ORIGINAL ARTICLE

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Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*)

Abstract In socially feeding birds and mammals, as group size increases, individuals devote less time to scanning their environment and more time to feeding. This vigilance "group size effect" has long been attributed to the anti-predatory benefits of group living, but many investigators have suggested that this effect may be driven by scramble competition for limited food. We addressed this issue of causation by focusing on the way in which the scan durations of free-living dark-eyed juncos (*Junco hyemalis*) decrease with group size. We were particularly interested in vigilance scanning concomitant with the handling of food items, since a decrease in food handling times (i.e. scan durations) with increasing group size could theoretically be driven by scramble competition for limited food resources. However, we showed that food-handling scan durations decrease with group size in an environment with an effectively unlimited food supply. Furthermore, this food-handling effect was qualitatively similar to that observed in the duration of standard vigilance scans (scanning exclusive of food ingestion), and both responded to changes in the risk of predation (proximity of a refuge) as one might expect based upon anti-predator considerations. The group size effects in both food-handling and standard scan durations may reflect a lesser need for personal information about risk as group size increases. Scramble competition may influence vigilance in some circumstances, but demonstrating an effect of competition beyond that of predation may prove challenging.

Introduction

In many socially feeding birds and mammals, an increase in group size leads to a decrease in individual levels of vigilance and an increase in time devoted to feeding (Elgar 1989; Lima 1990; Roberts 1996). For over 20 years the main explanation for this vigilance "group size effect" has been that it is driven mainly or entirely by anti-predator considerations. That is, the increase in both the collective probability of detecting attack and numerical dilution of risk with increasing group size can account for the basic group size effect (see McNamara and Houston 1992; Cresswell 1994; Roberts 1996; Bednekoff and Lima 1998a). Recent work has demonstrated a clear need to revise old tenets about the nature of risk dilution and collective detection (Lima 1995a, b; Lima and Zollner 1996, Bednekoff and Lima 1998b; see also Roberts 1996), but the "predation hypothesis" still provides the preeminent explanation of the ubiquitous group size effect (Roberts 1996).

A commonly mentioned, radical alternative to the predation hypothesis might be termed the "competition hypothesis", in which the vigilance group size effect reflects scramble competition for limited resources (Clark and Mangel 1986; Cezilly and Brun 1989; Elgar 1989; Krause 1994; Saino 1994). The basic idea behind the competition hypothesis is that, as group size increases in a food-limited environment, an animal increases its feeding rate (i.e., reduces its vigilance) in order to gain a greater portion of the food supply (e.g., Clark and Mangel 1986). Beauchamp and Livoreil (1997) suggest further that such competitive effects may be the primary driving force behind the vigilance group size effect, basing their suggestion on evidence that finches, in a strongly food-limited environment, speed up both search

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and food handling as group size increases in a manner consistent with the competition hypothesis (see also Shaw et al. 1995). Similar scramble competitive effects have a precedent in both empirical (Barnard et al. 1983; Dill and Fraser 1984; Vander Wall 1990) and theoretical (Clark and Mangel 1986; Yamamura and Tsuji 1987; Engen 1988; Shaw et al. 1995) studies of foraging behavior.

In this paper we address the issue of causation in the vigilance group size effect in a study of free-living dark-eyed juncos (*Junco hyemalis*). We focus on vigilance scanning concomitant with food handling (essentially seed-husking times) and independent of food handling or ingestion (standard vigilance scans), and argue that one need not invoke competitive effects to explain the group size effect observed in either of these behavioral measures. Competitive effects may well influence anti-predatory vigilance in some circumstances, but demonstrating an effect of competition beyond that of predation may prove challenging.

Background and rationale

A controlled manipulation of the competitive environment under field conditions is difficult to achieve, so we chose to eliminate competition for limited resources as a possible influence on junco behavior by providing an unlimited food supply over an entire winter season. The persistence of vigilance group size effects in such an environment provides strong evidence against the competition hypothesis. One might nevertheless argue that such a result would be inconclusive since juncos might perceive competition even when it does not exist. In a later section we argue that such a "fixed" perception of competition is unlikely in juncos. We also manipulated the risk of predation (via the proximity of protective cover) to determine whether a change in risk influences the duration of food handling and standard scans as expected under the predation hypothesis.

We focus in part on scanning while handling food because a decrease in handling times (and thus scanning times) with increasing sociality may reflect scramble competition for limited food (e.g., Street et al. 1984; Beauchamp and Livoreil 1997). A simple game theoretical model in Clark and Mangel (1986) suggests that handling times should be at a minimum when animals feed socially. A slightly more complex game theoretical model (see Appendix) shows that handling times under scramble competition for a limited resource might even decrease monotonically with group size in the absence of predation risk. Studies of vigilance do, in fact, provide indirect support for such an effect. In many such studies, time spent scanning the environment was probably to a large (but unspecified) extent, time spent simultaneously handling food items (e.g., Studd et al. 1983; Popp 1988; see also Bednekoff and Lima 1998a); this is particularly true for granivorous birds like juncos, which visually scan their environment while husking large seeds (see Lima 1988; Popp 1988; Beauchamp and Livoreil 1997; Benkman 1997). Thus the common observation that scan durations decrease with increasing group size (e.g., Studd et al. 1983; Metcalfe 1984a, b; Monaghan and Metcalfe 1985; Quenette and Gerard 1992; Cresswell 1994; see also below, but see Elgar and Catterall 1981; Blumstein 1996) suggests that handling time may routinely decrease with group size. If the group size effect in food-handling scan durations is indeed competition-driven (Appendix), it should disappear under conditions of unlimited food, and should not be influenced by an overall change in the risk of predation.

We focus also on the duration of standard vigilance scans, exclusive of food handling or ingestion, as envisioned in all models of anti-predator vigilance (Bednekoff and Lima 1998a). Our interest in standard vigilance scans relates to both competitive effects and the possibility that standard and food-handling scans are functionally similar. Regarding competitive effects, a decrease in standard scan durations with increasing group size could be driven by competition for resources: an animal using relatively shorter scans experiences a higher rate of food ingestion and thus obtains a greater overall portion of the available food. Such a shortening of scans, however, can also be explained by a reduced need for personal information about risk as group size increases (McNamara and Houston 1992; see also Desportes et al. 1991; Quenette and Gerard 1992). If the group size effect in standard scan durations is indeed driven by competition, then it should disappear under conditions of unlimited food; the predation hypothesis predicts the persistence of this group size effect, and that scan durations will increase with an increase in predation risk (i.e., an increase in the need for information about risk). Furthermore, a group size effect in both standard and food-handling scan durations under conditions of unlimited food would suggest that the food-handling effect may also reflect a lesser need for information about risk with increasing group size.

Methods

Study site, species, and food items

This study was carried-out from mid-January through mid-March 1998 at a site 9 km west of Terre Haute, Ind. (site 2 in Lima 1995a). The study site centered on a 6 × 3 m ground-level concrete pad aligned along an east-west axis parallel to (and 1.5 m from) the north side of an unoccupied building. All observations on feeding birds were made through a window in a darkened room in the building. This window was positioned 3 m from the center of the concrete feeding pad and was covered almost entirely by black plastic to further prevent birds from detecting the observer. The pad and building were in a small (0.5 ha) opening in a 20-ha hardwood forest (Kiewig Woods) managed jointly by Indiana State University and The Nature Conservancy.

Dark-eyed juncos accounted for over 80% of all feeding birds. Other bird species visiting the site were American tree sparrows (*Spizella arborea*), white-throated sparrows (*Zonotrichia albicollis*), song sparrows (*Melospiza melodia*), cardinals (*Cardinalis cardinalis*), and (during March) fox sparrows (*Passerella iliaca*). Each of

these additional species was rarely present in excess of two or three individuals.

Our study required a clear distinction between standard and food-handling vigilance scans. To this end, we used two types of food: whole white millet seeds and bits of corn meal (sifted to remove the powdery corn flour). Birds consuming bits of corn meal cannot simultaneously engage in vigilance scanning and the ingestion of food (Lima 1995b), hence scanning necessarily detracts from energy intake rate. The actual handling time for bits is minimal, and amounts to the time necessary to make a single peck (about 0.25 s; Lima 1995b). In contrast, a junco can visually scan its environment continuously while husking a whole millet seed (see also Benkman 1997, Lima 1998), which may take several seconds to complete.

Food was placed on the concrete pad at a density of about 40 bits cm^{-2} in a 1.75×1.75 m "patch". Depending upon the experimental conditions (see below), woody vegetative cover was placed over the patch of food (the "cover-overhead" condition), or placed 1 m away from the north edge of the patch (the "cover-away" position). This woody cover (with branch diameters < 1.5 cm) was secured to a moveable pyramidal wooden frame 1.5 m in height and 2×2 m square at the base. Leafless woody vegetation was applied to three sides and the interior (down to within 5 cm of the ground) at a density that would certainly thwart an attacking raptor (at least initially), while cover was applied to the fourth side at a density that would provide safety but also allow for the videotaping of birds feeding with cover overhead; this side always faced the observational window in the adjacent building. The nearest naturally-occurring woody cover was about 10 m to the east and 15 m to the west.

Finally, we emphasize that food was present continuously at the study site, 24 h each day, without interruption or significant depletion, from mid-December 1997 through the end of March 1998. Note also that food was present at the study site for a full month before the start of experimentation (in mid-January) to give juncos ample time to learn about the nature of their food supply. The food supply in such an environment should have been perceived by a junco as effectively unlimited.

Scan durations

We determined food-handling scan durations (effectively millet-husking times) and standard vigilance scan durations (for juncos feeding on corn meal) using a 2×2 factorial design with food type as one factor and cover position as the other. Only one combination of food type and cover position was present during any given observational session. The temporal ordering of these food-cover combinations was determined randomly with the restrictions that (1) all four combinations must have been used before progressing to the next round of four and (2) no two consecutive sessions could have the same combination. Switches to a given food-cover combination were done the evening before observations were to take place. Five complete rounds of combinations were performed for a total of 20 observational sessions. These sessions were conducted on consecutive days except during rainy weather. All five rounds were completed during a 25-day period from mid-January to mid-February 1998.

Observational sessions began each morning no earlier than 0.5 h after sunrise, and lasted about 1.5 h. These sessions consisted of videotaping the behavior of several focal juncos for at least 30 s each. During this period, flock size and species composition were dictated onto the audiotrack of the videotape. Observations were made only during periods when flocks were stable in size, defined as time periods with no arrivals or departures within the last 15 s; arrivals and especially departures often induce brief episodes of scanning (Lima 1995a). After videotaping a given focal junco, a different focal bird was chosen and the above process was repeated. The identity of previously taped juncos was monitored by noting their position on the pad and unique marks when such features were available. Thus focal juncos were not resampled on a given day within our ability to identify them. Previous observations on marked birds at this site indicate that individual juncos rarely visit the study site twice in a 1.5-hr period (P.A. Zollner, personal observation).

All videotapes so obtained were time stamped before analysis (using a Panasonic WJ-810 Time-Date Generator). To determine the average food-handling scan duration (or seed-husking time) for a focal junco feeding on millet seeds, we first divided its videotaped interval into five equal time segments. The time spent handling the first millet seed consumed during each time segment was then determined; these five values were averaged to obtain a single value for each focal junco. For focal juncos feeding on corn meal, we defined a vigilance scan as any period of time during which the bird raised its bill parallel to the feeding surface (cf. Ekman 1987). Average scan duration for a focal junco was based on five measurements of scan durations following the above procedure for food-handling scan durations.

All estimates of average focal junco behavior were themselves averaged according to flock size for a given observational session. We did not include a given flock-size-specific average unless it involved at least three focal birds for standard scans, and at least four focal birds for food-handling scans (food-handling scan durations were inherently more variable than standard scan durations). We considered flock sizes of one to five, and six or more birds; flock sizes larger than six were too "unstable" (by our definition) to generate the data necessary to be considered separately. This overall procedure yielded at least four and a maximum of six data points from each observational session for use in subsequent analyses. All statistical analyses were performed using the SAS statistical package (SAS Institute 1988).

Patch choice experiment

Juncos were given a simple choice of feeding either in the cover-overhead or cover-away conditions to determine whether they did, in fact, perceive the cover-overhead condition as the safer one in which to feed. This involved two food patches placed 1 m apart on the concrete feeding pad. Woody vegetative cover was placed over one patch, and the other was left exposed. Both patches always contained the same type of food item during a given session, and were prepared as described earlier. We used a 2×2 factorial design with food type (millet or cornmeal) as one factor, and cover location (east or west side of the concrete pad) as the other factor. The ordering of cover/food-type combinations between observational sessions was determined randomly as described above. Four complete rounds of combinations were performed for a total of 16 observational sessions. These sessions were conducted on consecutive days except during rainy weather. All 16 sessions were completed during a 20-day period from late February to mid-March 1998.

Observational sessions started each morning no earlier than 0.5 h after sunrise and lasted for a period of 1 h. During this hour (which began with the arrival of the first junco if none were initially present), the number and species of birds feeding in both patches were recorded at 1-min intervals. The data for each session were summarized by a single value: the proportion of all counted juncos which were recorded as feeding in the patch with cover overhead. These proportions were then arcsin-square-root transformed before being analyzed to assess patterns in patch use.

Results

Food-handling scan durations (seed-husking times) decreased with increasing group size (Fig. 1), and were generally greater in the cover-away treatment. A two-way ANOVA indicated a significant effect of both group size ($F_{5,31} = 4.35$, $P < 0.01$) and cover ($F_{1,31} = 7.38$, $P < 0.01$) on these scan durations. The cover-overhead
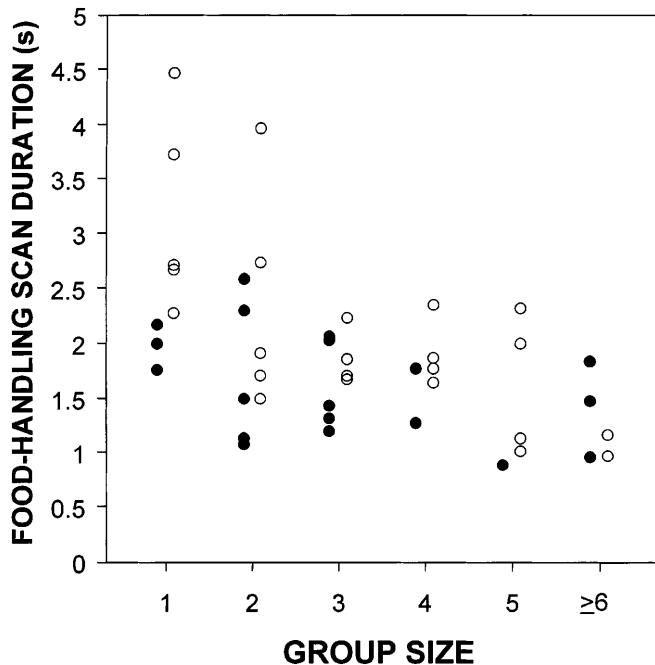
Fig. 1 Food-handling scan durations as a function of group size. *Solid* and *open circles* represent scan durations in the cover-overhead and cover-away treatments, respectively. Juncos fed on whole millet seeds, and scan durations were effectively millet-husking times. Plotted data represent average durations for focal juncos as described in the Methods

Fig. 2 Standard vigilance scan durations as a function of group size. *Solid* and *open circles* represent scan durations in the cover-overhead and cover-away treatments, respectively. Juncos fed on corn meal, and all scanning was done at the expense of food ingestion (i.e., scanning and food handling could not be done simultaneously). Plotted data represent average durations for focal juncos as described in the Methods

group size effect appears weaker than that in the cover-away treatment (Fig. 1), but the interaction between cover treatment and group size was not significant ($F_{5,31} = 1.03$, $P > 0.25$).

We also observed a significant effect of group size on standard scan durations (Fig. 2; two-way ANOVA, $F_{5,39} = 3.05$, $P < 0.025$). The tendency for shorter scan durations in the cover-overhead treatment was also significant ($F_{1,39} = 4.55$, $P < 0.05$), and there was no significant interaction between cover treatment and group size ($F_{4,39} = 0.16$, $P > 0.50$). The overall effect of group size on standard scan durations was similar to that observed in food-handling scan durations (Fig. 1), although the latter were much longer.

The interpretation of our results depends in part on the assumption that juncos perceive greater safety when feeding with cover overhead. During the patch choice experiment, an average of 83% ($n = 16$, SE = 0.058) of all juncos recorded were feeding in the patch with cover overhead; this average is significantly greater than the value of 0.5 indicating no patch preference (*t*-test, $t = 2.96$, $df = 15$, $P < 0.01$). A two-way ANOVA indicated no effect of cover location (east or west; $F_{1,12} = 0.10$, $P > 0.50$) or food type (millet or corn meal; $F_{1,12} = 0.003$; $P > 0.50$) on the tendency of juncos to prefer the cover-overhead patch. The fact that some juncos did feed in the exposed patch was due largely to occasionally crowded conditions under cover; juncos in the exposed patch usually fed as close to cover
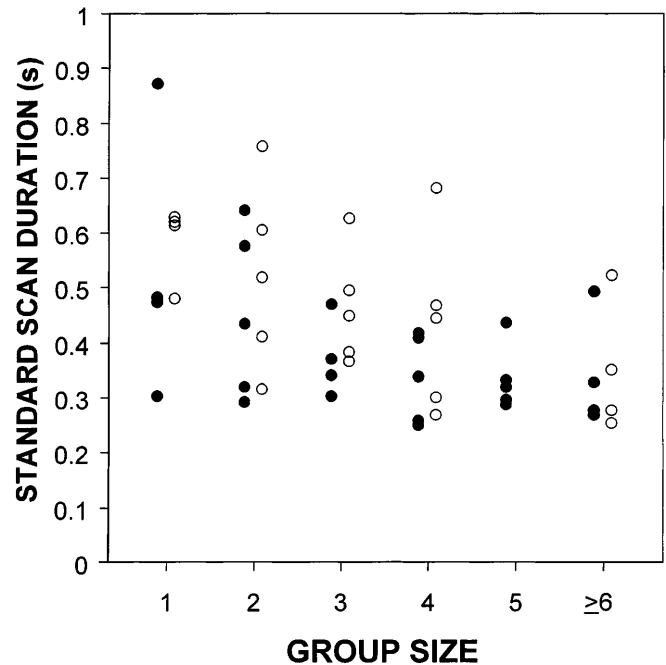
as possible. This overall preference for feeding in or near woody cover is congruent with that reported in scores of studies on the use of space by birds and many other animals (Lima 1998).

Discussion

Our results suggest that one need not invoke scramble competition to explain the group size effect in food-handling or standard scan durations, since both effects persisted in an environment with an effectively unlimited supply of food. Furthermore, both food-handling and standard scan durations were influenced by the proximity of protective cover as expected under the predation hypothesis.

As mentioned earlier, one might argue that even though our experiment excluded the possibility of competition for resources, juncos still perceived such competition; perhaps they follow the simple rule of thumb equating the presence of flockmates with competition (e.g., Clark and Mangel 1986). If this is the case, then it may prove impossible to distinguish between the predation and competition hypotheses, for it would be difficult to construct an environment more obviously free of competition than the one used in our experiments. We are reluctant to accept a simple competitive rule-of-thumb for juncos, because individual juncos

typically respond to significant food depletion by asserting their dominance and aggressively excluding others from the remaining food (S.L. Lima, P.A. Zollner, P.A. Bednekoff, personal observations). The fact that we observed no such aggressive behavior during our experiment suggests that juncos perceived an effectively non-depleting source of food. Furthermore, given the sorts of fine perceptual distinctions that animals make regarding their foraging environments (Stephens and Krebs 1986), it seems unreasonable to posit that juncos are unable to perceive a simple lack of food depletion and thus a lack of competition for food.

One result that might be interpreted in favor of the competition hypothesis is the existence of a group size effect in the cover-overhead treatment – why should there be such an effect in a refuge from predators? A pile of woody cover, however, cannot provide an absolute refuge from predators, hence vigilance would not be expected to drop to very low levels. This is especially true of the sort of isolated, semi-open pile of cover used in our experiment, into which *Accipiter* hawks may sometimes pursue small birds in an effort to force them back into the open (S.L. Lima, personal observation). Cover itself also provided a visually obstructive environment that may have warranted longer scans (e.g., Metcalfe 1984a; Arenz & Leger 1997) than might otherwise be expected in such relative safety.

The general similarity between the group size effects for food-handling and standard scan durations (Figs. 1 and 2) suggests that the longer millet-handling times observed in smaller groups represent an information-gathering effect analogous to that envisioned for standard scan durations (Desportes et al. 1991; McNamara and Houston 1992; Quenette and Gerard 1992). Also suggestive of such an effect is the fact that juncos given a choice between bits of ground millet and whole millet seeds preferred whole millet only when in small groups (Lima 1988). In the absence of the sorts of strong competitive effects outlined earlier (see Appendix), it is difficult to explain the group size effect in food-handling scan durations in any other way. The only other plausible alternative that we can offer involves "acoustic vigilance"; that is, listening for information about impending attack. Seed husking in granivorous birds is audibly noisy, and slower seed husking may allow a junco in a small group to gather additional (acoustic) information about its environment that can be forgone in larger groups. Such acoustical considerations might apply to most animals. Overall, we really do not understand the scanning process in any detail, nor the sorts of information sought by vigilant animals (Bednekoff and Lima 1998a).

In conclusion, our results do not support the idea that scramble competition for food is the main driving force behind the basic vigilance group size effect. The generality of our results is open to question, since strictly speaking they apply only to juncos. We nevertheless suspect that competition is generally unlikely to be the driving force behind vigilance group size effects. Perhaps

the best evidence we can offer in this regard is the fact that group size effects observed in the vigilance of drinking (Burger and Gochfeld 1992), sleeping (Lendrem 1984; Terhune and Brillant 1996) and preening (Roberts 1995) animals are difficult to interpret as some form of competition for limited resources. Furthermore, group size effects in mixed-species flocks of birds sometimes involve two or more species unlikely to be competing for resources (e.g. Sullivan 1984; Dolby and Grubb 1998). We also note that many ideas about scramble competition for limited resources are based upon theoretical and empirical studies that often make no allowance for the ubiquitous effects of predation on social behavior (e.g., Barnard et al. 1983; Parker 1985; Shaw et al. 1995; but see Street et al. 1984); such studies probably should not be taken as predation-free points of reference for the study of scramble competition and its possible influence on vigilance.

We do not rule out the possibility that scramble competition for resources could have an influence on the vigilance group size effect in addition to that of anti-predatory considerations. However, competitive effects may be difficult to demonstrate in the face of an already strong predation-driven group size effect; there may be little room for the further lowering of vigilance expected under competition. Perhaps competitive effects will be at their most detectable in groups of two or three animals; in this range, vigilance is still relatively high and thus there will be some possibility of detecting a competition-induced lowering of vigilance. Detecting the effects of scramble competition also depends on having animals that will not resort to interference competition (i.e., aggression) as food becomes scarce. We suspect that, in most animals, such aggression (not a lowering of vigilance) will likely be the main behavioral response to a limited food supply.

Appendix

Scramble competition and food-handling times
in social foragers

Assume that a group of animals is feeding on a stock of food items that depletes rapidly as group members feed. Under such competitive conditions, an individual can gain a greater proportion of the limited food supply by handling food items faster than its groupmates (assuming negligible search or travel time between food items). However, handling food faster leads to lower digestive efficiency since food items will be less broken-up before ingestion (Sibly 1981). Hence a group member can maximize its overall en-

ergy intake by trading off food ingestion against digestive efficiency.

We determine the handling time that maximizes overall assimilated food intake as an evolutionary "game against the field" (see Maynard Smith 1982). Consider a particular aberrant individual that takes some time h to handle each food item, while each of its $n-1$ groupmates employs a handling time $\hat{h}$. This aberrant animal will secure a portion of the available food given by:

$$F(h,\hat{h}) = \frac{\frac{1}{h}}{\frac{1}{h} + \frac{1}{\hat{h}}(n-1)} = \frac{1}{1 + \frac{h}{\hat{h}}(n-1)}.$$

This proportion increases as the aberrant individual handles food faster (as h decreases). As mentioned earlier, digestive efficiency is a function of handling time, $D(h)$. In broad terms we could use any function $D(h)$ in which digestive efficiency increases with handling time at a decreasing rate; we chose $D(h) = e^{-k/h}$ as a plausible and convenient function. Overall assimilated energy intake will depend on the product $E(h,\hat{h}) = F(h,\hat{h})D(h)$. To find the evolutionarily stable handling time we take the derivative $\partial E(h,\hat{h})/\partial h$, set this equal to zero, and then replace h and $\hat{h}$ with h^*. This yields an optimal handling time given by:

$$h^* = \frac{kn}{n-1}.$$

The optimal handling time decreases, at a decreasing rate, as group size increases ($\partial h^*/\partial n < 0$, $\partial^2 h^*/\partial n^2 > 0$). In other words, if scan durations are commensurate with handling times, they would show a classic group size effect purely as a function of a competitive game of food consumption between group members.

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