

Group size effect caused by food competition in nutmeg mannikins (*Lonchura punctulata*)

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When foraging group sizes increase, animals generally decrease the time devoted to antipredator detection and increase their foraging rate, the commonly reported group size effect. The increased foraging rate is thought to follow from increased safety from predators because as group size increases, more eyes are available to detect predators and the risk of being a predator's victim is diluted. This increased safety then allows higher feeding rates because individuals can reallocate time spent in vigilance to foraging. However, increased foraging rates can also be due to increased competition for resources as the number of companions increases. We tested whether increased feeding rates are the product of competition or antipredation when group size increases in nutmeg mannikins (*Lonchura punctulata*). We used edited video playbacks to change group size and type of competitor: vigilant only, feeding only, and controls. We found that the increased feeding rate associated with an increased group size only resulted when the companions were feeding. Video playbacks of nonforaging companions neither decreased an individual's use of vigilance while handling food nor did it release the full increase of feeding rate. Focal birds lowered their scanning time while feeding as the frequency of pecking by simulated nonvigilant companions increased. We conclude that the group size effect reported in nutmeg mannikins is not a product of safety benefits of group living but may also arise from the costs imposed by competition for resources. *Key words*: competition, group size effect, *Lonchura punctulata*, nutmeg mannikins, video playback. [*Behav Ecol* 20:421–425 (2009)]

When avian and mammalian foraging group size increases, individuals decrease the time devoted to antipredator detection and increase their foraging rate: the group size effect (Elgar 1989; Lima 1995; Roberts 1996; Lima et al. 1999). The increased foraging rate is thought to follow from increased safety from predators because as group size increases, more eyes are available to detect an approaching predator sooner and the risk of being the predator's victim is diluted (Pulliam 1973; Elgar and Catterall 1981; Lima 1990; Lima and Dill 1990; Lima 1995; Lima et al. 1999). This increased safety then allows higher feeding rates because individuals can reallocate time spent in vigilance to foraging (Lima et al. 1999).

Increased foraging rates, however, can also be the consequence of increased scramble competition for resources as the number of competitors increases (Clark and Mangel 1986; Beauchamp and Livoreil 1997; Beauchamp 2003; Randler 2005). In groups, the size of the share an individual obtains of a common resource is directly related to its exploitation speed. The group, therefore, should induce an exploitation arms race in which each individual attempts to outeat the others. Increased feeding speed may be achieved at the expense of antipredator vigilance and perhaps even optimal food-handling speed (Clark and Mangel 1986; Grand and Dill 1999; Beauchamp and Ruxton 2003). Although the competition hypothesis is entirely consistent with the group size effect, its role remains controversial (Lima et al. 1999; Bednekoff 2003).

The question of whether competition or predation is responsible for increased feeding rates within groups has been approached by studying how scanning and food handling

change with group size in dark-eyed juncos (*Junco hyemalis*) (Lima et al. 1999). Lima et al. (1999) found similar patterns between vigilance scanning that is concomitant with food handling and vigilance scanning that is independent of foraging. They argue that the similarity of the patterns for both types of scans is consistent with an antipredatory explanation for increased feeding rates. However, they also report a reduction of food-handling time as group size increases, a reduction that is also compatible with increased competition. So the question remains whether increased feeding rates are the product of competition or antipredation.

One way to resolve the question would be to have a subject feed with companions that are either never vigilant and just feed or instead are always vigilant and never feed. If the subject increases its feeding rate irrespective of whether companions feed or not, then the increase is likely the consequence of antipredatory benefits. However, if it only increases its feeding rate when companions are feeding, then the effect is likely attributable to competition in which case we also expect that scans associated with food handling will be shorter. We use this logic to test the group size effect in nutmeg mannikins (*Lonchura punctulata*), a granivorous estrildid finch from southeast Asia that feeds in groups with little aggression (Giraldeau et al. 1990). We used edited video playbacks to change group size and type of companions: vigilant only, feeding only, and controls.

MATERIALS AND METHODS

Study animals

Twenty-three 2-year-old adult nutmeg mannikins were purchased from a commercial supplier (L'oisellerie de l'Estrie, Québec, Canada) and individually identified with a unique combination of colored leg bands. Outside experimental periods, all birds were kept in the animal care facilities of the Université du Québec à Montréal in cages with ad libitum access to millet seeds and water under a 12-h photoperiod.

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Apparatus

The experimental apparatus consisted of a box covered with plastic wire mesh with a perch and a drinking trough located in an observation room. One of its long sides was transparent to allow the experimenter to see inside. One of its short sides was also transparent allowing the birds to see a TFT LCD computer monitor (Sony DSM-m61—resolution max: 1280 dots \times 1024 lines, operating frequency 48–85 Hz, horizontal blanking superior to 2.5 μ s and vertical blanking superior to 450 μ s) that broadcasts video sequences from a computer located outside the observation room.

Creating the virtual group foragers

We randomly chose (here and thereafter using random number tables) 6 nutmeg mannikins from the colony to produce the video sequences to be used during the experimental playbacks. First, using a remote controlled miniDV digital camera (Canon Optura 30) set on a tripod, we recorded the behavior of birds through a peephole in an opaque curtain. Each bird was introduced into the experimental box alone and allowed to feed ad libitum for 10 min, 4 times a day from a feeder containing mixed millet seeds. We repeated this familiarization for 3 consecutive days for each bird. To insure that all group members in a video playback were life size, we used a feeder that only allowed birds to feed side-by-side facing the camera lens.

We taped feeding groups 4 times per day at 90-min intervals. The birds were food deprived for 14 h (overnight + 2 h) as well as during the intervals between recording periods in the same day. After the last recording of the day, the birds were offered an ad libitum supply of mixed millet seeds until lights off. We recorded scenes using all group sizes from 0 to 6 individuals. The identity of birds that made up each group size was randomly selected just before the birds were introduced into the aviary.

Once sequences for all group sizes were recorded, they were edited using Pinnacle Studio 9 software (Avid Technology Inc., Mountain View, CA) to create 3 companion types: nonvigilant foragers, vigilant nonforagers, and control unedited foragers. We distinguished between vigilant and nonvigilant behavior on the basis of the bird's head orientation based on a line projected from its eyes through its nares. The birds were deemed vigilant when the line pointed above the horizon and nonvigilant when it pointed below (Figure 1). For vigilant nonforagers, we edited-out images when a bird's head pointed into the feeder followed by head up with seed handling. Inversely, to create nonvigilant foragers, we removed all images where a bird's head pointed up so that the birds appear never to raise their head and so the frequency of their pecking movements increased. We created four 6-min video sequences for each group size and each of the 3 companion types. The choice of the playback to be used for a given focal bird was random in order to control for pseudoreplication (McGregor 2000).

Training and experimental trials

Six of the 17 colony birds were randomly chosen as experimental subjects. They were caged together for 6 days before the start of the experiment. All the birds were food deprived for 14 h (overnight + 2 h after lights on) and during the intervals between successive trials in the same day. A trial starts when a focal bird is introduced into the apparatus that provided ad libitum access to mixed millet seeds. The lighting conditions, the feeder, and the seed mixture were identical to those used in the video playbacks.

To allow the birds to get used to feeding next to the TFT LCD screen, each was placed in the experimental box 4 times per day, at 90-min intervals, for 15 min during which it had access to the feeder placed next to the screen playing a sequence of a feeder with no companions. After 5 consecutive days, the same procedure continued but the screen played a feeder with a randomly chosen number of companions. The bird was considered trained once it obtained a seed within the first 30 s of its introduction into the apparatus. A trial started when the focal individual landed on the feeder and ended when it left it or stopped foraging for 30 consecutive seconds. Each focal bird was observed twice for each group size (alone, with 1, 2, 3, 4, 5, and 6 companions) and for each companion type (control, vigilant nonforagers, and nonvigilant foragers).

We analyzed the focal birds' foraging and scanning behavior from videotaped recordings of the trials. A bird was considered to be foraging when its head was oriented down into the feeder or while it was handling a seed with its head pointing up. The feeding rate is the number of seeds eaten per minute spent foraging. Scanning events while handling seeds were recorded. A food-handling scan occurred when the bird kept the head up while handling a seed and ended when the seed was swallowed. The mean food-handling scan duration was the mean of all focal birds' mean food-handling scan durations averaged over the whole trial.

Statistical analysis

Focal birds experienced each combination of the 3 fixed within-subject factors: companion type (control, vigilant nonforagers, and nonvigilant foragers), group sizes (0–6 companions), and replicates (2 for each companion type and group size). We used repeated-measures analysis of variance to examine the effects of group size and playback condition on food-handling scan duration and feeding rate. We carried out Mauchly tests to control for sphericity in conditions with more than 2 factors. In cases where the sphericity assumption was violated, *P* values were adjusted using the Huynh and Feldt correction. We investigated the potential interactions between treatments and group sizes for each behavioral variable. To identify differences between group sizes, we used Tukey's post hoc tests. All analyses were conducted with SPSS 10 (SPSS Inc., Chicago, IL) for Windows, and thereafter all results are expressed as a mean and its standard error.

RESULTS

There was a significant interaction between companion type and group size on the duration of food-handling scans (degrees of freedom [df] = 12, $F = 17.32$, $P < 0.01$). There were no significant differences in food-handling scan duration when birds fed with vigilant nonforagers (comparing 1–6 companions—Tukey's post hoc tests: $P = 0.07$) but mean food-handling scans were shorter when birds fed with controls (comparing 1–6 companions—Tukey's post hoc tests: $P = 0.001$) (Figure 2). We also found that birds lowered the duration of their food-handling scans for each group size of nonvigilant foragers compared with controls, even though the linear monotonic decrease found with normal companions was no longer observed (comparing 1–6 companions—Tukey's post hoc tests: $P = 0.38$).

There was also an interaction between the effects of companion type and group size on feeding rate (df = 12, $F = 7.36$, $P < 0.01$). Compared with when they foraged alone, the birds significantly increased their feeding rate when they foraged with 6 birds, irrespective of the companion type (control—Tukey's post hoc tests: $P = 0.026$; vigilant nonforagers—Tukey's post hoc tests: $P = 0.029$; and nonvigilant

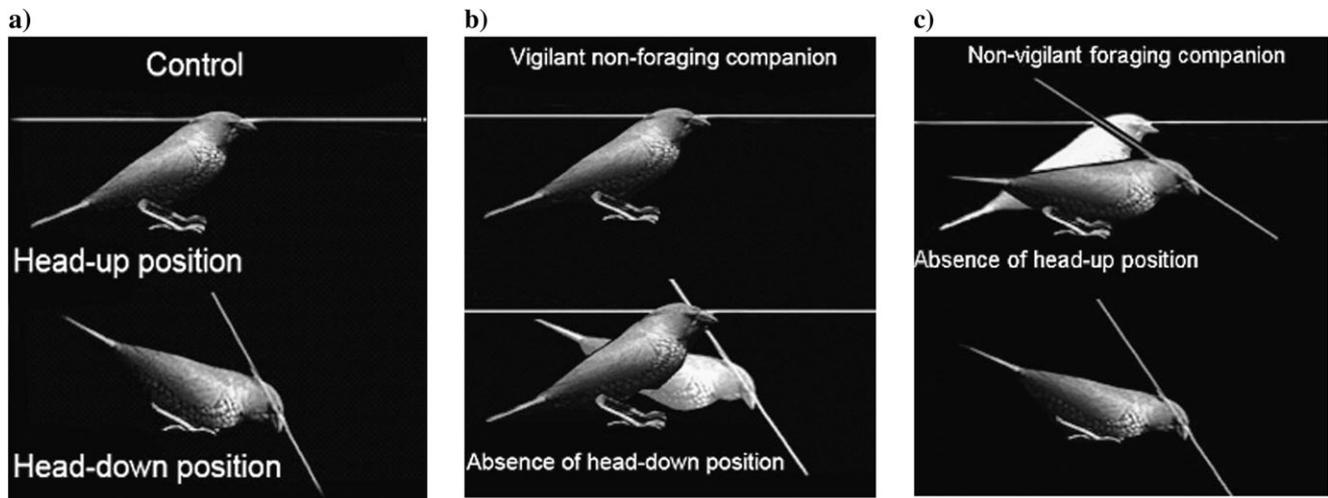


Figure 1
Representation of the 3 types of companions: (a) controls, (b) vigilant nonforaging, and (c) nonvigilant foraging companions.

foragers—Tukey's post hoc tests: $P = 0.019$) (Figure 3). Once a bird was with a companion, at the exception of when it was with 2 companions, group size did not influence its feeding rate with vigilant nonforaging companions. Indeed, feeding rates for birds with 2 vigilant nonforaging companions slightly differed consistently from all group sizes (group size 3 vs. group size 4—Tukey's post hoc tests: $P = 0.044$; group size 3 vs. group size 5: $P = 0.005$; group size 3 vs. group size 6: $P = 0.03$; group size 3 vs. group size 7: $P = 0.041$). However, the number of seeds eaten per minute did not differ significantly when birds foraged with 1 compared with 3 (Tukey's post hoc tests: $P = 0.67$), with 4 ($P = 0.78$), with 5 ($P = 0.32$), and with 6 vigilant nonforagers ($P = 0.11$). An increased feeding rate with group size was only found when companions fed (foraging with 1 compared with 6 controls—Tukey's post hoc tests: $P = 0.003$). In addition, nonvigilant foragers induced a rapid increase of feeding when focal birds were in company of at least one individual but they maintained a stable high feeding rate when group size increased (comparing 1–6 companions—Tukey's post hoc tests: $P = 0.39$). Focal birds feed more rapidly with small groups made up of nonvigilant foragers compared with control or groups of vigilant nonforagers. When group size increased beyond 3 birds, feeding rates tended to be similar with the nonvigilant foragers and the controls.

DISCUSSION

We found that nutmeg mannikins, like in most cases of reported group size effects, showed an increased feeding rate as group size became larger. However, our experiment provides experimental evidence in support of the increased competition hypothesis because the group size effect only occurs when the virtual companions are engaged in some feeding, in either the control or the feeding only conditions and not when companions are just vigilant. Moreover, the birds reduced their food-handling scanning time as the pecking frequency of simulated nonvigilant companions increased. We discuss possible biases introduced by the use of video playbacks and then address the implications of the result for studies of group foraging.

Potential biases of video playback

A number of earlier studies have established video playback as an efficient means of eliciting natural behavioral responses in

birds and many other animal taxa (reptiles: Clark et al. 1997; Ord et al. 2002; fishes: McDonald et al. 1995; Bolyard and Rowland 1996; Rosenthal et al. 1996; birds: Dittrich and Lea 1993; Evans et al. 1993; Adret 1997; mammals: Plimpton et al. 1981). However, in the case of playbacks meant to simulate groups of foraging individuals, 2 issues can be singled out as perhaps introducing some problem: 1) depth cues normally associated with a group cannot be transmitted directly due to the 2 dimensionality of video images and so spatial position corresponds to animals of different absolute sizes and 2) the video images of the competitors are not affecting or interacting with the food resource being exploited. We discuss both issues in turn.

The problem of depth perception and companions of different absolute sizes was addressed by our use, when taping the video playback sequences, of a linear feeding dish that forced companions to stand aligned on one of the feeder's side facing the video camera. In this way, all birds were at similar distances from the focal subject and so their images

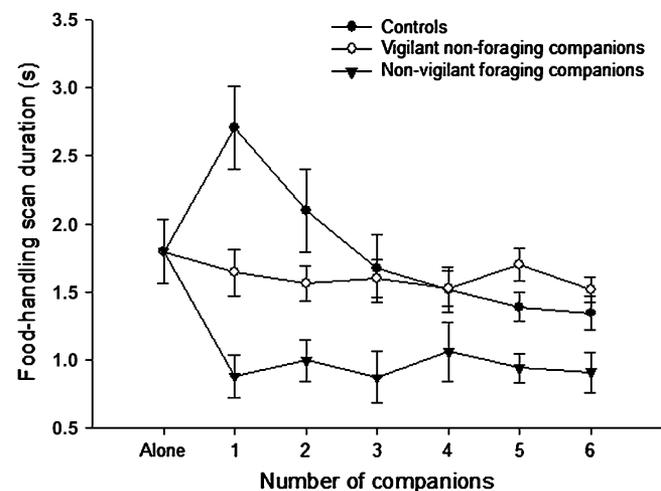


Figure 2
Variation of food-handling scan duration of focal nutmeg mannikins when group size increased with controls, vigilant nonforaging, and nonvigilant foraging companions. All the results are expressed as a mean and its associated standard error.

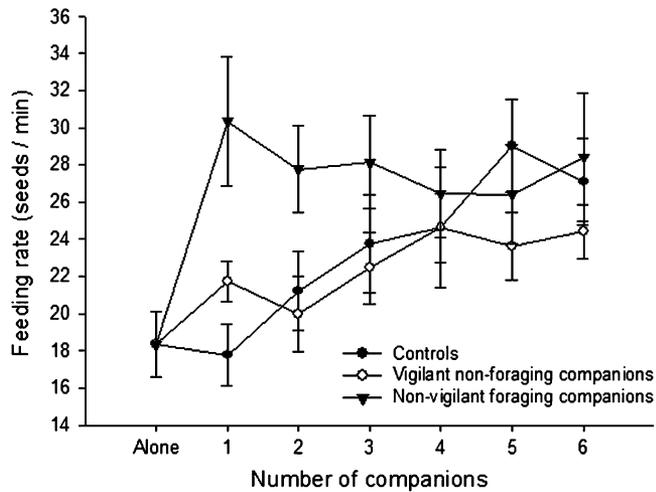


Figure 3
Variation of feeding rate of focal nutmeg mannikins when group size increased with controls, vigilant nonforaging, and nonvigilant foraging companions. All the results are expressed as a mean and its associated standard error.

had similar absolute sizes. It is possible, nonetheless, that the 2-dimensional representation of our linear foraging group still provided less effective releasers of the group size effect than a 3-dimensional group of real foragers. We feel this is unlikely because the detailed responses of our subjects were reminiscent of responses reported when birds feed within real groups. For instance, Beauchamp and Livoireil (1997) report that nutmeg mannikins feeding in larger group reduce their handling time, a reduction associated with a decline vigilance time. Our video playbacks elicited the same behavioral responses. We are confident therefore that the results we obtained are not an artifact of the video playback techniques used to simulate group foraging.

It could be argued that video companions are not appropriate simulations for foraging competitors because they do not actually have an effect on the focal bird's share of the resource. Some previous work where competition was simulated reported that the change in feeding rate does not necessarily require the presence of competitors within the food patch reducing the density of food available (McQuoid and Galef 1993; Grand and Dill 1999; Gauvin and Giraldeau 2004). We found a similar pattern; even in an unlimited food system and without any diminishing returns of the resource, the simulated presence of competitors induced the behavioral responses associated with an increasing group size. Thus, we feel that the focal individual's perception of competition did not rely on its ability to interact with the competitor increasing our confidence that the video playback technique is particularly reliable in addressing foraging competition questions.

Implications for studies of group foraging

Several factors have prevented earlier studies from providing an unambiguous understanding of the mechanisms driving the increased feeding rates observed with increasing group size. Among these is the difficulty of directly manipulating the efficiency of competitors within natural groups without also changing group size. As suggested by several authors, competitive influences on the behavioral responses induced by changes in group size can be difficult to demonstrate due to the confounding effect of changes in predation risk (Lima

et al. 1999; Beauchamp 2003; Bednekoff 2003). Here we present a way to address this question empirically by controlling competition intensity independently of group size. We show that edited video playback techniques provide a convenient way of ascertaining the antipredatory and competitive components of the response to changing group size by avoiding confounding effects of different competitive abilities or hunger states among nonfocal group members.

The decline of individual vigilance with increasing group size has usually been explained in terms of a lower need for animals to obtain information about predation (McNamara and Houston 1992; Lima et al. 1999). Our results do not support such an interpretation because if these were the case, vigilance would have declined with increasing numbers of vigilant nonforaging companions. The pattern we observed cannot be derived simply from hypotheses of reduced predation hazards with increasing group size. The results of our experiment indicate that the group size effect is not inevitably a product of safety benefits of group living but may also arise from the costs imposed by competition for resources.

It could be argued that our results can be explained by social facilitation. Social facilitation is generally defined as the increased probability of performing a class of behaviors in the presence of a conspecific performing the same class of behavior already in the observer's repertoire (Addessi and Visalberghi 2001). It predicts that an individual will be induced into being more likely to use the same class of behavior when exposed to a conspecific using that class of behavior. We do not think that social facilitation could account completely for our results on 2 counts. First, the facilitating effect of companions on feeding rate does not always require that the companion be feeding. When the birds were exposed to vigilant nonforaging companions, they reacted like when they were exposed to controls that both fed and were vigilant. A strict application of social facilitation cannot explain why nonforaging bird had the same effect as a foraging companion on an individual's feeding rate. Second, if social facilitation caused increased vigilance, its effect was not consistent. For instance, if social facilitation was responsible to the increased vigilance when individuals were exposed to vigilant companions (Figure 3), it remains a puzzle why it did not induce an increase in vigilance when individuals went from being alone to being exposed to increasing numbers of vigilant nonforaging companions (Figure 2). For these reasons, we are confident that social facilitation cannot be invoked as an effective alternative explanation for our results.

A surprising result was certainly the presence of a significant interaction between group size and replicates on feeding rates given that no such interaction between group size and replicates was found for food-handling scan durations (Table 1). The most likely explanation for this is that feeding rate increases over successive expositions to videos of a given group size, perhaps due to some familiarization. Given that during training we exposed individuals to a random selection of group sizes to allow the birds to familiarize themselves with feeding next to a video playback, it is possible that some birds had previous experience with some group sizes but not others and that this differed among birds.

In our study, we found that focal birds spent more time scanning when in small groups. Scanning may also serve to acquire foraging information from competitors; individuals monitoring competitors may be able to adjust their behavior to the behavior of companions. When foraging with only one companion in the control group, focal birds decreased their feeding rate and increased their food-handling scan duration, suggestive of a self-imposed costs: foraging costs independent

Table 1
The effects of increasing group size with controls, vigilant nonforaging, and nonvigilant foraging companions on feeding rate and food-handling scan duration

	Feeding rate			Food-handling scan duration		
	df	F	P	df	F	P
Companion type	2	8.96	<0.01	2	21.94	<0.01
Group size	6	13.1	<0.01	6	4.37	0.03
Replicates	1	1.04	0.35	1	5.49	0.06
Companion type × group size	12	7.36	<0.01	12	17.32	<0.01
Companion type × replicates	2	0.93	0.42	2	0.02	0.98
Group size × replicates	6	3.36	0.01	6	0.72	0.47
Companion type × group size × replicates	12	2.03	0.06	12	1.39	0.29

Interactions between type of companions and group sizes for each behavioral variable are also presented.

of resource availability but triggered by behavioral interference with companions (Vásquez and Kacelnik 2000). Evidence of such behavioral interference has been previously reported in socially foraging species such as starlings (*Sturnus vulgaris*) and nutmeg mannikins (Vásquez and Kacelnik 2000; Gauvin and Giraldeau 2004). These self-imposed costs are generally thought to represent a cost of maintaining cohesion within a group among foragers (Valone 1993).

Our results provide experimental evidence that the commonly reported group size effect can be the result of competitive pressure rather than release from predation pressure. It now remains to be seen whether the intensity of interference competition or even the occurrence of food scrounging strategies will affect the intensity group size effect?

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