Risk allocation and competition in foraging groups: reversed effects of competition if group size varies under risk of predation

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Animals often feed more quickly when in larger groups. This group-size effect is often explained by safety advantages for groups but an alternative explanation is that animals feed faster in larger groups because of greater scramble competition for limited food. We show that predation risk enhances the group-size effect if groups vary in size. By contrast, competition leads to the group-size effect only when individuals feed in groups of constant size. When individuals feed in groups that vary in size, the best strategy for dealing with competition is to feed intensely when in smaller groups and feed little when in larger (more competitive) groups. In all situations, the effects of competition interact with the effects of predation risk in a simple multiplicative way. Our results suggest that scramble competition is not a general explanation for the group-size effect on vigilance in situations where group size changes relatively rapidly.

Keywords: vigilance; predation; competition; foraging; group-size effect

1. INTRODUCTION

Animals often eat faster and look around less when in larger groups. This group-size effect on feeding and vigilance rates has been reported many times across a wide variety of taxa (Elgar 1989; Roberts 1996; Beauchamp 1998; Lima 1998; Treves 2000). Two processes have been suggested to explain this widespread pattern. First, larger groups may be safer and therefore allow faster feeding. Larger groups are safer because they are better able to detect or repel attacks and because each group member is less likely to be killed if an attack is successful (Cresswell 1994; Roth & Lima 2003). Second, larger groups might bring greater competition for limited food, and animals might compete by feeding faster. The potential effect of competition in foraging groups has enjoyed considerable recent interest (e.g. Slotow & Coumi 2000; Beauchamp 2001; Robinette & Ha 2001). Although models of competition in behavioral ecology are at least as old as the ideal free distribution (Fretwell & Lucas 1970; see also Shaw *et al.* 1995), the idea that competition could explain the group-size effect was not formally modelled until recently. In each of two simple models, foragers deplete a finite amount of food and their fitness depends on their energy intake. Faster foraging allows a forager to eat more of the food. Eating faster brings costs in digestive efficiency (Lima *et al.* 1999) or in predator detection (Beauchamp & Ruxton 2003). In both models, individuals are assumed to remain in a group of a set size.

Animals do not always spend their time in groups of a set size. Many feeding aggregations change rapidly in size and composition (e.g. Lima *et al.* 1999). Obviously individual animals can find themselves sometimes in larger and sometimes in smaller groups when group size changes rapidly. Most studies of the group-size effect have

gathered data from situations in which group size changes rapidly, although this effect has rarely been quantified (but see Roberts 1995). Therefore we ask whether changing group size affects the logic needed to explain the group-size effect.

Previously we developed the predation-risk allocation hypothesis for animals feeding in situations that differ in danger over time (Lima & Bednekoff 1999). Because fitness depends on overall survival and foraging success, the optimal feeding rate for each situation depends on the overall distribution of situations. In particular, anti-predator behaviour depends on the relative danger and length of that situation compared with other situations. When animals are exposed to a short period of great danger, they can cease feeding and make up for that lost feeding opportunity during the long period of lesser danger. Experimental tests of this idea have yielded mixed results with animals showing risk allocation in some situations and not in others (Hamilton & Heithaus 2001; Sih & McCarthy 2002; Van Buskirk *et al.* 2002; Pecor & Hazlett 2003). In this paper we combine safety and competition in the same modelling structure and explore the effects of allocation. For groups with fixed and changing group sizes, we show how predation and competition are expected to affect feeding rate. Our results suggest that intuitive ideas about group size and competition are likely to hold only when group sizes change little over time.

2. MODELS AND RESULTS

For a non-breeding organism, fitness is the product of probability of survival to breed and expected reproductive success. When attacks occur according to a Poisson process, survival is given by $\exp(-\text{attack rate} \times \text{time exposed to attack} \times \text{probability of dying per attack})$. Trade-offs between foraging and predation risk occur when increased foraging increases one or more of the terms in parentheses (see also Bednekoff 2004). Here, we assume that

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predators attack according to a Poisson process with a rate α that does not vary with group size and that each forager feeds across some period of length T . Each individual feeds at a proportional rate, u , between 0 and 1. Following Lima & Bednekoff (1999), we assume that the probability that an individual fails to detect an attack is the square of its feeding rate, u^2 . Thus, in the models in §§ 2a and 2b, attack rate and time exposed to attack are not affected by foraging effort, but probability of dying per attack is affected. Attack rate may increase with group size (Krause & Godin 1995; see also Bednekoff 2004). So long as larger groups are safer for an individual than smaller ones, an increase in attack rate with group size will not qualitatively alter the arguments presented below.

Expected reproductive success should increase with food intake. Here, we assume that this relationship is linear; that is, an animal that eats twice as much can expect to reproduce twice as much. This assumption simplifies the mathematics and allows us to contrast our findings with those of Lima & Bednekoff (1999), who assumed that animals fed to meet a fixed requirement. Because the situations in most animals are likely to lie between these two sets of assumptions, results that hold for the two contrasting models are likely to apply widely (see also Bednekoff 2001). After presenting our models and results, we will discuss why we believe our main points are general and robust.

(a) *Fixed groups*

(i) *Predation decreases with group size*

In groups of size n , a forager that fails to detect an attack is killed with a probability $1/n$. This dilution of risk corresponds to the logic of an earlier verbal model (Grand & Dill 1999) and assumes early targeting by the predator and no information transfer between foragers (Bednekoff & Lima 1998). Collective detection is probably important for many animal groups. Including collective detection would lead to greater safety advantages for larger groups and therefore make the effects of predation reported below even stronger. Combining these elements gives the fitness function

$$F = e^{-\alpha T \frac{u^2}{n}} k u T.$$

Here, group size enters into only the exponent of the survival term. The term kuT gives the expected reproductive success, where u is the foraging rate and T is the time spent foraging, so uT is the total foraging intake. The constant k converts foraging intake to reproductive success. Differentiating and solving for the optimal feeding rate, u^* , yields

$$u^* = \sqrt{\frac{n}{2\alpha T}}.$$

The optimal feeding rate increases with group size, n , and decreases when more attacks, αT , are likely (figure 1a). Unlike some subsequent models, for this model foraging intake equals foraging effort. If we compare the optimal feeding effort in a group of size m to that in a group of size n , the ratio of feeding effort is simply the square root of the ratio of group sizes

$$\frac{u_m^*}{u_n^*} = \sqrt{\frac{m}{n}}.$$

Figure 1. In groups of constant size, optimal feeding effort increases with group size under (a) predation, (b) competition and (c) their combination. Filled circles, effort ($\alpha T = 8$); open circles, intake ($\alpha T = 8$); filled diamonds, effort ($\alpha T = 32$); open diamonds, intake ($\alpha T = 32$). Foraging effort is lower when more attacks are expected (higher αT). Foraging intake equals effort under predation alone but decreases with competition or the combination of competition and predation.

(ii) *Competition increases with group size*

Now we assume that an individual's probability of being killed by a predator is not affected by the presence of others. Instead, food intake is affected by the presence and actions of others. We model competition by discounting an individual's feeding effort, u , by the proportion it is of the total feeding effort, $u/(u + (n - 1)v)$, where n is group size and v is the foraging effort of each other individual. This logic for competition (with different notation) is also

used by Shaw *et al.* (1995) and Beauchamp & Ruxton (2003). By this equation, if all individuals forage with the same effort, each has a food intake of u/n . When individuals have different foraging efforts, their intakes differ by even more. For example, the individuals in a group of two make efforts of $1/2$ and $1/4$, their intakes will be $1/3$ and $1/12$, respectively. Including this expression for competition leads to the overall fitness function

$$F = e^{-\alpha T u^2} k T u \left(\frac{u}{u + (n-1)v} \right).$$

Here, group size affects only competition for food. Solving for the evolutionarily stable feeding effort yields

$$u^* = \sqrt{\frac{2n-1}{2\alpha T n}}.$$

Because group size, n , appears in both the numerator and denominator, the effect of group size on feeding effort is not so obvious or strong. Effort does, however, increase with group size (figure 1b). Once again feeding effort decreases when more attacks, αT , are likely (figure 1b). If we compare the predicted feeding efforts for two different group sizes, n and m , it is

$$\frac{u_m^*}{u_n^*} = \sqrt{\frac{(2m-1)n}{(2n-1)m}}.$$

For each group, however, feeding intake is $1/n$ of feeding effort. Under competition feeding intake decreases quickly with increasing group size (figure 1b).

(iii) Competition and predation change with group size

Now we combine the elements of §§ 2a(i) and 2a(ii), so that group size affects both mortality and realized feeding intake. Now group size affects both the probability of being killed in an attack and food intake. The fitness function is

$$F = e^{-\alpha T \frac{u^2}{n}} k T u \left(\frac{u}{u + (n-1)v} \right).$$

Solving for the evolutionarily stable feeding effort yields

$$u^* = \sqrt{\frac{2n-1}{2\alpha T}}.$$

Feeding effort increases with group size faster than it does under either predation or competition alone and decreases when more attacks, αT , are likely (figure 1c). Although feeding effort increases quickly, feeding intake still decreases with increasing group size (figure 1c).

If we compare the predicted feeding efforts for two different group sizes, n and m , it is

$$\frac{u_m^*}{u_n^*} = \sqrt{\frac{2m-1}{2n-1}}.$$

This ratio for the combined effect is simply the ratio for predation multiplied by the ratio for competition. Thus the relative effect of the combination of predation risk and competition is simply their individual effects multiplied together.

(b) Fluctuating group size

Now we study the effects of changing group size. For simplicity, we limit ourselves to two group sizes, m and n . We assume that attack rate does not depend on group size and that each individual spends half the time in a group of size m and half the time in a group of size n . (For allocation across different mixtures see Lima & Bednekoff (1999)). For each situation we solve for two optimal feeding rates, one for each group size, by taking partial derivatives for each feeding rate, setting them equal to zero and substituting between the potential solutions for each rate (see also Lima & Bednekoff 1999).

(i) Predation decreases with group size

Now mortality is affected by feeding effort and group size in each situation, and future reproductive success depends on total feeding intake. Thus the fitness function is

$$F = e^{-\alpha \frac{T}{2} (\frac{u_m^2}{m} + \frac{u_n^2}{n})} k \frac{T}{2} (u_m + u_n).$$

This equation contains only elements that we have seen before. For each group size, predation risk depends on the square of the feeding rate divided by the group size. Expected reproductive success depends on total foraging intake. As half the time is spent in each situation, it is convenient to put $1/2$ outside the brackets for both predation risk and foraging intake. Solving simultaneously for the two evolutionarily stable feeding efforts yields

$$u_m^* = \frac{m}{\sqrt{\alpha T (n+m)}},$$

$$u_n^* = \frac{n}{\sqrt{\alpha T (n+m)}}.$$

Both feeding rates will increase as group sizes increase and decrease when more attacks are likely. The ratio of the feeding rates, which have the same denominator, is simply the ratio of the group sizes

$$\frac{u_m^*}{u_n^*} = \frac{m}{n}.$$

To illustrate the effect of group size clearly, we set the smaller group to size 1 and vary the size of the larger group (figure 2a). Foraging rate increases with group size, but the rate while feeding alone decreases when individuals spend half their time in larger groups (figure 2a). With allocation across several situations, the optimal feeding rate in any situation is affected by the other situations available. Animals should forage more in a particular situation if they will soon find themselves in even greater danger than if they will soon find themselves in relative safety.

(ii) Competition increases with group size

Here, fitness is affected by the realized feeding rate in each situation, and the realized feeding rate is affected by the feeding rates of others in each situation. This involves no new principles but yields the rather long fitness function

$$F = e^{-\alpha \frac{T}{2} (\frac{u_m^2}{m} + \frac{u_n^2}{n})} k \frac{T}{2} \left(\frac{u_m}{u_m + (m-1)v_m} + \frac{u_n}{u_n + (n-1)v_n} \right).$$

Figure 2. When foragers spend half of their time in a group of size n and half of their time alone, foraging effort in groups (filled diamonds) (a) increases with group size under predation, (b) decreases with group size under competition and (c) increases moderately with group size under the combination of predation and competition. Foraging effort when alone (circles) decreases with group size under predation alone but increases with group size under competition or the combination of competition and predation. Foraging intake in groups (open diamonds) equals effort under predation alone but decreases with competition or the combination of competition and predation.

Solving simultaneously for the two evolutionarily stable feeding efforts yields

$$u_m^* = \frac{(2m-1)n^2}{\sqrt{\alpha T m n [n^3(2m-1) + m^3(2n-1)]}},$$

$$u_n^* = \frac{(2n-1)m^2}{\sqrt{\alpha T m n [n^3(2m-1) + m^3(2n-1)]}}.$$

Both feeding rates decrease when more attacks are likely but the effect of group size on the rates is not obvious. We get a somewhat clearer picture if we look at the ratio of the feeding rates because, once again, the feeding efforts have the same denominator so their ratio is less complicated than the feeding rates themselves,

$$\frac{u_m^*}{u_n^*} = \frac{(2m-1)n^2}{(2n-1)m^2}.$$

In the ratio, the squares of the group sizes dominate the overall result and the squares are inverted. Thus foraging efforts actually decrease with group size, and feeding intake decreases even faster with group size (figure 2b). Foragers who spend half of their time in larger groups feed more intensely when alone (figure 2b). If animals can allocate their behaviour across two foraging situations, they do best to concentrate their feeding in the situation with less competition. Thus the possibility of allocation across situations reverses the intuitively expected effect of competition on foraging effort.

(iii) Predation and competition change with group size

Here, we have two group sizes and in each the presence of others affects both predation risk and feeding intake. Combining the elements from §§ 2b(i) and 2b(ii) yields the fitness function

$$F = e^{-\frac{T}{2} \left(\frac{u_m^2}{m} + \frac{u_n^2}{n} \right)} k \frac{T}{2} \left(\frac{u_m}{u_m + (m-1)v_m} + \frac{u_n}{u_n + (n-1)v_n} \right).$$

Solving simultaneously for the two optimal feeding efforts yields

$$u_m^* = \frac{(2m-1)n}{\sqrt{\alpha T [n^2(2m-1) + m^2(2n-1)]}},$$

$$u_n^* = \frac{(2n-1)m}{\sqrt{\alpha T [n^2(2m-1) + m^2(2n-1)]}}.$$

As in all the other models, feeding effort decreases when more attacks are likely. The effect of group size is less obvious but we find that both foraging efforts increase with group size, with the foraging effort increasing slightly while alone and considerably more when in a group (figure 2c).

Once again these two rates have the same denominator, so their ratio is the ratio of their numerators

$$\frac{u_m^*}{u_n^*} = \frac{(2m-1)n}{(2n-1)m}.$$

This ratio includes $(2m-1)/m$ countered by the inverted $(2n-1)/n$. Each of these terms can take on the values 1, 3/2, 5/3, 7/4, and so on, asymptotically approaching 2, and the larger group will contribute a somewhat larger term to the ratio. Thus as group size increases the ratio of feeding effort in a group to feeding effort alone will asymptotically approach 2 (see figure 2c).

By comparing this ratio with the previous two, we see that the combined effect of predation and competition is again their separate effects multiplied together. The

relatively weak increase seen in the combined model is a result of a strong increase because of predation countered by a moderate decrease owing to competition. Thus the expected group-size effect is restored in our model of competition and predation in groups of fluctuating size, but only because predation has a quantitatively stronger effect than competition in our model.

Although feeding effort increases somewhat, feeding intake is decidedly lower in larger groups (figure 2c). Thus feeding intake declines with group size in all situations involving competition. When all foragers feed with the optimal effort, u^* , each receives u^*/n in intake. Thus intake decreases unless feeding effort increases proportionally with group size. In all of our models, effort increases less than proportionally with group size.

3. DISCUSSION

Competition leads to opposite effects for fixed and changing groups. Foraging effort increases with competition for groups of fixed size but decreases for groups of changing size. In groups of fixed size, the only option for foragers is to work harder as competition increases. In groups of varying size, foragers can allocate their foraging to the situation in which they get the most for their efforts. Because they allocate their foraging to the least competitive situation and competition increases with group size, the usual group-size effect is reversed.

Our results suggest that scramble competition is not a general explanation for the group-size effect on vigilance in situations where group size changes rapidly. Our intuitive notion that competition should lead to greater feeding effort applies only to groups of fixed size. Previous models considered only groups of fixed size (Lima *et al.* 1999; Beauchamp & Ruxton 2003) and thus our previous thinking omitted a potentially critical element of the lives of animals.

Furthermore, in our models of competition, actual feeding intake decreases even when feeding effort increases with group size. If this decrease is a consequence of the food-finding process, it should be directly observable. We know of no reports of increasing feeding effort but decreasing ingestion with increasing group size. It is possible that ingestion increases but that net intake decreases under scramble competition because of poor digestion of hastily consumed foods (Lima *et al.* 1999). We know of little ecologically relevant evidence to support this conjecture. Thus a key assumption of scramble competition is yet to be documented for foraging groups.

By contrast, predation risk leads to faster feeding in larger groups whether or not group size fluctuates. The effect of group size was stronger with fluctuating group size than with constant group size. Our results extend our understanding of the importance of risk allocation. In a previous model (Lima & Bednekoff 1999) we assumed that animals fed to meet a fixed requirement and found that risk allocation accounted for all responses to risk. In other words, animals did not respond to their average predation risk, only to variation around that average. In this paper we assume that reproductive success increases linearly with feeding intake and find that foragers respond both to mean predation risk and to variations around the

mean. Risk allocation leads to responses to variation in predation risk. Risk allocation generally increases the magnitude of anti-predator behaviour above what would be seen otherwise, and what would be seen otherwise depends on the marginal value of extra food (see also Bednekoff 2004).

For both constant and varying group sizes, all effects of group size start with the same prediction for a lone animal and then move asymptotically towards all feeding or no feeding. Changing predation risk has the same proportional effect on each curve, contrary to predictions from the verbal model of Grand & Dill (1999). Thus the predicted effects of predation, competition and their combination do not differ in kind, only in 'slope'. In our opinion, there is no simple way to separate the effects of competition from those of predation risk without manipulating competition and predation risk independently of changing group size (see Bednekoff 2003). To date, changing predation risk has been demonstrated to alter feeding and vigilance while providing superabundant or limited food has not (Lima *et al.* 1999; Blumstein *et al.* 2002).

The findings reported in this paper are likely to be robust so long as risk of predation decreases with group size and competition increases with group size. Altering the strength of the changes with group size will alter the strength of the effects seen, but not their direction. Thus including collective detection would make larger groups even safer and lead to greater changes in foraging with group size. If predators attack larger groups somewhat more often (but not enough to make them more dangerous), this would decrease the differences in safety and foraging between small and large groups. We can also consider modifying the competition function. For example, the effect of foraging by others, v , could be weighted by some value between zero and one, and thereby the strength of competition could be adjusted from none to full. Analyses indicate that details of the competition function quantitatively change the effect of competition on foraging effort but that the qualitative change of effects between fixed and changing groups is robust.

The models above demonstrate the importance of allocation of risk and competition when feeding in groups. Generally the best action in a situation is affected by whether that situation is temporary or permanent. In foraging theory, animals should stay in bad patches for far less time if they can expect better patches later. In operant psychology experiments, animals should work harder for food in experiments where they feed only during the experiment than in experiments in which they are fed outside the experiment (Timberlake & Peden 1987; Houston & McNamara 1989). In life histories, an organism should invest heavily in reproduction when in a bad environment only if it is stuck there for life. If the organism can expect to spend part of its life in better conditions, it should invest in surviving to those better circumstances (Stearns & Koella 1986; Houston & McNamara 1992). These three examples show that the risk-allocation hypothesis is one form of the widely applicable principle that an organism's reaction to a situation may depend on what other situations it is likely to encounter.

We thank Tamara Grand, Guy Beauchamp, Graeme Ruxton and Dan Blumstein for stimulating discussions of the general subject. Comments by two anonymous reviewers improved the manuscript in many ways. P.A.B. thanks Eastern Michigan University for a Faculty Research Fellowship and a sabbatical in which he conceived of and completed this project, respectively. S.L.L. was supported in part by NSF grant IBN-0130758.

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