



COSTS AND BENEFITS OF WITHIN-GROUP SPATIAL POSITION: A FEEDING COMPETITION MODEL

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ABSTRACT

An animal's within-group spatial position has several important fitness consequences. Risk of predation, time spent engaging in antipredatory behavior, and feeding competition can all vary with respect to spatial position. Previous research has found evidence that feeding rates are higher at the group edge in many species, but these studies have not represented the entire breadth of dietary diversity and ecological situations faced by many animals. In particular, the presence of concentrated, defendable food patches can lead to increased feeding rates by dominants in the center of the group that are able to monopolize or defend these areas. To fully understand the tradeoffs of within-group spatial position in relation to a variety of factors, it is important to be able to predict where individuals should preferably position themselves in relation to feeding rates and food competition. A qualitative model is presented here to predict how food depletion time, abundance of food patches within a group, and the presence of prior knowledge of feeding sites affect the payoffs of different within-group spatial positions for dominant and subordinate animals. In general, when feeding on small abundant food items, individuals at the front edge of the group should have higher foraging success. When feeding on slowly depleted, rare food items, dominants will often have the highest feeding rates in the center of the group. Between these two extreme points of a continuum, an individual's optimal spatial position is predicted to be influenced by an additional combination of factors, such as group size, group spread, satiation rates, and the presence of producer-scrounger tactics.

INTRODUCTION

ALTHOUGH it is widely recognized that the costs and benefits of sociality differ between group-living individuals (Janson 1992; Krause and Ruxton 2002), less attention has been paid to how these differences are mediated by an individual's spatial position within their social group (Krause 1994;

Romey 1997; Parrish and Edelman-Keshet 1999). Krause (1994) found numerous lines of evidence that variation in individual fitness is related to within-group spatial position. In many species, certain individuals have preferences for particular spatial positions due to their differing fitness costs and benefits (Krause 1994). Animal groups are composed

of individuals seeking to increase their own fitness, and the combined costs and benefits of within-group spatial position of these individuals should determine the total geometry of the group (Parrish and Edelstein-Keshet 1999).

Feeding competition is a key factor that determines the major costs and benefits of spatial position, and also shapes the evolution of social systems. Competition often depends on food dispersion, and several authors have focused on how and why these differences lead to differing social systems (Wrangham 1980; Vehrencamp 1983; Janson and van Schaik 1988; van Schaik 1989; Sterk et al. 1997). Food items that are small and evenly dispersed generally lead to within-group scramble (WGS) competition, where individuals scramble to consume resources before others in their group encounter them. Large clumped food items generally lead to within-group contest (WGC) competition, where individuals or coalitions of individuals can defend food resources from others. WGC generally results in higher-ranking individuals having greater food intake rates, while feeding intake rates in WGS groups are generally not linked to rank. In primates, a link between competitive regimes and social systems has been found (Sterk et al. 1997). WGS generally leads to more egalitarian societies, while WGC generally leads to rigid dominance hierarchies.

Socioecological theory is largely based on the relative patchiness of resources (clumped versus evenly distributed), however, less attention has been given to how one measures this. Janson (1988) suggested that patchiness be measured in relation to the group spread, and a recent model (Vogel 2004) has provided practical methods to measure resource patchiness in relation to group spread in wild capuchin monkeys. This concept is crucial to understanding feeding competition because, for a given resource, the spread of a social group can determine whether the resource is perceived as patchy or evenly distributed. Differences in group spread between two similar sized groups can be enormous. A small cohesive group may only have one food item or patch at a given time, thus all members of the group will attempt to feed on this single re-

source simultaneously, which could result in some individuals being excluded. When a group is widely spread out, the group spread may contain several food items, thus many individuals will be able to feed at the same time. These differences in spatial scale are crucial to understanding how and why individuals compete for food, and may lead to the conclusion that traditional botanical measures of food distribution are inadequate to predict the manner and degree of feeding competition for a given animal species.

In this paper, I develop a qualitative model to determine the impacts of food size, food distribution, and prior knowledge of resources on within-group spatial position. These factors, along with predation, should be the primary determinants of where individuals are located in a social group. The sum of these individual spatial position choices will determine the overall group geometry, which is subsequently an important factor in driving the level of feeding competition. To fully understand the interaction between food size, food distribution, and feeding competition, one must take into account the spatial scale in which feeding competition takes place; it is crucial to have a clear understanding of the costs and benefits of within-group spatial position (Figure 1).

The feeding model discussed in this paper focuses on more or less stable animal groups, yet many of the factors mentioned are applicable to ephemeral animal groups as well (e.g., many flocking birds and fish aggregations). Various authors have used models of behavioral asynchrony to explain sexual segregation in ungulate species, noting that differential needs for rest and feeding could explain why many species have sexually segregated groups (Conradt 1998; Conradt and Roper 2000; Ruckstuhl and Neuhaus 2002). If an animal is unable or unwilling to leave a social group because of high dispersal costs, it may need to compromise its preferred behavior and activities to remain with the group. This tradeoff can cause inherent conflicts between the optimal behavior of an individual and the rest of the group. The feeding model incorporates many strategies that

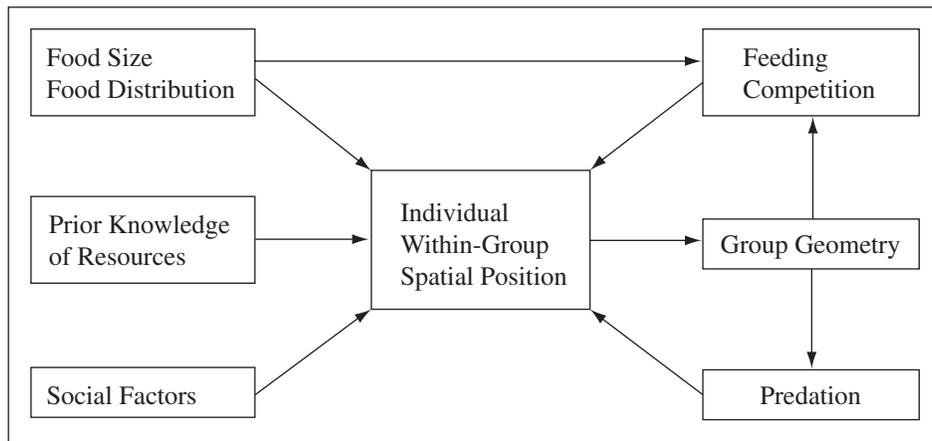


FIGURE 1. IMPORTANCE OF WITHIN-GROUP SPATIAL POSITION

animals utilize to reduce the costs of grouping while increasing the benefits to the individual.

In addition to the focus on nonephemeral animal groupings, the incorporation of dominance relationships means that portions of the feeding competition model are not applicable to some animals such as eusocial insects. Despite this limitation, a huge variety of vertebrate animal taxa have been observed living in fairly stable groups with individual recognition and dominance relationships: fish (Grant et al. 2000, 2002; Bshary et al. 2002; Croft et al. 2005; Sneddon et al. 2005), birds (Aubin and Jouventin 2002; Dubois and Giraldeau 2004; Drummond 2006), cetaceans (Pryor and Morris 1991; Sayigh et al. 1998), ungulates (Clutton-Brock 1976; Reby et al. 1998, 2001; Côté 2000), carnivores (Schaller 1972; Holekamp et al. 1996, 1999; Gompper et al. 1997; Clutton-Brock 2002), and primates (Cheney and Seyfarth 1990; Janson and Goldsmith 1995; Sterck et al. 1997).

In many species, the most important benefit of sociality is protection from predation. The “selfish herd effect,” coined by Hamilton (1971), is the major theory used to investigate the effects of within-group spatial position in relation to predation risk. Its basic premise is that the presence of neighbors reduces the risk of predation. Hamilton (1971) predicted that individuals at the periphery of the group

are under a higher risk of predation than central individuals because they have fewer neighbors. This “marginal predation effect” is hypothesized to be the main reason individuals benefit from central spatial positions within the group. The literature supports Hamilton’s theory rather well (see Viscido et al. 2001, 2002; Viscido and Wetthey 2002; James et al. 2004 for detailed theoretical and empirical analyses of Hamilton’s model), and numerous studies have found that mortality, per capita attack rate, and vigilance levels are higher in peripheral animals (mortality and attack rate: Krause 1994; but see Parrish 1989; vigilance: Lazarus 1978; Jennings and Evans 1980; Inglis and Lazarus 1981; Lipetz and Beckoff 1982; Underwood 1982; Alados 1985; DeRuiter 1986; Petit and Bildstein 1987; Janson 1990b; Burger and Gochfeld 1994; Steenbeek et al. 1999; Burger et al. 2000). If an animal group approaches a sit-and-wait predator, individuals at the front edge of the group will undergo particularly high levels of predation threat (Vine 1971; Busse 1984; Janson 1990b; Bumann et al. 1997; Carbone et al. 2003; Di Blanco and Hirsch 2006). In cases where the same spatial position results in both higher predation risk and lower feeding competition, individuals must balance the two factors to gain the highest total fitness levels (Janson 1990b; Romey 1995).

FEEDING COMPETITION

If predator avoidance is the only factor driving grouping patterns, individuals should seek to increase the number of close neighbors, and thus animal groups would be tightly packed with minimal interindividual distances. This type of group formation is not seen in most vertebrate species, which suggests there must be costs associated with grouping that also influence group geometry. The major cost of group living in most species is a reduction in food intake rate caused by an increase in feeding competition. When the number of neighboring conspecifics increases, feeding competition should also increase, causing individual food intake rates to decline (Janson 1988a). An increase in the distance between neighbors is predicted to reduce feeding interference (Di Bitetti and Janson 2001; Carbone et al. 2003).

Central individuals are predicted to have lower feeding intake rates compared to peripheral individuals due to an increase in neighbor density at the center of a group. Published results are contradictory, with several studies reporting higher feeding rates (or efficiency) at the edge of the group (Okamura 1984, 1986; Petit and Bildenstein 1987; Keys and Dugatkin 1990; Rayor and Uetz 1990, 1993; Black et al. 1992; Romey 1995; Stahl et al. 2001; Rowcliffe et al. 2004) and others reporting higher rates in the center of the group (Robinson 1981; Janson 1985, 1990b; van Schaik and van Noordwijk 1986, 1988; Barton 1993; Grant et al. 2002). This discrepancy could be the result of three factors: (i) depletion time (quickly versus slowly consumed food items); (ii) food distribution (rare versus abundant within the group spread); and (iii) whether the group has prior knowledge of food location. I will discuss how these three variables are predicted to influence an individual's within-group spatial position.

DEPLETION TIME

Depletion time is defined as the time it takes an individual to process and consume a food item or patch of food items. Although this can be measured in absolute terms, I will discuss depletion time in relation to different

aspects of group foraging. For simplicity, I have divided depletion time into three categories: quick, medium, and slow. Quickly depleted food items are small enough that an individual can put the entire food item in its mouth or consume it before the arrival of a conspecific group member. These items cannot be competed over aggressively, and thus animals will primarily compete through within-group scramble (WGS) (note an important exception in Grant et al. 2002). Food items with medium depletion times are defined as those that cannot be eaten completely before the arrival of a conspecific, but are not large enough to satiate a centrally foraging individual that usurps the item or patch. Medium depletion time foods should also lead to within-group contest (WGC). Large food resources are defined as containing enough food that a dominant central individual is able to be satiated after arrival at the resource. Some resources are so large that an entire group can be satiated (e.g., Janson 1988b) and no competition takes place; these super large patches are not a focus of this model and will not be discussed further. It is important to note that these definitions depend on the interindividual spacing of group members. If the average interindividual distance in a group increases, the same food item might change from medium to quickly depleted because of the extra time it would take a conspecific to reach another individual to compete for the food. I will use the above definitions with this caveat, but will address this issue later.

Quick Depletion Time (WGS)

If food items are quickly depleted, individuals will have higher feeding success at the front edge of the group. When individuals at the back of the group forage, they will roam over areas that have already been picked over by conspecifics. Several studies of invertebrates (Okamura 1984, 1986; Rayor and Uetz 1990, 1993; Romey 1995), birds (Petit and Bildenstein 1987; Keys and Dugatkin 1990; Black et al. 1992), and primates (Sigg 1980; Janson 1990b; Hall and Fedigan 1997) have shown that feeding success is highest at the edge of the group. More specifically, individuals at

the front edge have been found to have higher feeding rates in fish (O'Connell 1972; Krause et al. 1992; Krause 1993), birds (Black et al. 1992; Stahl et al. 2001; Rowcliffe et al. 2004), and primates (Robinson, 1981; Janson, 1990b; Hall and Fedigan 1997). An interesting and relevant behavior has been reported in white ibis (*Eudocimus albus*) flocks that forage for crabs (*Uca spp.*) in salt marshes (Petit and Bildstein 1987). When flocks of ibis approach, crabs retreat to underground burrows. Peripheral individuals are thus able to capture crabs before they can escape to their burrows, whereas central individuals have to probe the ground to extract the crabs. Although the authors did not find a difference in overall capture rates between central and peripheral animals, central animals spent more time foraging than peripheral ones (Petit and Bildstein 1987). This difference in handling costs from edge to center results in greater foraging efficiency for peripheral individuals.

When food items are quickly depleted, individuals gain the highest foraging success at the front edge of the group. Since this is also where predation should be the highest, a fitness tradeoff can arise between feeding and predation (Romey 1985, 1997). If both foraging efficiency and predator pressure increase at the periphery of the group, individuals should prefer locations that provide the greatest total fitness benefits. Romey (1985) and Krause et al. (1992) have found that when individuals are deprived of food, they prefer peripheral spatial positions. In these cases, the need to acquire food may be more important than the risk of predation (also see Ranta et al. 2006). This tradeoff is also exhibited in vigilance behavior. Two avian studies (Petit and Bildstein 1987; Keys and Dugatkin 1990) found higher foraging efficiencies in peripheral individuals, but no overall increase in food intake. The authors conclude that the benefits of higher foraging efficiency are countered by the increased time spent vigilant. Instead of increasing food intake rate, peripheral individuals maintain similar intake rates to central individuals and use the extra time (due to higher foraging efficiency) for vigilance to counter the increased predation threat. This balance between predation

and foraging efficiency could be affected by shifts in food distribution, hunger, group size, body size, and predator hunting strategies.

Medium Depletion Time (Producer-Scrounger)

Medium-sized food resources are defined in relation to how much of the resource a dominant individual can obtain. These food items are large enough to be contested over, yet small enough that a central dominant individual cannot be satiated upon arrival. When food items have medium depletion times, dominant individuals may place themselves behind the front edge of the group and in front of the center of the group. This spatial position has the advantage of increasing scrounging opportunities as well as the amount of food stolen from the finder (Di Bitetti and Janson 2001). To predict the preferred spatial position of dominant individuals feeding on medium-sized food resources, it is useful to examine the potential relevance of producer-scrounger models to within-group spatial position.

When animals forage in groups, the food discovered by a few can lead to the feeding success of many. This pattern can occur when individuals discover new information about food locations, share food patches, or engage in kleptoparasitism (Vickery et al. 1991; Giraldeau and Caraco 2000). Some models of group foraging focus on information sharing, where individuals both search for food and monitor conspecifics. When food is discovered, all group members converge on the patch and share (Clark and Mangel 1984). In species that utilize monopolizable resources, producer-scrounger models may be more appropriate. Individuals that discover food sites are deemed "producers," and individuals that join them after food has been found are deemed "scroungers" (Barnard and Sibly 1981). The number of producers and scroungers in a group should reach a stable equilibrium with equal payoffs, thus a mixed evolutionarily stable strategy (ESS) is reached (Giraldeau and Caraco 2000). Basic producer-scrounger models assume that an individual can be both a producer and a scrounger, but not at the same time. A more realistic model

is that of Vickery et al. (1991), who introduce a third opportunist strategy in which an individual can simultaneously be both a producer and scrounger, but at reduced efficiencies. If there is no tradeoff between producing and scrounging tactics in the rate of food discovery or opportunities to monopolize discovered patches, then the model is one of information sharing (Giraldeau and Caraco 2000).

One variable that has not been factored into most producer-scrounger models is the presence of dominance hierarchies. In many species, dominants often steal food from subordinates, and the costs and benefits of the producer-scrounger model change accordingly. One model has shown how dominance rank and competitive ability influence equilibrium numbers of producers and scroungers (Barta and Giraldeau 1998). If one assumes that individuals can only scrounge food from a lower ranking individual, dominants should play the scrounger role more often than lower ranking individuals. In both zebrafish and capuchins, it has been found that dominant individuals preferentially act as scroungers, and subordinates act as producers (Clifton 1991; Di Bitetti and Janson 2001). Additional models that allow for dominance in producer-scrounger situations predict that the decision of a dominant individual to act as a scrounger in a given situation will depend upon the amount of food available after stealing the item (Broom and Ruxton 2003; Broom et al. 2004).

Barta et al. (1997) modeled the effect of producer-scrounger models on group spatial structure. Their model indicated that scroungers should be found in the center of the group, and producers at the periphery. This model did not consider the issue of group mobility and the fact that scrounging opportunities are more available at the front of the group. When a group moves through the environment, producers should be located at the front periphery and dominants in the front central portion of the group. This spatial pattern has been found in four different populations of capuchin monkeys (Robinson 1981; Janson 1990a,b; Hall and Fedigan 1997; Di Bitetti and Janson 2001). In a set of experiments where unknown food sites were placed in the

home range of a capuchin group, subordinate individuals located at the front edge of the group discovered significantly more food platforms than individuals at other spatial positions (Di Bitetti and Janson 2001). Di Bitetti and Janson (2001) found that the spatial proximity of conspecifics had a significant influence on the finder's share, which is the proportion of a resource that the producer consumes before being joined by other foragers. The finder's share increased for both subordinate and dominant producers when they were farther away from conspecifics. Although subordinates can (and do) use this tactic to increase their finder's share, dominant individuals were still able to consume more total food at resources due to their aggressive monopolization of food. Dominant capuchins were most often found in the front-central spatial position, which is an ideal location for a dominant individual to increase its food intake (Janson 1990a,b; Di Bitetti and Janson 2001). By foraging behind the producers on the front periphery of the group, dominant individuals are better able to monitor the food discoveries of producers. Rather than being in the exact center of the group, ranging in the front-center allows dominant individuals to reduce the distance, and hence travel time, between themselves and the producers. Ruxton et al. (2005) used computer models to illustrate that the decision to join a food discovery depends on both the distance to the scrounging opportunity and the size of the food patch. If individuals actively choose spatial positions that will increase their food intake, dominant individuals should be located in positions that form a continuum in relation to food size. Small food items will drive dominants closer to the front periphery, and large items will steer them toward the center of the group.

Slow Depletion Time (WGC)

When food is contained in slowly depleted, defensible patches, individuals can aggressively compete over food (WGC). In these instances, dominant individuals at the center of the group will have higher feeding rates, while subordinates at the periphery wait for the dominants to finish eating before en-

tering the food patch (Robinson 1981; Janson 1986, 1990b; Grant et al. 2002). Reports of this "central-peripheral" spatial structure, wherein centrality is related to high dominance rank, has often been described in the primate literature (Kawamura 1956; Washburn and DeVore 1961; Sigg 1980; Robinson 1981; Sugiyama and Ohsawa 1982; Busse 1984; Collins 1984; Janson 1985; Wada and Matsuzawa 1986; van Noordwijk and van Schaik 1987; Janson 1990a,b; Barton 1993; Rasmussen and Farrington 1994; Ron et al. 1996).

The effects of WGC should be greatest when groups feed on one food patch at a time and when dominants are able to exclude subordinates. In many frugivores, fruit trees often form large defensible patches within the group spread. Janson (1986, 1992) has shown that dominant *C. apella* control access to fruit trees, and the rate of food intake is highly related to dominance rank or being tolerated by dominant individuals. If dominant and tolerated individuals are preferentially found in the center of the group, central individuals should have higher feeding rates on contestable items (Janson 1985, 1990a,b). Several studies have demonstrated that feeding rates are higher in central individuals (Robinson 1981; Janson 1986, 1990b; van Schaik and van Noordwijk 1986, 1988; Barton 1993; van Noordwijk and van Schaik 1999), and all of these species have a strong WGC component. In these cases, dominant individuals should not exhibit higher food intake rates when foraging at the front of the group. Even though ranging at the front would allow dominants to start feeding before other group members, if a resource is sufficiently large, the dominant individual will eat the same amount regardless of whether it ranges at the front or in center of the group. When single large food resources are contained in the group spread, dominants should be central. An important exception is when a resource is so large (or the group so small) that all individuals can peacefully eat at the same time with little or no feeding competition (Dubois et al. 2003).

FOOD DISTRIBUTION

A large literature has developed investigating the effects of resource distribution and

patchiness on various aspects of social foraging (Giraldeau and Caraco 2000). The crucial measures of resource patchiness for social foragers are the distribution and abundance of the items within the spread of the group (Janson 1988), although group spread itself may depend on food distribution (e.g., Isbell and Enstam 2002). The previous discussion of food size applies largely to instances when one food item or patch is found within the group at a given time. If multiple food patches are available to foragers at the same time, the relationship between individual spatial position and feeding intake rates changes, especially regarding valuable food items that elicit contest competition. If a group spread contains only one food patch, dominant individuals can exclude subordinates and gain a higher food intake rate. However, if there are multiple food patches, a subordinate can forage in another food patch. Janson (1996) conducted a relevant set of experiments by provisioning brown capuchin monkeys in Argentina with platforms filled with food to mimic fruit trees. Two food platforms were presented to the monkeys at varying distances. When the platforms were close together, the alpha male was able to defend both from competing conspecifics, but when placed 10 m apart, the alpha male was only able to monopolize one of the platforms. This experiment demonstrates two important concepts. First, multiple food patches lead to a smaller variance in feeding intake rate between group members. Also, defining a food item or patch can be difficult and subjective. In these experiments, when two patches are placed close together, they can be defended and monopolized as one large patch, but when placed farther apart, they are treated as two separate patches. When discussing patchiness of resources in relation to feeding competition, it is crucial to know at what size and distribution a resource can be defended for a particular species. For instance, in the previous example, a distinct patch of food for capuchin monkeys could be defined as any food source that is separated by 10 m or more from another one (Janson 1996).

When multiple defendable food patches are contained within the group spread, the importance of spatial position will decrease.

In long-tailed macaques (*Macaca fascicularis*), which regularly feed on multiple fruit trees simultaneously, van Schaik and van Noordwijk (1986, 1988) found that central individuals had significantly higher feeding rates than peripheral ones. This species regularly breaks into subgroups, with some individuals feeding on each tree within the group spread. The central dominant individuals often monopolize the most productive fruit trees, while others in the group forage at less productive trees nearby. This example illustrates that not all food patches are created equal. Koenig et al. (1998) discovered that although social rank and foraging rate in Hanuman langurs (*Presbytis entellus*) were not correlated, dominant individuals monopolized higher quality food items. These results indicate that even if multiple food patches are contained within the group spread, variance in patch quality can lead to significant relationships between spatial position and feeding competition.

The importance of spatial position on feeding competition should decrease if the ratio of food items to group members is high, even if the food items are quickly depleted. This measure, termed competitor-to-resource ratio (CRR), has been found to be highly related to levels of aggression (Grant et al. 2000). When resources are abundant relative to the number of individuals in the group, aggression levels decline. In these cases, one would expect that the costs of aggression are larger than the benefits of acquiring an abundant resource (Grant et al. 2000). This is analogous to the case of a single very large patch of food contained in the group; if one patch can satiate all group members, there is little reason to compete for food.

PRIOR KNOWLEDGE OF FOOD

Several studies have found patterns largely consistent with the hypothesis that animals, from bees to monkeys, have prior knowledge of food location (for reviews see Gallistel 1990; Janson 2000). If food sources are known, foragers generally move between food patches in straight lines to reduce travel time and increase travel speed while en route (Janson 1998, 2000; Pochron 2001). Foragers should memorize the locations of resources

that compose a large percentage of their diet, that are particularly preferred, and that are predictable in space and time (Janson 2000). Large fruit trees, food caches, salt licks, and water holes are likely to be remembered resources.

In this model, I am assuming that all individuals in the group have similar prior knowledge of large food resources. This public information differs from private information (Valone 1989; Dall et al. 2005). Ultimately, prior knowledge of food resources is a continuum between total public information, where everyone in the group has the same information, and total private information, where the location of any resource is known only to one individual. Despite intensive research on social learning with respect to foraging, the strategies animals use to monitor resources and their use of public versus private knowledge is still poorly known in most organisms (Valone 1989; Templeton and Giraldeau 1995; Dall et al. 2005). A previous model of group travel mechanisms assumed high levels of within-group private information (Couzin et al. 2005). This assumption is most appropriate in animals that live in unstable groups or fission-fusion social systems, where individuals commonly range apart from other group members for significant periods of time. This situation may be commonly found in fish shoals, temporary aggregations of birds, dolphins, spider monkeys, and chimpanzees. It may also be more prevalent in species where the monitoring of conspecific feeding is difficult. When prior knowledge is incorporated into the feeding model for within-group spatial position, large important resources are most likely to be remembered by group-living individuals. In general, these resources are eaten by most or all group members, and thus the assumption of total public knowledge of these resources is likely to be appropriate.

Prior knowledge of food sources should lead to changes in group geometry. In cases where food resources are rare with quick depletion times, both dominant and subordinate individuals should choose the front position to consume the resource before others arrive. Such scarce small resources are unlikely to form a major fraction of a forager's diet, thus this situation probably occurs only

for highly preferred items (e.g., fruit trees). When resources have slow depletion rates, dominant individuals should be in the center of the group since they can displace subordinates when they arrive, and thus have less incentive to rush rapidly to the resource. The degree to which dominants should be central when food resources are known should be a function of the resource depletion time in a similar manner to unknown food resources. The main difference is that when food items are known, quickly depleted, and rare, dominants should locate themselves in the vanguard position instead of anywhere at the front edge of the group. If dominants are in the exact center of the group and can satiate upon arrival at the food patch, there is little reason for them to be closer to the front of the group. If a dominant does choose to position itself at the front of the group, it will presumably increase predation risk and potentially shorten patch foraging times. If subordinates leave food patches before dominants, the dominants may have to leave the previous food patch at an earlier than optimal time to remain at the front of the group before arriving at the next fruit patch. This tradeoff should be affected by travel speed, group spread, and the distance between food patches. During cases in which a resource would be significantly depleted by subordinates at the front of the group, dominants should forage closer to the front to reduce the amount of food depleted before their arrival. In addition to resource depletion time, the number of individuals that reach the patch before the dominant, and the gut capacity of the species may affect the degree of centrality in dominants. The primary difference in the spatial position continuum in the case of known and unknown food resources is that, by definition, producer-scrounger strategies cannot occur when food resources are known. When dominant animals have prior knowledge of food resources, their best strategy is to optimize the spatial position that will allow them to be the most central (to reduce predation risk) without reducing their food intake. A similar strategy is found when food resources are unknown, but in these cases, dominants should strive to increase both the scroungers share

and the number of scrounging opportunities (Di Bitetti and Janson 2001).

Dominant individuals should have the ability to choose any spatial position in the group. This is not the case for subordinates. When food resources are clumped, dominants are able to monopolize central spatial positions, while subordinates are forced to the periphery. In mobile groups, subordinate individuals should go to the vanguard position of the group. In this position, subordinates can arrive at food resources and consume as much as possible before the arrival of kleptoparasitic dominants. Because subordinate individuals are more likely to be food stressed, an increase in food intake may outweigh the higher predation risk at the vanguard spatial position. When a group approaches a known food source, subordinates will often race ahead of the group and rapidly consume food before being displaced by the front-central dominants. This pattern has frequently been observed in brown capuchin monkeys (Janson 1990b).

However, this subordinates-first pattern could also be a simple consequence of the process of food visitation and use. Dominants may not be able to position themselves in the vanguard consistently because they are still feeding at previous rich food patches, where the subordinates have been excluded, which allows the latter the freedom to run ahead to the next patch. From this argument emerges an easily-tested prediction. If two or more successive known food patches are slowly depleted and close enough together to allow simultaneous feeding by individuals within a single group, then subordinates and dominants should arrive at the first of the food patches at about the same time. However, subordinates should arrive much sooner than dominants at the subsequent food patches. Subordinates will again lose their positional advantage when the distance to the next known patch becomes far enough that dominants can rejoin the subordinates after leaving the previous patch. In contrast, if the subordinate-first pattern is a consequence of subordinate versus dominant spatial preferences, then subordinates should arrive first to all patches, regardless of foraging sequence.

SUMMARY MODEL

The three previously discussed factors (food size, distribution, and knowledge of food items) can be combined to form a comprehensive model of feeding competition in relation to within-group spatial position. When food items are quickly depleted, individuals at the front edge of the group will have the highest intake rates (Figure 2A,B). This pattern is expected to occur whether food items are scarce or abundant, although the pattern may be less pronounced when items are very common relative to the number of foragers (Grant et al. 2000). When items are uncommon and slowly depleted, dominant individuals in the center of the group should have the highest intake rates. Panels A and C in Figure 2 form a continuum; the smaller the food items are, the closer to the front of the group dominant individuals are expected to be located. As previously noted, medium-sized food items lead to pro-

ducer-scrounger roles in the social group. The last combination of factors, large abundant food items, should dramatically decrease the relationship between within-group spatial position and food intake rates. This situation should be rare in nature except as a short-lived seasonal effect. Otherwise the consumer's population density should increase and consequently reduce the quantity or quality of patches encountered.

The model changes when known food items are introduced (Figure 2B,D). When food items are small and abundant, individuals will gain the highest food intake rate at the front edge of the group. When these small items are rare, the vanguard position will be the most advantageous. By ranging in the vanguard position, individuals will be able to reach the known food item before others in the group. If there are several food items encountered by the group per unit time, anywhere on the front periphery of the group

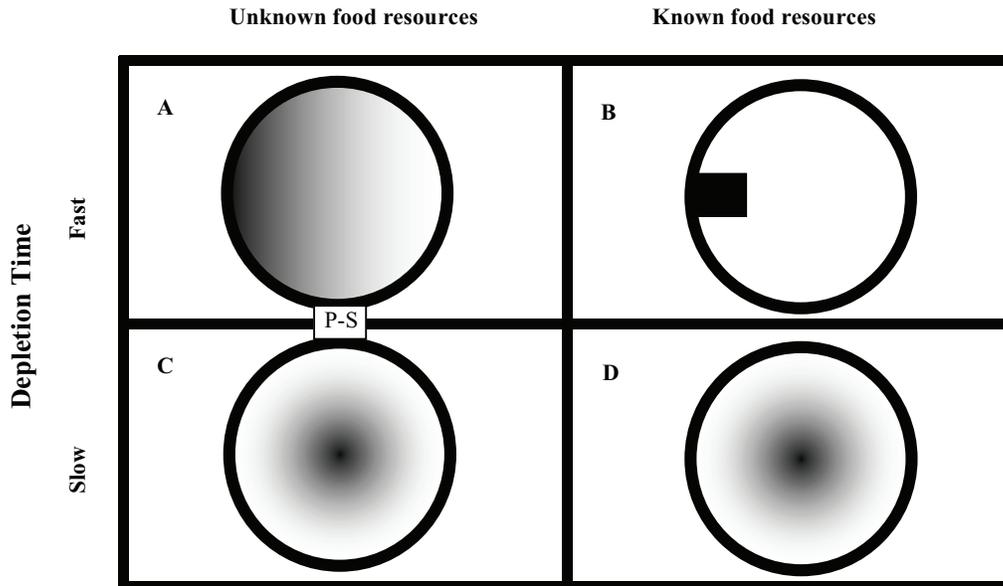


FIGURE 2. FEEDING COMPETITION MODEL FOR WITHIN-GROUP SPATIAL POSITION

These figures represent conditions when food is rare or uncommon in the group spread. Circles represent animal groups moving from right to left. Shading indicates areas of highest feeding success for dominant individuals. The area labeled "P-S" indicates where producer-scrounger relationships are predicted to occur. For cases when resources are previously known and slowly depleted (D), only dominant individuals will have the highest foraging success in the center of the group, and it is predicted that subordinates will have better foraging success at the vanguard position (the same pattern shown for dominants in panel B).

should lead to a higher foraging efficiency. The case where food items are both large and known is particularly important because organisms are more likely to remember these resources than smaller ones. When large food items are eaten, dominant individuals should range in the center of the group, as in the previous case, but subordinate individuals will gain the highest feeding rates when located in the vanguard position.

EFFECTS ON GROUP GEOMETRY

The spatial geometry of a group should be determined by the sum of individual costs and benefits of spatial position to all group members (Parrish and Edelman-Keshet 1999). Given the above relationships between spatial position and feeding competition, one can also make predictions about total group geometry and feeding competition. When foods are sparsely distributed and WGS (within-group scramble) is particularly strong, individuals at the front of the group have the highest food discovery and intake rates. In this situation, the predicted group geometry is a broad feeding swath, where the group spread is greater in width than length to maximize the number of individuals at the front edge of the group (Altmann 1974). This pattern also decreases the number of individuals forced to forage at the back of the group, which has been depleted of food, and should lead to an increase in the total amount of food consumed by the group. If resources are found in small, dense patches that are known to the group, the geometry of the group should be greater in length than width. This is expected because subordinates should rush to the front of the group to feed at food patches before dominants displace them. Groups should increase travel speed as they approach known resources, a result that has been found in baboons (Pochron 2001).

Another factor that could lead to elongated foraging groups was pointed out by Altmann (1974), who notes that if the time it takes an individual to finish consuming a food item is so long that the rest of the group has moved some distance, the foraging progressions can become elongated in the direction of travel. Reports of group spread are rare in the lit-

erature, and few studies have measured both width and length of the group, but some studies have shown that groups will spread out more when resources are scarce or widely distributed (Stoltz and Saayman 1970; Byrne et al. 1990; Janson 1990a; Hall and Fedigan 1997; Byrne 2000). By increasing inter-individual distances and group spread, individuals can reduce the amount of feeding competition and still remain in a group. Conversely, this should lead to increased predation risk, and a number of studies have shown that the spread of social groups decreases after predators have been encountered or in areas where predation risks are elevated (Altmann and Altmann 1970; Stanford 1985; Boinski 1988; van Schaik and Mitrasetia 1990; Viscido and Wetthey 2002).

In some bird and fish species, spacing within social groups is fairly even. This is not the case for many primate species. Researchers using spatial proximity to investigate social behavior have found a wide variety of within-group spacing patterns (Kinzey and Cunningham 1994; Stevenson et al. 1998). Stevenson et al. (1998) documented the internal spacing of four neotropical primates and showed that each species had different internal spacing, which the authors concluded was an adaptation for utilizing different sized food resources. When multiple resources are found within the group spread, individuals sometimes cluster on those resources, and the resultant group spacing is uneven, or subgrouping occurs (van Schaik and van Noordwijk 1986, 1988). This clustering of individuals within the group can be an effective strategy to optimize feeding intake and lower predation risk. By clumping together at food resources, individuals can increase their number of close neighbors, which may be the perceptible unit by which organisms measure their predation risk (Treves 1999; Hirsch 2002) without substantial increases in feeding competition (cf. Janson 1990b). If these subgroups spread out and avoid each other, the total group spread will be larger, which can increase the number of food patches within the group, thus increasing food availability. Kinzey and Cunningham (1994) suggest that primate spacing patterns form a continuum ranging from spe-

cies with tight, evenly clustered groups to fluid fission-fusion social systems. To fully comprehend the evolution and maintenance of this wide diversity of grouping patterns, it is necessary to understand the costs and benefits of within-group spatial position to individuals.

TRAVEL INITIATION, GROUP LEADERSHIP, AND SPATIAL POSITION

Other factors that can potentially influence an individual's within-group spatial position are group leadership and the initiation of travel. When an animal group decides which resource to visit next, the process may be despotic, where one individual determines where the group moves, or involve some degree of consensus decision making by the group (Conradt and Roper 2005). Collective decision making should result in higher payoffs to most individuals within the group (List 2004; Simons 2004; Conradt and Roper 2005). Although group leadership has been linked to dominance status in a wide diversity of primates and carnivores, this pattern is not universal (Boinski 2000; Byrne 2000; Holekamp et al. 2000).

Travel initiation and group leadership are two potentially different processes. When a group is resting or stationary foraging, members may differ in their desire to move to a new area or change activity pattern. This behavioral asynchrony can be caused by differences in hunger level or energetic reserves (Conradt and Roper 2000; Ruckstuhl and Neuhaus 2002). Individuals with a greater need for food should be more likely to move away from the group and start foraging when others are resting (Holekamp et al. 2000). Additionally, subordinate individuals excluded from food patches should move to the next food site before other group members. In order to coordinate travel initiation, a wide variety of taxa have been reported to increase grooming, vocalizations, activity, and movement toward the edge of the group immediately prior to travel (Boinski 2000; Byrne 2000; Holekamp et al. 2000).

Once a group is moving, the mechanisms by which the group decides where to travel are not well understood. Couzin et al. (2005) created a model showing how attraction to

conspecifics can lead to effective group coordination even when group members differ in their preferred direction of travel. One result is that individuals can often make incorrect travel decisions (Couzin et al. 2005). In this case, a front-edge individual may visit a food resource that the rest of the group does not. This behavior has commonly been witnessed in groups of ring-tailed coatis (*Nasua nasua*) and brown capuchins (*Cebus apella*) (personal observation). Individuals that jump ahead may increase their food intake and risk of predation (as noted above), and could also suffer an additional cost of becoming separated from their group. In cases where predation on solitary individuals is high and lost groups are difficult to relocate, major constraints on jumping ahead may occur.

Group leadership from the vanguard position has been assumed in theoretical models, and several empirical studies have found that group leaders are typically located at the front edge of the group (Boinski 2000; Holekamp et al. 2000; Reeb 2000; Couzin et al. 2005). By heading off in a particular direction, an animal may be signaling to other group members its desire for them to proceed in the same direction, and conspecifics may use this information to determine which direction to travel (Boinski 2000; Holekamp et al. 2000; Couzin et al. 2005). This pattern is not universal, and some species of primates exhibit central leadership in which a central dominant individual determines the direction of travel (Boinski 2000; Byrne 2000; Janson 2000). Leadership from central spatial positions is possible because individuals at the front edge are able to visually monitor the movements of conspecifics and often use contact vocalization to maintain group cohesion (Byrne 2000). These mechanisms of central leadership could not plausibly be used in many species of fish, and there may be phylogenetic and cognitive constraints on this method of group leadership. In some species, the mechanism of group leadership is unknown and unclear to human observers (coatis, *Nasua spp.* Kaufman 1962).

It is reasonable that group leadership can play a role in shaping an individual's spatial position. In the case of vanguard leadership,

if information about resource quality and location is roughly equivalent among group members, group leadership should be influenced by hunger level and foraging efficiency, as previously outlined in the feeding competition model. This pattern may not be universal, and the influence of group leadership on an individual's within-group spatial position preferences is a process that is too poorly understood to allow one to make predictions at present.

GROUP SIZE

Although most of the expected effects of food distribution on spatial structure should occur regardless of group size, some should be affected by the number of individuals in the group. If WGS occurs, there should be a decrease in individual food intake rates as group size increases, which will cause members of large groups to travel farther and have longer day ranges (van Schaik 1983; Janson and Goldsmith 1995). The cost of being at the back of the group should increase in larger groups because more individuals will be foraging and depleting food resources at the front of the group. The group spread should increase with group size, especially in species with high amounts of WGS. If WGC (within-group contest) is strong, higher ranking individuals should have significantly higher foraging intake rates in large groups. This occurs because more individuals are excluded from contestable food sources than in smaller groups. It may lead groups to become more fragmented and separate into subgroups. If the increased spread due to larger numbers allows the group to encompass more feeding sites, larger groups may have a reduction in WGC. In these cases, subgrouping would be an optimal strategy to reduce both predation risk and WGC at the same time. An increase in group size has important impacts on producer-scrounger models. As size increases, the frequency of scroungers in the group should increase as well (Giraldeau and Caraco 2000), which should lead to an increase in the overall spread, as subordinate individuals may range farther away from the group to avoid dominant scroungers (Flynn and Giraldeau 2001). More scroungers can lead to

increased competition, and thus a variety of optimal spatial positions may evolve for differently ranked members in a large group feeding on medium-sized resources. It should be noted that determining spatial positions in extremely small groups can be difficult. If there are very few group members, every time an individual moves, the total group geometry may change. In this case, it may be difficult for an individual to maintain one preferred position. One might expect that spatial preference, and thus the costs and benefits of spatial position within the group, will be stronger in larger groups.

SOCIAL EFFECTS

Virtually all studies of spatial position preferences have discussed either the predation or feeding competition hypothesis for spatial position (Krause 1994). Hemelrijk (1998, 2000) raises the possibility that patterns of group geometry can arise simply from social processes. Using individual-based computer models, Hemelrijk (1998, 2000) found that dominants are more central, and subordinate individuals peripheralized as a result of aggressive interactions. Indeed, these models are similar to observed patterns in fish (Clifton 1991; Krause 1994), spiders (Rayor and Uetz 1990), and primates (Robinson 1981; van Schaik and van Noordwijk 1986; Janson 1990a,b). If central-peripheral spatial structure can arise in the absence of predation and feeding competition effects, these computer models offer an important insight into the origin and formation of within-group spatial preferences. It must be noted that the dominance relations modeled by Hemelrijk (1998, 2000) can be influenced by feeding competition. If WGC is strong, dominance relationships should be more pronounced than in species with high WGS (Vehrencamp 1983; Janson and van Schaik 1988; Sterck et al. 1997). Hemelrijk (1998, 2000) predicts that spatial differences in rank will be greater when dominance relationships are more pronounced. If within-group feeding competition did not exist, there would be little reason for individuals to compete, and thus dominance relationships would not arise. However, individuals can compete for resources

other than food. Although the avoidance of dominants may be an important proximate factor in determining spatial position, the ultimate cause is presumably competition for food or some other resource.

The model discussed in this paper has dealt primarily with individuals that differ only in rank. In most species, group-living individuals also differ in size, sex, and age. These demographic and social factors can play a large role in shaping the costs and benefits of individual spatial position. A good example is that of infants or juveniles within a group. Because of their small size, most infant animals have higher predation risk and lower metabolic needs than adults. This greatly shifts the costs and benefits of within-group spatial position, and infants and smaller individuals are preferentially found in the center of groups in a large number of species (Collins 1984; Pereira 1988; van Noordwijk et al. 1993; Beise 1996). There are numerous other reasons infants might gain benefits from being spatially central, including protection from infanticidal males, more learning opportunities, retaining spatial proximity to the mother, and increased numbers of playmates. These advantages to infants can drive their mothers to alter their spatial positions as well (Collins 1984; Cowlshaw 1999; Boinski 2000).

CONCLUSION

Within-group spatial position is an important factor in determining the type and levels of feeding competition. Despite this fact, few studies have investigated the costs and benefits of within-group spatial position, and those that have generally have not taken food properties into account. Only by understanding the complex relationship between food properties and spatial position can one understand the proximate factors driving individuals to certain within-group spatial positions. This knowledge is crucial to gain deeper insight of how feeding competition occurs and how this, in turn, affects social patterns.

The feeding competition model for within-group spatial position presented here is qualitative but not quantitative. For simplicity, this model expresses food size and distribution in relation to the spread of the group, thus a food item can vary both in size and distribution depending on properties of the animal group. I advocate two tests of this model. First, field studies that measure relevant food properties need to be undertaken. When researchers are studying social groups, it is advisable to take data on social foraging variables such as food depletion time. Not only is it important to calculate depletion time, but also how long it takes a conspecific to join or usurp a feeding individual. Very few naturalistic field studies report the number of food items contained in the group spread at a given time. This is crucial data to understanding feeding competition, yet is mysteriously absent from the literature. Although some researchers have focused on the presence and properties of known food items, not enough work has been done in this area. It is important to differentiate between known and unknown food items when making conclusions about social foraging parameters (Pochron 2001). Second, although qualitative models can be useful, a quantitative model must be developed to gain a more accurate knowledge of how these factors affect an organism's within-group spatial position. I believe the best method to develop a quantitative model is by using individual-based dynamic modeling to mimic social groups as well as varying food properties and food knowledge of actors within the model.

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