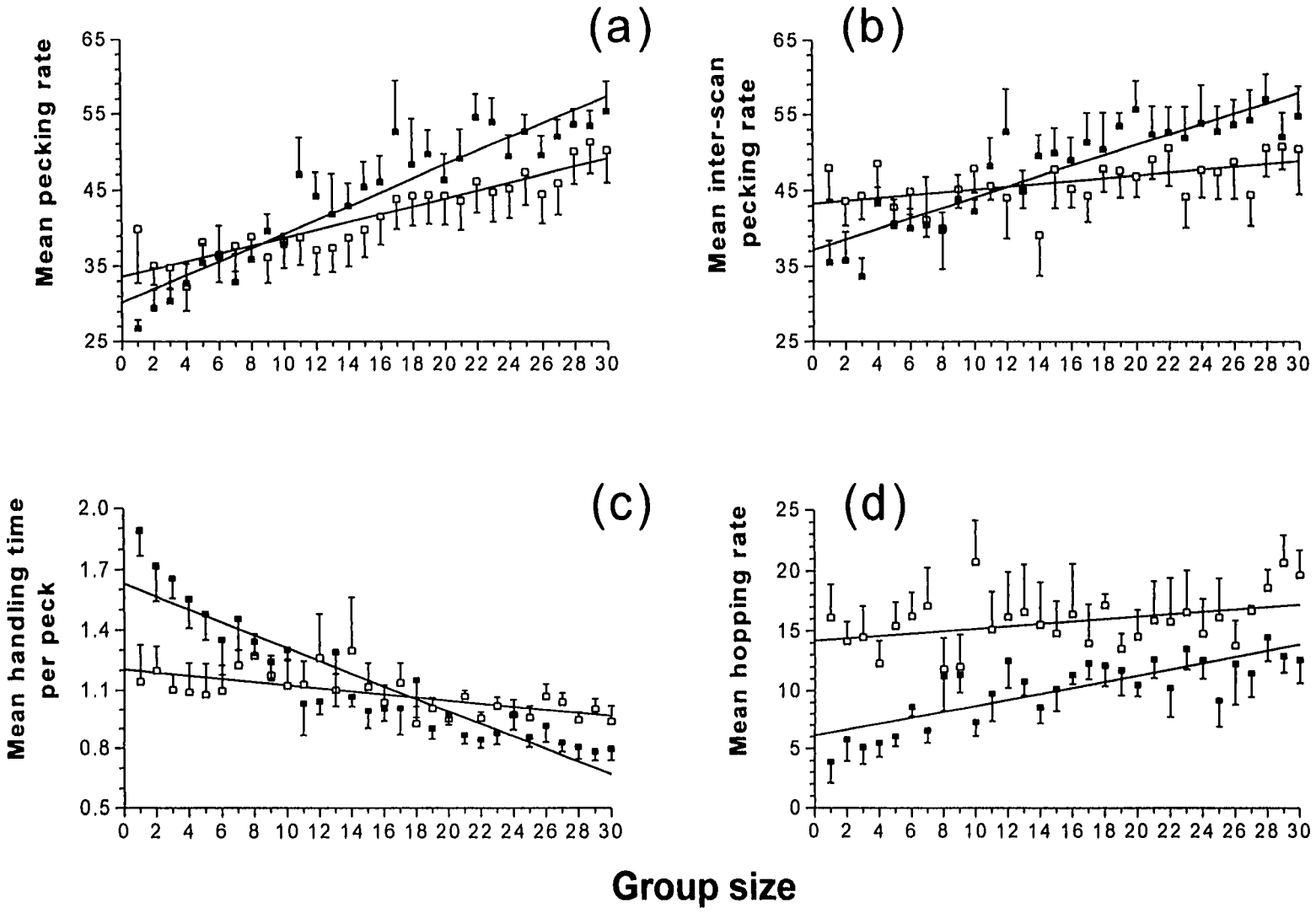

(a)
(b)
1.5
1.0
0.5
0.0
-0.5
5
10
15
50 63 50 55 50 59 51 62 52 63 55 57 69 53 66
50 63 50 55 59 50 51 62 52 63 55 57 69 53 66
Slopes
Dominant
Subordinate
Dominance rank

Figure 6


(a)
Mean pecking rate
(b)
Mean inter-scan pecking rate
(c)
Mean handling time per peck
(d)
Mean hopping rate
Group size