Within-group spatial position in ring-tailed coatis (*Nasua nasua*): balancing predation, feeding success, and social competition

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Abstract of the Dissertation

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Charles Janson

Several factors shape the within-group spatial position preferences of animals, most notably; predation, dominance rank, food abundance and depletion time, and prior knowledge of food location. Individuals are predicted to choose spatial positions which maximize their personal fitness, and various factors can affect the costs and benefits of these spatial positions. The total summed spatial position preferences of all group members determines the group geometry which has a major effect on the type and degree of feeding competition, and thus impacts social structure. I first present a qualitative model predicting where individuals should locate themselves in groups. To test this model, I studied groups of wild ring-tailed coatis in Iguazu, Argentina.

Survivorship rates for coatis in Iguazu were high, and individuals often lived in groups with many close relatives. These coatis had an odd dominance structure in which small juvenile coatis would regularly attack older individuals and win agonistic interactions during feeding. This system was likely driven by a combination of fast life histories which led juveniles to value food more than older individuals, close genetic relatedness between group members, and adult female support of juveniles. This agonistic behavior of juveniles was likely a form of extreme juvenile tolerance rather than juvenile dominance in the traditional sense.

Coatis almost always discovered food by olfaction. Individuals at the front of the group found far more experimental food plots than individuals in other spatial positions, but were almost always joined by other group members. Juveniles were found at the front edge of the group more than all other age/sex classes. This led to higher fruit foraging success, especially on pindo fruit trees. At the same time, these juveniles were essentially ignoring the increased predation threat from being at front of the group. Subadults were located in areas to best avoid feeding competition and receiving aggression from adult females. The spatial position preferences shown by coatis were different from that predicted, but still conformed to the essential principles discussed in the model.

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Chapter 1

Costs and Benefits of Within-Group Spatial Position: A Feeding Compeittion Model

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 who 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 affects 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 Edelstein-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 and Janson in press) 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 resource 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 simultaneously. 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, as well as 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. This group geometry is subsequently an important factor in determining the level of feeding competition. Thus 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. To understand this interaction fully, 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 here 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 animals use 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 Wethey 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 on 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 inter-individual 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; van Schaik and van Noordwijk 1986, 1988; Janson 1985, 1990b; 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 long. 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. Quickly depleted food 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 who 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 inter-individual spacing of group members. If the average inter-individual distance in a group increases, the same food item might change from medium to quickly depleted because of the extra time it takes a conspecific to reach another individual to compete for that food item. 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 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 which 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 as well. Two avian studies (Petit and Bildenstein 1987; Keys and Dugatkin 1990) found higher foraging efficiencies but no overall increase in food intake in peripheral individuals. 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. Medium sized 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 kleptoparastism (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 who discover food sites are deemed "producers," and individuals who join producers 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 which 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 which 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 further 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 (Janson1990a,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 towards the center of the group (Figure 2.).

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 dominant individuals to finish eating before entering the food patch to consume food (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; Rassmussen 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 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; van Schaik and van Noordwijk 1986, 1988; Janson 1986, 1990b; van Noordwijk and van Schaik 1999; Barton 1993), 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 of the group would allow dominant individuals to start feeding before other group members, if a resource is sufficiently large, the dominant individual will eat the same amount of a given food item or patch regardless of whether it ranges in the front or 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. The second is that 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 further 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 which is separated by 10 m or more from another food source (Janson 1996).

When multiple defendable food patches are contained within the group spread, the importance of spatial position in the group will decrease. In long-tailed macaques (*Macaca facicularis*) 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) found that although social rank and foraging rate 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, are particularly preferred, and 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 likely 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 (Figure 2a&b). 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 in 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 subordinate individuals in the front of the group, dominant individuals 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, dominant individuals 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 use 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. The cells in figure 2a and 2c form a continuum, wherein 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 producer-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 should be the most advantageous. By ranging in the vanguard position, individuals will be able to reach the known food item before any 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 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 used, 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 Edelstein-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 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 wider 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 which 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 literature, 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 Wethey 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 (Stevenson et al. 1998; Kinzey and Cunningham 1994). 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 species 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

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 (Conradt and Roper 2005; List 2004; Simons 2004). 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 the group is 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 travel to a food resource that the rest of the group does not visit. This behavior has commonly been witnessed in groups of ring-tailed coatis (*Nasua nasua*) and brown capuchins (*Cebus apella*)(personal observation). Individuals who 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; Reebs 2000; Couzin et al. 2005). By heading off in a particular direction, an animal may be signaling to other group members its desire for the rest of the group 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 further and have longer day ranges (van Schaik 1983; Janson and Goldsmith 1995). The cost of being in 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 as group size increases, especially in species with high amounts of WGS. If WGC 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. This 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 predation risk and WGC at the same time. An increase in group size also 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 also lead to an increase in the overall spread, as subordinate individuals may range farther away from the group to avoid dominant scroungers. An increase in 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; Janson 1990a,b; van Schaik and van Noordwijk 1986). 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). Hemelirijk (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 may 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 here 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, increased 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; Cowlishaw 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 these studies have generally 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 which 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). Secondly, although qualitative models can be useful, a quantitative model needs to 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, and vary food properties and food knowledge of actors within the model.

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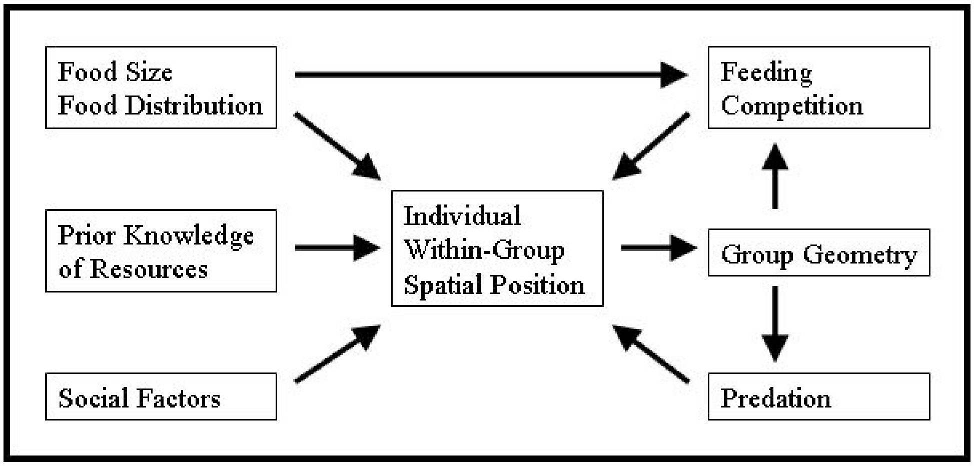
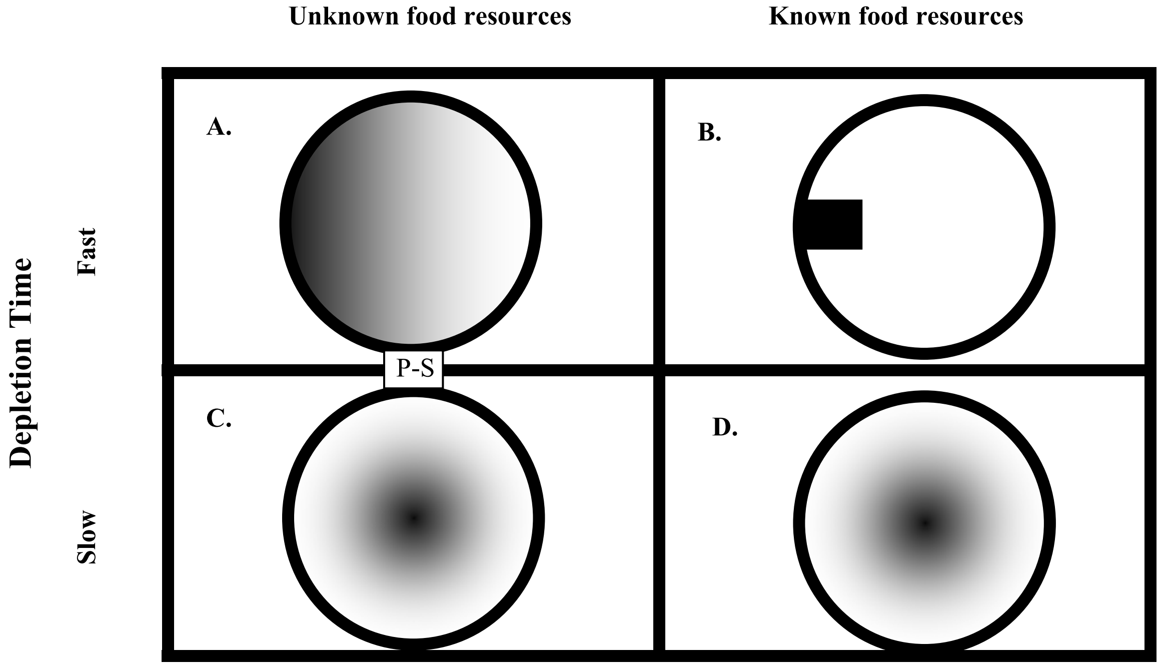


Figure 1.1. Importance of within-group spatial position.



Note: 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 in the front-most or vanguard position (the same pattern shown for dominants in square B).

Figure 2.2. Feeding Competition Model for Within-Group Spatial Position.

Circles represent hypothetical animal groups, moving from right to left. Shading indicates areas of highest feeding success for dominant individuals. All figures represent conditions when food is rare or uncommon in the group spread. When food is abundant in the group spread and quickly depleted, dominants will find the highest feeding success in the front edge of the group (the same as condition A).

Chapter 2

Measuring within-group spatial position: methods for field biologists

Abstract

Within-group spatial position is an important variable which can affect an individual's risk of predation, foraging success, and social relationships. Studies relating behavior to within-group spatial position often use differing methods to measure spatial position, which has lead to difficulties comparing studies. In a recent study (Christman and Lewis 2005), the statistical powers of four methods used to record spatial position were tested, yet most of these methods are not practical for studying wild animals. Four methods which have been previously used by field biologists are discussed here; 1) nearest neighbor (NN), 2) neighbor density (ND), 3) minimum convex polygon (MCP), and 4) Janson's elliptical clock (JEC), as well as one new measure, the angle of vulnerability method (AoV). When field biologists measure within-group spatial position it is important to address several factors before deciding which methods are the most useful and appropriate in a given study. When measuring predation risk, the preferred method is dependent on the detection or hunting distance of the predator. When this distance is short, the AoV or JEC methods are most useful, and in cases with long distances the MCP is preferable. When studying feeding competition, a combination of

the ND and JEC method is ideal. When studying social interactions, the ND method is often the best available measure.

Introduction

Within-group spatial position has important effects on predation rates, the proportion of time devoted to anti-predator behavior, food intake rate, and social interactions (Reviews: Krause 1994, Krause and Ruxton 2000, Caro 2005, Hirsch submitted). One notable problem in the literature is that different authors use different criteria to determine if an individual is classified as central or peripheral. A recent paper tested the statistical power of four methods for recording spatial position (1. geometric centre, 2. MCP, 3. mean resultant vector, and 4. Nearest neighbor of all individuals)(Christman and Lewis 2005). Three of the four methods require that the observer know the location of all individuals in the groups and the authors concluded that the Minimum Convex Polygon (MCP) method is easier for most field biologists to use because the observer only needs to know the identity of the individuals who make up the MCP.

Although this comparison provided a step in the right direction, in most cases field biologists are not able to use the methods tested in Christman and Lewis (2005). The ability to accurately record the location of all individuals in a group is either difficult or impossible in most animal study systems. To use such methods, one either needs to study animals in captivity (Romey 1995, Romey 1997) or use overhead video cameras on a wild population (Viscido and Wethey 2002). Although Viscido and Whethey were able to collect accurate data on groups of fiddler crabs using video recording, many species spread out to such a large degree that video camera methods are not feasible. Because using video cameras and total group scan samples is often not feasible, previous authors have typically used individual focal samples to address questions of animal behavior in relation to within group spatial position (Janson 1990ab). This paper will discuss the advantages and disadvantages of four previously used methods of recording within group spatial position, and suggest a new method for estimating predation risk, which may be useful in some study systems.

Why spatial position?

Krause (1994) discussed several factors, which lead to differential fitness with respect to within group spatial position. In this manuscript I will discuss the three factors which are most important to researchers studying animal behavior 1) predation, 2) feeding competition, and 3) social factors.

Predation

Hamilton's (1971) selfish herd hypothesis is the basic foundation in which predation with respect to spatial position has been studied. Hamilton (1971) stated that because edge individuals have higher domains of danger (defined as the area of an individuals Voronoi polygon), their risk of predation is higher. If a predator appears anywhere at random within or near a group, the likelihood that the predator will attack a given individual is proportionate to their domain of danger. Because edge living individuals often have no neighbors on one side, their domains of danger are by definition larger then central individuals. This pattern also persists if using bounded Voronoi polygons or limited domains of danger (Viscido et al. 2001, 2002, Viscido and Wethey 2002, James et al. 2003). Several studies have indicated that the risk of predation is highest on the edge of animal groups. Studies have found higher death rates, attack rates, and vigilance levels on peripheral individuals (Review: Caro 2005). In addition, predation risk has been shown to be higher on the front edge of moving groups (Busse 1980, Janson 1990b, Bumann *et al.* 1997, Carbone *et al.* 2003, Di Blanco and Hirsch in press). This latter result is commonly predicted to occur in cases where individuals at the front of the group have higher encounter rates of sit and wait predators. If predators move, or stalk their prey, an additional increase in predation threat is predicted to occur at the side and back edges of animal groups (Bumann et al. 1997, Di Blanco and Hirsch in press).

Although Hamilton's hypothesis is an important theoretical foundation, the circumstances described in his model are not always applicable. In Hamilton's model, the predator always attacks the closest prey and can randomly appear at any point in the group. In the case of two dimensional prey groups with terrestrial predators, it is assumed that the predator will attack from outside the group, thus peripheral individuals will undergo a higher threat (Vine 1971). Unless there are substantial differences in prey type (such as sick/weak individuals, non-vigilant animals, or preferred age/sex classes of prey), predators are predicted to attack the closest individual and not skip over peripheral prey on route to central ones (but see Parrish 1989 and discussion in Stankowich 2003). If it is assumed that predators attack groups in this manner, any useful definition of prey centrality should take this predator behavior into account. A notable example in which predators can behave more similarly to Hamilton's predation scenario is when aerial predators attack a group (see: Brunton 1997 and Stankowich 2003).

Feeding competition

Most previous studies relating food intake to within group spatial position have found that individuals in the edge and front edge positions have higher food intake rates (review: Krause 1994, Krause and Ruxton 2000). These results make sense with respect to small evenly distributed food items where food can be depleted by individuals in the front of the group before the individuals in the back and center have fed (most previous studies have been conducted in birds). The density of individuals is often highest in the center of the group, thus central animals will often have higher levels of scramble and interference competition. Romey (1985) manipulated hunger levels of whirligig beetles and found that hungrier individuals positioned themselves at the group edge more than other group members. Additionally, limited food items may be depleted from front to the back of the group (Krause 1994). For species which feed on depletable resources, measuring an individual's spatial position in relation to the direction of travel may be a more important indicator of feeding competition than centrality. Several studies of frugivorous primates have found the reverse effect of centrality on food intake rates (Robinson 1981, van Schaik & van Noordwijk 1986, 1988, Janson 1985, 1990b, Barton 1993). In these primates, dominant individuals will often be located in productive fruit trees and force out subordinate individuals. The central dominant individuals then have higher food intake rates than the peripheral subordinates. Given that food patch size and distribution can lead to differing effects of spatial position with respect to food intake, it is important to understand the feeding ecology of a species when choosing any method to record within group spatial position.

Social factors

Many of the studies relating spatial position to social factors such as dominance have been undertaken in primates (Sigg 1980, Collins 1984, Janson 1990ab, Ron et al. 1996). Janson (1990ab) has suggested that individuals of varying rank and sex/age classes choose spatial positions within the group to maximize food intake and possibly to reduce the risk of received aggression. Hemelrijk (1998, 2000) used computer simulations to demonstrate that simple social dominance interactions could result in the spatial segregation of individuals of different rank. Thus, the ability for an animal to choose its spatial position in a group can be affected by its dominance status. Given the importance of spatial position on feeding rates and predation risk, the social factors which can lead to differences in individuals spatial positions are crucial to understanding the spatial structure of animal groups. These social factors are not solely important in primate studies. Studies have found spatial position differences with respect to age, size, and dominance status in a large variety of invertebrate and vertebrate taxa (Janson 1990ab, Rayor & Uetz 1993, van Noordwijk et al. 1993, Ranta et al. 1994, Ron et al. 1996, Krause et al. 1996, 1998). These broad spatial patterns with respect to age/sex class and dominance have also been investigated in finer-scale detail. Several studies have shown how individuals prefer to be located near individuals of their own matriline or others of similar age/sex and dominance classes (O'Brien and Robinson 1993).

Measures of spatial position

Four commonly used measures of spatial position will be discussed: 1) nearest neighbor (NN), 2) neighbor density (ND), 3) minimum convex polygon (MCP), and 4) Janson's elliptical clock method (JEC). These four methods are not all encompassing, and other methods not discussed here have been used in previous studies (see: Stankowich 2003). Because the concentric circle and layers of protection methods (Balda and Bateman 1972, Rayor and Uetz 1990) are sufficiently similar to the JEC method, only the latter, more detailed method will be discussed. Additionally a new method of recording spatial position, the angle of vulnerability (AoV) will be discussed and defined.

Nearest neighbor

Authors have previously used the distance to the nearest neighbor to calculate centrality, and this is the single easiest method to record for many field biologists (Underwood 1982). If animals are distributed randomly, central individuals should have, on average, shorter NN distances than peripheral individuals (Hirsch unpublished data). The major problem with this method is that it may be a poor measure of within group spatial position. If an edge individual happens to have a close neighbor, they may appear to be central despite being on the edge. For example, if the group geometry is ringed shaped (which, to my knowledge, has never been observed in nature) or exhibits subgrouping, the central individuals may have similar or higher nearest neighbor distances than edge individuals (Figure 1). As shown by Christman and Lewis (2005), this method also may not be useful in species which space themselves evenly (Figure 1B). In this case, the average NN distance should be similar regardless of an individual's spatial position.

Neighbor density

A similar method of measuring spatial position to the NN method is neighbor density (ND). For this method the observer records the number of individuals within a circle of a given radius around the focal animal. Like the NN method, researchers can also record the identity of these neighbors to determine spatial relationships between individuals. The ND method should have a smaller variance than the NN method, because it makes use of information from several neighbors, not just one. In cases where animals are evenly spaced, the number of individuals in an animal's radius should be similar except when the individual is on the edge of the group. Because of this, the ND method may identify individuals at the edge of the group, but would fail to further distinguish between central and "middle ring" individuals in species with even spacing (Christman and Lewis 2005).

Minimum convex polygon

The MCP method defines any individual found on the minimum convex polygon of the group spread as peripheral. The advantage of this method is that defining an individual as central or peripheral is generally unambiguous (Krause and Tegeder 1994). As long as an observer is able to accurately see the relevant fraction of the group edge in relation to the focal animal, it is not difficult to determine where the MCP is. Despite the advantages of using this method, some problems may result from its use. The proportion of peripheral individuals using the MCP is inversely related to group size for a given shape. This is a biologically reasonable feature of this method, as the edge-to-area ratio in fact must decrease with increasing dimensions of an object. Additional changes in the proportion of peripheral animals can emerge because of changes in group shape. This can be biologically important. For instance, in a study of vigilance levels in geese, Lazarus (1978) found that average group levels of vigilance changed not solely as a function of group size, but as a function of the percentage of peripheral animals in the group. One disadvantage of the MCP method (as well as the NN and ND methods) is that it does not take group direction into account. Although this may be reasonable when measuring non-mobile groups such as orb-weaving spiders (Rayor and Uetz 1990, 1993), strong front-back effects on individuals in moving groups have been found with respect to foraging and vigilance levels (Janson 1990, Bumann et al. 1997, Hall and Fedigan 1997, Di Blanco and Hirsch in press).

Janson's elliptical clock

The JEC measure of spatial position has only been used in a handful of studies of social mammals (Robinson 1981, Janson 1990ab, Hall and Fedigan 1997, Di Blanco and Hirsch in press). This measure was created to define within-group spatial position based on the overall group geometry, including group directionality. Using this method, the observer places an imaginary ellipse over the group spread. The observer then divides the radius into three equal portions which create three ellipses; center, middle, and edge (Figure 2). The observer records centrality based on these ellipses, and further subdivides the three ellipses into twelve portions, with twelve representing the front of the group and six the back of the group. The 36 resultant spatial positions can then be pooled into categories, which may be biologically meaningful (example: 1. front edge, 2. front middle, 3. center, 4. back middle, 5. back edge). One advantage of this method is that it takes into account group directionality. The difficulty with this method is that it requires that the observer has some idea of where all or most group members are in the group. The studies which have used the JEC method all used social mammals with contact calls and make considerable noise when foraging. This method may not be feasible for when the determination the group shape is difficult, or when groups are so small that the observer has difficulty determining spatial geometry.

Behavioral factors

Of the four previously listed methods for determining within group spatial position, some are predicted to be more applicable depending on the underlying questions being studied. These four methods of recording spatial position have advantages and disadvantages when assessing the effects of predation, feeding competition, and social relationships. I address each of these in turn.

Predation

The most common reason for recording within-group spatial position has been to measure the association with predation risk, yet there have been many inconsistencies in the methods used (Stankowich 2003). NN and ND provide some information useful to determine predation threat. If a predator attacks the closest individual, individuals with closer neighbors and higher neighbor densities are likely have lower predation threats. Although this measure of predation threat may be appropriate in cases where aerial predators are attacking a group, it may not be for terrestrial predators. An individual in the center of a group which has a low neighbor density or a nearest neighbor further away than individuals on the edge of the group would still be under lower predation threat from a terrestrial predator than are edge individuals because a predator would likely encounter and attack the edge individuals before reaching the center of the group (Vine 1971, Stankowich 2003). In practice the previous scenario that a central individual has a lower ND value than edge individuals is unlikely to occur in nature (Figure 1C). Generally, individuals in the center of a group have closer nearest neighbors and higher neighbor density (Hirsch unpublished data). As noted by Christman and Lewis (2005) if a species spaces evenly, measuring NN is unlikely to be an accurate or useful measure of spatial position (Figure 2B). Another potential problem with using the NN and ND methods is that both make assumptions as to the patterns of individual spacing within the group. The act of group movement often creates higher densities at the front edge of the group, which is also where food availability is often highest (Bumann et al. 1997). In one study, Di Blanco and Hirsch (in press) found that levels of anti-predatory vigilance were higher at the front edge of the groups despite having higher neighbor density. The heterogeneous spacing of many animal groups makes both NN and ND poor measures of within-group spatial position in relation to predation threat.

The MCP method is most often used in studies of predation threat (Fitzgibbon 1990, Krause and Tegeder 1994, Brunton 1997). As a general rule, if a terrestrial predator attacks the first available individual, an individual on the MCP of the group will be attacked. Depending on the starting point of the predator, in some cases an individual inside the MCP would be at greater risk of predation. For example, in Figure 3, if predator #1 attacks the nearest prey, individual D is under the highest predation threat despite being on the inside of the MCP. An ideal measure of spatial position should take this situation and the hunting behavior of the predator into account (Lima 2002, Stankowich 2003). The ability of a terrestrial predator to approach an individual within the MCP will likely be more probable in cryptic sit-and-wait forest living predators (such as several felid species), where the distance at which the prey can detect the predator is probably low (Janson unpublished work).

A major problem with the MCP method is that it provides no information about group directionality. One possible solution to this problem is to record group direction in conjunction with the MCP. Additionally, the MCP treats all individuals on the edge of the

MCP as the same. In reality some edge individuals could be much more vulnerable than others (such as individuals A versus B in figure 3). In some studies of fish predation, certain individuals have been defined as "stragglers," or individuals who are farther than a criterion distance from the group (Morgan and Godin 1985, Parrish et al. 1989). These stragglers have much higher predation risk, yet the MCP method would treat them equally as other non-straggler members on the MCP.

The JEC method has proven useful in studies of the influence of within-group spatial position on anti-predator scanning (Janson 1990b, Hirsch 2002, Di Blanco and Hirsch in press). The chief advantage of this method is that it is currently the only method which explicitly measures an animal's location with respect to the groups' direction of travel. Additionally, individuals on the outer edge of the group, yet inside the MCP can be classified as peripheral using the JEC method. In some cases this may be advantageous. For example, individual D in figure 1 would be described as central using the MCP, yet individual D is clearly near the edge of the group, and would presumably have higher risk of predation than individuals in the center such as individual C. The drawback to using this method in studies of predation threat is that it does not take into account neighbor density. In this case, it may be advantageous to record both the JEC and ND simultaneously (e.g. Di Blanco and Hirsch in press)

One possible solution to various problems with these methods is a new method which I term the Angle of Vulnerability (AoV). This method can be used on individual focal animals, who are assigned a level of risk depending on the angle at which they are vulnerable to predators. An individual's AoV is the maximum angle in a radius around a focal animal in which a predator has direct access to the prey (in this respect, the method resembles that of Krause and Tegeder 1994). For example individuals in figure 3 would have AoV values of A= 325°, B= 215 °, C= 45°, and D= 170° respectively. This angle is bounded by conspecifics, thus although an individual may have several portions of its radius that are vulnerable to a predator (for example; individual C could theoretically be approached by a predator from many sides), only the maximum angle is used to record an animal's AoV. For a field biologist to calculate the exact AoV value in the field may be difficult or impossible, but it is typically easy to calculate an approximate measure and individuals could be assigned AoV values based on a coarse scale which would reflect major differences in predation risk (for example high risk= 240° -360°, medium risk= 120° -240°, low risk= 0° -120°). Using a graded scale would be an advantage over course central-peripheral classifications (Stankowich 2003), yet is not too detailed as to prevent easy utilization in field. A graded system would be particularly convenient for measuring central individuals where several small (<120°) AoV angles may be found around the focal animal, and the ability of the observer to determine the largest could be difficult.

This method would successfully differentiate predation risk between stragglers and non-stragglers on the MCP (Figure 3, A and B). Additionally, the MCP treats all individuals inside the MCP the same. Individual D would be classified as central according to the MCP method, yet the predation risk of individual D would conceivably be similar to individual B (a MCP individual) but much greater than individual C. The AoV could result in a similar predation risk assessment between B and D (despite one not lying on the MCP), but distinguish between the different predation risks of C and D. The AoV method may be the most analogous to actual predation situations because the measure is derived from the viewpoint of the predator (note that if predator behavior does not conform to the assumptions of the AoV method, this method should be modified or not chosen). The AoV method is predicted to be most biologically realistic in cases where sit-and-wait predators are able to approach a prey group from relatively close distances. In cases where predators attack groups from very long distances relative to the group spread, the closest prey individual will almost always fall on the MCP. The importance of detection and attack distance on predation threat is an understudied phenomenon and further research is needed to accurately estimate differential predation threat in social animals. In the interim, researchers should either *a priori* categorize the hunting style of potential predators, or should record the predator attack distance before deciding which method to use. This may be complicated if multiple predators with different hunting styles are present. Regardless of hunting style, the AoV is the least susceptible measure to uneven distributions of individuals and odd group shape. The only crucial information not recorded by the AoV is group direction. Combining the AoV with the JEC method for assigning group directionality or an even cruder classification (for example: front, middle, and back of the group) should be a more accurate predictor of an individuals risk of predation than many previous measures used by field biologists.

Feeding competition

In most previous work it has been assumed that a greater number of nearby individuals leads to an increase in scramble feeding competition. For small quickly depleted resources in which animals compete in scramble competition, measuring NN or ND may be a good estimate of competitive interference. Unfortunately, these measures may not be ideal for moving groups. Numerous papers have found a positive relationship between “frontedness” in the group and food intake rates (Review in Krause 1994). By using NN or ND methods, one may be using a good measure to describe the degree of potential scramble competition, but without any concurrent understanding of food depletion effects from the front to the back of the group. In other circumstances, neighbor density may not be negatively related to food intake. In some primate species, which engage in contest competition, dominant individuals in the center of the group are able to monopolize contestable resources, thus leading to positive relationships between food intake and centrality/neighbor density (e.g., Janson 1990b).

When measuring spatial position in relation to feeding competition, it is probably not appropriate to use the MCP method. As with the NN and ND methods, the MCP method gathers no information about group directionality and individuals “frontedness” in the group. Even though peripherality, as defined by the MCP method, is predicted to be positively correlated to high NN and low ND values, the NN and ND methods are likely to be much more reliable measures of scramble competition than the MCP method. In the case where groups feed on patchy contestable resources, the MCP could potentially be useful in determining whether an individual is in the center of the group at a food resource, or on the periphery and being excluded. It is likely easier for a researcher to simply note whether a focal animal is inside or outside of a food patch rather than using an unreliable proxy such as the MCP (Vogel and Janson in review). This latter method is applicable in cases where one food patch is found within the group spread but may be more difficult to use in cases where groups contain multiple resources of dissimilar quality and dominant individuals use higher quality resources in the group center (Koenig et al. 1998).

Of these four methods, only the JEC method measures directionality, thus is likely the best method for use in studies of feeding competition. Despite this advantage, the JEC method does not result in a measure of conspecific density, and thus is not ideal to measure scramble competition. Depending on the distribution of food resources, the density of conspecifics may be a more important measure of feeding competition than within-group spatial position. For example, if a group of animals feeds on small dispersed resources which are abundant enough to not be depleted from the front to the back of the group, the feeding success rate of individuals may be limited by localized feeding interference. In this case, the NN or ND method would be a preferable measure of feeding competition. When possible, it is probably best for researchers to use the JEC method simultaneously with either the NN or ND method (e.g. Janson 1990b).

When groups are small, determining an individual's spatial position is not only difficult or impossible in practice, but any spatial position effects should decline precipitously. Because of this, both the JEC and MCP methods may be essentially useless if used with very small groups. In these cases, it may be possible to use the NN or ND methods in combination with a travel progression, or numerical ordering of individuals from front to back of the group. This latter method has been used in several studies of baboon travel progressions (Washburn & DeVore 1961, Rhine & Westlund 1981, Altmann 1979), but is typically difficult to record in the wild. In the case that groups have fewer than nine individuals, it may be possible to record the order of individuals at a feeding site without missing any individuals. This method might be appropriate for the study of frugivorous animals which live in small groups such as many lemur species (Overdorff et al. 2005).

Social Factors

Several studies have recorded the identity of a focal individuals' nearest neighbor as a measure of social proximity. The attractiveness of this method is that it's an easy measure to collect on wild populations of group living animals. Using the NN method, the observer only has to identify two individuals, which is very useful when studying groups of animals which are difficult to quickly identify. Despite its widespread usage, and ease of use, the NN method has some major drawbacks. The NN method can be a crude measure of social proximity because it only records information about two individuals per sample (unlike the ND method). This can lead to problems when drawing conclusions about the social proximity of group members. For example, assume that there is a group of five individuals; A, B, C, D, and E, and the average distance between A&B= 1m, A&C=3m, and D&E= 5m (Figure 4). Assuming that the positions of individuals are more or less fixed, the association between A&B would be just as strong as between D&E,

despite the much greater average distance between the latter. If the average distance between individuals is a good measure of social proximity, the NN method might not accurately reflect these patterns. One solution to this is for researchers to record both the identity and distance between the focal individual and its nearest neighbor. Additionally, the NN method is not always symmetrical. In figure 4, A will be the most frequent NN of C, yet the most frequent NN of A is B. In some cases, this asymmetry may be useful in the study of partner preferences, although measuring individual approaches would be a more direct measure. An additional problem with the NN method is the presence of infants. Studies often exclude dependent infants as being counted as a focal individuals' nearest neighbor (O'Brian and Robinson 1993). Although this correction may help, once the infant becomes independent the NN spatial proximity measures between the mother and other individuals may change despite no change in actual proximity between the individuals. For example, if individual A was the mother of individual B, and the average proximity between A&C were constant, in the period before the birth, A&C will have a stronger proximity level than after the birth of C, despite the absence of any change in proximity between A&C.

Many of the problems associated with the NN method are not encountered when using the ND method. When using the ND method for social proximity, the researcher records the identity of all individuals within a given radius of the focal individual. The ND method should be symmetrical, take into account multiple relationships simultaneously, and not be adversely affected by the presence of infants. The major problem with the ND method is the difficulty of collecting the data on wild animals. In some species, the quick and accurate determination of all individuals within a given radius is too difficult to implement. Despite this, researchers have used this method on fast moving forest living mammals (capuchins: Janson 1990b; DiBitetti unpublished data, Hirsch unpublished data). The other problem associated with the ND method is determining the distance of the radius used in data collection. A radius which is too short will likely result in too little information, and only collect information on individuals who are practically touching each other (which for some study systems may be appropriate). A radius which is too long might encompass such a large area that a large fraction of the group is included in each focal sample. Additionally, it may be difficult to record data accurately using a large radius. Researchers should ideally choose a distance that corresponds to the distance over which social interactions can develop quickly; for instance, in capuchin monkeys, the distance beyond which the presence of a dominant no longer inhibits subordinate feeding rates is 10m (Janson 1996). Although the NN and ND methods are commonly used for measuring social proximity, they are not appropriate for measuring the relationship between age/sex class or dominance and particular within-group spatial positions.

Previous researchers have used the MCP method to investigate the degree of peripherality as a function of dominance rank in some species (Christman and Lewis 2005). Because the MCP method cannot measure differences in centrality of individuals inside the MCP, a large amount of information may be lost. The MCP method provides no measure of inter-individual proximity, thus cannot be successfully used to determine within-group social proximity. Other than giving a rough measure of an individual’s or age/sex class's degree of peripherality in the group, the MCP method does not add any information that could not be better gleaned using other methods.

The JEC method has been used to measure differences in spatial preference by age/sex class in capuchin monkeys and ring-tailed coatis (Robinson 1981, Janson 1990ab, Hall and Fedigan 1997, Hirsch in prep). The JEC is not able to measure the social proximity between individuals, but is a useful tool to understand differences in spatial preference in relation to age/sex class. In many cases, the spatial preferences of different age/sex classes are in turn related to feeding competition, thus the JEC method can be very useful in studies investigating connections between social factors and feeding rates. If a researcher wants an understanding of the relationships between individuals, the NN and ND methods are the best and the JEC method is useful for investigating spatial position preferences by age/sex class.

Conclusion

Previous studies relating within-group spatial position to predation, feeding competition, and social proximity have used a wide variety of methods (some of which are not discussed here: Stankowich 2003, Christman and Lewis 2005). No single method is best for all circumstances. To choose the "best" methods, it is crucial that the researcher have a good understanding of both the biology of the study animal and the exact reason for recording within-group spatial position. When studying the effect of within-group spatial position on predation threat it is also important to know the behavior of the predator. In the case of terrestrial predators, the AoV method along with recording the relative "frontedness" of the focal may provide the most meaningful results. If the predators are aerial predators, it may be appropriate to record the ND. In some predator-prey systems, aerial predators hunt in the canopy at roughly the same height as their prey, and thus resemble terrestrial predator-prey systems, but several meters from the ground. Either way, it is important to know something about the general hunting behavior of the predator (or suite of predators) before choosing a method (Stankowich 2003). When recording spatial position with respect to feeding competition in moving groups, it is essential that one records the focal animal's relationship to the direction of group travel. In cases where scramble competition is expected, measuring the ND is likely an important measure. In cases where contest competition is predicted, measuring the spatial position using the JEC and/or whether the focal is inside/outside a food source is likely the most appropriate method. When both types of feeding competition are expected, both ND and another measure need to be recorded. Finally, in studies of social interactions NN might not be useful unless it is impossible to use the ND method. If a researcher is forced to use the NN method, at a minimum, they should record the distance to the NN. In cases where researchers want to investigate spatial position preference differences by age/sex class, the JEC is typically adequate (Janson 1990ab).

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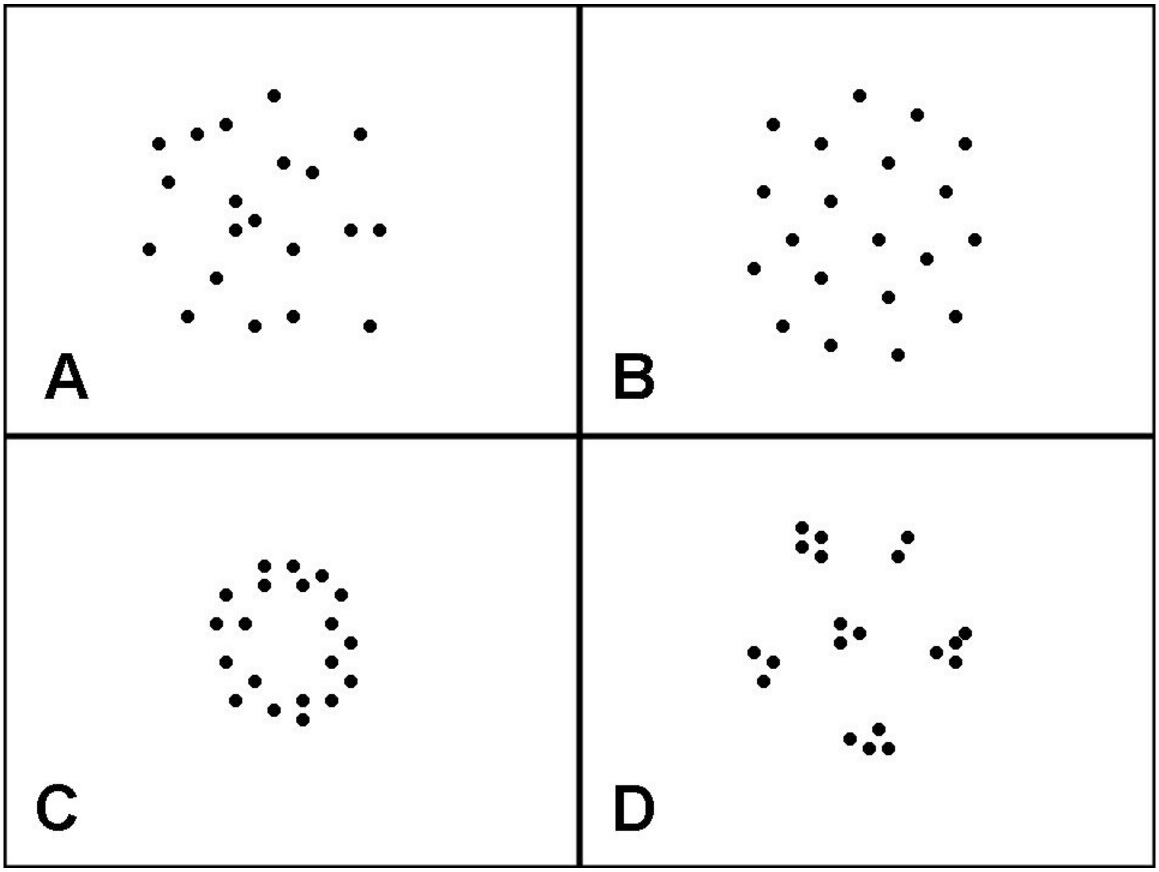

Figure 2.1. Spacing of four hypothetical animal groups. Each dot represents one individual. A. Random spacing, B. Even spacing, C. Ring formation, D. Subgrouping. C is unlikely to occur in nature, but the remaining examples have all been observed.

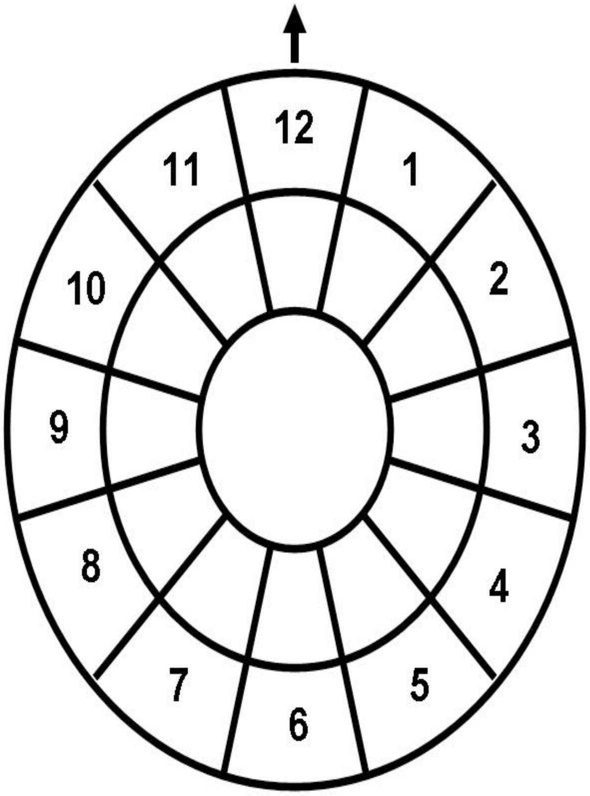

Figure 2.2a. Spatial positions divided according to the JEC method. The arrow represents the front of the group. The center spatial position is often not subdivided, and the middle and outer spatial positions are often summed into biologically relevant categories.

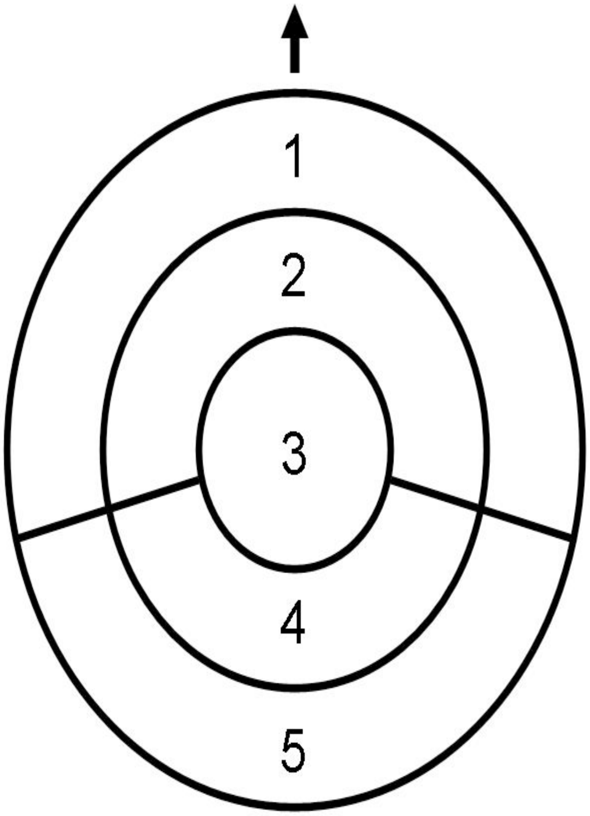

Figure 2.2b. Summarized spatial positions using the JEC method. 1. front edge, 2. front middle, 3. center, 4. back middle, 5. back edge.

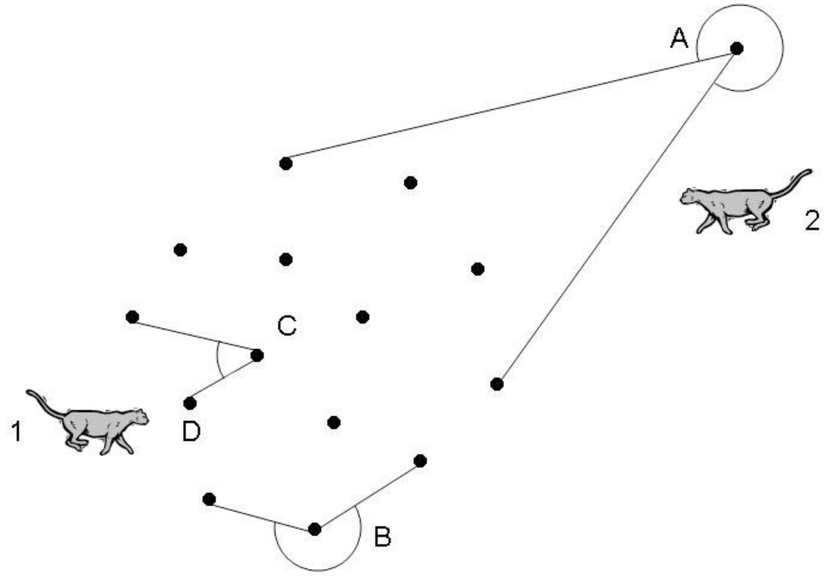

Figure2. 3. Overhead view of a social animal group. AoV values for A= 325°, B= 215 °, C= 45°, and D= 170°. Predators 1 and 2 are indicated by the felid drawings.

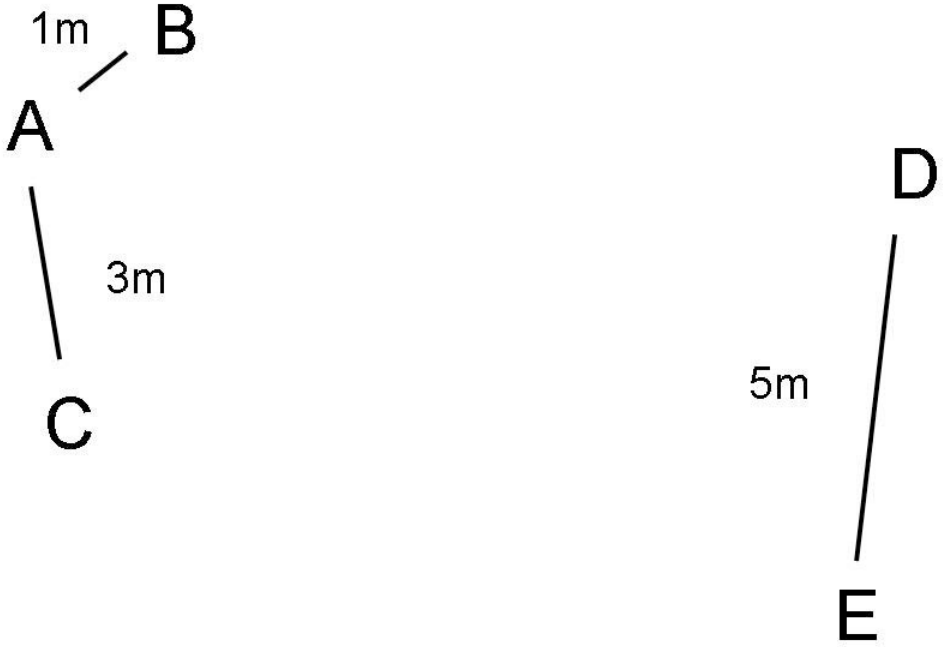

Figure 2.4. Five individuals (A-E) in a hypothetical social animal group. Lines represent the average distance between individuals in meters.

Chapter 3

The natural history of ring-tailed coatis (*Nasua nasua*) in Iguazu, Argentina

Abstract

To understand how diet and ecology affect the social behavior of ring-tailed coatis, detailed measures of feeding behavior were recorded from two well-studied groups over a two year period. The feeding behavior of ring-tailed coatis (*Nasua nasua*) in Iguazu was very similar to white-nosed and ring-tailed coatis studied at other sites. Most feeding time was spent foraging for ground litter invertebrates, and fruit foraging constituted most of the remaining foraging time. Consumption of vertebrates was rare. The proportion of time spent feeding on invertebrates and fruit generally matched the abundance of these foods in their environment. During the winter, when invertebrate and fruit availability was low, coatis spent a large amount of time feeding on an exotic fruit species (*Hovenia*). Coatis spent about 44% of their feeding time foraging for fruits of pindo palm (*Syagrus romanzoffianum*), and this species likely plays a major role in the ranging and feeding behavior of these coati groups. The time in which a coati group depleted a fruit tree ranged from 2.5-12.5 minutes, and coati groups ate an average of 2.5-250 fruits when visiting a fruit tree. When groups visited a fruit tree, the total number of individuals feeding at a given time was generally low, but this number varied depending on the plant

species. This quick depletion of fruit trees, especially pindo, differs from other frugivorous species in Iguazu such as capuchin monkeys, and likely plays an important role in shaping the social dominance system of coatis.

Introduction

Feeding ecology is an important factor influencing the biology of animals. Food properties such as handling time, nutrient content, caloric energy, and depletion time can greatly influence the behavior of animals (Krebs 1986, Kamil et al. 1987). When groups of animals (as opposed to lone individuals) encounter food patches, properties such as food size, food availability, and whether individuals have prior knowledge of the resource can lead to changes in both individual and group behavior (Giraldeau and Caraco 2000). The size and distribution of different food types is a particularly important variable which can influence feeding competition (Wrangham 1980; Vehrencamp 1983; Janson and van Schaik 1988; van Schaik 1989; Sterk et al. 1997, Grant et al. 2002, Dubois et al. 2003). In general, food items which are small and quickly depleted lead to within-group scramble competition (Isbell and Young 1991). Conversely, large patchy food resources can lead to within-group contest competition. To understand how feeding ecology may shape the social structure of a species, it is important to record measures of food depletion time, and patch size. The purpose of this study was to describe the diet, seasonal patterns, and fruit tree use by groups of ring-tailed coatis in Iguazu, Argentina, Coatis are medium-sized social mammals which are found throughout Central and South America (Gompper 1995). Coatis are generally described as omnivorous, and have diets composed of fruit, ground litter invertebrates, and occasional vertebrate prey (Kaufman 1962, Gompper 1996, Alves-Costa et al. 2004). Most previous work on coatis has focused on the Central American white-nosed coati (*Nasua narica*), and little is known about the behavior and ecology of ring-tailed coatis (*Nasua nasua*). Recent work on ring-tailed coatis has focused on ranging and dietary trends in two populations in Brazil (Alves-Costa et al. 2004, Beisiegal 2006), but detailed behavioral data were not collected. In a study of ring-tailed coati diet in Mangabeiras Park, Brasil, coatis were found to mostly eat insects, millipedes, spiders, and fruit (Alves-Costa et al. 2004). The proportion of millipedes and spiders in the diet increased during the wet season (October-March), which should have been the period of highest invertebrate abundance (Di Bitetti 2001, Beisiegal and Mantovani 2006). The proportion of coati feces containing fruit seeds varied seasonally. Fruit seeds were more common in the dry season during some years, but not in others (Alves-Costa et al. 2004).

As part of this study, detailed behavioral data was collected on two groups of ring-tailed coatis in Iguazu, Argentina. Coatis regularly fought over food items, and food size and distribution are likely to be important factors shaping social behavior and dominance relationships (Hirsch in press). Agonism occurred during pindo fruit (*Syagrus romanzoffianum*) foraging more often than any other activity; thus, understanding the manner in which coati groups utilize this fruit species may be particularly important to understanding the dominance and social system of this species (Hirsch in press).

Methods

Study site

The study was conducted in Iguazu National Park, Argentina, between August 2003 and September 2004 (for details of the field site see: Brown and Zunino 1990; Di Bitetti 2001a,b). This area of Atlantic Coastal forest is dominated by secondary growth forest and has a high fleshy fruit tree density (3-5 per/hectare, Janson and Placci unpublished data). The forest areas used by the coatis were not homogeneous. Some areas were composed of mature primary growth forest, while others were altered by humans for the convenience of tourists and park employees. The coatis would often travel through areas with mowed grass to reach fruit trees, but did not typically search for ground litter invertebrates in these areas. The coati groups spent most of their foraging time in areas with secondary forest. The coati groups would regularly travel and feed on and below steep 80m cliffs, where we were not able to observe them easily (Appendix, Table 1). The coatis also regularly used a series of small islands in the Iguazu River.

The abundance of fruit in the study area was determined using previously published data (Di Bitetti 2001a). The average number of grams of dry fruit per hectare per day was averaged by month. The fruit species recorded by Di Bitetti were consumed by sympatric capuchin monkeys (*Cebus apella*), whose fruit component of their diet is roughly similar to coatis. All fruits seen eaten by coatis were also eaten by capuchin monkeys, thus using the abundance of fruit species eaten by capuchins should be a useful proxy measure of fruit available for coatis. Several fruit species were observed being consumed by capuchins and not by coatis, which was in part due to the shorter period of the coati study (coati = 2.5 years versus capuchin = 10 years at the time of study). Di Bitetti (2001a) sampled fruit trees in an area which was within the home range for all four coati groups, and immediately north of the waterfall area. Large numbers of introduced fruit species were present in some areas of the park, especially near the waterfall area. *Hovenia dulcis* had originally been introduced into the area before the park was granted protected status (1937), and this invasive species was commonly found in disturbed areas. Tangerine, grapefruit, and orange trees were also introduced in this time period, but were less common than *Hovenia*. In addition, these citrus trees were not as invasive. Several *Eriobotrya japonica* trees were planted in the park as ornamentation, and these trees were concentrated in the waterfalls area of the park as well. Although most *Ficus* trees used by coatis were native, an introduced *Ficus* species was planted in some areas for ornamentation. These exotic *Ficus* trees were originally pollinated by a species of fig wasp not present in Iguazu. Despite a lack of pollinators, some exotic *Ficus* fruits would occasionally become fertilized, and the ripened fruits were eaten by the coatis.

The area near the waterfalls also contained restaurants, snack bars, and trash cans (Appendix Figure 1). The coatis were able to enter many of the trash cans, and would eat discarded foods when available. I was not able to ascertain the exact behavior of the coatis when they were not followed, but when observers were present, we were able to prevent tourists from directly feeding coatis. The number of tourists typically increased during the peak winter months of June-August.

Study species and behavioral sampling

Coati groups used in this study ranged from 8-31 individuals. One to three adult females per group were fitted with radio-collars to facilitate locating the groups. Coatis were captured using Tomahawk or similar traps, anesthetized, and either fitted with radio-collars or given multi-colored plastic ear tags for individual identification (Dalton Rototags). Ear tags were placed on juveniles older than four months of age, and we were able to individually recognize all group members after this age. Groups of coatis were usually habituated within two to three weeks. Habituated coatis would allow observers to silently walk within 2m of a focal animal recording the feeding behavior of individuals. Dietary data was recording using individual focal samples, and group scan samples.

Individual focal samples were taken on known individuals from two groups (PQ and PSG) from August 2002 until October 2004. Focal samples were ten seconds in duration, and the same individual was not resampled within ten minutes. During the focal sample, I recorded the identity of the focal individual, a variety of behavioral variables, and the number of food items ingested. Short focal samples were used because many of the associated variables recorded during the focal samples changed frequently and rapidly. Individuals were selected opportunistically. Due to poor overall visibility in the dense forest, it was not feasible to select individuals based on a pre-determined order. Adults were preferentially targeted over juveniles, especially during 2004 when both groups had large numbers of juveniles. When individuals were feeding on fruit, I recorded the total number of fruits eaten during the sample (to the nearest ¼ fruit). Coatis ate one fruit per bite for four of the six most common fruits (*Cecropia* and *Hovenia* being the exceptions). *Hovenia* fruits were sufficiently large, that I was able to see the proportion of an individual fruit that the coati ate during the sample (coatis typically bit off 1/2-1/4 of a *Hovenia* fruit during each bite. When coatis were eating *Cecropia*, it was difficult to determine the percentage of fruit eaten, but it was possible to count the number of bites taken by the individual. These coati bites were converted into fruit number by estimating that it took a coati 12 bites to eat an entire *Cecropia* fruit. When coatis were eating ground litter invertebrates, I was only able to see the ingested item in a small percentage of cases. When I was able to determine the type of invertebrate, I recorded this information. In several cases, I was not able to see the item, but heard a distinctive crunching sound when the coati was chewing the prey item. In these cases, it was assumed that the prey item had a thick exoskeleton, and was likely an arthropod. In some cases, the coati rolled a prey item in its paws before ingesting, which is typically an indication that the prey had irritating morphological features such as spines or was covered with a noxious substance.

Data on monthly diet patterns was taken from 15-minute group scan samples. During these scans I recorded the percentage of individuals searching for food or feeding. If more than two thirds of the group were foraging, this was classified as a foraging scan. The relative proportion of individuals searching or feeding on fruit, invertebrates, or trash was recorded. If some individuals in the group were not visible, the percentage of individuals foraging on each food type was based on the individuals seen at the time of the scan. In general, scans were only recorded when two-thirds or more of the group was visible. If any fruit trees were contained in the group spread, the number of trees of each species was recorded.

Fruit tree depletion times and the amount of fruit eaten per tree were calculated using tree focal samples. When I was able to arrive at a fruit tree before the group, the number of coatis feeding and searching for fruit was recorded every minute for the duration of the time that the coatis fed at the tree. Prior to the start of the sample, a timer was set to beep once every minute. The tree focal sample started with the first beep after the arrival of the coatis, and at each beep, the number of all individuals feeding and searching for fruit was recorded. From these tree focal samples, it was possible to determine the average depletion time for different species of fruit trees, and the amount of total feeding at the fruit tree in "coati minutes" (the total minutes all coatis spent feeding on a tree). By multiplying the number of coati minutes times the average number of fruits eaten during the ten second feeding samples (times 6), it was possible to determine the average total number of fruits eaten from a tree. These values were then averaged for major fruit species. Approximately 80% of tree focal samples were recorded during 2004, thus the average group size during most tree focal samples was between 25-30 individuals (the exact percent of samples recorded by year varied depending on the fruit species).

Statistical analyses

Ten second focal samples were used to test the relationship between feeding success and spatial position. Two GdLM models were constructed with fruit or invertebrate feeding success as the dependent variable, and several other potentially confounding variables were entered into the models. To test for nonlinear seasonal patterns, both the month (represented by numbers 1-12), and month squared were entered as variables in these models. An unequal sample size was recorded for each age/sex class due to differences in the number of individuals in each age/sex class and opportunistic sampling (adult males N= 238, adult females N= 1902, subadults N= 835, juveniles N= 1499).

Results

Coatis primarily ate fruit and ground litter invertebrates. Coatis spent between 69.7-97.5% of their monthly feeding time foraging for ground litter invertebrates (N= 4648 feeding scan samples). The amount of time spent invertebrate foraging was highest during the summer months of November-February, which is also when invertebrate abundance is typically the highest (Figure 1) (Di Bitetti 2001b). The feeding success rate on invertebrates was higher during these months as well (Figure 2, Table 1).

It was possible to observe or infer the type of invertebrate consumed in 11.5% of the successful invertebrate foraging focal samples (77 of 671). In 54.5% of these cases, I observed the coatis eating annelid worms (N=42). During 26.0% of these samples, I heard a distinctive crunching sound indicating the consumption of an exoskeleton (N=

20). Coatis were observed rolling the prey item between their paws before consuming the item during 11.7% of the samples (N=9),and it was likely that the coatis were consuming millipedes and tarantulas during these samples. Coatis were also observed eating Formicidae larvae (N= 3), Scarabaeidae larvae (N= 2), and an individual Orthoptera during the focal samples (N=1).

With the exception of a spike in trash foraging during September 2003, the group consistently spent less than 5% of their monthly foraging time searching for human foods. Coatis were rarely observed eating vertebrates. Coatis were observed consuming vertebrates (Order: *Anura*) during two scan samples (N=4648). The most commonly observed vertebrate prey was frogs. During 32 months of study, 14 frogs were either seen or heard being consumed (including ad libitum data). When frogs were captured, the frogs often emitted loud screams, which attracted other coatis. When conspecifics approached the possessor of the frog, there were often aggressive fights for control of the carcass. Other than frogs, coatis were observed consuming a dead bird (N=1) and turtle eggs buried in the ground (N=1, ad libitum data). Although coatis were seen chasing rabbits and small lizards, they were never observed catching or consuming these vertebrates.

The remaining foraging time was spent searching for or consuming fruit. In many cases, when a fruit tree was present within the group spread, only a fraction of the group was actually feeding or searching for fruit. Trees containing ripe fruit were found within the group spread during 6.3-39.9% of the scan samples, and varied by month (Figure 1).

When foraging for fruit, coati groups contained an average of 1.45 trees within the group spread (N=826). The percentage of time spent fruit foraging varied by month. In general, fruit foraging was lowest during the summer months of November-February, when invertebrate feeding was highest (Figure 1). The occurrence of fruit feeding appeared to be closely linked to the availability of fruit but the correlation was not significant (N= 12, R^2= 0.154, one tailed P= 0.104)(Figure 3). During June-August, there was a major discrepancy between the amount of fruit foraging scans and fruit availability. During June and July, the coatis spent large portions of time feeding on *Hovenia* fruits (Figure 4). Because Di Bitetti (2001ab) censused an area immediately north of the waterfall area, he likely recorded far fewer *Hovenia* trees in his sample than were commonly available for the coatis in and near the waterfall area. Excluding these months from the analysis is probably a more accurate reflection of the amount of fruit available to coatis. When values from June-August were excluded from the sample, fruit availability and the percentage of time spent foraging for fruit were significantly correlated (N=9, R^2= 0.424, one tailed P= 0.029).

A total of 29 species of fruit were observed being eaten during the scan samples (Table 2). Although the coatis were observed eating some additional species outside the scan samples, these species were not commonly eaten during the study period. All of these additional species were also present in the diet of sympatric capuchins (Di Bitetti 2001a). Pindo trees were the major fruit source for coatis and over 43% of fruit foraging scan samples contained pindo trees. The next most commonly eaten fruit was *Hovenia*. *Hovenia* trees were ripe during the winter months when the availability of other fruits was low. In addition, both the abundance of invertebrates, and the invertebrate foraging success of the coatis was lowest during the winter. Exotic fruit species made up a significant portion of the coatis fruit foraging time (27.9%).

The average depletion time of fruit trees varied by species. Some species such as *Cecropia* only contained 1-4 ripe fruits at a time, and the coati groups consumed these very quickly (2.5 min). Other species such as *Ficus* and *Eriobotrya* took 11.4-12.5 min respectively to be depleted (Table 2). The differences in depletion time were related to the amount of fruit available and the coati feeding rate. The average number of fruits eaten in one visit to a *Ficu*s tree was 270 individual fruits. The amount of fruit eaten per fruit tree visit was roughly in agreement with calculations of fruit tree productivity in Iguazu (Placci, Di Bitetti, and Janson unpublished work). In general, the entire group was not observed feeding in the same tree at the same time, although this was occasionally observed when the group fed on a particularly large *Ficus* tree. The mean number of individuals that fed on a fruit tree per minute can be calculated by dividing the number of coati minutes by the depletion time. For most tree species, approximately 4 individuals simultaneously fed on the same tree at any given time. This value was lower for *Hovenia* and *Cecropia* fruit trees (averages of 3.0 and 2.0 individuals respectively).

Discussion

Ring-tailed coatis in Iguazu had diets similar to other previously studied coati populations (Kaufman 1962, Alves-Costa et al. 2004). Coatis on average spent just over

80% of their feeding time foraging for ground litter invertebrates. The seasonal and monthly variation in diet appears to be driven by resource abundance. Coatis spent more time foraging for and had higher feeding rates on invertebrates during the summer months, which had the highest abundance of invertebrates in the environment. The summer months were also the period in which fruits were less abundant in the environment. It was predicted that coatis would spend more time foraging for insects in the winter due to low fruit availability. This pattern was not observed. Instead, coatis ate large quantities of fruit of exotic species during the lean winter months. At this time, coatis spent large fractions of time feeding on two exotic fruit species, *Hovenia dulcis* and *Eriobotrya japonica*. These two species were most commonly found in the waterfall area of the park, and the presence of these fruit trees probably drove the coati groups to use these areas more frequently during the winter season (Hirsch unpublished data).

Fruit tree depletion times ranged from 2.5-12.5 minutes per tree. In some cases, only one or two coati individuals would feed at a fruit tree, while the rest of the group would forage for invertebrates or use other fruit trees. This was common during *Cecropia* feeding. In a few cases, all or most of the group would feed at a large *Ficus* or *Eriobotrya* tree. When feeding on larger fruit trees most, or all group members spent some time feeding at the tree, although the entire group did not arrive at and leave the fruit tree together. When feeding on pindo, coati behavior was particularly variable. In some cases, only one or two individuals would feed at a tree, in other cases, most or all of the group would feed at the pindo tree. This variability was likely the result of different quantities of fruit available. In many cases, coatis visited relatively unproductive pindo trees, or visited the same tree multiple times per day (in some cases 4-5 times per day). The circuitous nature of coati travel patterns led groups to use the same areas multiple times per day, thus even if a fruit tree had already been visited, when the group passed by the same tree later in the day, some individuals would typically visit the tree and feed (if possible). In other cases, a large, productive pindo which had not recently been visited contained enough fruit that all or most of the coati group was able to simultaneously forage under it.

When foraging for ground litter invertebrates, coatis ate approximately one item every 40 seconds. In general it was not possible to determine what type of invertebrate was consumed. Of the items that were visible, annelid worms made up more than half the items. This result may have been influenced by sampling bias. Because of the long shape of the worms, it was probably easier for me to see annelid worms compared to other smaller items which the coatis swallowed directly. Although annelid worms have been observed to be eaten by white-nosed coatis (Kaufman 1962), no previous study has reported that annelid worms comprised a large component of the invertebrate portion of the coati diet. This latter pattern may have been due to the use of fecal sampling in other studies, because the digestion of soft tissue parts may not have been visible in feces. It appeared that the coatis preferentially ranged in areas with high annelid densities. Annelid feeding was particularly noticeable in areas near the waterfalls which were damp and mossy year round due to water sprayed from the falls.

Conclusion

The diet of coatis in Iguazu was similar to other populations. Coatis mostly ate fruit and ground litter invertebrates, and vertebrate consumption was rare. In Iguazu, coatis appear to be eating large amounts of annelid worms, a pattern not recorded in other study sites. The foraging success of coatis was highest during the summer when invertebrate abundance was the highest (Di Bitetti 2001b). Higher amounts of fruit feeding also coincided with periods of increased fruit availability, with one exception. During the winter, when most natural fruit species do not produce fruit, the coatis extensively exploited two exotic fruit species, *Hovenia* and *Eriobotrya*. The presence of exotic trees in the park may have benefited several of the coati groups during the winter, when both invertebrate and natural fruit availability was low. It is uncertain if the availability of these foods during the resource scarce season may have increased the reproductive rate and survivorship of the coatis in Iguazu (e.g. Janson and Di Bitetti 2001, Hirsch in prep). Coatis spent a large amount of time foraging for pindo fruits, was and they did so more than sympatric capuchin monkeys. Capuchins typically visited pindo fruits during 5% or less of their fruit tree visitations (April-January), with a seasonal peak of 38% of visits during February-May (Janson unpublished data). Coatis spent 30% of fruit foraging time at pindo trees (April-January), with a seasonal peak of 60% of fruit foraging time during February-May. This is a major difference in fruit usage for these two conspecific frugivorous mammal species. It appears that coatis specialized on pindo, while capuchins specialized on larger fruit sources with slower depletion times. This specialization on smaller, more quickly depleted fruit resources may help shape patterns of feeding competition in ring-tailed coatis.

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Table 3.1. Results of generalized linear model for factors affecting the food intake of coatis searching for ground litter invertebrates. N= 3429. DF=10, Chi^2=23.739, P=0.008.

Variable	**DF**	**Estimate**	**Standard Error**	**P value**
Month	1	-0.195	0.067	0.004
Month^2	1	0.014	0.005	0.007
Time of day	1	0.000	0.000	0.402
Group speed	1	-0.129	0.076	0.088
Group size	1	-0.019	0.006	0.003
Age/Sex	3			
Adult female		0.000	-	-
Adult male		0.106	0.140	0.448
Subadult		-0.128	0.096	0.181
Juvenile		0.045	0.085	0.591
Neighbor density	1	0.031	0.023	0.187
Spatial position (front to back)	1	0.000	0.028	0.994

Table 3.2. List of all plant species consumed during group scan samples. Percent values per fruit species were calculated from the total number of scans when fruit was observed inside the. Species with an * indicate exotic species, which made up a total of 27.94% of fruit scan samples.

Family	**Genus and species**	**% of scans**
Annonaceae	*Rollinia emarginata*	0.32
Araceae	*Philodendron bipinnatifidum*	0.08
Bromeliaceae	*Pseudananas sagenarius*	0.16
Caricaceae	*Carica papaya* *	0.40
Lauraceae	*Nectandra sp.*	1.83
Leguminosae	*Inga sp.*	0.24
Melastomataceae	*Ossaea sp.*	0.24
Melastomataceae	*Miconia pusilliflora*	5.65
Moraceae	*Cecropia pachystachia*	0.80
Moraceae	*Maclura tinctora*	1.59
Moraceae	*Ficus sp.*	6.68
Moraceae	*Ficus sp.* *	0.16
Moraceae	*Morus alba*	0.16
Moraceae	*Sorocea bomplandii*	0.32
Myrtaceae	Unknown genera	1.27
Myrtaceae	*Eugenia involucrata*	0.08
Myrtaceae	*Eugenia sp.*	0.64
Myrtaceae	*Psidium guajaba*	2.23
Palmae	*Syagrus romanzoffianum*	43.76
Phytolacceae	*Tricostigma octandrum*	0.08
Piperaceae	*Piper sp.*	0.88
Rhamnaceae	*Hovenia dulcis* *	16.15
Rosaceae	*Eriobotrya japonica* *	6.37
Rutaceae	*Citrus sp.* Tangerine *	3.42
Rutaceae	*Citrus sp.* Orange *	0.80
Rutaceae	*Citrus sp.* Grapefruit *	0.64
Sapindaceae	*Allophyllus edulis*	0.48
Sapotaceae	*Crysophyllum gonocarpum*	4.06
Unknown	little round berries	0.56

Table 3.3. Average depletion time and food intake for six common fruit species. The depletion time was the average number of minutes that the group spent feeding on a fruit tree. The coati minutes are the summed number of minutes all individuals in a group spent feeding. The feeding rate was the number of individual fruits consumed by one coati in one minute. The number of coati minutes was multiplied by the feeding rate to determine the average number of fruits per tree that the coatis ate when they visited.

	Depletion time	**Coati minutes**	**Feeding rate**	**#fruits per tree**	**N**
Crysophyllum	7.24	30.55	2.91	89.02	42
Cecropia	2.49	5.04	0.52	2.64	37
Ficus	11.4	48.25	5.59	269.81	20
Hovenia	9.68	29.07	2.67	77.50	41
Eriobotrya	12.52	50.19	3.31	166.13	27
Syagrus (Pindo)	5.69	22.65	4.36	98.80	438

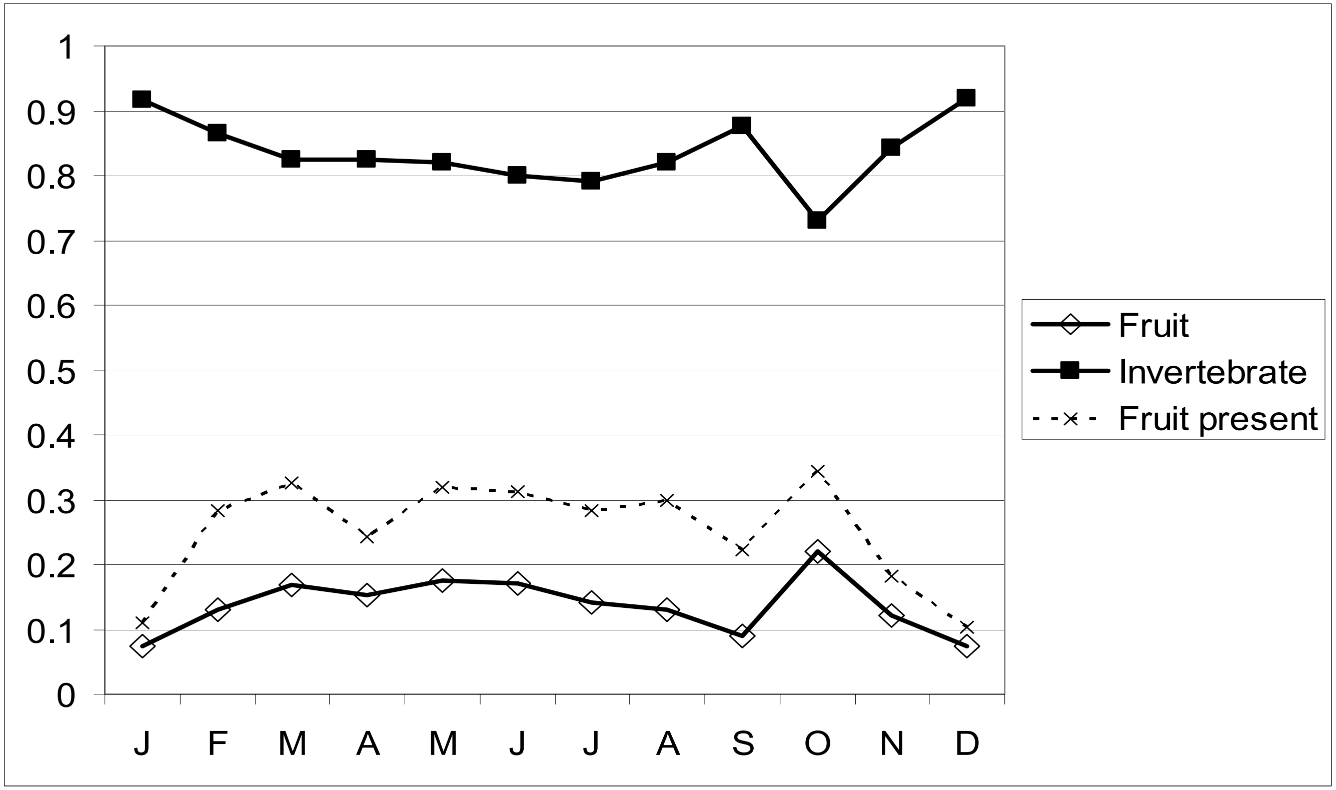

Figure 3.1. Diet by month. Values indicate the percentage of scan samples in which the group was foraging for invertebrates or fruit. The presence of fruit within the group is indicated by the dashed line.

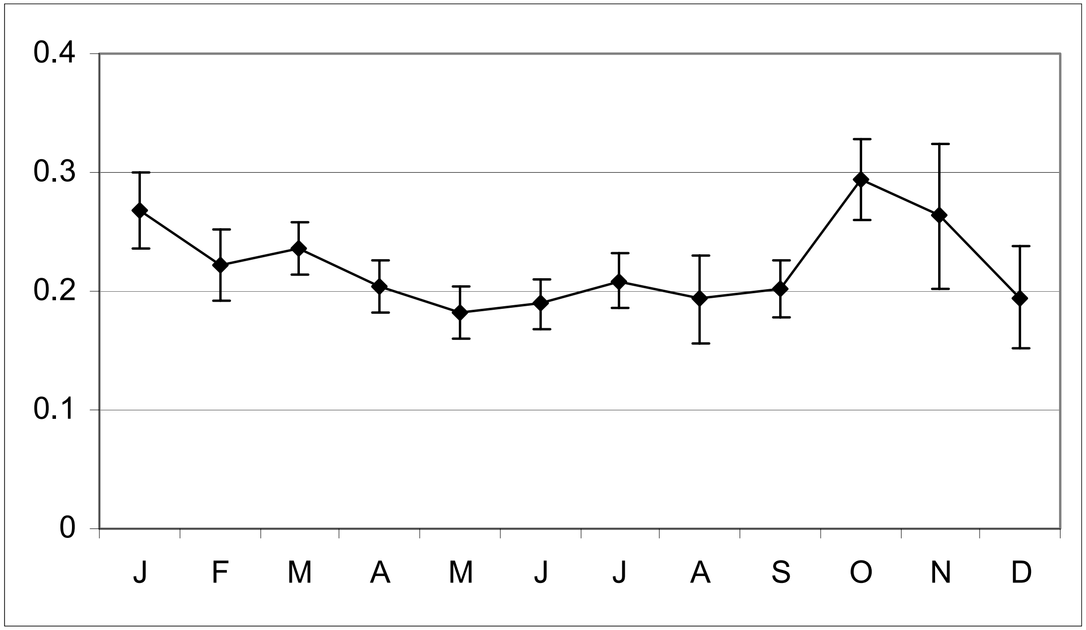

Figure 3.2. Invertebrate feeding success by month. Values represent the percentage of scan samples in which at least one invertebrate were eaten, summarized by month.

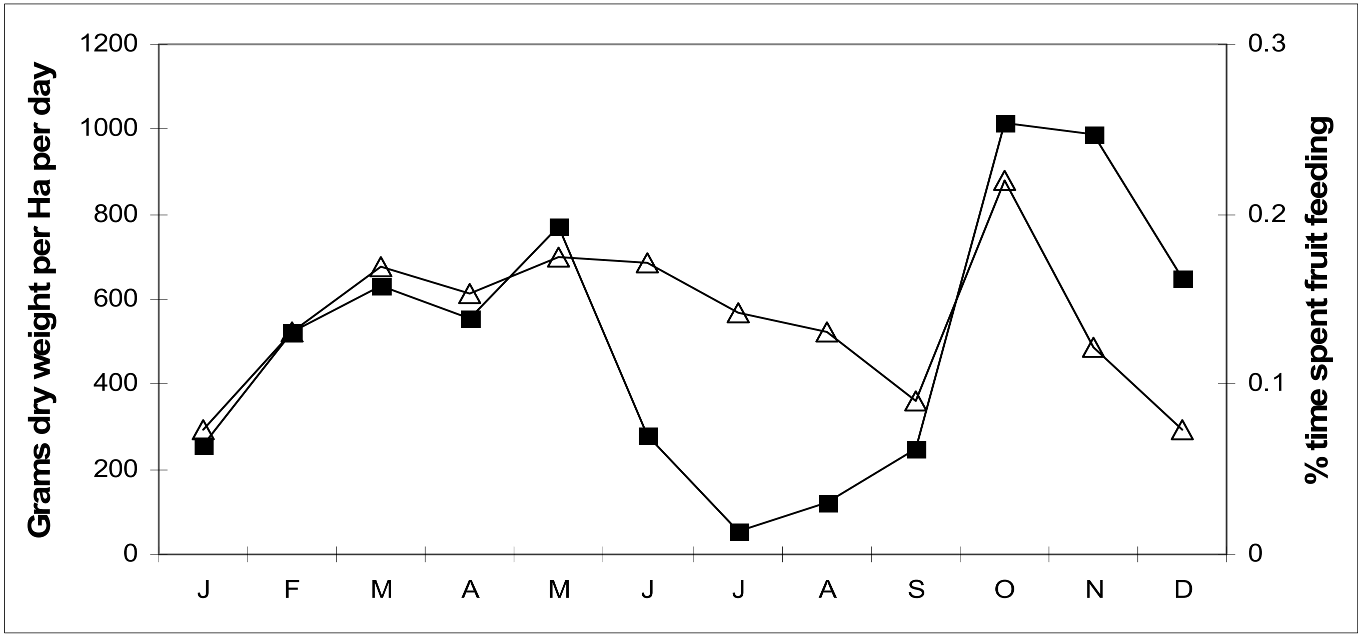

Figure 3.3. Availability of fruit (black squares; from Di Bitetti 2001a) and percent of time spent fruit feeding (open triangles) by the coatis per month.

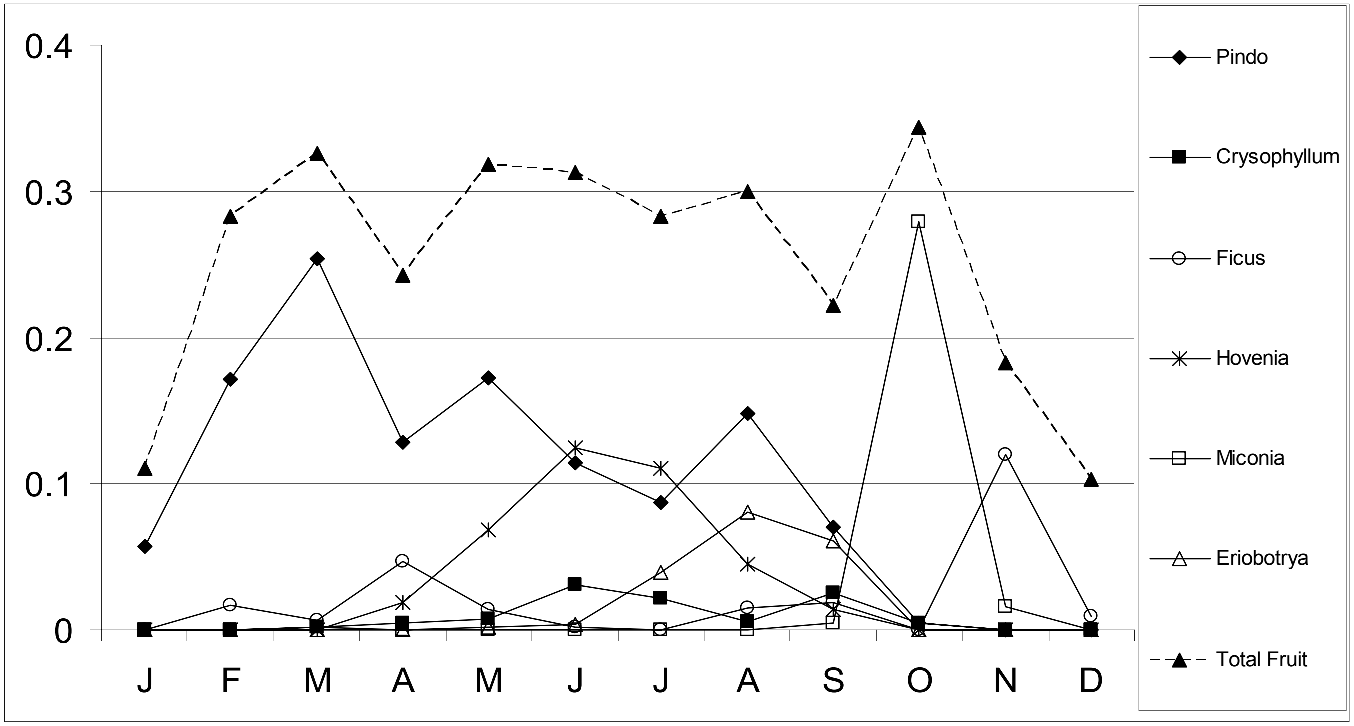

Figure 3.4. The percentage of feeding scan samples in which the six major fruit species were observed in the group spread. The total fruit values were calculated using all fruit species.

Chapter 4

Adult male sociality, group membership, reproduction, and mortality in ring tailed coatis (*Nasua nasua*)

Abstract

Four groups of ring-tailed coatis (*Nasua nasua*) were monitored and studied in Iguazu National Park, Argentina. Group sizes varied from 8-65 individuals, and many groups included a relatively high proportion of juveniles. Survivorship for subadults and adult females, at 74.8% and 70.8% per year, was equal to or higher than other coati populations. Juvenile survivorship of at least 56.6% was relatively high, and most deaths probably occurred during the nesting period. Five adult females lost their entire litter during the nesting season, and juvenile mortality during this period may have occurred in an “all or none” pattern. Adult female mortality was also highest during the nesting period, when they were solitary, which provides support to the hypothesis that sociality lowers predation risk. The high survivorship rates found in three of the four groups may have been caused by the presence of humans and the use of steep cliffs, both of which were predicted to deter predators. Unlike white-nosed coatis (*N. narica*), ring-tailed coatis in Iguazu regularly had one adult male incorporated into the social group outside the mating season. The natal groups of four immigrant adult males was also known, and all of these males had dispersed from nearby groups. During the mating season, up to five

males were observed following some groups. Adult females were also observed leaving their group to mate with outside group males. Adult male sociality may be widespread in the species, but the benefits of adult male sociality are still uncertain.

Introduction

Demography and life histories are important constraints on the evolution of social behaviors (Kappeler and Pereira 2003). In order to understand the evolution of social behavior in ring-tailed coatis, it is necessary to understand patterns of demography and life history. Compared to other social mammals, little is known about the behavioral and population ecology of the ring-tailed coati. Although some authors have studied dietary patterns and ranging behavior, no extensive studies of social behavior exist (Beisiegal 2001, Alves-Costa 2004, Beisiegal and Mantovani 2006). The ring-tailed coati is found throughout much of South America, but is much less studied than its northern cousin, the white-nosed coati (*Nasua narica*) (Kaufman 1962, Gilbert 1972, Russell 1982, 1983, Gompper 1994, Gompper 1995, Hass and Valenzuela 2002, Booth-Binczik et al. 2004). Previous authors assumed that ring-tailed coatis have similar or identical social systems to white-nosed coatis (Gompper 1995, Beisiegal 2001), which has a unique social system among carnivores in that adult males are mostly solitary and females are social (Gittleman 1989). Coati groups are composed of between 1-16 (often related) adult females and their offspring (Kaufman 1962, Gompper *et al.* 1997). Total group sizes have been reported ranging from 2-162 individuals, with most groups between 6-26 individuals (Kaufman 1962, Gompper 1997, Hass and Valenzuela 2002, Booth-Binczik et al. 2004).

Group sizes of white-nosed coatis fluctuate from year to year (Russell 1982, Gompper 1997). Adult females typically give birth to 1-6 offspring per year, and predation and mortality rates vary at different research sites (Kaufman 1962, Gompper 1997, Hass and Valenzuela 2002). Previous research found that smaller groups have higher predation rates than larger groups (Hass and Valenzuela 2002). Predation is particularly high for solitary adult male coatis or adult females foraging alone during the birthing season (Hass and Valenzuela 2002). Studies of both white-nosed and ring-tailed coatis have found an inverse relationship between vigilance levels and group size (Burger and Gochfeld 1992, Di Blanco and Hirsch 2006).

During the one-month mating season, adult male white-nosed coatis often enter social groups to breed (Kaufman 1962, Gompper 1994, Booth-Binczik et al. 2004). Coatis are highly seasonal breeders, but unlike other medium sized social carnivores, they do not use communal nests (Rood 1990, Creel and Waser 1994, Clutton-Brock *et al.* 2001). During the birth season, coati groups often disband and each female uses a different nest site (Kaufman 1962, Russell 1982, Gompper 1994). Gompper (1996) argued that adult males are asocial due to increased feeding competition when traveling in social groups. Adult females were observed forming coalitions against adult males at fruit trees, and this female dominance over adult males was likely related to group size (Gompper 1996). The cost of increased feeding competition in white-nosed coati groups potentially outweighs the increased predation risk for solitary adult males. Even though adult male white-nosed coatis are primarily asocial, they have been observed traveling with social groups over a period of weeks (Gompper and Krinsley 1992). In these cases, it was not always clear whether the adult male was related to the group, although in some known cases, social adult males were observed traveling with their natal groups (Gompper and Krinsley 1992). The purpose of this study is to describe the structure of ring-tailed coati groups, calculate rates of mortality, and to discuss how these patterns may have shaped the social system of the ring-tailed coati.

Methods

Study area and population

The study was conducted in Iguazu National Park, Argentina (54°W, 26°S) (see: Brown and Zunino 1990; Di Bitetti 2001ab, Di Bitetti et al. 2006a). This area of Atlantic Coastal forest is dominated by secondary growth forest and high fruit tree density (3-5 per/hectare, Janson and Placci unpublished data). The home ranges of all four groups overlapped in the "waterfalls" area of the park. This area has several walking trails for tourists interspersed through the forest. This area contains a series of large waterfalls on the Iguazu River. Just above of the waterfalls area, there were several small islands along the river that the coatis use (and where we could generally not follow the groups). Below the waterfalls, >80m steep cliffs were found on the shore of the Iguazu River. The coati groups would frequently use these cliffs for sleeping and foraging.

Predators

Iguazu forest has an intact suite of carnivorous mammals, including jaguars (*Panthera onca*), puma (*Puma concolor*), ocelots (*Leopardus pardalis*) and tayra (*Eira barbara*) (Crawshaw 1995, Di Bitetti et al. 2006a). Although poaching occurs, Iguazu National Park is comparably well protected, and park rangers regularly patrol the park. Because the coati study area was close to the park guard headquarters and tourist infrastructure, the likelihood of poaching in the coati study area was low. Although poachers in the area have been found hunting top predators and their prey (peccary and tapir), park guards have not reported the hunting of coatis. Compared to tropical forest sites, ocelot populations densities in Iguazu were low (Iguazu= between 12.8±2.7 and 20.0±4.2 individuals per 100km^2), and it appears that their population densities are relatively stable over time (Di Bitetti et al. 2006a). Jaguar and puma densities in Iguazu were also low (jaguar = 0.67 and puma = 2.9 per 100 km^2) (Di Bitetti et al 2006b, Di Bitetti and Paviolo unpublished work). The felid densities in Iguazu were lower than three well studied coati field sites. Ocelot densities on Barro Colorado Island, Panama are at least five times higher than Iguazu (minimum of 1 individual per 1km^2), and pumas are occasional but non-permanent residents on the 1500 hectare island (Moreno et al. 2006). Comparatively high felid densities were recorded in Jalisco, Mexico (180 ocelots, 1.7 jaguars, and 3.5 pumas per 100 km^2)(de Villa Meza et al. 2001, Hass and Valenzuela 2002, Nunez et al. 2002). Although exact population densities for predators in the

Huachuca Mountains are not available, during the coati study period, puma densities appeared to be very high (Hass and Valenzuela 2002, C Hass personal communication).

Although the above carnivores are the only likely predators of weaned coatis in Iguazu, other animals may be responsible for nest predation. Raptors, margay (*Leopardus wiedii*), tayra, and capuchin monkeys (*Cebus apella*) could all potentially raid coati nests. In Costa Rica, white-faced capuchins (*Cebus capucinus*) are major nest predators of white-nosed coatis (Newcomer and DeFarcy 1985, Fedigan 1990, Perry and Rose 1994, Saénz 1994, Rose et al. 2003). In the Iguazu study area, there were large numbers of these monkeys which may have attacked and consumed nestling coatis. A recent paper claimed that brown capuchin monkeys have never been reported to eat nestling coatis, and that in one study area brown capuchin monkeys were observed playing with ring-tailed coatis (Resende et al. 2004). This pattern was not observed in Iguazu. Coati-capuchin interactions were generally hostile, and capuchin groups would often chase coatis out of and away from fruit trees. Although a series of primate researchers studying brown capuchins in Iguazu have never witnessed a capuchin consume a coati nestling during over 15 years of research, there was one reliable report from a park employee who witnessed this behavior. Coati mothers generally chose nest sites that are either high in the canopy in areas of high liana density, or on the edge of a cliff. The placement of these nests would make it very difficult for capuchin monkeys to find them (C. Baldovino personal communication). Even if the capuchins did find these nests, they were often in areas where the researchers may not have been able to witness the predation event (dense liana tangles, several meters below the edge of a steep cliff).

Group membership

Three to four coati groups were monitored during two study periods totaling 32 months of research (Table 1). During the initial study period of winter 2001 (May-August), I regularly walked along trails in the waterfall area searching for coati groups. During the first month, whenever a group was encountered, I took as much demographic information as possible, and attempted to follow the group. One individual from the GR group was captured during 2001, and I habituated and followed that group until late August. Two other groups (PQ, SF) were encountered during the 2001 study period.

During the second study period (June 2002-December 2004), individuals from four study groups were radio-collared and studied. Coatis were captured using 32x10x12 inch Tomahawk or similar traps. The coatis were anesthetized with the assistance of a veterinarian. Individuals were tagged with by multi-colored plastic eartags (Dalton Rototags) and radio-collared. The coati groups were usually habituated within two to three weeks, and it was possible to follow the coatis within 3m without disturbing them. The PQ and GR groups were the first to be radio-collared (August 2002). Following the death of the radio-collared female in group GR (November 2002) I lost contact with the group. In February 2003, another adult female in the GR group was captured and radio-collared. Shortly after this female was tagged, the GR group split into two groups (GR and PSG). It is possible that the GR group split up before February, but was temporarily reaggregated during the capture. The GR and SF groups were radio-collared during July and August 2003, and virtually all individuals in those groups were eartagged.

The two primary study groups were the PQ and PSG groups. During March 2003-October 2004, both groups were followed at least five complete days a month. During a typical day the group was followed from nest site to nest site with at least one observer in the field. Whenever possible, the SF and GR groups were followed and censused, but in some months it was not possible to accurately count these two groups. It was still possible, however, to determine the time of disappearances of individuals in these two groups within a one-month accuracy. The major exception was the GR group juveniles born during October 2003. During 2004, the GR group was not encountered frequently, and when contacted, they were usually not seen in areas where counting unmarked juveniles was easy. When disappearances occurred, I checked the last known sighting of the individual, and calculated the range of possible days in which the individual could have disappeared. In some cases, when a group was censused for the first time during the winter (June-August), it was not possible to determine whether some coati females were adult females or large subadults (SF and GR during 2001 and 2002). This differentiation was possible when individuals were captured, and coati weight and tooth wear could be measured. One additional census of the PQ and PSG groups was taken in May 2005 by two former field assistants (Yamil Di Blanco and Carolina Ferrari).

A Kaplan-Meier survival curve was calculated using the census and disappearance data. All adult females, subadults, and juveniles who disappeared from their group were classified as mortalities. Individuals were classified according to age as follows: juveniles= 3 months (the approximate time of weaning) to 12 months, subadults= 12 to 24 months of age, and adults= 24 months of age or older. Male subadults typically split from their groups at 22 months of age, thus these subadult males were censored. Adult males were not included in the survival curve. In white-nosed coatis, there is evidence that females occasionally transfer or change groups (Gompper 1997). During the length of this study, no adult female transfers were observed, thus female disappearances were likely due to mortality. In two cases, subadults were found to leave their groups earlier than normal. In these cases, mortality was determined by censusing the subsequent subgroup (PQ subgroup). In one case, a subadult male left its natal group earlier than October, but was seen in the area afterwards (TM). This male was censored on the last day it was seen. The group census data only included weaned coatis (six weeks or older). Because of the highly seasonal birth pattern, it was possible to determine the age of most captured coatis. In the case of adult female coatis, adult females were assigned the youngest age possible based on census data. For example, if a 42 month old coati was captured and its age could not be determined with certainty, it was assigned an age of 30 months (the youngest possible adult age).

Individuals were entered into the sample database when they were captured and tagged, or when they could be identified by distinctive morphological traits (fur color, torn or ripped ears, missing the tip of the tail). In the case of young juveniles, census data taken immediately after group reformation was used to determine the number of disappearances that occurred before tagging occurred. For example, if 31 juveniles were observed returning to the group, then if we found less than 31 individuals on a subsequent day, we knew that an individual disappeared. Because adult females could not always be accurately assigned the correct age in months, monthly mortality for adult females older than 36 months of age may be inaccurate. Not all coatis were first observed at the same starting age, thus the Kaplan Meier survival model could not be constructed in the typical manner. Instead, a staggered entry model was created. For each age/month, the number of individuals who entered and exited the database was calculated (total N=137 individuals). This resulted in a monthly mortality rate which was graphed as a Kaplan Meier survival curve (Figure 1). Six individuals who died after being hit by vehicles were censored from the analysis at the time of death since their mortality was not due to natural causes. Adult males were not entered into the model because only group living individuals had sufficiently detailed census data for inclusion.

Because it was not possible to enter nests or observe coati births, it was impossible to determine the number of offspring born to each female. Previous studies have found that white-nosed coatis can give birth to 1-6 offspring per year, and in this study it was assumed that adult females could give birth to a maximum of six juveniles per year. It was possible to determine whether an adult female had given birth, because they showed obvious signs of pregnancy beforehand (enlarged nipples and swollen stomach). Adult females typically dispersed from their groups two to seven days before giving birth. In some cases, pregnant females returned to their groups soon after birth, presumably because their offspring had died. In other cases, previously pregnant adult females were observed without swollen nipples immediately after the birthing season. In these cases, it was assumed that their offspring had died in the nest. To determine the average juvenile nest mortality rate, two calculations were made. The minimum nest mortality was calculated assuming that each nest held an average of four juveniles per nest. This assumption was chosen because the average number of weaned offspring found per adult female was 4.25 (this number was rounded down to 4 individuals per nest, which was the same estimate used by Hass and Valenzuela 2002). This minimum estimate was based on the number of females which lost all of their offspring during the season. Nest deaths may not have occurred purely in an “all or none” pattern. It is possible that one or two coatis may have died in a nest, while the rest of the litter survived. If this was the case, a maximum nest death estimate may be more appropriate. The maximum nest death was calculated by assuming that all adult females gave birth to six juveniles per nest, and that the difference between the number of individuals observed at weaning and the maximum birth rate was the result of nest deaths (Table 2).

The birth date of juveniles was determined through the behavior of adult females. In cases where mothers were wearing radio-collars, I was able to monitor their movements during the birthing season. When a pregnant adult female chose a nest site for two consecutive nights, I regularly monitored her movements. When the adult female was monitored in her nest multiple times per day (3 or more), it was determined that she may have given birth. After the presumed day of birth, the nest was monitored twice per day. At the first movement of the signal outside the nest tree, or the first sighting of the adult female, the last possible date of birth was determined. In some cases, adult females without radio collars were observed both before and after giving birth. In these cases, the earliest and latest possible birth days were determined from these fortuitous coati sightings. The best mating and birth seasonality data was recorded during 2003 when several adult females had functioning radio collars and some mating behaviors were observed.

Statistical procedures

Yearly survival rates were determined with the same census data used to create the Kaplan Meier survival curves. Three different values were calculated for first year survivorship. First, the known survivorship of individuals between the time of weaning and one year of age was calculated (10-12 months of age). This weaned juvenile survivorship rate was multiplied by the minimum and maximum nest mortality numbers to calculate minimum and maximum yearly juvenile survivorship estimates. The second and third year survivorship rates were based on individuals of known age, but fourth and fifth year survivorship rates may have been biased because the age of some individuals was not properly classified. Because of this uncertainty, a summary of adult female survivorship was estimated. Thusly, survivorship rates were calculated for three age classes; juveniles, subadults, and adults.

To determine if mortality rates were higher during the birth season (October-December), the number of expected disappearances for the birth period was calculated for each age class. If mortality was random across months, roughly one fourth of all disappearances should have occurred from October to December. The observed number of disappearances was compared to expected values using G-tests for each age class. In addition, average monthly survival rates were calculated for the three birthing months and the nine non-birthing months.

Results

Upper and lower estimates of nest survivorship were 91.7% and 64.6% respectively. Juvenile survivorship after weaning was 87.6%, thus total survivorship through the end of the juvenile phase was in the range of 56.6-80.3%. Yearly subadult survivorship (between 12-24 months of age) was 74.8%. This estimate for subadult survival may have been influenced by the premature dispersal of the PQ group subadults during 2004. In February and March 2004, all nine PQ subadults left their natal group and formed their own subgroup. Three of the five subadult disappearances recorded during the study were from this subgroup, thus typical rates of subadult survivorship are likely higher than 74.8%. Yearly adult female survivorship (all individuals over 24 months of age) was 70.8%. Adult female mortality during the birth season was higher than during the non-birth season (Figure 2). Nine of fourteen adult female disappearances occurred during the three months when adult females split from their groups and gave birth, which was significantly different from random (test name?, F= 24.23, P=<0.001). The average monthly survivorship for adult females was 94.3% during nesting, and 98.2% during the rest of the year. This seasonal mortality pattern was not found in group-living subadults (F= 1.73, P=0.189).

Both mating and births were highly seasonal (Table 3). In many cases, it was possible to determine the approximate length of the receptive period by examining genital swellings of the estrous females. In one case, an adult female was observed to be in estrus on August 9th, 2003, was observed mating on August 16th, and the gave birth between October 24-27th, which resulted in a 70-73 day pregnancy (EK, group SF). Individual females were observed in estrus for up to one week. The mating period generally lasted longer than one week, and in the case of the SF group during 2003, extra-group males were seen following the group for 19 days (July 31st to August 18th). There may have been a connection between the number of estrous females and the presence of more than one adult male. Groups with five or fewer adult females typically had only one adult male present during the mating season (PQ 2002, PQ and PSG 2003), while groups with multiple adult males all contained more than five adult females (GR 2002, SF 2003, SF, PSG, and GR 2004). In cases where mating was observed, offspring were born between 65-73 days afterwards. All births occurred during October, and we were able to determine accurately the age of older individuals in months by assuming that they were born during this month. In some cases, adult females in one group gave birth 1-2 weeks before females in other groups. Although the sample size was too small to test statistically, it appeared that births were highly synchronous within groups (all within 2-4 days), while females from different groups were less synchronous (within 3 weeks). In some cases, all births from the same group occurred within three days of each other.

Of the 12 radio-collared adult females, four died during the course of the study. One was killed by a car during the birth season (LP). An adult female which died from unknown causes during the birthing season, disappeared down a cliff and the body presumably rolled into the river (BR). One adult female disappeared from her group, and we could not find her signal (NC). This female was last heard in an area far from any accessible forest trails. Her remote location may have made it more difficult to find a weak signal. It is possible that her radio-collar was damaged during a predation event. Another female died from unknown causes after a serious injury (CY). This female was observed with a severe limp on her back left leg, and she was later observed to be unable to keep up with her group. After several days of ranging alone, her body was found at the base of a tree where she had remained inside or nearby for over 4 days. It was not certain whether she starved to death in the tree and the body was scavenged by a predator soon after, or whether she was killed by a predator after descending. Given that the corpse was found a few feet from the tree, the former scenario seems more likely. The corpses of two non-tagged coatis were found in the study area. The skull of one had a large tooth puncture in the crania which matched the size of an ocelot canine tooth. The other body had no visible markings on the skeleton, but was found under an uprooted tree in a manner which appeared to be the result of placement by a felid predator.

In 2004, an event occurred which influenced the calculations of subadult survival. During January 2004, the nine subadults in the PQ group dispersed and formed a new group. Although none of these subadults were radio-collared at the time, we regularly observed this subgroup throughout the year. Three of these subadults disappeared early in the year (February, March and April), one of the remaining six was last seen in June (which may have been the result of either dispersal of mortality), and the last five were seen alive through August. The mortality seen in this subgroup was much higher than subadults which remained in their natal groups. Of these nine subadults, two females survived to adulthood (AA, CC). These females were seen being followed by an adult male (IK, the adult male associated with the PQ group) after the PQ estrous period was finished, and it is possible that IK mated with them. During December 2004, these two adult females rejoined the PQ group with their newly born juveniles.

All four groups contained an adult male outside the mating season (Table 4). These males were socially integrated into the group, and regularly interacted with group members. If an adult male was temporarily separated from the group, when he rejoined, high pitched vocalizations, mutual sniffing, and mutual grooming were often displayed. In four cases, it was possible to determine the natal group of adult males. IK and TV were originally tagged as subadults in the GR group (born in 2000), and Dr.H and NR were originally from the SF group (born in 2001). These males ranged from 29 to 42 months of age when they were first observed in their (non-natal) groups. It is noteworthy that all four groups were spatially close, thus these four males did not disperse very far from their natal groups. In all four cases, these males lived solitarily for several months before entering another group. Group membership of adult males often changed just before the mating season (GR 2001, GR & PQ 2003). During the mating season, some groups attracted five or more adult males at the same time. These adult males were observed viciously fighting with each other, presumably for access to the estrous females (Booth-Binczik et al. 2004). In some cases (N= 6), adult males did not actually enter the groups during the mating season, and adult females were observed to drift away from their group, mate with an outside group male, then return to their group.

The adult male in the PSG group (VI), was observed more than any other adult male and his actions may be particularly useful for understanding adult male behavior in this species. VI accompanied PSG group for at least 21 months. The census taken in May 2005 found that he was no longer in the PSG group, and another adult male (NR) was found with the group. During 2003, VI was observed mating with at least two of the PSG adult females. A few days after mating, VI left the PSG group and temporarily joined the SF group. It appeared that the PSG group females came into estrus sooner than the SF females during 2003, thus after the PSG females were not in estrus, VI took the opportunity to mate with the SF females. After the SF females were no longer in estrus, VI returned to the PSG group. A similar behavior was seen in 2004, when VI left to pursue the GR group. In 2004, several of the PSG adult females were still in estrus during VI's absence. Two other adult males were found associated with the PSG group during this time, and two PSG females were observed mating with IK (the PQ adult male).

Discussion

Survivorship

In general, total survivorship in the Iguazu coati population was relatively high, especially for juveniles. Adult female survivorship was similar to study populations in

Mexico and BCI, but much higher than in the US (Hass and Valenzuela 2002, Gompper unpublished data). The low survivorship in the Huachuca Mountains may have been related to the reportedly high population density of pumas (C Hass, personal communication). Mortality of adult females was concentrated during the birthing season, which was also found in other populations (Hass and Valenzuela 2002). This seasonal mortality risk is likely evidence for the increased risk of predation when solitary, and further evidence of the anti-predation benefits of grouping (reviews: Krause and Ruxton 2002, Caro 2005). Subadults did not have higher mortality during this time, presumably because they remained in groups composed of other subadults and any adult females which failed to give birth (or females who returned to their group after losing their nestlings).

Juvenile survivorship in Iguazu was much higher than other coati populations, even when comparing the upper mortality estimate for nest deaths. Juvenile coatis had higher monthly mortality rates during the nesting season than during the rest of the year (minimum monthly survivorship estimates during nesting = 95.8%, monthly survivorship for the remaining ten months = 98.7%). This pattern of high nest mortality is consistent with previous work (Hass and Valenzuela 2002). However, it seems highly unlikely that the upper estimate of GG% is accurate. In Hass and Valenzuela's study, they assumed that adult females gave birth to an average of four offspring per year. If this assumption were applied to Iguazu, this would result in a nest mortality rate much lower than the upper estimate, and would be closer to the lowest possible estimate of nest mortality. When juveniles were seen immediately after returning to their groups in early to mid

December (PQ and PSG 2003, 2004, SF 2004), the mother to juvenile ratio was high (31:143= 4.61 juveniles per adult female). This estimate is lower if the complete dataset was used, which includes juveniles first contacted as late as mid-January (53: 221=4.25). Because adult females returned to their groups with such high numbers of juveniles per female, it appears that if a female had any surviving offspring, very little mortality occurred within a nest. On the other hand, other adult females had 100% nest mortality. The demographic data are consistent with the hypothesis that nest mortality resembled an "all or nothing" pattern. This makes sense if nest deaths are primarily due to predation. It seems plausible that if a predator encountered a coati nest, they would eat all of the juveniles rather than just one or two (assuming an unlimited predator gut capacity). Even given total loss of offspring in attacked nests, nest mortality was low compared to other coati sites (Saenz 1994). Because adult females nested in highly inaccessible and well-hidden locations, it may have been difficult for potential predators to find and enter the nests. Regardless of which nest mortality estimate is used, the overall juvenile survivorship was fairly high compared to other populations. The high overall juvenile survivorship led to groups with high ratios of juveniles to adult females (often 5:1 or higher). This pattern is unusual, and it is plausible that group demography could have influenced other aspects of the coati social system, such as dominance relationships.

It is currently unclear what impact predator densities have on coati survival. The population densities of felid predators are lower in Iguazu than other coati study sites. On BCI, no jaguars were present and pumas were not present year round, but there were many more ocelots on BCI than in Iguazu. Although coatis were not the major prey item of BCI ocelots, coati remains were regularly found in ocelot scats (6.8% of scats, Moreno et al. 2006). Felids were more abundant in Jalisco, Mexico, than Iguazu. Although ocelots were especially abundant in Jalisco, coati remains were never found in ocelot scats (de Villa Meza et al. 2001). Coatis are known to be preyed on by jaguars and puma in Iguassu National Park, Brazil (present in 8.2% of jaguar scats and an unknown percentage of puma scats), but coati remains were not found in 56 ocelot scats (Crawshaw 1995). I found evidence of at least one ocelot-coati predation event, and my impression was that ocelots were much more common in the coati home ranges than all other felids (based on footprint sightings). Even though Iguazu has lower predator densities than other coati field sites, adult female mortality in Iguazu was within the same range as other populations (Hass and Valenzuela 2002). The major differences in mortality between coati study sites appeared to be linked to juvenile survivorship (during both nesting and post weaning). It is plausible that lower predation pressure benefits juveniles more than other age/sex classes.

One notable aspect of these survivorship patterns is that there is net positive recruitment into established groups. If adult females give birth to 4.6 offspring per year, with approximately 10% of those lost to nest predation, 2.7 of these will survive to adulthood. Even if coati females gave birth to only 4.6 offspring over the course of their lifetime, these survivorship rates would lead to an increase in total group size. The pattern of increasing group size is exactly what was seen over time, as some groups got larger each year. In one case, the GR group split in half, and this may be why extraordinarily large groups were never seen (e.g. Booth-Binczik 2001). Even then, it appears that the coati population in Iguazu is not stable. The one group that shifted their home range away from the waterfall area suffered an increase in mortality (GR), and it seems plausible that something akin to a source-sink population dynamic is occurring. Groups near the waterfalls and cliffs may be expanding at unstable rates, but when these groups split up and disperse, they may go to areas of the park where they suffer much higher mortality. The long-term impacts of these high survivorship rates are unclear, and long term monitoring needs to be conducted to fully understand the population dynamics at this site.

It appears that there is a link between a group's habitat use and its predation rate. It is plausible that the use of the tourist areas would decrease predation threat, because the presence of humans could scare away predators (Isbell and Young 1993). Ocelots and puma were observed in and near the tourist areas, but it is likely that they visited these areas less frequently than areas with no human disturbance. If human presence was the primary reason for low mortality rates, it seems reasonable that groups which used these areas less often would have higher mortality. In general, the PQ and PSG groups spent the most time near the tourist areas. GR was frequently observed in there areas during 2001 and 2002, much less during 2003, and almost never in 2004. The SF group rarely used the tourist areas during all study years. Of these four groups, all had similar survivorship patterns except for the GR group during 2004. This was the year that the group spent almost all of their time ranging south of the waterfalls. During 2004, the GR juveniles had a 57.4% survivorship after 8 months (yearly survivorship was not known). In addition, the adult female survivorship during this period was 55.5%, which was far lower than any other group during any year. In this study, the only adult female disappearances outside the birth season occurred in the GR group during 2004 (N=4). The SF group also rarely used the tourist areas, but did not suffer similar mortality rates. If tourists were largely responsible for scaring away predators, it stands to reason that the SF group would have had similarly high mortality rates. A reason why the SF group did not have higher mortality rates may have been their use of steep cliffs along the Iguazu River. It was common to find the SF group ranging in or near the cliff. This behavior made it difficult for us to follow the group, but might have deterred predators as well. The PQ and PSG groups also spent a considerable amount of time on or below the cliffs. When the PQ group ranged to the north of the waterfalls, they were typically found below the cliff edge. On the other hand, the GR group did not have access to cliffs in the area above the waterfalls. It is plausible that the reason group GR suffered such high mortality during 2004 was because they ranged in areas with little or no protection from predators. In contrast, the other groups typically spent large amounts of time in or near cliff edges or tourist areas.

Premature subadult dispersal

The premature dispersal of the PQ subadults may have been the result of an increase in feeding on trash and tourist food. During late 2003, the PQ group began spending significant amounts of time nearby a tourist restaurant where they would raid trash cans and steal food from tourists. Although the percentage of time that the group actually spent feeding on these foods was not high (<5%), these foods appeared to be highly preferred and easily contestable. Although these foods did not appear to change normal dominance patterns in the group, they may have caused an increase in the frequency of aggression (Hirsch in press). Because subadults were the lowest ranking group members, and because fights between adult females and subadults are especially common from December- April, the PQ subadults may have been subjected to frequent violent aggression during the time of their dispersal (Hirsch in press). Additional evidence supports this conclusion. As the PQ juveniles born in 2003 became subadults, they were also found to prematurely disperse from their group during December 2004. In addition, after the conclusion of this study, it was reported that the PSG started to spend significant amounts of time searching for human foods. During 2005, the PSG subadults split from their natal group (Yamil Di Blanco and Carolina Ferrari personal communication). Although the presence of these man-made foods did not appear to influence the patterns of dominance, it may have led to drastic changes in the makeup of the social groups. These results support the contention that wildlife and park managers should prevent wild animals from feeding on human foods in order to assure that the social groups do not develop atypical social patterns.

Mating and birth seasonality

Mating and births were highly seasonal. Although the exact length of estrus could not be determined, it appeared to vary between 5-7 days for an individual female and the maximum total mating period for a group (SF 2003) was 19 days. Direct observations of births were not possible, but it appeared that births were highly synchronized within groups. The lack of synchrony between groups made it possible for at least one male to mate with females of more than one group (VI 2003). Adult males may have been able to prevent others from entering the group and mating with adult females when few adult females were present (five or less), while higher numbers of females were typically accompanied by an influx of adult males during the mating season (cf. Cords 2000). It is plausible that adult males within a social group are better able to fight off non-group males, or have preferential mating relationships with group living adult females. This may lead to increased mating success, but not monopolization of mating (Gompper et al. 1997). Adult females were observed temporarily leaving their groups to mate with outside group males. The degree to which adult male group membership leads to increase reproductive success needs to be addressed in future genetic studies.

Adult male sociality

Adult males were found in all four social groups for several continuous months outside the mating season. This pattern contrasts sharply to patterns observed in white-nosed coatis (Gompper and Krinsley 1992). Given this difference, it is important to discuss the applicability of Gompper's (1996) hypothesis of male asociality in white-nosed coatis. Adult males were found to have lower food intake rates when with a social group compared to being solitary. Because predation rates on BCI are not particularly high, Gompper hypothesized that the foraging benefits of living alone outweighed the increased predation risk. It is also notable that this pattern of adult male asociality occurs in populations of white-nosed coatis with higher predation levels (Hass and Valenzuela

2002). If male sociality is determined through a balance of predation threat and foraging costs, why would adult male ring-tailed coatis in Iguazu live in groups?

The predation threat in Iguazu is comparatively low, thus it was unlikely that increased predation pressure was driving adult male sociality. Although no foraging data were recorded for solitary adult male coatis, group size was inversely related to invertebrate foraging rates (Hirsch in prep). When feeding on fruit, adult males had similar intake rates to other age/sex classes, but adult males were found at fruit trees significantly less frequently than all other age/sex classes (Hirsch in prep). It appears that even though adult males are the highest ranking age/sex class in coati dominance hierarchies, there was a trend for adult males to be lower ranking in larger groups (Hirsch in press). This pattern suggests that adult males may be vulnerable to coalitionary aggression from teams of related females, which could explain their avoidance of fruit trees relative to other age/sex classes (e.g. Gompper et al. 1997, Hirsch in prep).

It appeared that adult male coatis in Iguazu also had incentives to forage alone (Hirsch in prep). Given that adult male sociality patterns in ring-tailed coatis appear to contradict the predictions of Gompper (1996), why are adult males in groups? It is plausible that adult males live in groups for other reasons such as parasite reduction or access to females (Gompper 2004). Living in a group may make it easier for an adult male to gain access to females during the mating season. It seems plausible that group living adult males could have mated with most or all adult females in their group, and living with a group outside the mating season may lead to increased mating opportunities during the mating season. In some cases, adult male membership changed less than one month before the mating season, and it appeared that the new male was bigger and stronger than the previous male (N= 3). By aggressively entering the group just prior to the mating season, these new males may have gained increased access to females (cf. Cords 2000). This access to females may not translate into mating success. Males in white-nosed coati groups during the mating season were not found to sire the majority of offspring in the group (Gompper et al. 1997). To test this hypothesis in ring-tailed coatis, further genetic work needs to be conducted.

Observations of other ring-tailed coati populations have demonstrated that male sociality might be a species wide behavioral pattern. Adult males have regularly been seen in groups outside the mating season in three different coati populations in Brazil; Mangabeiras Park, Minas Gerais; Tiete Ecological Park, Sao Paulo; and Campeche Island, Santa Catarina (Alves-Costa et al. 2004, Resende et al. 2006, and Juliano Bonatti personal communication). Even though the ecology of these ring-tailed coati sites is presumably very different, adult male sociality has been observed in all four sites. This supports the hypothesis that adult male sociality is a species wide trait, and may not be a flexible behavior which is heavily influenced by localized costs and benefits. More detailed work on adult male sociality is needed to sufficiently test this hypothesis.

Conclusions

Average birth cohort size (minimum average = 4.6) was higher than estimates for white-nosed coatis (4 individuals, Hass and Valenzuela 2002). The time of highest mortality risk was during nesting, and nest deaths likely occurred in an “all or nothing” pattern. The high reproductive rate combined with high survivorship, particularly for juveniles, resulted in non-stable groups which increased in size over time. This ecological condition was likely related to the presence of humans and large cliffs, which may have reduced the threat of predation. Previously studied populations of ring-tailed coatis were also studied in areas with a significant human presence (Mangabeiras Park and Tiete Ecological Park, Brazil). In order to determine the exact effects these growing populations have on coati demography, and group membership, it would be preferable to study coatis in populations which have little or no human influence.

The group structure of ring-tailed coatis in Iguazu, Argentina is different from that reported for white-nosed coatis in that adult males were regularly observed associated with groups for extended periods of time. It is unlikely that these adult males were traveling with their natal groups, and in four cases, it was known that group living adult males transferred from another group. Although this behavior was flexible and some groups were found without an adult male for more than three consecutive months, the typical ring-tailed coati group included one adult male. This pattern may be normal for the species, as adult males have been observed in groups outside the mating season in at least three other ring-tailed coati populations. The exact reasons for these patterns are unclear. Because similar patterns have been reported for other ring-tailed coati populations, this behavior may not be heavily influenced by local ecological conditions.

Solitary white-nosed coati males have been observed in a wide variety of ecological conditions as well (Kaufman 1962, Hass and Valenzuela 2002, Booth-Binzcik et al. 2004), and it appears that sociality (or lack thereof) in coatis may be driven by something other than local ecological conditions.

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Table 4.1. Group membership by age/sex class in the four study groups. Question marks indicate cases when it was difficult to determine whether some individuals were large subadults or adult females. Numbers for 2005 were taken during late December 2004 and represent the upper estimate of group membership during 2005.

Group	Year	Adult males	Adult females	Subadults	Juveniles	Total group size
PQ	2001	1	1	0	6	8
	2002	1	1	3	3	8
	2003	0-1	3	2	9	14-15
	2004	0-1	5	0	19-25	25-30
	2005	1	7	0	31	40
PSG	2003	0-1	5	0	6	11-12
	2004	1	5	6	15-17	27-29
	2005	1	6	14	31	52
GR	2001	1	?	?	32	51
	2002	1	?	?	?	54
	2003	0-1	7	10	0	17-18
	2004	0-1	5-10	0	23-40	28-51
SF	2001	1	?	?	11	23
	2002	1	?	?	?	~25
	2003	1	9?	6?	12	28
	2004	1	8	11-12	23	43-44
	2005	1	10	20	34	65

Table 4.2. Calculated minimum and maximum survivorship estimates of juveniles in coati nests. Minimum values were derived from estimates that adult females gave birth to at least four offspring per nest. Maximum values were calculated with the assumption that all coatis gave birth to the maximum of six offspring.

Group	**Year**	**# females**	**lost litters**	**max #**	**observed #**	**min. nest deaths**	**max. nest deaths**
PQ	2002	3	0	18	9	0	9
	2003	5	0	30	30	0	0
	2004	7	0	42	31	0	11
PSG	2002	2	?	12	6	0	6
	2003	3	2	30	17	8	13
	2004	6	1	42	31	4	11
GR	2003	10	?	60	40	0	20
SF	2003	6	2	48	23	8	25
	2004	10	?	60	34	0	26
	Totals:	**52**		**342**	**221**	**20**	**121**
						Minimum % survivorship	**Maximum % survivorship**
						0.917	0.646

Table 4.3. Reproductive seasonality data for 2003. The first nine females had radio-collars placed on them at the time of study. The first and last possible day of birth was determined as described in the text.

ID	Collar	Group	Mating seen	First possible day	Observed/movement
AY	Yes	PQ	no	Oct. 20	Oct. 25
AN	Yes	PQ	no	Oct. 20	Oct. 27
GZ	Yes	PQ	no	Oct. 20	Oct. 28
PS	Yes	PSG	prob 8/4/2003	Oct. 9	Oct. 11
GH	Yes	PSG	prob 8/4/2003	Oct. 9	Oct. 15
SD	Yes	GR	no	Oct. 19	Oct. 25
NC	Yes	GR	no	Oct. 17	Oct. 20
EK	Yes	SF	8/16/2003	Oct. 24	Oct. 27
BR	Yes	SF	no	Oct. 25	Nov. 3
PT	No	SF	no	?	Oct. 28
MA	No	PQ	no	After Oct. 16	Oct. 24
DA	No	PQ	no	After Oct. 16	Oct. 27
NY	No	PSG	8/4/2003	After Oct. 7	Oct. 22
JW	No	PSG	8/4/2003	After Oct. 1	Oct. 14
HA	No	GR	8/13/2003	?	?

Table 4.4. Adult male residency in four coati groups. – denotes that the group was not yet formed. A question mark indicates that the group was not censused during that month. Unmarked adult males were recorded as LA (light adult) or DA (dark adult) depending on coat color. In two cases, unmarked adult males were recognizable by morphological features; LA males CT (cut tail) and NM (notch missing). Adult males with a question mark after their ID are ambiguous, these adult males were either untagged, and looked similar to the previous years adult male (DV), or appeared to be a marked adult male with a missing ear tag (BF). Numbers in parentheses are the age in months of males when first entering the group.

Year/month	**PQ**	**PSG**	**SF**	**GR**
2001				
June	LA male	-	LA male	SF
July	LA male	-	LA male	SF
August	LA male	-	?	DV
2002				
June	EH	-		DV?
July	EH	-	LA male (CT)	?
August	EH	-	LA male (NM)	DV?, VI
September	EH	-	LA males (CT and NM)	MD
October	none	-	?	MD
November	none	-	?	MD
December	none	-	?	MD
2003				
January	none	-	LA male (CT)	MD
February	none	-	?	MD, VI
March	IK (29)	VI	?	?
April	IK	VI	?	?
May	IK	VI	?	None
June	IK	VI	?	LA male
July	OB1	VI	LA males (CT and NM)	MO
August	OB1	VI	VV, WW, VI, BF, MP	MO
September	OB1	VI	IK/LA male (CT)	?
October	none	VI	?	MO
November	OB1/none	VI	IK	?
December	none	VI	IK	None

2004				
January	none	VI	IK	None
February	IK/none	VI	IK	None
March	IK	VI	?	None
April	IK	VI	TV (42)	BF?
May	IK	VI	TV	?
June	IK	VI	?	Dr. H (32), BF?, NR (32)
July	IK	VI	?	NR
August	IK	VI, BF?	TV, LA male, DA male	NR, VI, DA male
September	IK	VI, DA male	?	?
October	?	?	?	?
November	?	?	?	?
December	IK	VI	TV	?

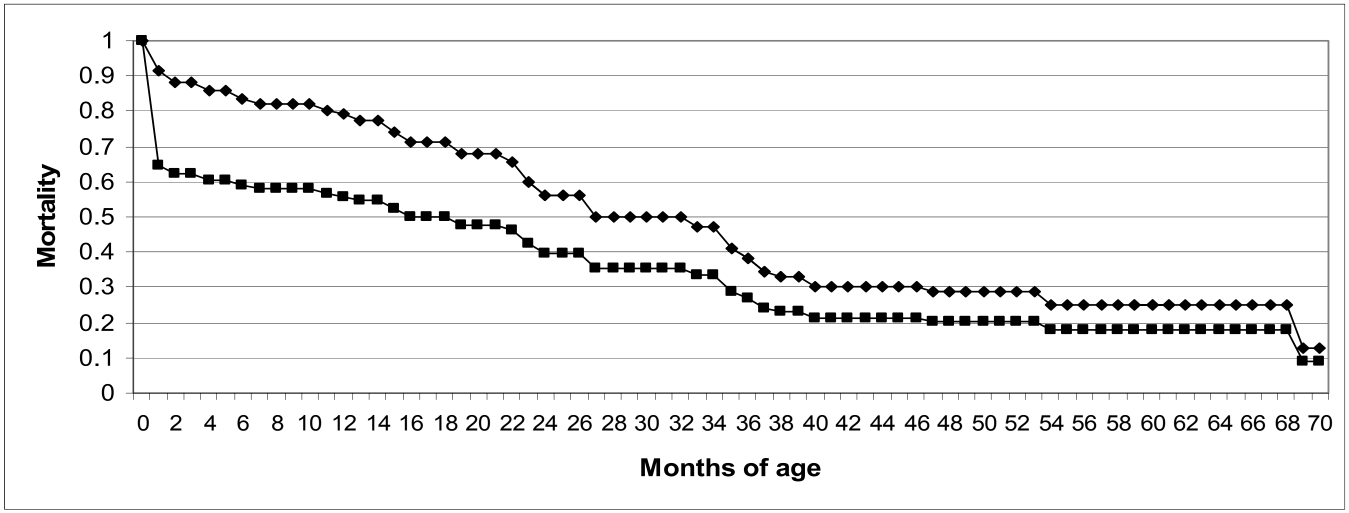

Figure 4.1. Kaplan-Meier survivor curves. Upper line was calculated using the minimum nest mortality estimate, and the lower line was calculated using the maximum nest mortality estimate.

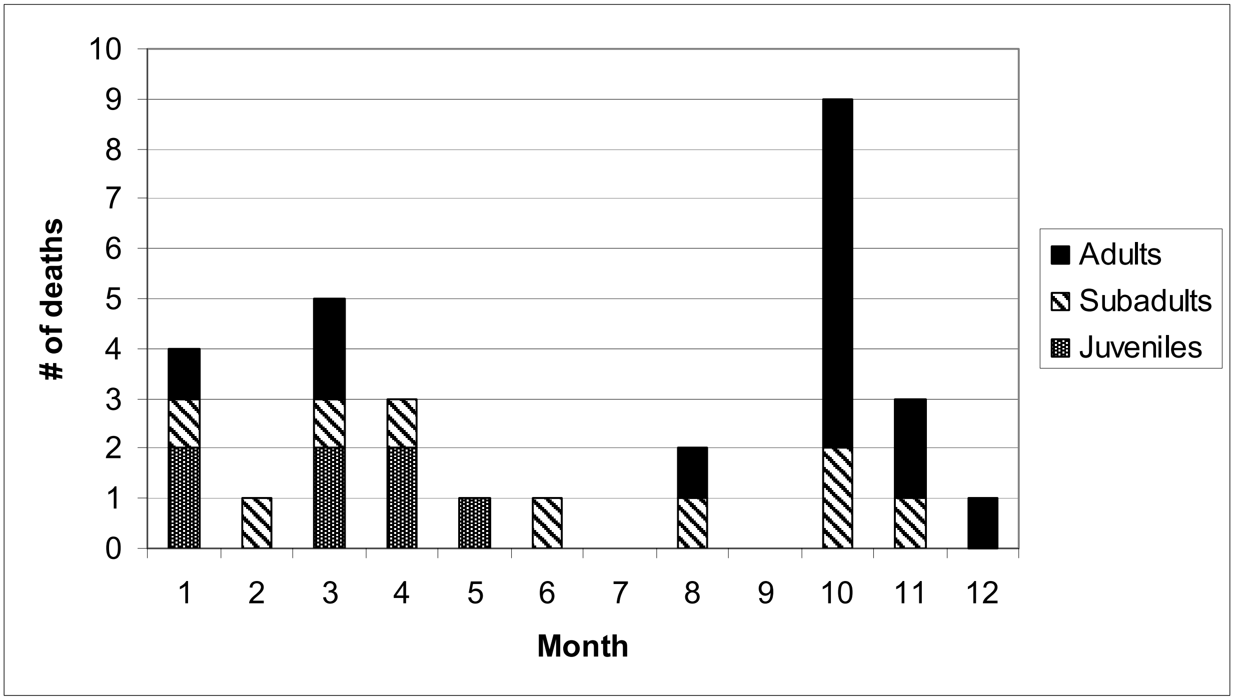

Figure 4.2. Age class mortality/disappearances by month. Only weaned coatis were included, and juvenile nest deaths were excluded. Months 10-12 represent times when adult females could have been separated from their group to give birth.

Chapter 5

Spoiled Brats: is Extreme Juvenile Agonism in Ring-Tailed Coatis (*Nasua nasua*) Dominance or Tolerated Aggression?

Abstract

Ring-tailed coatis exhibit an extreme form of juvenile agonism not found in other social mammals. Two groups of habituated, individually recognized, coatis were studied over a 2.5 year period in Iguazu National Park, Argentina. Dominance matrices were divided by year and group, resulting in four dominance hierarchies which were analyzed using the Matman computer program. Strong general patterns were seen in both groups during both years. Adult males (one per group) were the highest ranking individuals, followed by male juveniles, female juveniles, adult females, and male and female subadults. The pattern in which young, physically inferior individuals were able to outrank larger adults is different from other social mammal species in that the juvenile coatis aggressively defended food resources and directed aggression towards older individuals. These agonistic interactions may not reflect "dominance" in the traditional sense, and appear to be a form of "tolerated aggression." This tolerated aggression leads to increased access to food, and should help juveniles during a period in which they need to gain weight and grow rapidly. Because this tolerance of juvenile aggression is reinforced through coalitionary support of juveniles by adult females, agonistic patterns are also consistent with the hypothesis that juvenile rank is being influenced by high

degrees of relatedness within coati groups,. Although some interesting parallels exist, these dominance patterns do not appear to be the same as those found in other social mammals such as hyenas, lions, meerkats, or Cercopithicine primates.

Introduction

Juvenile dominance over older individuals has been reported in some species of social mammals, especially matrilineal primate species. In many macaque societies, young juvenile monkeys are able to usurp resources and direct aggression towards older, larger group members due to maternal support (Kawamura 1958, van Noordwijk & van Schaik 1999). In some species of macaques, a pattern of "youngest ascendancy" occurs in which young female offspring are supported by their mothers over older sisters (Datta 1988, Chapais 2004). In Hanuman langurs, which exhibit the classic "age-inversed" dominance hierarchy, female rank is inversely related to age. In this case, young breeding females are assumed to have a greater need to obtain high dominance rank to increase their reproductive success, while older females at or near the end of their reproductive lifespan have less need to maintain a high dominance rank (Borries *et al.* 1991). Authors have hypothesized both juvenile tolerance and juvenile-juvenile coalitions as the proximate mechanisms driving age inversion in langurs (Hrdy and Hrdy 1976; Borries *et al.* 1991). Tolerance for juveniles is also found in cooperatively breeding meerkats. Small juvenile meerkats are tolerated during feeding and actively supported by older group members. Clutton-Brock and collaborators (Clutton-Brock *et al.* 1999; Kokko *et al.* 2001; Clutton-Brock 2002) found that larger meerkat groups are able to outcompete other groups, have lower costs of raising offspring, lower mortality, and higher breeding success. These authors conclude that meerkats likely aid young juveniles to augment group size, thus resulting in higher fitness levels for older group members.

Coatis (*Nasua spp.*) exhibit similarities to other social mammals with juvenile dominance or tolerance. Coatis are female philopatric and have the ability to form matriline based dominance hierarchies (Gompper 1996). Coati growth rates and litter sizes (2-6) are similar to other social carnivores such as meerkats, but unlike meerkats, most or all adult females give birth (Clutton-Brock et al. 1999). Births are highly seasonal and adult females nest independent from one another. Previous authors have stated that adult female white-nosed coatis (*Nasua narica*) exhibit juvenile "tolerance," yet do not fully describe or quantify this behaviour (Russell 1982, Gompper 1995). In addition, no authors have suggested a proximate or evolutionary mechanism for the presence of this behaviour. The purpose of this report is to 1) describe the system of dominance for the ring-tailed coati (*Nasua nasua*), and 2) evaluate the possible proximate and evolutionary functions of juvenile dominance/tolerance in ring-tailed coatis.

Methods

The study was conducted at the Iguazu Falls National Park, Argentina (see: Brown and Zunino 1990; Di Bitetti 2001a,b). Dominance interactions were recorded opportunistically from the PQ and PSG groups between July 2002 and December 2004 (Table 1.). In order to place radio collars and mark animals, the coatis were captured using 32x10x12 inch Tomahawk or similar traps. The coatis were anesthetized with the assistance of a veterinarian. All individuals were individually recognized by multi-colored plastic eartags (Dalton Rototags), or radio-collars. Eartags were not placed on juveniles less than four months of age. The coati groups were usually habituated within two to three weeks. We were able to follow habituated individuals within 2m without disturbing them in areas of open forest. Because the coatis were scared by loud noises such as broken branches, the observers followed the groups as quietly as possible.

Coatis spent most of their time foraging for ground litter invertebrates, which is consistent with another study of ring-tailed coati diet (Alves-Costa et al. 2004, 70-92% of all group scans Hirsch unpublished data). Fruit and invertebrate food availability is lower during the winter months (Di Bitetti 2001b, Beisiegal and Montovani 2006, Hirsch unpublished data). The most important fruit species for coatis in Iguazu are pindo fruits which are available year round, but typically peak during February-May (Di Bitetti 2001b). Coatis fed on pindos during 44% of all scan samples in which fruit was being eaten (Hirsch unpublished data). Both groups would occasionally use areas which overlapped with human visitors. During these periods, trash or human foods were sometimes available inside the group spread (<3-4% of scan samples). When coatis were in these areas, we guarded trash cans or any non-natural food to prevent the coatis from attempting to feed.

Coatis were divided into three age classes: juveniles, subadults, and adults. When young coatis (7-8 weeks of age) descended from their nests and first join the groups they were defined as juveniles, and were two to four times smaller in weight than subadults and adults (BT Hirsch unpublished data). By this age they were weaned and ate fruit and ground-litter invertebrates. During October, when pregnant adult females leave their groups to give birth, the previous year's juveniles are then 12 months old. Subadults are defined in this study as male and female coatis between 12-24 months of age. This definition is not perfect, but appears to reflect true behavioural differences. Subadult female coatis are able to conceive at 24 months of age. At 24 months of age, the "newly adult" males disperse from their natal groups and become solitary. Despite being defined as "adult" these 24 month old male coatis were never seen mating with an adult female, and they did not reach typical adult male body weights until 26-30 months of age (BT Hirsch unpublished data). Unlike white-nosed coatis (*Nasua narica*), ring-tailed coati groups typically have one adult male associated with each group (Resende et al. 2004, BT Hirsch unpublished work, Alves-Costa personal communication). In cases where age could be determined, these group living adult males were all over 28 months of age (N=4). During the mating season, some groups were followed by several solitary males and adult females likely mated with multiple males. During this 2.5 year study period female ring-tailed coatis were never observed or suspected of changing or entering other groups. This pattern of 100% female philopatry in Iguazu differed from Gompper et al. (1997) who found several examples of white-nosed coati adult females that were not related to other group members.

All agonistic interactions were recorded ad libitum by the author, or by field assistants trained for at least 2 months. When both myself and one of the four field assistants simultaneously recorded an agonistic interaction, over 95% the samples were identical (N=63). When an agonistic interaction was observed, the initiator, recipient, winner, context of the aggression, and type of agonism were recorded. In some cases, the individual who initiated the interaction was not seen, but the winner and loser were observed. The winner was defined as in Gompper (1996). If one individual directed agonism towards a conspecific, and the recipient did not defend themselves, the recipient was considered the loser. If an individual gained or maintained possession of a food item after an agonistic interaction, they were defined as the winner. All interactions with unknown individuals were not used in the dominance hierarchy analyses. A larger data set (N= 1575) which also included unknown individuals was used in an analysis of effects of age, sex, context, and type of agonism. In this larger data set, some individuals were recognizable by age class but not by individual ID. Six types of agonism were recorded (in order from least to most aggressive); avoidance, displacement, aggressive vocalization, lunge, bite, chase, and escalated fighting. The most common type of agonism, lunging, occurred when one coati would lunge their head in the direction of another. This type of interaction was typically, but not always, accompanied by a sharp aggressive vocalization. Any interaction which involved more than two individuals was noted and used in a separate analysis. Polyadic interactions were often difficult to fully observe, thus the percentage of coalitionary interactions in the data set is likely an underestimate. Agonistic events were classified as a coalition when two individuals directed agonism at a third, or a third individual came to the aid of another during an agonistic event.

Dominance matrices of dyadic interactions were constructed using two groups (PQ and PSG), with the 2003 and 2004 seasons separated (Nov. 2002-Oct. 2003, Nov. 2003-Oct. 2004). The four dominance matrices were reordered and all matrix statistics were determined using the Matman program version 3.1 (de Vries et al. 1993; de Vries 1995). Average dominance ranks were adjusted for group size. The rank of each individual was divided by group size, and then averaged by age/sex class. This resulted in a value between 0 and 1 for each age sex class, which was then multiplied by the average group size (20.75). The resultant values represent the average rank per age/sex class in a standardized average group of 20.75 individuals. Any agonistic interaction that simultaneously involved more than two individuals was classified as a coalitionary interaction. These interactions were not necessarily coordinated. For example, if two juveniles simultaneously attacked an adult male, it was recorded as a coalition. If the two juveniles attacked the adult male sequentially, they were recorded as two separate dyadic interactions. Coalitionary interactions were broken down by age/sex class. In the analysis of adult female support for juveniles, maternity was assigned using grooming data (Hirsch unpublished work). All observed grooming interactions were entered into a similarity matrix, and juveniles were assigned maternity based on the number of grooming bouts received by each adult female (which were highly skewed towards the presumed mothers). Only individual juveniles that were groomed significantly more by one female than any other females was assigned a mother. Maternity of juveniles in the PQ group during the 2003 season were excluded from the analysis because the grooming data was not sufficient to statistically determine maternity.

Results

Dominance patterns.

A total of 1079 dyadic interactions were used in the dominance matrix analyses (PQ 2003= 93, PQ 2004= 266, PSG 2003= 184, PSG 2004= 539)(Tables 2abcd). Adult males had the highest average rank of any age/sex class (4.3), followed by male juveniles (5.9), female juveniles (11.3), adult females (16.3), subadult females (17.6), and subadult males (18.4). With the exception of the PQ group during the 2003 season, all dominance hierarchies were significantly linear (Table 3). The directional consistency indexes varied from 0.63-0.78, and a high proportion of two-way interactions were recorded (Table 3). Even though the number of reversals was relatively high, the patterns found by age/sex class were still robust. Adult males won 68.0% (N=100) of interactions against juveniles, 85.5% (N= 62) against adult females and 92.3% (N= 52) against subadults. Juveniles (both male and female) won 84.2% (N=234) of interactions with adult females and 82.8% (N=87) against subadults. Juvenile dominance over adult females did not vary in relation to the adult female:juvenile ratio (percentage of interactions won and adult female:juvenile ratios; PSG 2003= 80.7%, 5:6, 2004= 89.0%, 5:15; PQ 2003= 82.4%, 3:9, 2004=82.2%, 5:23)(P=0.730, linear regression). Juveniles directed aggression towards their presumed mothers in 19.9% of interactions towards adult females (33 out of 166). During years in which maternity could be assigned, the PQ and PSG groups contained five adult females; thus, juveniles were not directing more or less aggression towards their mothers than at random (G-test, DF=1, Chi^2=0.001, P=0.975).

Adult females won 78.8% (N= 118) of interactions against subadults. These interactions were more common when juvenile coatis were less than six months old. A total of 83 cases of adult females winning agonistic interactions versus subadults were observed (from the PQ 2003 and PSG 2004 group years). Of these interactions, 83.13% occurred when juvenile coatis were 6 months of age or less (December-May). Few or no interactions were recorded from October and November when most groups had disbanded. The lopsided pattern was further evident when compared to the total number of agonistic interactions recorded (December-April= 274, May-September= 488). Adult female domination of subadults represented 25.18% of all agonistic interactions during the first time period, and then dropped to 3.07% when juveniles were older than six months of age. Although average rates of aggression could not be assigned because of the ad libitum sampling protocol, it appears that rates of aggression between adult females and subadults vary significantly over time.

Context and type of agonism.

Almost all agonistic interactions where the context was known occurred during feeding and foraging (96.8%). A small fraction (3.2%) occurred in social contexts such as grooming, rest, or play. It was not possible to accurately determine the context in 14.6% of the interactions. These indeterminate samples were often observed after the initiation of the agonistic interaction or the context appeared ambiguous to the observer. Differences were found in the type and context of agonism by age class. When an agonistic interaction was instigated by a juvenile, it typically occurred during fruit feeding (51.1%). Adults and subadults instigated agonism during fruit feeding much less than juveniles (28.6% and 26.4% respectively). When juveniles initiated an agonistic encounter, they were more likely to lunge at their opponents (78.4%) than subadults and adults (57.6% and 42.4% respectively), and less likely to chase or fight with their opponent (juveniles= 13.5%, subadults= 26.3%, adults= 40.5%). Fights between adults and subadults were particularly violent, and 47.1% involved chasing or escalated fighting (Table 4). Additionally, in 18.9% of the interactions between adults and subadults, the subadults actively avoided the adult. This high number of avoidances compared to other age/sex classes probably reflects a strategy of the subadults to escape aggression from adults by using spatial avoidance. There were no significant differences between the sexes in the type of agonism used.

Pindo palm fruits were the most common resource at which food-related agonism took place (33.6% of all agonistic interactions). Coatis were observed feeding on pindo fruits during 8.45% of foraging scan samples, and pindo made up 43.76% of fruit foraging time. The amount of agonism observed during pindo foraging was statistically more than expected based on foraging time (G-test, DF=1, Chi^2=540.65, P<0.001). Although some coatis would climb into palm tree fronds to eat fruit (typically 1-5 individuals at one time), the bulk of the group usually consumed fallen fruits in the fruit shadow (which typically ranged from 1.5-3.5m in diameter). When feeding below these fruit trees, juveniles and adult females were rarely forced to leave the fruit shadow, but would aggressively compete for individual fruits. In contrast, subadults were sometimes chased out of these feeding patches or avoided them altogether (Hirsch unpublished data). The common usage and clumped distribution of pindo fruits may be important in driving the type of agonistic encounters found. These dietary patterns appear analogous to the reliance of *N. narica* on *Scheelea* fruits on BCI. There were no differences in agonistic patterns when coatis fought over non-natural foods. There was also no indication that agonistic patterns changed during the peak tourist season (July and August), which also corresponded to the period of lowest natural food availability.

Coalitionary patterns.

Coalitionary interactions occurred at similar levels as recorded in *N. narica* (Gompper *et al.* 1997) (N= 79, 6.8% of all interactions with known individuals). Coalitions occurred in almost every age/sex class combination possible. Thirty-three of these coalitionary interactions involved adult females supporting juveniles. Adult females aided juveniles against subadults (N=6) and adults, both male and females (N=22), more frequently than against juveniles (N= 5) (G test, X^2= 43.47, P<0.001)(Figure 1). Out of these 33 cases, the maternity was known/suspected in 19 cases. In 12 out of the 19 cases, the supported juvenile was not the offspring of the adult female who helped. The females who supported juveniles were likely their aunts or grandmothers. In one case a subadult female was observed supporting a juvenile versus an adult male. No other instance of a juvenile being aided by subadults, or an adult male were seen. No coalitions were recorded which only involved juveniles and not at least one older individual. Juveniles formed coalitions among themselves towards older individuals a total of 14 times, 8 times against adult females, 4 times against subadults, and 2 times versus adult males.

Discussion

Despite a high number of reversals, patterns of coati dominance were clear. Adult males were the highest ranking on average, followed by juvenile males, juvenile females, adult females, and subadults. The patterns found with respect to adult females and juveniles are different compared to previously studied dominance patterns in primates and other social mammals, but may fall somewhere between the nepotistic aggressive social systems of macaque societies, and the tolerant cooperative breeding system of meerkats. The relationship between adult females and subadults was particularly hostile when juveniles were six months of age or less. During this period, there was a large number of escalated aggressive interactions between adult females and subadults, and subadults were commonly seen avoiding adult females. This agonism likely played a large factor in the premature emigration of the PQ subadults during 2004.

Possible mechanisms leading to juvenile "dominance"

Matrilineal support.

The patterns of dominance found in ring-tailed coatis were not similar to female bonded primate and hyena societies with matrilineal dominance hierarchies. In these social systems, juveniles typically rank just below their mothers, and above females of lower ranking matrilines (Cheney 1977, Hausfater *et al.* 1982, Chapais 1992, Holekamp et al. 1996, Engh et al. 2000, Chapais *et al.* 2001). In ring-tailed coatis almost all juveniles were ranked above all adult females, a pattern unlikely to be produced through maternal coalitionary support. Even though support from mothers is not driving juvenile dominance in ring-tailed coatis, support of all juveniles by all group living adult females appears to play an important role in shaping the dominance system. Females did not preferentially support their own offspring, but did support juveniles over older individuals more than expected by chance. Adult female white-nosed coatis have been found to direct more aggression towards unrelated females (Gompper et al. 1997), but it is unclear if this behavior would transfer to within-group offspring of unrelated females as well. In order to properly test the effects of inclusive fitness on juvenile support and tolerance, it would be ideal to study a group where at least one of the adult females had immigrated into the group and was not closely related to the other adult females.

Juvenile coalitions and mobbing.

Juvenile coatis may be able to form coalitions with each other in order to dominate older individuals (Chapais and Gauthier 2004**.** Little evidence was obtained to support this hypothesis. Only 14 coalitions of juveniles against older individuals were recorded. Even if juveniles do not actively form coalitions against older individuals, their sheer numbers in the group might allow them to "mob" other group members. In several cases, we observed an adult female run away from small concentrated food patches (such as pindo fruit shadows) after being repeatedly attacked by several juveniles acting independently. It appeared that the aggression directed towards the adults and subadults was so bothersome and annoying that the costs of aggression outweighed the benefits gained by feeding. If this mobbing hypothesis is correct, juvenile dominance patterns should vary depending on the relative numbers of adult females and juveniles. However, the patterns of juvenile dominance were the same for all group years despite wide variance in the adult female/juvenile ratio (from 5/6 to 5/25). Juveniles in the group with the highest adult female to juvenile ratio (PSG 2003= 5/6) won a similar percent of interactions versus adult females compared to other group years, thus there was no discernable effect of adult female juvenile ratios on patterns of juvenile dominance.

Female tolerance for group augmentation.

If group augmentation is driving female tolerance, one would expect to find similar circumstances to those found in meerkats. However, coatis are not cooperative breeders, thus most adult females have offspring in the group and would be predicted to act in their offspring's interest over that of others. Although longer term demographic data would be ideal for hypothesis testing, it appears that no clear relationship is present between group size and mortality or breeding success, thus group augmentation does not appear to be a plausible reason for juvenile dominance in ring-tailed coatis. In addition, juvenile coatis regularly attacked and were aggressive towards older individuals, which is not a pattern predicted by the group augmentation hypothesis. One parallel between ring-tailed coatis and meerkats is that both species have relatively rapid life histories compared to primates and hyenas. Because juveniles in species with faster life histories are particularly vulnerable, and need to gain weight rapidly, the relative value of food items may be greater for juveniles versus older, more self sufficient individuals.

Female tolerance for inclusive fitness benefits.

Demographic patterns appear to provide ideal conditions for high r values between adult females (Hirsch unpublished work). If this is correct, the high degree of relatedness between adult females and assorted juveniles may influence the costs and benefits of aggression. If this is true, it is predicted that ring-tailed coati groups will exhibit degrees of relatedness far higher than similar matrilineal mammals such as cercopithicine primates, white-nosed coatis, and hyenas. In order to properly test this hypothesis, a comprehensive analysis of the DNA samples taken from the PQ and PSG groups will need to be conducted.

Further discussion

Why do adult females support juveniles but not subadults? Presumably, subadults and juveniles are equally related to the adult females. In some species of primates, adult females support their younger offspring over older offspring (Kawamura 1965, van Noordwijk & van Schaik 1999). This pattern has been ascribed, in part, to the higher reproductive values of younger siblings (once they have reached the age of first reproduction) compared to their older sisters (Schulman and Chapais 1980). In some cases, juvenile dominance can occur due to the support of non-kin allies (Chapais and

Gauthier 2004). In these cases, non-kin were forming bridging alliances versus older sisters, (i.e. in an A>B>C rank order, A helps C outrank B). This hypothesis is an unlikely explanation for the evolution of juvenile dominance/tolerance in coatis because juvenile coatis are not likely to be consistent or effective coalition partners which would allow bridging coalitions against higher ranking individuals. Although juveniles and adult females sometimes formed coalitions versus subadults, the major source of aggression towards subadults was direct dyadic aggression from adult females and juveniles. These agonistic interactions were concentrated in periods when the juveniles were particularly young (<6 months of age). The increased aggression towards subadults during this time period could coincide with the period in which the juveniles have the highest nutritional needs and may also be a result of the adult females reinforcing the new dominance relationships between subadults and their conspecifics.

Juvenile support may be the result of the greater relative nutritional requirements and higher vulnerability of juvenile coatis (cf. Datta 1988). It is presumed that high juvenile growth rates need to be accompanied by high energy intake, thus the need for food may be higher in juveniles compared to subadults. Support of juveniles would thus serve to increase a female's long term reproductive success (Kaufman 1962, Gittleman and Oftedol 1987). Tolerance of juvenile aggression by adult females may allow coati juveniles to force their way into spatial positions with the highest foraging success, and effectively give the juveniles priority access to resources (Hirsch unpublished data). The pattern of increased aggression towards subadults when juveniles are six months or less may provide additional support for the hypothesis that adult females are aiding juveniles when they have greater nutritional needs.

Why don’t other social mammals exhibit similar dominance patterns to ring-tailed coatis? Despite observations of youngest ascendancy and age-inversed hierarchies in primates, and juvenile tolerance in meerkats, no other known social animal has a system of dominance exactly like ring-tailed coatis. Coatis may fall somewhere between macaques and meerkats. In some macaque species juveniles aggressively fight over food against older larger individuals. The success of these interactions depends on coalitionary support from other group members, particularly close kin (Chapais *et al.* 2001). The resulting macaque dominance hierarchies are in large part organized by matrilines, with daughters being ranked just below their mothers. On the other end of the spectrum, cooperatively breeding animals exhibit juvenile tolerance with little or no matrilineal basis. In the case of meerkats, large cohorts from one female are present in the group, and juveniles are tolerated by all group members (Brotherton et al. 2001). These juveniles can then non-aggressively steal food from others at will. This tolerance of juveniles during feeding is also found in cooperatively breeding primates (Goldizen 1987). Lion social systems are a useful comparison because they can contain multiple juveniles and subadults from different mothers, which is similar to coatis. In this case, adult females are dominant over both age/sex classes but cubs may gain access to carcasses because the dominant adult male tolerates their presence (Schaller 1972). This behavior is not seen in ring-tailed coatis and is consistent with the pattern that group living adult males are unlikely to have fathered many juveniles currently in the group (although it may have occurred in the PSG group 2004).

The social system of ring-tailed coatis differs from all of the previous examples in that coati juveniles are actively and aggressively fighting for food items, rather than being passively tolerated by older individuals, yet, unlike macaques, this system is not based on direct matrilineal support. Despite the lack of matrilineal dominance hierarchies, coalitionary support from closely related adult females may drive, or at least help reinforce juvenile dominance. Demographic factors could lead to high r values between adult females and juveniles which could lead to adult female tolerance during aggressive interactions.

The presence of juvenile "dominance" in ring-tailed coatis could be influenced by their feeding ecology. Unlike many small-medium sized social carnivores such as meerkats and mongoose, coatis spend a significant percentage of their foraging time eating fruit (Hirsch 2007). Fruit trees are often found in clumped defensible patches which promote contest competition, wherein dominant individuals could defend the resource and prevent subordinates from feeding (Vogel 2005). Small ephemeral items such as leaf litter invertebrates are not predicted to promote contest competition (unless long handling times are necessary) and should thus result in scramble competition (van Schaik 1989). The patterns of coati aggression do not precisely fit into these two categories. Coatis were often observed fighting while foraging on leaf litter invertebrates. These fights typically occurred when a coati was digging a large pit to extract an invertebrate, after which the victorious coati usurped the hole and resumed pursuing the prey. In other cases, coatis fought over large invertebrates such as annelid worms or large crickets which could not be eaten in one bite. Although aggression occurred during invertebrate foraging, fruit feeding was the most common context in which aggression was recorded (pindo fruits in particular). The distribution of fruits underneath and on pindo trees is spatially clumped and thus predicted to promote contest competition. When a group arrived at a pindo tree, the juveniles would often aggressively defend individual fruits and their immediate personal space. Unlike some species of primates, dominant coatis did not regularly defend entire fruit patches, and most aggression occurred within the fruit patch. In a study of *N. narica*, Gompper (1996) found that subadults had lower foraging success than adult females when feeding on *Scheelea* fruits which is probably related to aggressive competition. Because juvenile coatis did not exclude older individuals from the foraging patches, the feeding success of adult females was not predicted to have been substantially reduced due to juvenile aggression. Pindo foraging rates of the different age/sex classes were all similar, but the total time spent feeding on Pindo was lower for subadults than adult females and juveniles (Hirsch unpublished data). This pattern is consistent with the hypothesis that subadults are either being pushed out of fruit patches, or actively avoid them to reduce their level of received aggression. These patterns indicate that their may be very little cost to adults for tolerating juvenile aggression, while subadults are suffering a reduction in feeding due to their subordinate status.

Conclusion

The patterns of dominance exhibited by ring-tailed coatis are different from any previously published system of dominance relationships. Whether this behaviour only occurs in Iguazu, or is a species-wide phenomenon is currently unknown. Although previous work on white-nosed coatis has suggested that adult females are "tolerant" of juveniles, nothing resembling the patterns described here has been reported. It is unclear if these patterns have not been described because no researchers have collected data on juvenile dominance, or because it does not occur. Because patterns of juvenile dominance are so visibly obvious in ring-tailed coatis, I believe the latter is more plausible, and white-nosed coatis simply do not exhibit this pattern. If high within-group relatedness is helping to drive juvenile dominance, it is predicted that this social system might not be found in every population of *N. nasua*. In order to test these hypotheses further, it would be ideal to study populations with higher predation rates, occasional female transfer, or lower reproductive rates.

It is not surprising that adult females would support offspring and close kin, but it is not clear why coati "tolerance" is actually quite violent. Even though juvenile coatis were less aggressive during dominance interactions than older individuals, they still attacked older individuals during feeding (passive interactions like avoidance and displacements occurred in only 2.6% of the dominance interactions that juveniles won). If adult females coatis choose to tolerate juveniles and allow them to have priority access to food, why do the juveniles regularly attack the adult females? In order to fully test questions regarding the origin of these patterns it is first necessary to confirm that the coatis in the Iguazu study groups are in fact closely related. Tissue samples taken from the coatis during the trapping procedure can be used for a genetic analysis to determine the degree of relatedness between females and confirm suspected/inferred matrilineal relationships. In the future it would then be ideal to investigate patterns of dominance in groups where at least one adult female is not closely related to the other group members. If so, this could provide a strong test of the theory that inclusive fitness is helping drive the evolution and maintenance of juvenile dominance in ring-tailed coatis. Another useful experiment would be to change the costs of feeding competition. There currently appears to be little evidence that adult females are suffering a reduction in food intake because of their tolerance of juveniles. It is currently unknown if adult females would tolerate food theft and aggression from juveniles during a period of extreme food scarcity.

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Table 5.1. Group structure of the PQ and PSG groups. Absence of PQ subadults during 2004 was due to premature emigration not mortality.

Group	Year	Adult males	Adult females	Subadults	Juveniles	Total group size
PQ	2001	1	1	0	6	8
	2002	1	1	3	3	8
	2003	1	3	2	9	15
	2004	0-1	5	0	19-25	25-30
PSG	2003	0-1	5	0	6	12
	2004	1	5	6	15-17	27-29

	Age/sex	IK	CL	LW	PB	PU	AK	TC	SB	AA	MA	AY	GZ	AN	DA	CC	Total
1 IK	AM	-	2	1	1	1	0	0	2	1	2	0	1	0	0	2	13
2 CL	JM	0	-	2	1	0	0	0	0	0	1	0	1	0	0	1	7
3 LW	JM	0	0	-	1	1	1	0	0	1	1	0	1	0	0	0	6
4 PB	JM	0	0	1	-	2	1	0	0	0	0	0	1	0	0	0	5
5 PU	JM	1	1	0	0	-	1	0	0	0	0	1	1	1	1	2	9
6 AK	JM	0	0	1	0	0	-	1	1	1	0	0	3	0	0	1	8
7 TC	JM	0	0	0	3	0	0	-	0	0	0	0	1	0	0	1	5
8 SB	JF	0	0	0	0	0	0	0	-	0	0	1	0	0	0	0	1
9 AA	JF	0	0	0	0	0	0	0	0	-	0	0	0	2	0	1	3
10 MA	AF	0	0	0	0	0	0	0	0	0	-	0	0	5	1	0	6
11 AY	AF	0	0	0	0	0	0	0	0	0	0	-	1	1	2	0	4
12 GZ	AF	0	0	1	1	0	0	0	0	0	0	1	-	12	1	1	17
13 AN	SF	0	0	0	0	0	1	0	0	0	0	1	1	-	0	1	4
14 DA	SF	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0
15 CC	JF	0	0	0	0	0	0	0	0	1	0	0	1	0	0	-	2
Total		2	3	6	7	5	4	1	3	4	5	4	12	21	5	10	93

Table 5.2a. Dominance hierarchy for the PQ group during 2003. Rows represent winners and the columns the losers in agonistic encounters. Age/sex classes are coded as follows; Adult males= AM, juvenile males= JM, juveniles females= JF, adult females= AF, subadult females= SF.

	Age/sex	AE	OV	JK	ED	RR	LO	OG	AD	OZ	SV	IK	VL	GL	AL	RX	TL	GD	RY	AY	RQ	SN	DI	MM	GZ	AN	DA	JF	SZ	MA	Total
1 AE	**JM**	-	6	0	0	0	1	4	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	4	1	3	0	0	26
2 OV	**JM**	0	-	3	1	1	2	3	2	2	2	0	3	0	1	2	2	1	1	1	0	1	3	2	3	2	2	1	0	0	41
3 JK	**JM**	0	1	-	0	2	0	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	2	1	0	16
4 ED	**JM**	0	1	0	-	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	7
5 RR	**JM**	0	0	1	0	-	1	1	1	0	0	1	0	0	0	2	0	0	1	2	1	0	0	0	3	1	1	2	0	2	20
6 LO	**JF**	1	0	0	0	0	-	1	0	0	0	0	0	1	2	0	1	1	0	0	0	0	1	0	0	0	0	2	0	0	10
7 OG	**JF**	0	1	0	0	0	0	-	1	0	2	1	0	0	2	0	0	0	0	1	0	0	1	0	1	2	0	0	0	0	12
8 AD	**JM**	0	1	0	0	1	0	0	-	0	2	0	0	0	1	0	0	1	0	0	0	0	1	1	2	1	0	0	1	1	13
9 OZ	**JM**	0	0	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
10 SV	**JM**	0	0	0	0	0	0	0	0	0	-	1	1	0	0	1	1	1	0	0	0	1	0	0	3	0	0	1	0	0	10
11 IK	**AM**	0	1	0	0	1	0	0	0	0	0	-	1	1	0	0	1	0	0	1	1	0	2	0	2	2	1	2	0	0	16
12 VL	**JF**	0	0	0	0	1	0	1	0	0	0	0	-	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	6
13 GL	**JF**	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	4
14 AL	**JF**	0	0	0	0	1	1	0	0	0	0	2	1	0	-	0	0	2	0	1	0	0	0	1	1	0	1	0	0	1	12
15 RX	**JF**	0	1	1	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0	0	2	0	2	0	0	0	1	8
16 TL	**JF**	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	4
17 GD	**JF**	0	0	0	0	0	0	2	1	0	1	0	0	0	1	0	0	-	1	0	0	0	0	0	3	0	0	0	0	0	9
18 RY	**JF**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	0	0	0	0	1	0	0	0	1	1	4
19 AY	**AF**	0	2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	-	1	0	0	0	1	1	0	0	0	2	9
20 RQ	**JF**	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	3	1	0	1	1	0	1	0	8
21 SN	**JF**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	0	1
22 DI	**JF**	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	1	0	0	1	0	0	4
23 MM	**JF**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	1
24 GZ	**AF**	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	-	1	1	0	0	1	5
25 AN	**AF**	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	1	1	0	6
26 DA	**AF**	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	4
27 JF	**JM**	0	1	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	-	0	0	8
28 SZ	**JF**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	-	0	1
29 MA	**AF**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0
Total		1	16	7	1	14	5	15	7	2	12	11	7	4	11	8	7	8	4	9	4	3	13	10	26	19	10	16	5	11	266

Table 5.2b. Dominance matrix for the PQ group 2004. Rows represent winners and the columns the losers in agonistic encounters.

Age/sex classes are coded as follows; Adult males= AM, juvenile males= JM, juveniles females= JF, adult females= AF.

	Age/sex	DM	VI	BS	JS	TM	KG	PS	GH	JW	SX	NY	CM	Total
1 DM	**JM**	-	4	0	4	6	4	3	3	2	2	1	3	32
2 VI	**AM**	2	-	3	5	5	4	6	2	5	3	7	4	46
3 BS	**JF**	0	0	-	2	3	0	0	1	0	2	2	0	9
4 JS	**JM**	5	2	0	-	6	4	2	6	1	4	5	4	39
5 TM	**JM**	2	2	0	2	-	1	2	2	2	3	2	2	20
6 KG	**JF**	1	0	1	1	0	-	1	0	0	1	3	3	11
7 PS	**AF**	0	0	1	0	1	0	-	0	0	0	0	0	2
8 GH	**AF**	0	1	0	1	1	0	0	-	1	1	1	0	6
9 JW	**AF**	1	1	0	0	1	0	0	0	-	1	0	0	4
10 SX	**JF**	1	0	1	2	0	1	0	0	0	-	1	0	6
11 NY	**AF**	0	4	0	1	0	0	0	0	2	0	-	1	8
12 CM	**AF**	0	0	0	1	0	0	0	0	0	0	0	-	1
Total		12	14	6	19	22	14	14	14	13	17	22	17	184

Table 5.2c. Dominance matrix for the PSG group 2003. Rows represent winners and the columns the losers in agonistic encounters.

Age/sex classes are coded as follows; Adult males= AM, juvenile males= JM, juveniles females= JF, adult females= AF.

	Age/sex	IP	BO	AS	BK	RS	VI	RO	AM	KH	DH	BM	IB	CV	ZS	ES	NY	PS	BJ	BS	GH	DM	SX	CM	JS	KG	JW	TM	Total
1 IP	**JM**	-	3	2	1	1	2	1	1	3	1	4	3	1	4	0	3	1	1	1	3	3	0	3	0	1	0	2	45
2 BO	**JM**	0	-	1	2	1	0	0	1	1	0	1	0	2	1	0	0	1	1	1	1	0	0	0	0	4	1	0	19
3 AS	**JM**	0	0	-	4	2	2	2	2	3	0	2	2	2	3	1	1	0	0	3	0	1	1	1	1	2	2	1	38
4 BK	**JM**	2	0	1	-	2	3	2	0	1	0	1	2	1	0	0	4	1	0	3	1	6	2	2	2	1	0	0	37
5 RS	**JM**	0	1	1	0	-	1	3	1	2	1	1	0	1	2	1	2	1	1	1	2	0	0	0	3	0	2	0	27
6 VI	**AM**	6	0	1	3	0	-	1	1	1	1	4	2	3	0	2	6	5	0	3	3	12	4	2	17	3	3	6	89
7 RO	**JF**	0	1	0	0	0	0	-	1	1	0	1	2	2	1	0	1	1	1	0	3	2	2	2	0	0	0	2	23
8 AM	**JF**	0	0	0	0	1	0	0	-	1	0	1	1	1	1	0	0	1	0	1	2	0	3	1	0	0	0	0	14
9 KH	**JF**	0	2	1	0	0	0	0	0	-	0	1	0	1	3	0	3	1	1	0	0	1	0	0	3	0	0	0	17
10 DH	**JF**	0	0	0	0	0	0	0	0	0	-	1	0	1	0	1	0	1	0	0	1	0	0	0	0	1	1	0	7
11 BM	**JM**	0	0	1	0	2	2	0	0	0	0	-	2	2	2	0	2	1	0	2	1	0	0	2	0	1	1	0	21
12 IB	**JM**	1	0	2	1	1	1	0	1	2	0	1	-	1	0	1	1	1	0	1	2	0	0	0	0	0	1	0	18
13 CV	**JM**	0	1	2	0	1	1	0	0	1	0	1	0	-	0	2	0	1	0	0	0	1	0	0	1	0	0	0	12
14 ZS	**JM**	0	0	2	1	0	0	0	0	0	0	2	0	0	-	0	0	0	1	0	0	0	1	0	2	0	0	0	9
15 ES	**JM**	0	0	1	0	0	1	0	0	0	0	0	0	1	0	-	3	1	0	2	4	0	0	1	0	2	1	0	17
16 NY	**AF**	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	-	1	0	5	0	4	6	1	4	4	0	1	28
17 PS	**AF**	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	-	1	2	1	1	2	0	2	0	0	1	14
18 BJ	**JF**	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	0	0	1	0	1	0	0	0	0	4
19 BS	**SF**	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	-	1	1	1	2	0	1	0	0	10
20 GH	**AF**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	4	1	0	3	1	1	2	13
21 DM	**SM**	1	0	1	1	0	2	1	0	0	0	0	0	0	0	1	1	1	0	1	1	-	3	6	3	2	0	2	27
22 SX	**SF**	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	-	1	0	2	0	1	7
23 CM	**AF**	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	-	7	1	0	2	14
24 JS	**SM**	1	0	0	0	0	2	0	1	1	0	0	0	0	0	0	0	2	0	0	2	1	0	1	-	5	1	1	18
25 KG	**SF**	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	-	1	0	4
26 JW	**AF**	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	1	3
27 TM	**SM**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	-	4
Total		13	8	17	16	11	18	11	9	17	4	23	15	19	18	11	27	23	7	29	28	45	27	27	48	31	15	22	539

Table 5.2d. Dominance matrix for the PSG group 2004. Rows represent winners and the columns the losers in agonistic encounters. Age/sex classes are coded as follows; Adult males= AM, juvenile males= JM, juveniles females= JF, adult females= AF, subadult males= SM, subadult females= SF.

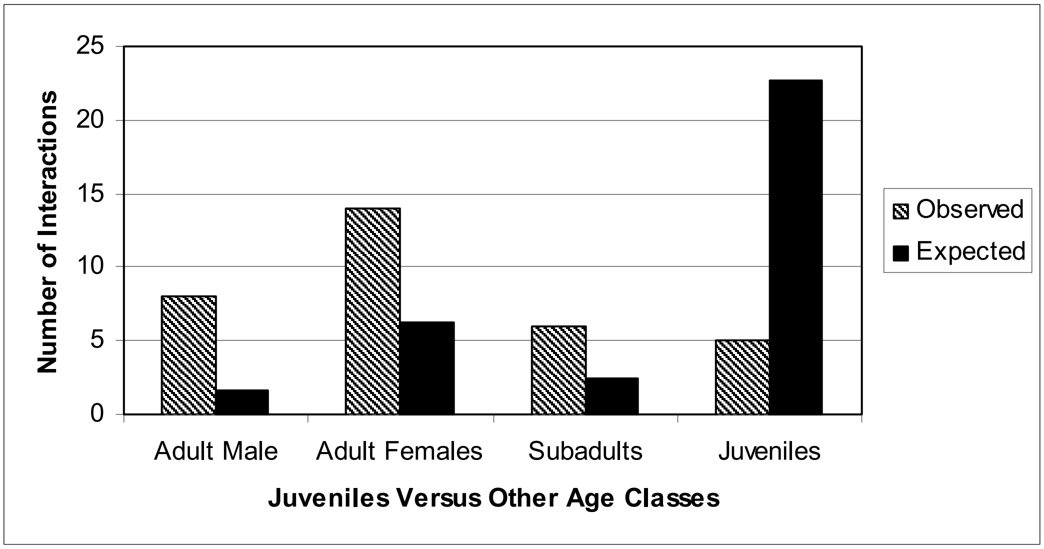
Table 5.3. Dominance hierarchy statistics.

Group/year	**PSG 2003**	**PSG 2004**	**PQ 2003**	**PQ 2004**
Matrix total	184	539	89	266
Landau's linearity index (h)	0.629	0.270	0.161	0.125
Landau's corrected index (h')	0.675	0.306	0.257	0.185
Expected value of h or h'	0.231	0.107	0.188	0.100
Directional consistency index	0.630	0.703	0.775	0.752
% of unknown relationships	19.70%	33.62%	51.43%	59.61%
% of one-way relationships	46.97%	47.86%	39.05%	32.51%
% of two-way relationships	33.33%	18.52%	9.52%	7.88%
% tied relationships	1.52%	6.84%	8.57%	3.94%
Improved linearity test (R tailed probability)	<0.001	<0.001	0.225	0.019

Table 5.4. Percentage of different types aggression recorded during dyadic encounters separated by age class. Type of aggression is ordered from least to most aggressive.

Winner-Loser	**Avoidance**	**Displacement**	**Vocalization**	**Lunge**	**Bite**	**Chase**	**Fight**	**N**
Adult-adult	6.45	1.08	8.60	43.01	1.08	35.48	4.30	93
Adult-juvenile	5.13	3.42	17.95	58.12	0.00	14.53	0.85	117
Adult-subadult	23.40	6.38	3.55	17.73	1.42	42.55	4.96	141
Subadult-adult	9.09	0.00	3.03	33.33	9.09	39.39	6.06	33
Subadult-juvenile	6.06	0.00	3.03	69.70	15.15	6.06	0.00	33
Subadult-subadult	0.00	0.00	0.00	73.08	3.85	19.23	3.85	26
Juvenile-adult	1.16	1.54	14.29	59.07	5.41	17.37	1.16	259
Juvenile-juvenile	0.48	0.73	3.15	84.99	4.36	5.57	0.73	413
Juvenile-subadult	1.15	1.15	1.15	73.56	1.15	19.54	2.30	87

Figure 5.1. The number of fights in which adult females supported juveniles. Columns separated by age/sex class of opponent with whom the juvenile fought against. G test (43.47, $X^2 < 0.001$)



Chapter 6

Behavioral mechanisms of olfactory food detection by ring tailed-coatis (*Nasua nasua*)

Abstract

The food discovery behavior of ring-tailed coatis (*Nasua nasua*) was studied using experimental feeding plots. Coatis primarily used olfaction to detect these new food sources, and visual food discovery appeared plausible in only 5 of 148 experiments. The probability of an individual discovering an experiment reached 50% at a distance of 19.6m, and no experiments were detected from more than 24.5m. Coatis were less likely to find the feeding experiments when traveling, and an increase in travel speed resulted in longer detection distances. The experiments were more likely to be found when the group size was larger. The distance measure taken from the closest individual (the nearest approach distance; NAD) was a better predictor of whether the plot was discovered than a group level measurement (perpendicular distance; PD). The number of fruits and the presence and direction of wind did not have significant effects on the probability of finding the experiments or the distance of detection. The average distance of detection was negatively related to the percentage of fruit in the diet per month. This relationship suggests that coatis are using olfactory search images which vary by season. The coati experiments were compared to similar experiments testing visual food detection in

capuchin monkeys. The visual detection abilities of capuchins were similar to the olfactory detection abilities of coatis.

Introduction

How animals detect and search for food is an important factor influencing their optimal foraging strategies. For instance, animals with relatively large food detection distances are predicted to have higher food encounter rates in comparison to animals with shorter detection distances (Giraldeau and Carcao 2000). Higher encounter rates should in turn favor earlier departure from food patches and greater choosiness in entering food patches (Stephens and Krebs 1987). If an animal has poor detection abilities and uses replenishing food sources, they may be predicted to increasingly exploit known food items rather than search for new food items (Janson and Di Bitetti 1997). This option is predicted to be particularly relevant in organisms which feed on large food patches with slow depletion times (such as large fruit trees). But despite this potential importance few studies have actually investigated the influence of detection on foraging decisions.

Because of thick vegetation found in some forests, the distance at which foraging animals in forested environments can see food items may be quite short. In a previous study of visual food detection in brown capuchin monkeys (*Cebus apella*) Janson and Di Bitetti (1997) found that the probability of visually discovering a new food site reached 50% when the distance between the food and the nearest individuals was 25.5m. Three major predictor variables influenced the probability of detection 1) distance to the experiment, 2) size of the experiment, and 3) travel speed. The authors found that capuchin monkeys discovered experiments from longer distances when traveling slowly, and when the food platforms were larger. To examine the distance at which capuchins visually detect food, the authors took both group and individual level measures. The nearest approach distance (NAD) was either the distance at which an individual detected the feeding experiment, or the closest distance an individual came to the experiment without detection. The authors also measured the groups' perpendicular distance (PD), which is the shortest perpendicular distance between the experiment and the groups' line of travel. The authors found that the group PD was a better predictor of whether an experiment was discovered than the individual NAD.

Very little attention has been paid to investigating how various sensory modalities could potentially affect food detection distances. Dominy et al. (2001) stated that forest living primates are able to detect food from longer distances by using olfaction because smells are not blocked by vegetation and suggests that primates may have the ability to detect food using olfaction from 200m. This suggestion is not consistent with existing detection distances (Janson and DiBitetti 1997), but these animals were most likely using vision as the major modality of detection. Thus, it is of interest to carry out such an experiment in the same habitat with a species that relies primarily on olfaction.

This paper reports on a series of experiments conducted to test the olfactory food detection abilities of ring-tailed coatis (*Nasua nasua*). The earliest reports of coati behavior note their keen ability to detect food by use of smell (Chapman 1938). Coatis typically search for invertebrates by sticking their nose in the leaf litter and soil, and use their sense of smell to detect prey items (Kaufman 1962, Gompper 1996). Coati nasal and cranial anatomy are consistent with a heavy reliance on olfaction (Gompper 1996). Coatis are commonly seen pointing their flexible noses in an upwards position and sniffing in the air making it easy for the observer to note coatis' detection of food. Based on existing theory and previous experiments the following predictions were tested: If olfactory food detection is much more efficient than visual food detection for coatis, a large difference in detection distance between coatis and capuchins is predicted. In addition, the different sensory modes may change how detection distance depends on food quantity, individual behavior, travel speed, and other variables.

Additional factors may also affect detection ability, such as food "smelliness," temperature, height in the canopy, learning, and search images (Nams 1997, Dukas and Kamil 2001). Olfactory search images could change the ability of coatis to detect particular food sources at different times (Nams 1991, 1997). This study used a standard detection stimulus across several seasons and two years, which was used to test for temporal variation in detection ability and examine its causes. Because the distance of detection is an important variable influencing social foraging decisions, it is important to know what variables are driving these abilities and how a reliance on olfaction could change the costs and benefits of various feeding strategies.

Methods

The study was conducted in the Iguazu Falls National Park, Argentina between March 2003 and September 2004 (for details of the field site see: Brown and Zunino 1990; Di Bitetti 2001a,b). This is the same study site used in Janson and DiBitetti (1997) and the fruit component of the diets of both species is similar (unpublished work). Experiments were conducted on two study groups (PQ and PSG) which ranged between 3-35 individuals during the experiments. Upper and lower group size values were the result of experiments conducted on subgroups or temporary group fusions. Coatis were captured using Tomahawk or similar traps, anesthetized, and either fitted with radio-collars or given multi-colored plastic eartags for individual identification (Dalton Rototags). Eartags were placed on juveniles older than four months of age, and it was possible to recognize all individuals older than four months. Between one and three adult females per group were fitted with radio-collars in order to locate the groups. Groups of coatis were habituated and observers would silently walk within 2m of a focal animal without disturbing the animals. With the exception of occasional accidental loud noises made by the observers (such as breaking a branch), it did not appear that the coatis changed their travel and foraging behavior due to being observed. For instance, if a food item such as a pindo fruit was encountered nearby an observer, the coatis would approach the food regardless (even if the fruit was below the boot of an observer).

Feeding experiments were conducted using medium sized green table grapes. Because grapes are not a natural food item for coatis, the two study groups were presented with large quantities of grapes before the experimental regime so that all individuals would have a previous opportunity to smell and feed on grapes. The coati groups were given grapes at least three times before the start of the experiments, and this procedure was repeated in 2004 to train the recently born juveniles. 5, 10, 20, 50 or 100 grapes were placed in a $1m^2$ plot. During the 100 grape treatments, the experimental plot varied between $0.3m^2$ and $2m^2$ ($0.3m^2$, $0.7m^2$, $1m^2$, and $2m^2$). This variation in plot density was used for another concurrent study of feeding competition. A DVC video camera was set up on a portable tripod approximately 2.5m from the experiment site to record feeding and other behaviors. Feeding experiments were always conducted with two or more observers who communicated with radios and hand signals. One researcher would typically stay with the group, while the other arranged the fruit and video camera. When a group approached within 25m of the experiment, the researcher walking with the coatis positioned themselves in a location where they could see those individuals closest to the experiment, while the other researcher remained near the experiment and started the video camera. In order to not disturb the coatis during the detection process, both researchers tried to remain stationary, or walk as quietly as possible. Observers would often coordinate their data collection to observe multiple individuals who were most likely to discover the experiment. A total of 229 experiments were conducted. In 44 of these experiments, the detection behavior of the coatis was either not observed or was not completely clear, and therefore excluded from the analysis (for a total N of 185). The coati groups did not discover the food in 37 of these 185 experiments.

Janson and DiBitetti (1997) noted that upon discovery of a new food source, brown capuchin monkeys generally changed direction towards the food site and increased travel speed. This behavior was also observed in coatis, but with a notable addition. During a typical food discovery, the coatis would hold their heads up from the ground and sniff in the air. This was particularly noticeable due to the flexion of the tip of the nose, which was an indication of olfactory behavior. Coatis typically followed this behavior by orienting toward the food site then increasing their travel speed. By using these two behavioral cues to determine the presence of olfactory detection, the methods used here closely resemble those of Nams (1991, 1997; see below). In some cases it was clear that the coatis discovered a food site due to their speed and change in direction, but no sniffing was observed. During the discovery experiments we were especially careful to minimize any possibilities that the coatis could detect the experiments by "cuing" in on our actions. To prevent the coatis from cuing on the sight of the tripod or the sound of the radios used during the experiment, hand held radios and the DVC video camera were regularly used outside the context of feeding experiments. Despite these controls, in some cases it appeared plausible that coatis may have been able to use visual information to detect the feeding experiments. In the cases in which coatis would look in the direction of the experiment without sniffing in the air before approaching, we noted that visual detection might have occurred. If the area between the coati and the experiment was sufficiently closed or blocked as to prevent visual detection (such as when the experiment was behind thick vegetation) we coded the detection as olfactory by default.

When a discovery occurred, the identity, behavior, travel speed, travel direction, and spatial position of the discoverer were recorded. If the experiment was not discovered, the same data was taken on the individual who came closest to the experiment. At the point of discovery or the closest approach without a detection (NAD), the group behavior, group speed, group travel direction, group spread (length and width), distance from the experiment to the center of the group, and wind speed and direction were recorded. Behavior was divided into three categories; travel, invertebrate foraging, and fruit eating. We tried to avoid placing the experiments near fruit trees, but in some cases the group traveled to a nearby fruit tree that was unknown to the observers. The travel speed was recorded and graded on a scale of 0-3 (0= no movement, 3= rapid travel). Travel directions and angles were measured with a handheld Suunto sighting compass. All distances were measured using 50m fiberglass tape after the experiment was completed. The group length and width were determined through visual estimation. These visual estimations were also used during 15min scan samples of group behavior. Average group length and width were determined using these group scans (N=2210).

Spatial position of individuals was recorded in the same manner as Janson (1990a,b). The group spread was visually divided into three concentric circles: 1) center, 2) middle, 3) edge. Coati location within these circles was then further subdivided into 12 positions based on the number of a clock, with 12 being the front most position and 6 representing the back of the group. These 36 spatial positions were then summarized into 7 spatial position categories (as in Di Blanco and Hirsch submitted); 1) front edge, 2) front middle, 3) center, 4) back middle, 5) back edge, 6) outer sides, and 7) middle sides (Fig. 1). Wind speed was difficult to record due to the low amount of wind in the forest. Attempts to measure wind speed using a digital wind meter were inadequate because the wind was only strong enough to set off the meter in one instance. The presence and direction of wind was determined by using the flame of a lit match held next to a compass (after the experiment was completed).

Distance measurements during a group approach were taken in the same manner as Janson and Di Bitetti (1997). The nearest approach distance (NAD) was either the distance at which an individual discovered the feeding site, or the distance to the nearest individual who did not discover the site. The perpendicular distance (PD) is the distance between the experiment and the major axis of group movement regardless of detection. The PD was calculated using the trajectory of group movement recorded by the observer who was in direct contact with the coati group. By entering the direction of group movement and the distance and direction between the experiment and group center at the time of discovery, it was possible to calculate the perpendicular distance between the groups' line of travel and the experiment. The NAD measure provides information on the individual detection ability, while the PD is a group level measurement. In seven cases, a coati group did not approach the experiment close enough to accurately measure the NAD (>25m), but we were able to measure the PD.

The percent of time spent feeding on fruit and invertebrates was determined using 15min group scan samples (Hirsch unpublished data). During the instantaneous scan, we defined the behavior of the group by whatever activity >66% of the group was engaged in. All feeding scans were separated from the raw data set and analyzed for seasonal differences in percent of time spent feeding on fruit and ground litter invertebrates (feeding scans during months in which experiments occurred N=4134).

Statistical analyses

Each experiment in which at least one coati in the group came within 25m of the experiment was treated independently (N=185). A generalized linear multiple logistic regression was run with twelve group level variables (year, month, group activity and speed, group length and width, group size, individual NAD, group PD, presence of wind, the log number of grapes, and experiment density) entered as the independent variables, and experiment detection as the dependent variable (yes or no). These variables were chosen because it was hypothesized that they may have an effect on detection. The Akaike criterion was used to choose among possible best-fit models. Another such analysis was run on only the experiments which were successfully discovered (N= 148) with eleven independent variables pertaining to the discoverer (year, month, month squared, age, sex, individual activity and speed, presence and direction of wind, the log number of grapes, and experiment density). Because only 3 experiments were discovered when an individual was not moving (travel speed 0), these observations were lumped into the slow moving travel speed category for the analysis. The square of the numerical value for ‘month’ was entered into the analysis of detection distance after an initial inspection of the data indicated the possibility of a U shaped pattern over time. The variables identified in the Akaike analyses were then entered into best subsets generalized linear models (GdLM).

The distances at which the chances of detection were 50% were originally calculated using the ‘inverse prediction’ function in the JMP 3.1 statistical program (see: Janson and Di Bitetti 2001). Due to a relatively small number of non-detections (especially at larger NAD and PD values) the results of these tests appeared to be skewed upwards, and the values contrasted strongly with observed behavior. Instead, revised 50% probability values were calculated by plotting the percentage of experiments discovered at averaged distances (0-5m, 5-10m, 10-15m, 15-20m, 20-25m, 25-30m) weighted by the number of observations. The polynomial formula obtained from this plot was then used to determine the distance at which detection of experimental food sites reached 50% (hereafter called the ‘average’ detection distance).

The average experimental detection distance by month was regressed against the average time spent eating fruit (weighted by experiment sample size). To test the effect of fruit consumption on experimental detection distance, the mean percentage of time spent feeding on fruit per month was entered into a regression with average detection distance weighted by the square root of detection sample size per month.

Results

Of the 148 discoveries, visual detection appeared plausible in only 5 cases. It appeared that the coatis discovered the experiment sites by olfaction in the remaining 143 experiments. The average distance at which the coatis detected the experiment sites was 8.9m (SE ± 0.39, N = 143). The probability of detecting the food site reached 50% at a

NAD of 19.6m (Figure 2). The probability of detection reached 50% at a PD of 27.5m. The average length and width of the groups were 23.2m and 14.3m respectively. The difference between the 50% NAD and PD values should approximately equal one half the group width (7.15m), thus these values are in accordance with coati group geometry. The average detection distance by capuchin monkeys of 1x1m experimental food platforms suspended from tree limbs was 13.7m (SE± 1.19, N=18; Janson and Di Bitetti 1997). The latter is significantly greater than the detection distance by the coatis (Kruskal Wallis Chi^2= 8.399, p=0.004).

There were no significant effects of year, month, group speed, group length and width, group PD, number and density of grapes, and presence of wind on the probability of detection (Table 1). The three significant predictor variables which affected the detection probability were the individual NAD, group activity, and group size. Because the effect of group size leveled off as the group size increased, the square root of group size was entered into the model. Coati groups had a higher probability of detection as the NAD decreased (slope=-0.141, P=0.011), group size increased (slope=0.114, P=0.006) and during invertebrate foraging as opposed to group travel (slope=4.035, P=<0.001).

Some variables, which did not affect the probability of detection by the group, did have significant effects on the distance, at which the experiment was detected by individuals (NAD). The variables, which had significant effects on NAD, were individual activity, individual speed, and the interaction of those two variables (Table 2). Coatis discovered the experiments at significantly shorter distances during rapid travel, compared to slower travel speeds (slope=-2.892, P=0.007). This pattern was apparent only for travel behavior rather than during terrestrial foraging. When coatis were foraging for terrestrial invertebrates, travel speed had no significant effect on the distance of experiment discovery (Kruskal-Wallis DF= 2, Chi2= 1.277, P= 0.528). Coatis were more likely to discover experiments when foraging in the front and side edges of the group (front edge F= 137.3555, Chi^2= <0.001, side edge F= 54.52291, Chi^2= <0.001; Figure 1).

There were seasonal patterns of detection ability by coatis. The month, and month squared variables were included in the best subset model as indicated by the Akaike analysis. The slopes of these variables in the GdLM indicated that the relationship between month and detection distance is U shaped, with the shortest detection distances being found during mid-April (month slope=-1.265, p= 0.163, month squared slope=0.124, p=0.075). A further analysis revealed that the average detection distance was negatively correlated with the average percentage of time spent feeding on fruit (slope = -33.271, p=<0.0165). This pattern occurred during both 2003 and 2004, but was not significant for either year alone (2003; slope= -37.051, p=0.082, 2004; slope= -15.317, p=0.412). Additionally, when only data for the most commonly used fruit tree in the coati diet was analyzed (pindo fruits), the relationship between the amount of time spent feeding on pindo was not correlated with the experimental detection distance (slope= -0.020, p=0.732).

Discussion

Probability of detection versus distance

The NAD was a better predictor of the probability that the coati group would discover an experiment than the group PD. This result is opposite to that found by Janson and DiBitetti (1997), who found that the PD was a better predictor. These authors concluded that the PD is a better predictor variable because PD is a group level measurement, while the NAD more accurately represents the discovery ability of individuals. The NAD measure during experimental discovery represents one point between the animal and the experiment, while the PD takes into account the entire approach of the group to the experimental site, and is thus a more integrative measure. The authors mention that in cases of non-detection, the NAD is always shorter than the PD. When the experiment is detected, the NAD can be larger than the PD, especially if the group center is traveling directly to the experiment (NAD= 0). To predict whether a group of animals will discover a feeding site, the group PD should be a more reliable and stable predictor of the group's ability to detect an experiment than the NAD.

The poor link between the group PD and the probability of experiment detection may be the result of imprecision in the calculation of the coati group PD. In general, the travel routes of ring-tailed coatis are much more circuitous than capuchins. Coatis often travel in circles and other travel trajectories that deviate widely from a straight line. Although coatis will travel in straight lines when traveling to known fruit resources (Hirsch unpublished data), or when using commonly used travel "routes," most experiments were conducted during periods of foraging for ground litter invertebrates (so the presence of nearby fruit trees did not influence the experiments). It is precisely during these times when the group tends to travel in non-straight lines. Because the coatis twist and turn so frequently during their travel, the ability to calculate the predicted group PD based on the travel trajectory at the time of experimental discovery is likely to be weak. The NAD in contrast, was much less affected by the circuity of the group's progression.

Effects of group size

Larger groups detected food experiments at larger PD values. It was important to test whether this pattern might be due to another collinear variable. Changes in group size coincided with the year because both the PQ and PSG groups were larger during 2004. It is conceivable that if the coatis increased their discovery abilities over time due to learning, that this could have been expressed in conjunction with the yearly effect. The Akaike analyses indicated that the coatis were more likely to detect the experiments during 2004, but group size was a better predictor variable determining the detection outcome. There was no effect of group width and length variables on detection probabilities, even when group size was excluded from the analysis. This pattern is consistent with the hypothesis that the increased probability of detection at a given PD value is caused by the larger number of individuals searching for food rather than a function of larger group spread or group "swaths" found in larger groups. Some authors have posited that increases in group size can lead to increases in food encounter rates (Clark and Mangel 1986). In this study system, the slope of this effect is small. The group reaches a 90% discovery rate at a group size of 29 individuals, thus any additional increase in individuals above this group size will likely result in relatively few additional discoveries (*N. nasua* groups up to 64 individuals have been observed). This is an important result with respect to the evolution of sociality and optimal group size. If the additional chance of discovering food per added individual levels off after a certain group size, the cost of feeding competition is more likely to outweigh the benefit of additional individuals at these larger group sizes (Janson 1988, Janson and Di Bitetti 1997).

Number of fruit and the presence of wind

Neither the number of fruits nor the presence and direction of wind had a significant effect on the ability of the group to detect the experiments or the distance at which individuals detected the plots. Given that both factors would presumably increase the ability of coatis to smell the experiments, this result was not expected. The result that wind had no effect could have resulted from the fact that wind was present during only 24 experiments and that the wind was generally very light.

Spatial position

Individuals on the front and side edges of the group discovered significantly more experimental plots than predicted by chance. This pattern is similar to those found in other species (Janson and DiBitetti 2001, Stahl et al. 2001). The larger number of novel food discoveries by front edge individuals may be a major reason why some individuals prefer to forage at the front of the group, although this is also the spatial position with the highest associated predation risk (DiBlanco and Hirsch in press).

Activity and speed

Group activity affected the probability of food detection, and individual activity and individual speed influenced the distance at which the plots were detected. The group was significantly more likely to detect the experiments during foraging for leaf litter invertebrates, than during travel. The effect of fruit feeding is indeterminate because of the small sample size (n=2). Although the groups were less likely to discover experiments during travel, the group speed had no effect on the probability of discovery (after controlling for activity).

Similar results were found with the detection distance. Coatis discovered experiments from longer distances while foraging versus traveling. The speed of the individual had a negative effect on detection distance when traveling, but no effect when foraging. Both results indicate that coati groups and individuals are more likely to discover new food items when searching for food at slower speeds as opposed to rapid traveling. These results are similar to those of Janson and DiBitetti (1997). Thus even though coatis and capuchin monkeys are using different sensory abilities to find new food items, both olfactory and visual detection abilities decrease when traveling.

Seasonal effects

Because these experiments used a novel food item, it was predicted that there might be a learning curve in detection, despite efforts to minimize this (Nams 1997). In addition to individual learning over time, during 2004 both groups had several new juveniles, which were not available to participate in the experiments the previous year. A pattern indicating olfactory learning was not seen in the analyses of year or month. A U shape pattern of detection distance was found with respect to month during both 2003 and 2004. Although the month and month squared variables were not significant in the GdLM model, the Akaike analysis included these two variables in the best subsets model. This pattern indicates that the coatis started off the year detecting experiments from longer distances, then shorter distances during the fall, followed by an increase during the spring (Figure 3.). This U-shaped pattern of detection distance coincides with changes in fruit availability and inter-patch travel distances. During late fall (especially April-June) the amount of time spent feeding on fruit increases (Hirsch unpublished data). The average fruit experiment detection distance was negatively correlated to the average time spent feeding on fruit per month, thus as the groups used more fruit trees in their environment, they were detecting the experiments at shorter distances. There are some plausible reasons for this pattern. As the number of alternate feeding sources increased, coatis may have been less willing to go to the feeding experiment, and simply skipped over these resources in favor of the more abundant natural fruit trees. This reasoning is unlikely because the coatis were never observed to detect an experiment and not approach. In addition, the experiments were generally placed far from fruit trees, thus there was typically no alternate fruit source nearby. It is also plausible that the coatis are forming olfactory search engines for fruit, which was found in olfactory food detection experiments using striped skunks (Nams 1991, 1997). If the formation of an olfactory search image is leading to a tradeoff in grape detection ability versus natural food items, one could predict that particular important food sources should be negatively correlated with experiment detection distance. Over 10% of coati feeding time is spent feeding on pindo fruits, and pindos are eaten more than twice as much as the next most commonly utilized fruit species (*Hovenia dulcis*). However, there was no relationship between pindo consumption and experimental detection distance, despite the importance of this fruit in the diet of the coatis.

Coatis versus capuchins

The experimental design for coatis was similar but not identical to the capuchin experiments of Janson and Di Bitetti (1997). The results from these experiments resembled the capuchin experiments in terms of the importance of traveling. Both series of experiments found that traveling or increased travel speed could lead to lower discovery rates. These experiments support the hypothesis that travel not only affects visual detection abilities but negatively affects olfactory detection abilities as well. The size of the experiment had a significant effect on the ability of capuchins to see the experiment, but neither the number of grapes nor the size of the experimental patch had an effect on the ability of coatis to detect the experiment. In both cases, the size of the experiments ($0.3m^2$-$2m^2$) was much smaller than some of the natural fruit resources available in Iguazu, which can be found commonly in crowns of up to 20m in diameter (Janson personal communication).

A major difference in the results for the capuchin and coati experiments is that the group PD was a poor predictor value for coati experiment detection. This result is likely due to major differences in straight line travel between the two species. Although the capuchin experiments were conducted with one social group, it was suggested that effects of group width were somewhat analogous to changes in group size (Janson and Di Bitetti 2001). While group size had a significant effect on food discovery in coatis, the group width was not a significant predictor variable (even when group size was removed from the GdLM). This result might also be a byproduct of the circuitous travel routes of coatis or reflect a fundamental difference in the way that food is discovered using olfaction and vision. It was not possible to ascertain whether the detection abilities of capuchins changes seasonally.

Conclusion

The experimental results are consistent with the hypothesis that coatis typically locate food by smell rather than sight. It appears that olfactory food detection does lead to quantitatively different detection abilities compared to visual detection. As with capuchins, there is a tradeoff between food detection and traveling. In cases where the coatis are traveling, they experience a significant decrease in their ability to detect new food items. This result remains to be fully incorporated into foraging models. As predicted, an increase in group size does lead to higher detection probabilities but it is highly unlikely that the small increases observed would offset the increased cost associated with increased group size, especially at larger group sizes. New food sources were mostly discovered by individuals in the front edge of the group which may lead to greater net foraging rates at the front of the group (Hirsch in prep). Finally, smaller detection distances for the experiments during months with more natural fruits available are compatible with the possibility that coatis may have olfactory search images.

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Table 6.1. GdLM model for the probability of detection. DF= 3, Chi^2= 21.499, p=<0.001

	DF	Estimate	Error	P	
Individual NAD	1	-0.141	0.055	0.011	**
Group PD	1	0.007	0.040	0.862	
Group activity	2				
Invertebrate foraging		0.000	-	-	
Travel		-4.035	0.657	0.000	***
Fruit eating		9.417	-	-	
Group speed	3				
Stationary		0.000	-	-	
Slow movement		0.562	0.429	0.189	
Medium		0.515	0.494	0.297	
Rapid travel		0.096	0.811	0.905	
Group length	1	0.003	0.025	0.910	
Group width	1	0.009	0.037	0.814	
Group size	1	0.114	0.042	0.006	**
Presence of wind	1	0.196	0.387	0.612	
Month	1	0.235	0.137	0.086	
Number of grapes	1	-0.001	0.006	0.824	
Density of grapes	1	-1.003	0.695	0.149	

Table 6.2. GdLM model for experiment detection distance. DF= 7, Chi^2= 35.058, p=<0.001

	DF	Estimate	Error	p	
Age	2				
Adult		0.000	-	-	
Juvenile		-0.597	0.647	0.356	
Subadult		0.302	0.542	0.578	
Individual activity (travel)	1	2.219	0.745	0.003	**
Group Speed	2				
Slow movement		0.000			
Medium		0.814	0.867	0.348	
Rapid Travel		-2.892	1.072	0.007	**
Activity X Speed					
Slow travel		0.000			
Medium travel		1.553	0.891	0.082	
Fast travel		-3.261	1.047	0.002	**
Spatial position	6				
Front edge					
Front middle		1.422	1.949	0.466	
Center		-1.378	2.221	0.535	
Back middle		0.698	2.731	0.798	
Back edge		-0.953	1.437	0.507	
Side edge		-0.197	0.997	0.844	
Side middle		-0.360	2.640	0.892	
Presence of wind	1	-0.499	0.717	0.487	
Experiment upwind	1	-0.089	0.931	0.924	
Month	1	-1.265	0.906	0.163	
Month squared	1	0.124	0.070	0.075	
Number of grapes	1	0.033	0.905	0.971	
Density of grapes	1	-0.135	0.330	0.683	

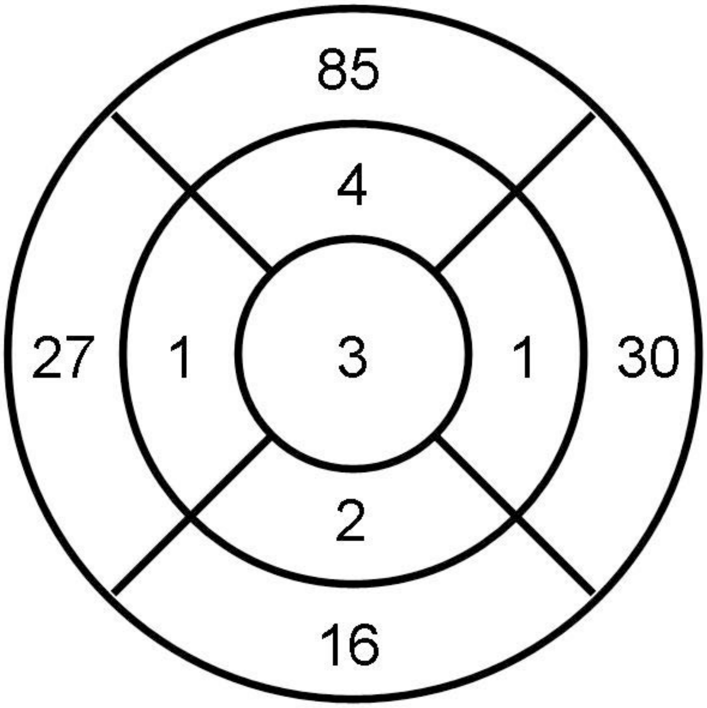

Figure 6.1. Number of discoveries per within-group spatial position. The top of the figure denotes the front edge of group movement.

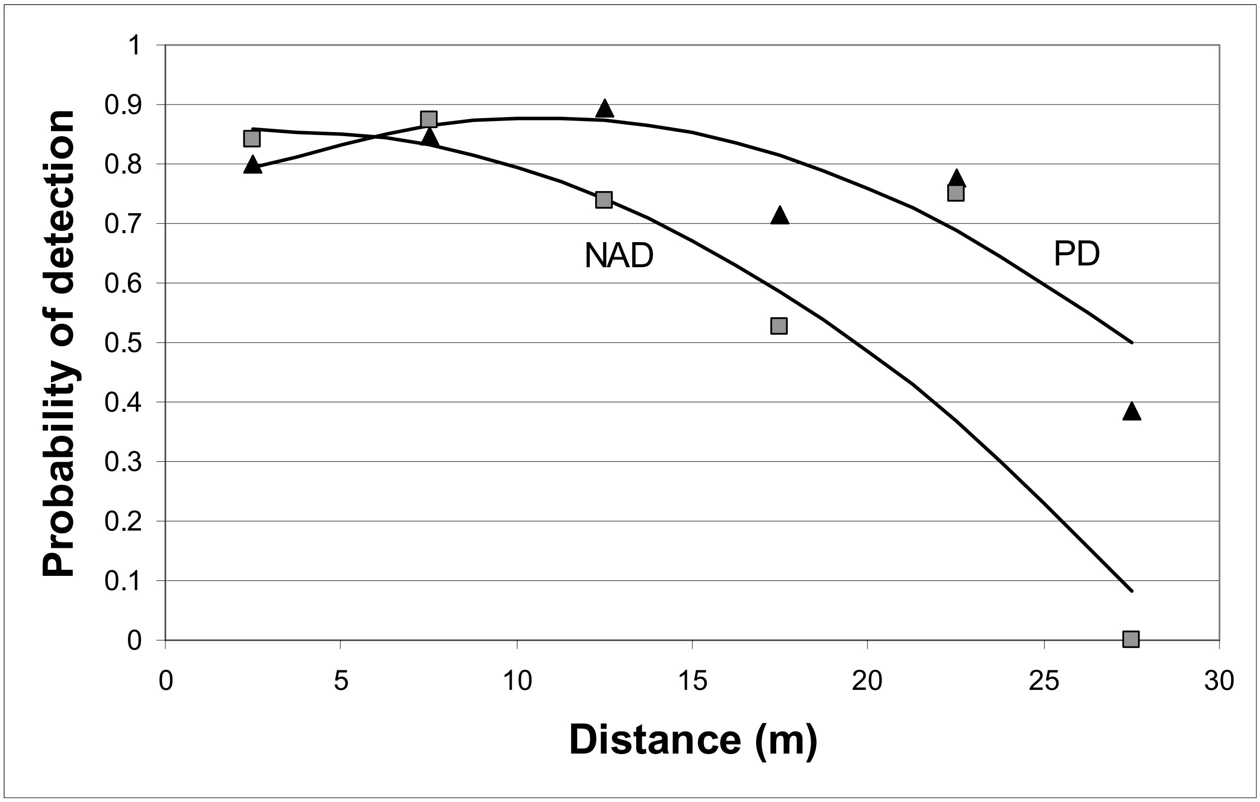

Figure 6.2. Probability of detection as a function of nearest approach distance (NAD= boxes), and group perpendicular distance (PD= triangles). Slope equations for discovery probability= 0.846+0.00793*NAD- 0.0013*NAD^2, and 0.73213+0.02757*PD- 0.00131*PD^2.

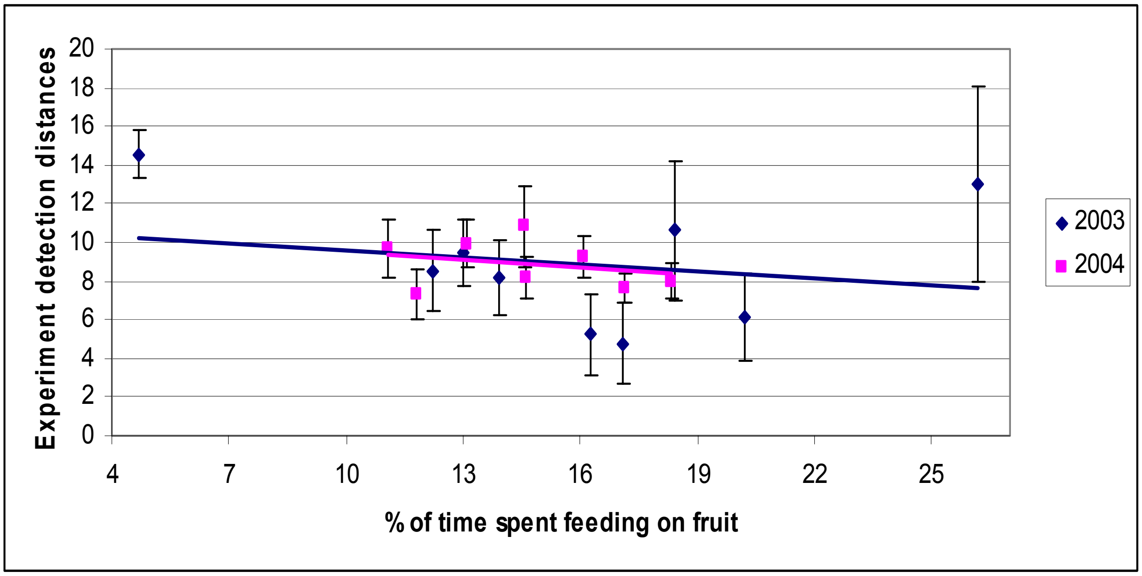

Figure 6.3. Relationship between the percentage of time spent feeding on fruit per month and experiment detection distance (in meters); ±SE.

Chapter 7

Inter-individual spacing affects the finder’s share in ring-tailed coatis (*Nasua nasua*)

Abstract

Social foraging models are often used to explain how group size affects an individual’s food intake rate and foraging strategies. The proportion of food eaten before the arrival of conspecifics, the finder’s share, is hypothesized to play a major role in shaping group geometry and feeding competition. The variables which affect the finder’s share were tested by presenting groups of ring-tailed coatis with 5-100 grapes, and groups varied between 3-35 individuals. The number of grapes in the experiment had a strong negative effect on the finder’s share and the probability that the finder was joined. The arrival of a conspecific, the time to arrival of a conspecific, and the nearest neighbor distance all had independently significant negative effects on the finder’s share. Although group size did not have a direct effect on the finder’s share, group size was found to influence the finder’s share through the latter three spatial variables. The benefit of discovering a greater number of experiments at the front of the group was offset by the lower finder’s advantage at this spatial position. These results highlight the crucial importance of considering the manner by which individual spacing shapes social foraging strategies.

Introduction

In many animals, sociality leads to increased feeding competition, while simultaneously reducing predation risk. Within cohesive social groups, food intake rate can vary according to age/sex class, dominance status, within-group spatial position, foraging strategy, and a variety of other factors (Janson 1990ab & 1992, Black et al. 1992, Altmann 1998). By understanding how these factors influence an individual's food intake rate, researchers can better understand mechanisms leading to sociality and varying social systems. Most current social foraging models focus on how group size affects individual food intake rates and foraging strategies (Caraco and Giraldeau 2000). However, the manner by which group size mediates foraging strategies, e.g., via group spread, inter-individual distances, and joining times, is unclear. The aim of this paper is, therefore, to determine the spatial mechanisms by which group size affects social foraging.

Increasingly, individual foraging strategies have been modeled using game theoretical approaches (Barnard and Sibley 1981, Vickery et al. 1991, Ranta et al. 1996, Ruxton et al. 2005). In particular, a growing body of work has used producer-scrounger models in which animals can either search for food or join conspecifics who have found food (which can also be termed finders and joiners; see also Caraco and Giraldeau 1991, Ruxton et al. 1995, Ranta et al. 1996). When an animal finds a patch of food, it typically consume a fraction of the resource before the arrival of conspecific, which is defined as the "finder's share." As the finder's share increases, the frequency of scroungers in a group is predicted to decline and the proportion of producers is predicted to increase. This proportion is hypothesized to play a major role in shaping group geometry, feeding competition, and competitive regimes (Barta et al. 1997, Giraldeau and Caraco 2000, Di Bitetti and Janson 2001, Dubois and Giraldeau 2004). The finder's share and size of resource patches are particularly important factors in the evolution of competitive regimes and kleptoparasitism. When food patches are small, they are often consumed before the arrival of a conspecific, thus the finder's share is essentially one, and it is generally not possible to compete aggressively over food (Dubois et al. 2003, Dubois and Giraldeau 2004). When food items are larger, the ability to compete over food depends on a combination of the finder's share, competitive inequalities between group members, food dispersion, group geometry, and the ability to monopolize food (Di Bitetti and Janson 2000).

Caraco and Giraldeau (2000) note that the distance between individuals, group spread, foraging area, and food detectibility are likely to be important factors which influence social foraging, yet few authors have incorporated inter-individual spacing into foraging models. In order to address these questions, a series of feeding experiments was conducted using wild groups of ring-tailed coatis (*Nasua nasua*) feeding on patches of introduced fruit. Coatis were chosen because they are typically terrestrial, we were able to observe easily their food finding and joining behaviors, and we could videotape these experiments. Coatis are opportunistic foragers, and have been known to exploit trash bins, exotic fruits, and other novel food items (Kaufman 1962, Booth-Binczik 2001). This latter behavior allowed us to rapidly train the coatis to use a new food source (seedless table grapes). A series of hypotheses concerning the outcome of the coati feeding experiments were made based on previous empirical and theoretical work:

1. Group size and the finder's share will be negatively related. (Giraldeau and Livoreil 1998). The group size effect should occur because as the number of potential joiners in a group increases, the chance that the finder will be joined, or joined more quickly will increase. This increase in joining, or quicker joining behavior should lead to a decrease in the finder's share.

2. The finder's share will be positively related to group spread, the distance between the finder and the nearest conspecific, time to the arrival of a conspecific, and the presence of a conspecific joiner. (DiBitetti and Janson 2000, Flynn and Giraldeau 2001). All four of these measures could be lead to more time for the finder to feed before the arrival of a conspecific, or lower the probability that the finder would be joined. This increased feeding time should lead to a higher finder's share.

3. The finder's share will be largest when finder is located in the rear of the group. If fewer individuals are located behind the finder, the probability of being joined should be smaller.

4. The amount of food available in a patch will be negatively related to the finder's share. (Giraldeau and Caraco 2000). For example, if an animal always eats five food items

before the arrival of a conspecific (regardless of all other factors), the finder's share would be 100% for a patch of five food items, and 10% for a patch of fifty items.

Methods

Study area and species

The study was conducted in the Iguazu National Park, Argentina between March 2003 and September 2004 (for details of the field site see: Brown and Zunino 1990; Di Bitetti 2001a,b). Observations were conducted on two study groups (PQ and PSG). During 2004, the subadults in the PQ broke off and formed their own subgroup (3-6 individuals). To increase the sample size for small groups, the PQ subadult subgroup and temporary foraging subgroups were used in the experiments whenever possible (N= 7 experiments). In general, the PQ and PSG groups foraged cohesively, and the group sizes remained relatively stable within a given year (PQ 2003= 15, 2004= 25-31; PSG 2003= 9-12, 2004= 25-27). In one case, the PQ group was joined by the PQ subgroup leading to a group of 35 individuals.

One to three adult females per group were fitted with radio-collars to help in locating the groups. Coatis were captured using 32x10x12 inch Tomahawk or similar traps, anesthetized, and either fitted with radio-collars or given multi-colored plastic ear-tags for individual identification (Dalton Rototags). Eartags were placed on juveniles older than four months of age, and we were able to recognize all individuals older than four months.

Groups of coatis were usually habituated within two to three weeks. Habituated coatis would allow observers to silently walk within 2m of a focal animal. It did not appear that the coatis changed their foraging and travel behavior due to being observed, with the exception of startle reactions to occasional accidental loud noises made by the observers (such as loudly breaking a branch). If a food item such as a pindo palm fruit (*Syagrus romazoffianum*) was encountered nearby an observer, the coatis would approach the food (even if the fruit was below the boot of an observer).

Experiments

Feeding experiments were conducted using medium sized green table grapes, and the methods were similar to DiBitetti and Janson (2001), although terrestrial rather than arboreal feeding sites were used. In order to mimic naturally occurring fruit trees, between five and one hundred (5, 10, 20, 50 or 100) grapes were placed in a $1m^2$ area. For the 100 grape treatments, four experimental areas were used ($30cm^2$, $70cm^2$, $1m^2$, and $2m^2$). This variation in density was designed for a concurrent study of feeding competition, which will be described elsewhere. A DVC video camera was set up on a portable tripod approximately 2.5m from the experiment site. Feeding experiments were always conducted with two or more observers who communicated with radios and hand signals. One observer would stay with the group, while the other arranged the fruit and video camera. When a group approached within 25m of the experiment, the researcher walking with the coatis positioned stopped in a location where he could see the coatis closest to the experiment, while the other researcher remained near the experiment and started the video camera. In order not to disturb the coatis during the detection process, both researchers tried to remain stationary, or walk as softly as possible. When coati groups approached the experiment, both observers carefully watched the behavior of the coatis nearest to the site. The observers would often coordinate their observations in order to track those multiple individuals which were in the best positions to discover the site. To prevent the coatis from cuing on the sight of the tripod or the sound of the radios used during the experiment, the hand held radios and video camera were regularly used outside the context of the feeding experiments.

Coatis regularly find food by olfaction, and not by sight (Hirsch in prep). The behaviors associated with olfactory food detection allowed us to pinpoint the distance at which coatis detected the feeding experiments, and what factors influenced food discovery (Hirsch in prep). Although we were able to observe the finder's discovery readily, the method by which joiners found food items were not regularly observed, and is not discussed in this manuscript. Coatis do not emit food calls. It is the impression of the author that the joiners used three cues to find the experiments: 1) visual detection of the finder eating the grapes, 2) olfactory detection of the experiment (with and without visual confirmation of the finder's presence), and 3) auditory information. The last method seemed to coincide with periods of loud fighting. It appeared that the likelihood of further joiners detecting the experiment was much greater following periods of loud fighting at the experiment site, although this needs to be confirmed.

The observers recorded several variables in conjunction with the experimental discoveries, including the identity and spatial position of the finder, and the distance from the finder to its nearest neighbor. Additional group levels factor recorded were the group length and width, and the distance of the experiment to the group center (at the time of arrival of the finder). The group length and width were estimated visually by the two observers. All other distances were measured using a 50m fiberglass tape after the experiment was completed. The group spread estimates were double checked when measuring the distance between the experiment and group center. When the detection distance was subtracted from this latter number, the resulting number should have been close to the radius of the group, which was the case during all experiments. The author later watched the recorded tapes to determine the number of grapes which the finder ate before the arrival of a conspecific (the finder's share), whether a finder was joined, and if so, the time to arrival of the finder. All times were measured to the nearest second.

The spatial position of the finder was recorded in the same manner as Janson (1990a,b). The group spread was visually divided into three concentric circles: 1) center, 2) middle, and 3) edge. The coati's location within these circles was then further subdivided into 12 positions based on the numbers of a clock, with 12 being the front-most position and 6 representing the back of the group. These 36 spatial positions were then summarized into five spatial position categories (as in Janson 1990a,b); 1) front edge, 2) front middle, 3) center, 4) back middle, and 5) back edge (Figure 1). A total of 179 experiments were conducted, but because we could not always accurately record all variables, only the 160 experiments with sufficient data were used.

Statistical methods

All data were entered into the STATISTICA statistical program (version 5.5, StatSoft, Inc. 2000.). Two separate Generalized Linear Models (GdLM) were analyzed using the Akaike index (AIC) to identify best subsets models. The first analysis used the arcsine transformed finder's share as the dependent variable, with year, month, age of the finder, presence of a joiner, time to arrival of conspecifics, distance to nearest neighbor, distance to group center, group length and width, spatial position of finder, group size, experiment density, and the number of grapes (log transformed) as the independent variables. Because the number of experiments detected in the center and middle positions was low (Hirsch in prep), the spatial position variable was treated as a continuous variable with one being the front edge of the group and five the back edge. A second GdLM analysis used the presence or absence of a conspecific joiner as the dependent variable with the previously listed variables entered as independent variables (with the exception of presence of a joiner, and the time to arrival). A best subset model was calculated indicating which factors best determined the finder's share, and another best subset model indicating which factors influence the likelihood that the finder will be joined by a conspecific. The inclusion of variable interactions did not change the resultant best subsets models in either analysis. For the full model results presented in Tables 1&2, these interactions are excluded for purposes of clarity.

Results

The two GdLM's were significant overall (finder's share, p=<0.001, arrival, p=0.021). The best subset model identified by the Akaike analysis of the determinants of the finder's share included the arrival of a conspecific, distance between the finder and its nearest neighbor, time to the arrival of a conspecific, and the number of grapes as being significant predictor variables (Chi^2= 209.5223, p=<0.001; Table 1.). Using the arrival of a conspecific as the dependent variable resulted in a best subsets model which included the distance to the finder's nearest neighbor, distance between the experiment and the group center, group width, spatial position of the finder, and the number of grapes (Chi^2= 58.581, p=<0.001; Table 2.). The average time between the finder's arrival and the arrival of a joiner was 23.22 seconds. Whether an individual was joined or not had a large influence on the finder's share. Finders who were not joined had much greater finder's shares (joined=0.15%, not joined=0.77%) and ate almost four times more grapes (number of grapes eaten before being joined= 4.43, if not joined=21.68).

When a conspecific did not arrive during an experiment, the finder's share was not always equal to one. The maximum number of grapes eaten by one coati was 42, which is an estimate of the maximum satiation amount for coatis eating grapes. If all experiments with less than 50 grapes are excluded, the average satiation amount for adults and subadults was 38.4 grapes (N=10) compared to 18.5 grapes for juveniles (N=2, maximum number of grapes eaten = 26). During the experiments in which the finders were not joined, they ate an average of 0.28 grapes per second. There was no effect of age/sex class on the feeding rate (Kruskal-Wallis p=0.442). The spatial density, which varied during the 100-grape experiments ($30cm^2$ to $2m^2$), had no influence on the encounter rate, and was conducted solely to test for its influence on feeding contest competition. The density of grapes in the experiments had no effect on the finder's share (paired T test, p=0.912). The lack of effect is logical given that these results only concern feeding rates before the rest of the group arrives, not afterwards.

The distribution of food discoveries was highly biased towards the front edge position (front edge= 78.11%, back edge= 15.38%, Figure 1). The front of the group also contained a higher density of individuals than the back. The average number of individuals within 3m of a focal animal was almost twice as high as at the back of the group (front edge= 1.50, back edge= 0.88). As the number of individuals in a particular spatial position increases, the number of conspecifics who can discover the experiment in that position increases, as well as the number of potential joiners in close proximity. As a consequence, the finder's advantage was higher at the back of the group (front edge= 7.31 grapes, back edge= 15.93 grapes). This difference was in part due to variation in the chances of being joined. Of the 132 experiments, which were discovered by front edge individuals, all but 15 finders were joined by conspecifics (88.6%), compared to half of the finders in the back periphery (13 of 26=50%; chi-square test for independence Chi^2=22.24, p<0.001). Although the discovery rate at the front of the group was over five times higher than the back, the benefits of being in the front of the group are roughly balanced out by the almost twofold increase in density at the front edge, and twofold increase in the finder's advantage at the back of the group. The exact payoffs to individuals foraging at the front and back edges of the group will be addressed in a future manuscript.

A single coati was never able to monopolize an entire experimental food plot (in part due to the deliberately even distribution of the food offered), and several coatis could simultaneously feed at an experiment site. Despite a situation resembling scramble competition, high levels of aggression were observed during the experiments. Although it was not possible to directly compare rates of aggression during the experiments to cases when the groups fed from natural fruit trees, it appeared that the level and style of aggression was similar in both cases. In most cases, coatis would fight over individual grapes and were not able to monopolize a patch of several fruits. Competition over grapes occurred only after a joiner appeared and thus is not discussed here, but the impact this competition has on food intake rates will be addressed in a future manuscript. In summary, the social foraging system of ring-tailed coatis resembled an information sharing system with incomplete sharing (see: Ruxton et al. 1995), and a combination of scramble and contest competition (see: Ranta et al. 1996).

Discussion

Number of fruits

The number of grapes used in the experiments had a large effect on the finder's share (Giraldeau and Carcaco 2000). As the number of grapes increased, the finder was able to eat a proportionally smaller amount of the total before the arrival of a conspecific. Additionally, the number of grapes was significantly and positively correlated with the probability of being joined. This result makes sense, because the probability of being joined should increase as the time spent feeding increases, which in turn increases with the number of fruit in the patch. The probability of being joined ranged from 72.7% when only five grapes were used, to a 90.4% probability when one hundred grapes were used. Most coati fruit patches are larger than the 5-20 grape experiments in both the number of fruits available and the time needed to deplete the resource (Hirsch unpublished work). The most common fruit species used by coatis in Iguazu, pindo palms, typically contain between 280-500 fruits per tree, with 56-100 of them being ripe at a given time (Di Bitetti personal communication). This estimate is consistent with data showing that the mean number of fruits eaten by coatis from underneath pindo trees was 106.7 fruits, and a median of 56.2 fruits (Hirsch in preparation). Because of the size of the natural fruit patches, and the ability of coatis to remember their location in time and space, it is predicted that coatis will almost always be joined by conspecifics when feeding at a single food source. In many cases, coatis had to either arrive at a food source first or aggressively compete with conspecifics to increase their individual food intake rates when eating fruit. This prior knowledge of food resources leads to cases which are by definition not able to generate producer-scrounger tactics. Producer-scrounger tactics in this population could probably only be used when discovering a fruit tree for the first time.

Group size and spatial factors

Group size had no direct significant effect on the finder's share or the probability that a finder would be joined by a conspecific. This result is contrary to expectations (Giraldeau and Carcaco 2000). Despite this finding, spatial factors, which are influenced by group size, did have large effects on the finder's share. The finder's share increased as the distance to the nearest individual increased, as the time to arrival increased, and when the finder was not joined by a conspecific. Additionally, the probability that a finder was joined was negatively related to the distance to the nearest neighbor and the distance between the experiment and group center. These results indicate that foraging away from other group members leads to an increase in an individual's finder's share. Despite being positively correlated with increased neighbor density and group size, the probability of being joined increased as group width increased. This demonstrates that group width is acting independently from these other variables to increase the likelihood of joining. It seems plausible that groups with wider spreads (or swaths) are able to detect more resources (or joining opportunities) than skinnier groups, which is consistent to previous work on baboon and capuchin monkey groups (Altman 1974; Janson and Di Bitteti 1997). Although group size is positively correlated with group spread, distance from the group center, and neighbor density (Table 3), when entered into the GdLM model with the presence of a joiner as the dependent variable, these spatial variables all resulted in significant effects, while group size did not. These results indicate that the behavioral strategies of individuals when foraging in social groups are accounted for more readily by their spacing behavior than by group size, a result that accords with recent work on vigilance behavior in primates (Treves 1998). By locating themselves away from other conspecifics, individuals may be able to mitigate or even avoid the negative effects of living in larger groups (Di Bitetti and Janson 2001).

Traditional producer-scrounger models have primarily focused on the effects of group size, but the results here indicate that inter-individual spacing is the likely mechanism driving the group size effect (see: Flynn and Giraldeau 2001). In some species, the ability for an individual to vary their within-group spacing may be highly constrained due to predation pressure. In some species individuals under low predation threat may be able to completely split off from a social group. Gompper (1996) has suggested that this imbalance between foraging costs and predation benefits has led to solitary foraging in adult male white-nosed coatis. In order to fully understand constraints on social foraging strategies, it is also important to understand the costs and benefits of spacing in relation to predation. Previous work on these coati groups had shown that vigilance levels rise when coatis have fewer neighbors and are in the front edge spatial position (Di Blanco and Hirsch 2006). These patterns indicate that individuals, who choose to forage away from others to increase foraging, simultaneously increase their risk of predation (Romey 1995, 1997).

Spatial position

An individual’s spatial position within the group had no direct effect on the finder’s share once all other factors were controlled for. This lack of pattern does not mean that spatial position does not affect foraging strategies. Instead, three variables that influence the finder’s share changed predictably with spatial position: 1) the arrival of a conspecific, 2) the time to arrival, and 3) the distance to the nearest neighbor. The probability that a finder was joined by a conspecific was positively correlated with being in the front of the group. The later result is likely due to the higher density of conspecifics at the front of the group, and from group members trailing the discoverer. If a food item is found at the front of the group, the cumulative likelihood that it will be discovered increases from back to front of the group, thus resulting in food depletion from back to front, a pattern found in several studies (Janson 1990b, Hall and Fedigan 1997, Bumann *et al.* 1997, Carbone *et al.* 2003). If an individual discovers a food item while in or near the back of the group, it will have far fewer (or no) conspecifics behind them that could stumble upon the discovery.

Coatis may be locating themselves in a manner similar to an ideal free distribution (e.g. Parker and Sutherland 1986). The higher discovery rate at the front of the group is offset by the higher density of individuals and reduced finder’s advantage. Once differences in food discovery and neighbor density are accounted for, the payoffs for individuals in the front and back of the group approximately balance out. Even if coatis are distributing themselves in this manner with respect to the finder’s share, it does not mean that all individuals have equal food intake. The finder’s share is a measure of the payoff before conspecifics arrive, thus any differences in dominance or fighting ability could affect the total final payoff after all fruit has been eaten (which will be addressed in a future manuscript). Additionally, even though the finder's share measures payoffs which occur before dominance interactions can occur, dominance relations may constrain where individuals are able to locate themselves within the group (Ron et. al. 1996, Hemelrijk 1998, 2000, Hirsch in press). In addition, individuals at the front of the group perceive a higher risk of predation, which would need to be incorporated into a full analysis of the costs and benefits of sptial position in ring-tailed coatis (DiBlanco and Hirsch 2006, Hirsch in prep).

Conclusion

Spacing is a crucially important factor influencing the foraging payoffs to group living organisms. By locating themselves away from others, individuals can increase the amount of time spent feeding on newly discovered food patches. They can also decrease the probability of being joined by locating themselves in the back of their social group. The heterogeneous nature of animal groups interacting with the environment results in a suite of potential foraging strategies which are influenced by an animal's dominance status, group size, predation pressure, and size and distribution of utilized food resources.

To date, very few studies have used spatially explicit foraging models (e.g. Rands et al. 2004, 2006). Barta et al. (1997) used individual based modeling to predict that finders (or producers) will be preferentially located at the group periphery. This and other studies are consistent with this prediction (Di Bitetti and Janson 2001). A major advantage of using individual based models is that spatial factors can be incorporated into the model (food detection distance, neighbor distance, and predation threat). Because the group size effects on social foraging variables are largely mediated through spatial factors as shown in this paper, individual based modeling may be a more biologically realistic form of modeling used to understand the costs and benefits of sociality in many organisms.

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Table 7.1. Generalized linear model for factors affecting the finder's share.

	DF	Estimate	Standard error	P	
Number of grapes (log)	1	-0.039	0.004	<0.001	***
Arrival of conspecific (no)	1	0.076	0.007	<0.001	***
Time to arrival of conspecific	1	0.001	<0.001	<0.001	***
Distance to NN	1	0.004	0.001	<0.001	***
Distance to group center	1	0.001	0.001	0.209	ns
Group length	1	0.000	0.000	0.694	ns
Group width	1	-0.001	0.001	0.077	ns
Spatial position of finder	1	0.003	0.003	0.390	ns
Group size	1	0.000	0.001	0.742	ns
Month	1	0.004	0.002	0.060	ns
Age	2				
Juvenile		-	-	-	
Subadult		0.002	0.008	0.779	ns
Adult		0.007	0.006	0.227	ns
Grape density	1	-0.002	0.011	0.838	ns

Table 7.2. Generalized linear model for factors affecting the probability that the finder is joined by a conspecific.

	DF	Estimate	Standard error	P	
Number of grapes (log)	1	0.570	0.245	0.020	*
Distance to NN	1	-0.296	0.082	0.000	***
Distance to group center	1	-0.084	0.039	0.033	*
Group length	1	0.005	0.022	0.839	ns
Group width	1	0.112	0.045	0.013	*
Spatial position of finder	1	-0.533	0.156	0.001	***
Group size	1	-0.096	0.051	0.060	ns
Month	1	-0.058	0.154	0.705	ns
Age	2				
Juvenile		-	-	-	
Subadult		0.029	0.472	0.952	ns
Adult		-0.336	0.354	0.342	ns
Grape density	1	0.092	0.761	0.904	ns

Table 7.3. Correlation coefficients for significant continuous predictor variables, and group size (N= 141 for all variables except arrival time, N= 116).

	Neighbor distance	**Group center**	**Group width**	**Group size**	**Spatial position**
Group center	0.288	-			
Group width	0.246	0.456	-		
Group size	-0.025	0.136	0.292	-	
Spatial position	0.238	-0.024	0.036	0.160	-
Arrival time	0.592	0.044	0.068	-0.122	0.072

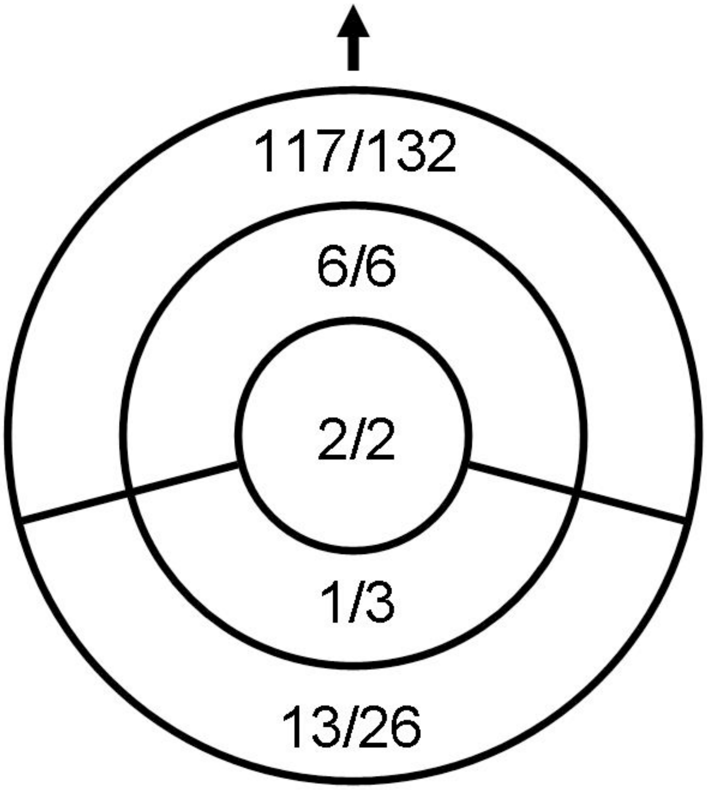

Figure 7.1. Number of discoveries when the finder was joined by a conspecific divided by the total number of discoveries per spatial position. The top of the figure represents the direction of group movement.

Chapter 8

Spatial position and feeding success in ring-tailed coatis.

Abstract

Spatial position within a social group has important effects on feeding success. When animals consume small, quickly eaten food items, individuals located at the front-edge of a group typically have greater foraging success. When groups of animals feed on large clumped resources, dominant individuals can monopolize the resource, leading to higher feeding success in the center of the group. The foraging success of ring-tailed coatis in Iguazu, Argentina did not fit this pattern. When feeding on small ground litter invertebrates, coatis had equal foraging success at all spatial positions. When feeding on fruit, individuals in the front of the group had greater feeding success. The first pattern likely resulted from an abundance of invertebrates in the environment. The within-group spatial position preferences of the four age/sex classes differed significantly from each other. Juveniles avoided the back of the group, while subadults were much more likely to be found in this spatial position. These preferences did not change when feeding on fruit versus invertebrates. Although groups typically became more elongated and traveled faster when feeding on fruit, it did not appear that the coatis were switching their spatial position strategies when switching food types. When feeding on pindo fruits, adult males

were found at the fruit tree less often than other age sex classes. During the first two minutes, juveniles were found at a fruit tree more often than other age sex classes. This behavior of the juveniles to locate themselves in the front of the group should result in higher feeding success on fruits, but increase their risk of predation.

Introduction

As an animal group moves through the environment, members consume food items encountered during travel. If these food items are small and quickly eaten, as individuals pass over or near the same locations, food availability may be reduced. This food depletion can lead to individuals in the back of the group having lower feeding success. This pattern of front-to-back food depletion has been found in several studies (O'Connell 1972, Robinson 1981, Janson 1990b, Black et al. 1992, Krause et al. 1992, Krause 1993b, Hall and Fedigan 1997, Stahl et al. 2001, Rowcliffe et al. 2004). However, when food is abundant, it may be impossible for individuals in the front of the group to deplete the food resource before the arrival of individuals in the back of the group. This food abundance leads to equal feeding rates from front to back of the group (e.g. Hall and Fedigan 1997 during the wet season).

Food items occurring in large patches may also lead to conditions in which no front to back food depletion is found. In many frugivorous primate species, central individuals have higher feeding intake rates (Robinson 1981, Janson 1986, 1990b). This often occurs because central dominant individuals are able to aggressively monopolize concentrated resources (Janson 1996, Grant et al. 2002). Other subordinate group members are then left to seek alternate food sources or wait for the dominants to leave the food patch before entering (Vogel and Janson in press). This can lead to a pattern where dominant individuals are more commonly found in the center of the group, which has been found in many primate species (for review see: Hirsch 2007). The same food resources which can lead to higher feeding success in central individuals are often important food resources such as fruit trees which individuals may remember (Garber and Paciulli 1997, Janson 1998, 2000, Janmaat et al. 2006). When individuals remember the location of food resources, individuals of different rank may change their decisions about spatial choice in order to increase food intake while avoiding aggression (Hirsch 2007). In particular, subordinate brown capuchin monkeys have been observed to "jump ahead" of the group before approaching a fruit tree (Janson 2000). By jumping ahead of the group, subordinates are often able to consume a share of the food resource before dominants arrive and monopolize the resource.

In cases where food items are not previously known, some individuals can act as "scroungers." Rather than independently search for food, these scroungers search for conspecifics who have found food, and then join the food discoverers (Giraldeau and Caraco 2000). When food joining opportunities are present, central and front-center spatial positions may be ideal for joining individuals to monitor food joining opportunities (Barta et al. 1997, Janson and Di Bitetti 1997). Because food joining often takes the form of aggressive kleptoparastism, dominants are predicted to be scroungers more often than subordinates, and thus may choose front-center spatial positions more than food finders (Janson and Di Bitetti 1997, Hirsch 2007). The combination of food abundance, depletion time, and prior knowledge of resources are predicted to influence an individual's choice of within-group spatial position differently depending on their dominance status (Hirsch 2007).

Coatis are an ideal species to test predictions related to within-group spatial position because they are mostly terrestrial, have linear dominance hierarchies, and eat both large clumped items and small dispersed items (fruit and ground litter invertebrates) (Hirsch in press). To make predictions as to how coatis choose their spatial position, it is important to understand if and how food is depleted. The purpose of this paper is to determine whether individuals in certain spatial positions have greater feeding rates than individuals in other spatial positions and if coatis choose spatial positions consistent with maximizing their food intake.

Methods

The study was conducted at the Iguazu National Park, Argentina between March 2003 and September 2004 (for details of the field site see: Brown and Zunino 1990; Di Bitetti 2001a,b). Two coati groups (designated PQ and PSG) were studied; these groups size varied between 8 and 30 individuals. Group composition changed over time, and subadults were only present in the PQ group during 2003, and the PSG group during 2004 (see Table 1 in Hirsch and Di Blanco 2006). Between one and three adult females per group were fitted with radio-collars to locate the groups. Coatis were captured using

Tomahawk or similar traps, anesthetized, and either fitted with radio-collars or given multi-colored plastic eartags for individual identification (Dalton Rototags). Eartags were placed on juveniles older than four months of age, and we were thus able to recognize individually all group members older than four months of age. Groups of coatis were usually habituated within two to three weeks. Habituated coatis would allow observers to silently walk within 2m of a focal animal.

Individual focal samples were taken on known individuals from August 2002 until October 2004. Focal samples were ten seconds in duration, and the same individual was not resampled within ten minutes. During the focal sample, I recorded the identity of the focal individual, within-group spatial position, individual and group activity (terrestrial foraging, rest, alert, travel), individual and group terrestriality (arboreal or terrestrial), group speed (ranked from 0-3 with 0 being no movement and 3 being rapid travel), the number and identity (when possible) of all individuals within 3m of the focal, and the number of food items ingested. Short focal samples were used because many of the associated variables recorded during the focal samples changed frequently and rapidly (particularly neighbor density). Individuals were selected opportunistically. Due to poor overall visibility in the dense forest, it was not feasible to select individuals based on a pre-determined order. Adults were preferentially targeted over juveniles, especially during 2004 when both groups had large numbers of juveniles.

Spatial position of individuals was recorded in the same manner as Janson (1990a,b). The group spread was visually divided into three concentric circles: 1) center, 2) middle,

3) edge. The coatis location within these circles was then further subdivided into 12 positions based on the number of a clock, with 12 being the front most position and 6 representing the back of the group. These 36 spatial positions were then summarized into 5 spatial position categories (as in Di Blanco and Hirsch 2006); 1) front edge, 2) front middle, 3) center, 4) back middle, 5) back edge (Fig. 1).

Additional data on group geometry was taken from 15-minute group scan samples. During these samples, the length and width of the group was estimated to the nearest 5m. All samples were taken by the author and these estimations were periodically checked for accuracy. When double-checking the group spread estimations, one field assistant and I would stand at the far ends of the group spread, in areas of good visibility, and measure the group spread using 50m fiberglass tape. Group behavior and feeding data taken during these scan samples included: the percentage of arboreal individuals, group activity, group speed, the number and location of fruit trees in the group spread (if present).

To detect if coatis arrived at fruit trees in a particular order, a series of tree focal samples was recorded. When I was able to arrive at a fruit tree before the arrival of the group, I recorded the number and identity (or age/sex class) of all individuals eating at the fruit tree every minute. Prior to the start of the sample, I set the timer on my watch to beep every minute. The tree focal sample started with the first beep after the arrival of the coati group, thus the sample could have started between 1-59 seconds after the arrival of the group. At each beep I recorded either the number of all feeding individuals, the number of feeding individuals in each age/sex class, or the ID of all feeding individuals. For this analysis I used the later two measures and lumped all known individuals into their respective age/sex classes. For consistency, I restricted the analysis to periods of feeding on pindo fruit (*Syagrus romanzoffianum*) and only data from the PSG group during 2004 were used. The number of individuals feeding per age/sex class was divided by their total number in the group to control for differing numbers of group members by age/sex class.

Statistical analyses

Ten second focal samples were used to test the relationship between feeding success and spatial position. Two GdLM models were constructed with fruit or invertebrate feeding success as the dependent variable, and several other potentially confounding variables were entered into the models. To test for nonlinear seasonal patterns, both the month (represented by numbers 1-12), and month squared were entered as variables in these models. An unequal sample size was recorded for each age/sex class due to differences in the number of individuals in each age/sex class and opportunistic sampling (adult males N= 238, adult females N= 1902, subadults N= 835, juveniles N= 1499). Unequal sample sizes were recorded for each within-group spatial position because the area of outer spatial positions was larger than inner spatial positions and because coati density varied by spatial position. All samples taken during periods of invertebrate foraging and fruit feeding were entered into a JMP dataset. To test whether age/sex class had a significant effect on spatial position, the focal samples were entered into a contingency table with four age/sex classes and five spatial positions (N= 20 cells). The total Chi-square models were significant for both fruit feeding and invertebrate foraging. Expected cell wise values were calculated for each age/sex class and spatial position, based on the total number of samples recorded for each age/sex class and the total number of samples recorded at each spatial position. The relative deviations from these expected values were calculated by subtracting the observed values from the expected values, and then dividing these by the expected values.. To test whether different age/sex classes were more or less likely to be found in certain spatial positions, G-tests were used to determine if age/sex class spatial preferences differed from random, and if so, cell wise Chi^2 values were calculated for each age/sex class and spatial position combination. All significant values (P=<0.05) are noted on Figure 3. This same analysis was repeated for samples taken during fruit feeding. To test whether the spatial position preferences of the four age/sex classes were different when feeding on fruit versus ground litter invertebrates, a multiple regression was run with spatial position as the dependant variable (as a categorical 1-5 variable). Age/sex class, fruit feeding, and the interaction of fruit feeding and age/sex class were entered as independent variables. Data from pindo fruit tree focal samples was entered into a JMP dataset. Tukey-Kramer paired comparisons were used to test for differences in the presence of the four age/sex classes at the pindo trees for each minute.

Results

When feeding on ground litter invertebrates, coatis typically consumed prey items in one second or less. In some cases, they would spend over 15 seconds consuming a particularly large annelid worm. Even though the consumption of invertebrates was generally quick, coatis could sometimes spend much longer excavating the prey. Coatis would sometimes spend over two minutes digging holes which reached up to 20cm in depth searching for subterranean invertebrates. In general, invertebrate search times were much shorter, and it appeared that most items were found directly beneath leaves or only a few centimeters below the leaf litter.

The eight most common fruit tree species fed upon by coatis were used in the analysis of fruit consumption. Fruit trees were depleted more slowly than invertebrates, ranging from 2.50-12.5 minutes on average. Some large *Ficus* trees were particularly productive, and coatis were recorded feeding continuously for up to 45 minutes in one tree. On the other hand, small *Cecropia* trees were generally depleted very quickly (average= 2.5 minutes, N=37). The most common fruit species eaten by coatis was pindo palm fruit (*Syagrus romanzoffianum*) which were depleted in an average of 5.68 minutes (N= 406).

The average length and width of the groups was 23.23m by 14.34m respectively (SE length= 0.387, SE width=0.198). Both group length and width were significantly positively correlated with group size (length, F=244.10, $P<0.001$, width, F=160.66, $P<0.001$). The average length and width of small groups (between 8-15 individuals) was 16.83m by 11.67m (SE length= 0.302, SE width=0.202). The group spread in large groups (25-31 individuals) was 28.87m by 17.10m (SE length= 0.668, SE width=0.323).

The group spread was generally greater in length than width and this elongation increased as the group increased travel speed (Chi^2= 109.05, DF=3, $P<0.001$) (Figure 1). There was a significant relationship between fruit feeding and group elongation. When group speed, group size, and the percentage of individuals eating fruit was entered into a multiple regression model, fruit eating was positively related to an increased group length/width ratio (F=10.11, p=0.002).

The spatial position preferences of the four age/sex classes during fruit feeding appeared to be similar to foraging patterns (whole model, R^2=0.026, DF=28, Chi^2=364.92, $P<0.001$). Adult females, subadults, and juveniles had statistically significant spatial position preferences during invertebrate foraging, but only subadults differed from random during fruit feeding (G-test P values for age/sex class = <0.05). These results are likely influenced by the lower sample sizes recorded during fruit feeding (fruit feeding N= 1045, invertebrate foraging N= 3429), and low sample sizes recorded for adult males (fruit feeding N= 50, invertebrate foraging N= 188). Subadults were less likely to be found in the center and more likely to be found at the back edge of the group when feeding on fruit (front edge, Chi^2=5.21, P= 0.023, back edge, Chi^2=5.99, P= 0.014) compared to other age-sex classes. During fruit feeding, it was much more common to record individuals in the center of the group compared to terrestrial foraging, which is either a result of biased data collection or a higher density in the group center during fruit feeding (Chi^2=115.28, $P<0.001$). Although both fruit feeding and age/sex class were highly significant in the final multiple regression model with spatial position as the dependant variable, the interaction was not (Table 3). The lack of effect of the interaction variable is consistent with the hypothesis that the spatial position preference of the age/sex classes does not change when feeding on fruit versus invertebrate foraging.

When feeding on ground litter invertebrates, individuals at the front of the group did not have higher food intake rates. Three predictor variables had significant effects on invertebrate foraging rates; group size, month, and month squared (Table 1). Invertebrate feeding success was negatively related to group size (slope estimate = -0.019, P= 0.003). Feeding rates were lowest during the winter. Winter months are typically colder and invertebrate abundance declines during this period (Di Bitetti 2001a, Beisiegal and Mantovani 2006). Spatial position had no effect on food intake even during the winter months when fewer invertebrates were available. Invertebrate feeding success was negatively related to group speed (slope estimate= -0.129, one tailed p=0.044).

Feeding rates differed depending on the species of fruit being eaten (Table 2). Individuals eating fruit had higher intake rates at the front of the group (slope estimate front-to-back = -0.103, p=0.034). When the interaction of the fruit species and spatial position variables was entered into an additional GdLM model, both variables remained significant and the interaction did not. Fruit intake decreased with increasing neighbor density, and was positively correlated with larger group size, time of day, and increased group speed. Although no differences in fruit intake rates were seen between the different age/sex classes, age/sex classes differed in their use of pindo fruit trees over time (Table 2.). Juveniles were more likely found feeding in pindo trees than subadults and adult males during the first minute (Tukey-Kramer paired comparison with adult females=

0.008, subadults= 0.011, adult male= 0.057). The presence of adult females and subadults did not differ during the first minute of pindo feeding (T-K= -0.022). During the second minute, juveniles were present more frequently than subadults (T-K= 0.001) and adult males (T-K= 0.037), and adult males were less likely to be present than all other age/sex classes. During minutes 3-4 the only significant difference was that adult males were less likely to be found pindo feeding than juveniles. From 5-10 minutes, no significant differences in the presence of individuals of each age/sex class at pindo trees was found. Not all pindo trees were depleted in the same amount of time, thus an analysis was conducted using only samples taken during the last minute of pindo feeding (all samples >1min., N=129). Tukey-Kramer analyses on the last minute of pindo feeding failed to identify any significant age/sex class differences.

Discussion

Invertebrate feeding success

There was no significant relationship between an individual's within-group spatial position and their feeding success on ground litter invertebrates. This effect remained throughout the year. This pattern suggests that invertebrates were so common that coatis were not able to deplete them from the front-to-back of the group. This same pattern was found by Hall and Fedigan (1997) except that they found a depletion effect during periods of invertebrate scarcity. Even during the Argentine winter when invertebrates were less abundant, coatis were still not able to deplete invertebrate food from the front to the back of the group. The significant negative effect of group size on invertebrate foraging success may be evidence of invertebrate food depletion in large groups, but this hypothesis is contradicted by the lack of effect of spatial position and neighbor density on invertebrate foraging rates.

A potential strategy to avoid conspecific interference and spatial depletion during foraging is to travel in a phalanx. By spreading the group out further in width than length, individuals may be able to increase the amount of food items encountered, while simultaneously reducing the amount of food depletion from front-to-back of the group (Altmann 1974, Hirsch 2007). Although invertebrate foraging was inversely correlated to group elongation, coati groups rarely traveled in a phalanx formation (15% of all samples). If the detection distances for ground litter invertebrates were extremely short, the group may have effectively traveled in a phalanx even when it didn't (i.e. apparent overlap in search fields would be negligible if search fields are narrow enough). The frequently elongated group spread may have been the result of the frequent traveling to fruit trees (once every 27 minutes, Hirsch unpublished data).When the group speed increased, coatis had lower invertebrate foraging success (one tailed P value= 0.044).

Fruit feeding success

Individuals at the front of the group had higher fruit feeding rates than individuals in the back. This effect remained when the species of fruit was controlled for in the GdLM analysis, meaning that front to back food depletion was found in all fruit species.

Alternately, insufficient sample sizes were collected to detect differences in depletion parameters between distinct fruit species. The fruit species had a significant effect on intake rate. Smaller, more abundant fruits (such as *Hovenia dulcis* and *Ficus sp.*) led to higher intake rates compared to fruits which were larger or more spread out in the tree canopy (*Citrus sp.* and *Crysophyllum gonocarpum*). Unlike invertebrate foraging, there was a significant negative relationship between the number of neighbors within 3m of the focal animal and fruit intake rate. Group size was positively related to fruit feeding success. The two main study groups almost doubled in size during 2004 (Hirsch in press), so that it was difficult to separate the effects of group size and year of the study. When year was entered into the GdLM, neither the year nor the group size variable were significantly related to fruit intake rate.

Within-group spatial position

Spatial position preferences differed between the four age/sex classes but did not differ when feeding on fruit versus invertebrates (see companion paper for further details on age/sex class differences). Fruit feeding patterns were very similar to invertebrate foraging, but age/sex class spatial position preferences generally did not reach significance, which was likely the result of lower sample sizes recorded for fruit feeding (Figures 3&4). The patterns of spatial position preference during focal samples are somewhat similar to patterns recorded during fruit tree focal samples. During periods of invertebrate foraging, juveniles were found to be on the front-edge of the group more often than chance. The over representation of juveniles during the first 1-2 minutes at a fruit tree, is an indication that they are more likely located at the front of the group during fruit feeding as well. Although the juveniles would not increase their invertebrate feeding rates at the front-edge position, their fruit intake should increase.

Although the use of the front-edge spatial position by juveniles may lead to higher fruit intake rates, is it advantageous for juveniles to consistently locate themselves in the front of the group? If coatis have no prior knowledge of fruit tree locations, this may be a good strategy by the juveniles. However, it is highly likely that coatis do know the location of fruit trees before visiting them. Coatis generally travel between fruit trees in straight lines, and increase travel speed before re-visiting fruit trees (Hirsch unpublished data). These patterns are highly consistent with the hypothesis that coatis have prior knowledge of fruit trees (Janson 2000, Pochron 2001). If juveniles have prior knowledge of fruit tree locations, it seems plausible that they would switch their within-group spatial strategies depending on the food source being used. During invertebrate foraging, they could range in the center of the group, where predation pressure is lowest, then, before arriving at a fruit tree, they could run up to the front of the group to feed before others (Di Blanco and Hirsch 2006, Hirsch 2007). It appears that the juveniles were not spacing themselves according to this strategy, but instead, consistently foraged near the front edge of the group, despite an increased predation risk in this position (Di Blanco and Hirsch 2006). A possible reason for this seemingly sub-optimal pattern displayed by the juveniles was that fruit trees were so common in the environment, and they were visited so frequently, it always payed to be located at the front of the group. The average distance between fruit trees visited by coatis was 108m (median= 53m, N=423, Hirsch unpublished data). Coati groups visited 17.8 fruit trees per day on average, or one tree every 27mins. (Hirsch unpublished data). It appeared that the distance between fruit tree visits was generally too short to allow juveniles to switch spatial strategies depending on the resources used. In many cases, individuals in the front of the group entered a new fruit tree while individuals at the back of the group were still feeding on a previous fruit tree.

Because subadults were subordinate to all other age/sex classes, they may be predicted to use the "jumping ahead" strategy as well. This pattern has commonly been seen in subordinate capuchin monkeys, and may allow subordinates to feed upon resources before the arrival of dominant individuals who may later monopolize the resource (Janson 1990b, Hirsch 2007). The evidence for this is conflicting. There was a trend for subadults to be found more often at the front edge during fruit feeding ($Chi^2=3.081$, $p=0.079$). The evidence from the spatial position data, supports the hypothesis that subadults were using a bimodal strategy of ranging in either the front-edge or back-edge of the group. This pattern was not detected during the fruit tree focal samples. Subadults were significantly less likely to be found at pindo trees than juveniles during the first minute. Subadults were also not found to be more frequently found feeding on a pindo tree during the last minute of visitation.

Although adult males were less likely to be in the front-middle spatial position during invertebrate foraging (Figure 3), no statistically significant differences were found due to low sample sizes (only one male was associated with each group). Adult males were consistently underrepresented at fruit trees during the first four minutes. It seemed that adult males did not rush ahead to fruit trees, but generally avoided the front position regardless of foraging type. Given that adult males are typically the most dominant group members, there seems to be little reason for adult males to avoid a concentrated source of food (Hirsch in press). In white-nosed coatis, Gompper et al. (1997) found that adult female coatis in larger groups were able to form coalitions and chase away adult males from fruit tree shadows. Despite adult male dominance in dyadic interactions, adult males may have chosen to avoid pindo trees to avoid the possibility that the multiple individuals concentrated there would form a coalition to drive them out. Additional data or field experiments are needed to further test this hypothesis.

Conclusion

The relationship between food size and feeding success within-the group was different than expected. Although fruits were depleted from the front to the back of the group, ground litter invertebrates were not. This is evidence that ground litter invertebrates in Iguazu National Park are too abundant to be easily depleted. Given these patterns of feeding success, the distribution of age/sex classes within the group was different than expected as well. The most dominant individuals, adult males and juveniles were predicted to locate themselves at the front-edge of the group during fruit feeding more than other group members. Some evidence of this pattern was found in juveniles, but adult males were consistently absent at fruit trees. A previous study of coati anti-predator behavior demonstrated that the perceived risk of predation is highest at the front-edge of the group (Di Blanco and Hirsch 2006). The spatial position preferences of juvenile ring-tailed coatis appear to be more reliant on foraging benefits than predation risk. Additionally, social factors such as avoiding aggression, may drive individuals to locate themselves in positions that are suboptimal for obtaining the highest foraging success possible (Hirsch companion paper). Such social effects may explain why adult males that were dominant during dyadic agonistic encounter, but had few or no allies, chose not to forage in the optimal spatial position for feeding.

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Table 8.1. Results of generalized linear model for factors affecting the food intake of coatis searching for ground litter invertebrates. N= 3429. DF=10, Chi^2=23.739, P=0.008.

Variable	**DF**	**Estimate**	**Standard Error**	**P value**
Month	1	-0.195	0.067	0.004
Month^2	1	0.014	0.005	0.007
Time of day	1	0.000	0.000	0.402
Group speed	1	-0.129	0.076	0.088
Group size	1	-0.019	0.006	0.003
Age/Sex	3			
Adult female		0.000	-	-
Adult male		0.106	0.140	0.448
Subadult		-0.128	0.096	0.181
Juvenile		0.045	0.085	0.591
Neighbor density	1	0.031	0.023	0.187
Spatial position (front to back)	1	0.000	0.028	0.994

Table 8.2. Generalized linear model for factors affecting the food intake of coatis feeding on fruit. N= 1045. DF=17, Chi^2=87.481, P=<0.001.

Variable	**DF**	**Estimate**	**Standard Error**	**P value**
Month	1	-0.133	0.153	0.385
Month^2	1	0.000	0.013	0.972
Time of day	1	0.000	0.000	0.070
Group speed	1	0.300	0.127	0.018
Group size	1	0.034	0.014	0.011
Age/Sex	3			
Juveniles		0.026	0.127	0.839
Subadults		-0.232	0.162	0.151
Adult females		0	-	-
Adult male	1	0.179	0.242	0.459
Neighbor density	1	-0.045	0.020	0.021
Spatial position (front to back)	1	-0.103	0.048	0.034
Species	7			
Arecastrum romanzoffianum		0	-	-
Cecropia pachystachia		-0.425	0.459	0.355
Maclura tinctorea		0.530	0.369	0.151
Ficus sp.		0.747	0.225	0.001
Citrus sp.		-0.782	0.220	0.000
Crysophyllum gonocarpum		-0.685	0.251	0.006
Hovenia dulcis		0.463	0.187	0.013
Eriobotrya japonica		-0.070	0.360	0.845

Table 8.3. Multiple regression model for factors affecting the number of samples recorded in each individual spatial position (categorical 1-5). N= 4474, DF=7, R^2= 0.007, Chi^2=101.92, P=<0.001.

Variable	**DF**	**Chi^2**	**P value**
Food (fruit or invertebrate)	3	5.79	<0.001
Age/sex class	3	13.89	0.003
Food x Age/sex	1	34.42	0.122

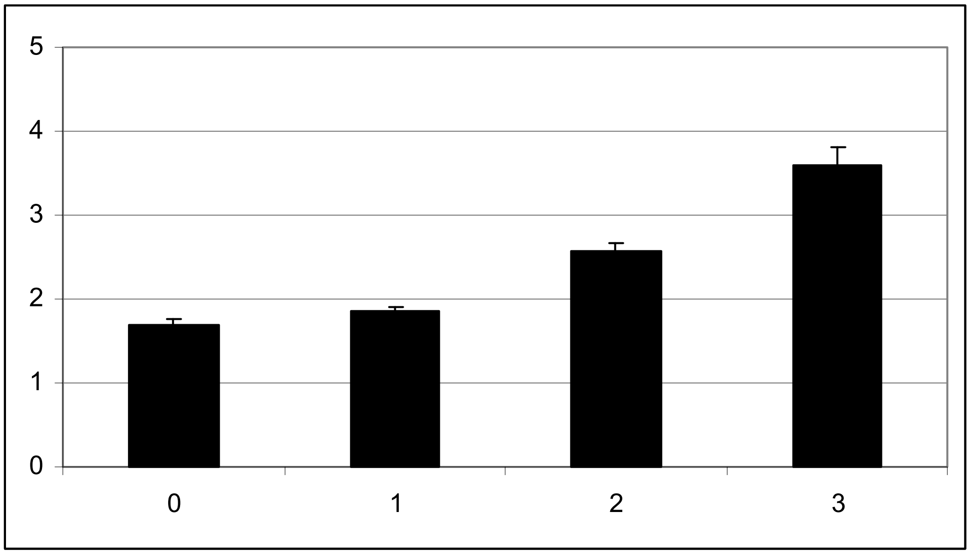

Figure 8.1. Length/width ratio of the group spread by group speed. Group spread was ranked from 0-3 with 0 being no movement and 3 being rapid travel. Higher L/W ratios indicate a more elongated group spread. Errors bars represent the standard error.

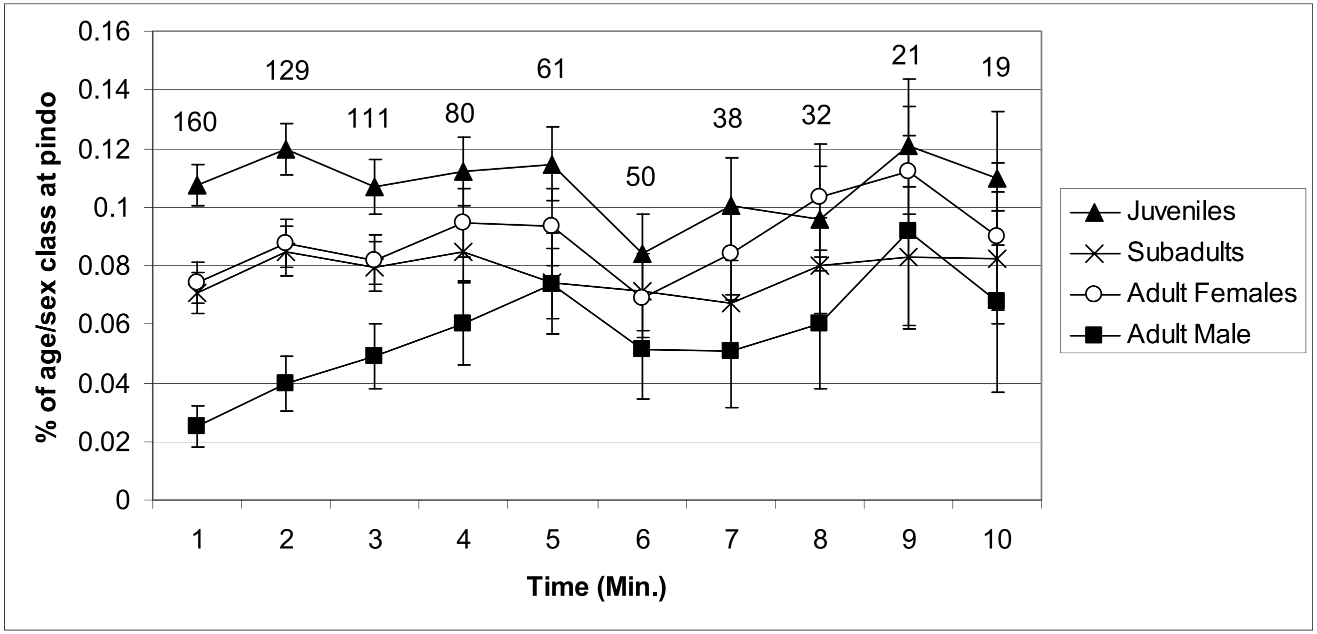

Figure 8.2. The proportion of individuals of each age/sex class at a target pindo fruit tree per unit of time. Time 1 equals the first minute of arrival at the fruit tree. Error bars = ±Standard error. N= number of fruit tree focal samples

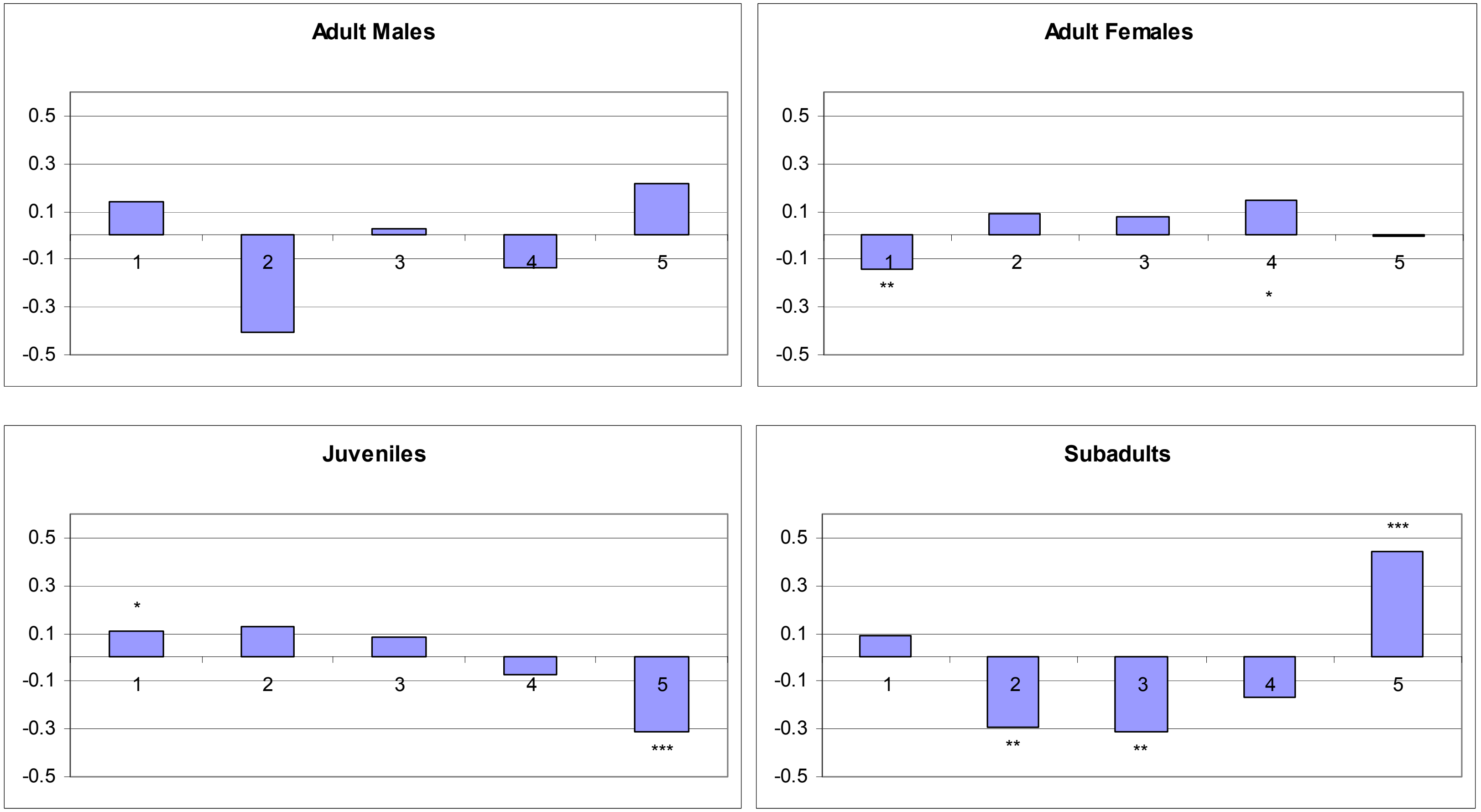

Figure 8.3. Deviations from expected values of within-group spatial position when feeding on terrestrial invertebrates during the entire year. Spatial position numbers are continuous with 1= front edge of group 5= back edge of group. * P = <0.05, ** = <0.01, *** = < 0.001. N=3429. Total model R^2= 0.010, DF= 12, Chi^2= 110.018, P= <0.001, N= 3429.

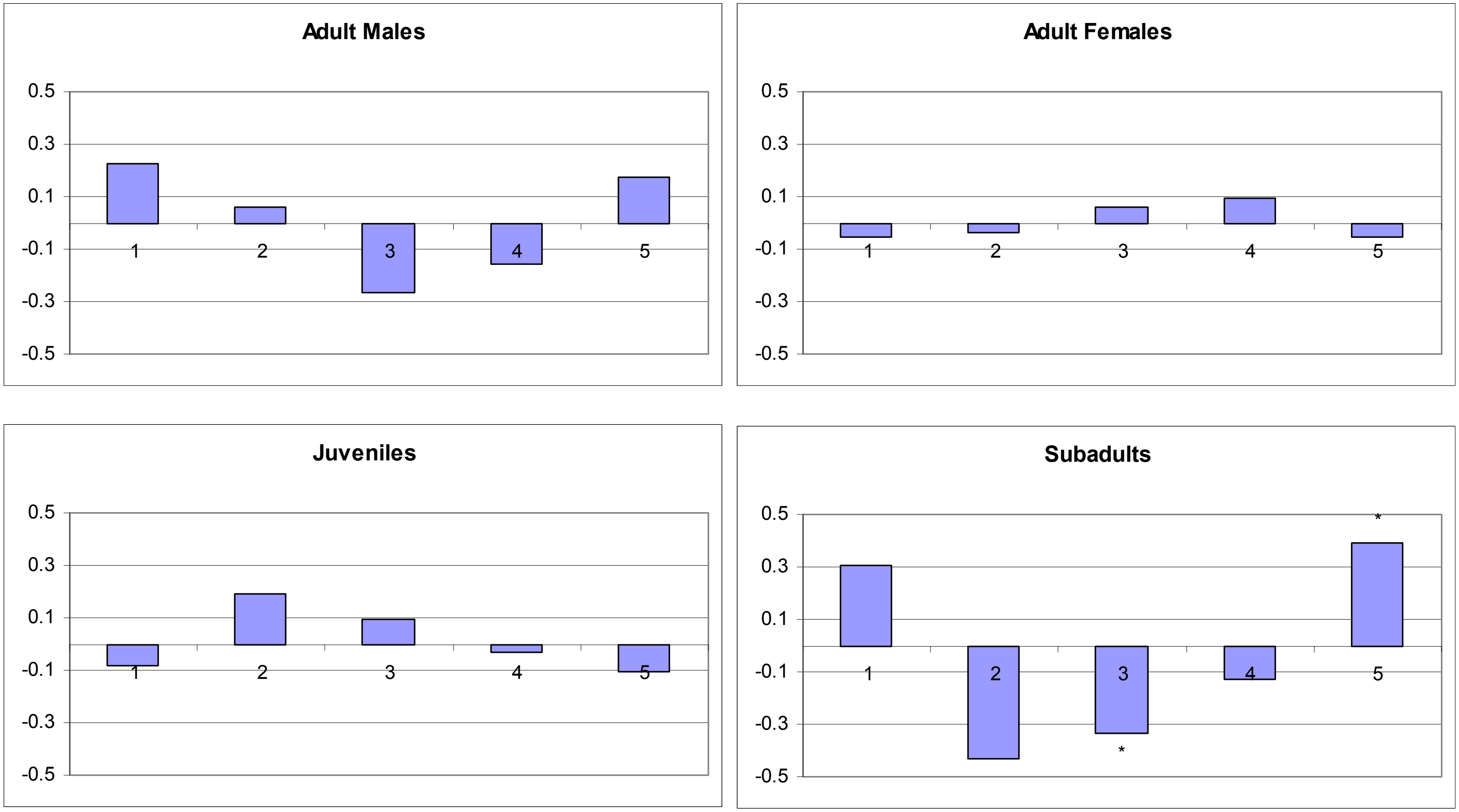

Figure 8.4. Deviations from expected values of within-group spatial position when feeding on fruit during the entire year. Spatial position numbers are continuous with 1= front edge of group 5= back edge of group. * P = <0.05, ** = <0.01, *** = < 0.001. N=1045. Total model R^2= 0.008, DF= 12, Chi^2= 26.688, P= <0.001, N= 1045.

Chapter 9

Within-group spatial position in ring-tailed coatis: balancing predation, feeding competition, and social competition

Abstract

A variety of factors can influence the costs and benefits of within-group spatial positions. For terrestrial group living animals, predation, feeding success, and social competition are thought to be three of the most important variables. The relative importance of these three factors was investigated in groups of ring-tailed coatis (*Nasua nasua*) in Iguazu, Argentina. Previous work found that coatis at the front-edge spatial position have higher predation threat and greater fruit feeding success. Different age/sex classes responded differently to these costs and benefits. Coatis preferred nearby neighbors of the same age/sex class, and these age/sex classes were found at certain spatial positions more or less frequently than expected. Juveniles were rarely found at the back of the group, while subadults were found there more frequently than all other age/sex classes. The spatial behavior of subadults was likely a strategy to avoid aggression, particularly from adult females. Subadults were typically subordinate to adult females, and their relationships were characterized by high levels of aggression. This aggression was especially common during the first half of the year when the juveniles were six months of age or less. During this half of the year, subadults were most often

found in the front or back of the group, and adult females were typically central. It appears that subadults were choosing within-group spatial positions to avoid aggression. On the other hand, juveniles appeared to choose spatial positions based on feeding success and not predation avoidance.

Introduction

Within-group spatial position is influenced by feeding competition, predation threat, social dominance, and other variables (Hirsch 2007). In general, individuals in central spatial positions are under a lower threat of predation and experience an increase in feeding competition (Krause 1994b, Krause and Ruxton 2000, Caro 2005). In moving groups, individuals at the front typically have higher foraging success and predation threat compared to the back of the group (Busse 1980, Janson 1990b, Bumann *et al.* 1997, Carbone *et al.* 2003, Di Blanco and Hirsch 2006). This pattern arises due to increased predator encounter rates at the front of the group, and food depletion from front to back. But, contest competition can lead to increased feeding success in the center of the group, which has been seen in several species (Robinson 1981, van Schaik & van Noordwijk 1986, 1988, Janson 1985, 1990b, Barton 1993, overview in: Hirsch in press).

In some cases, within-group spatial choice has a large social component. Several studies have reported a correlation between dominance status and centrality (Robinson 1981, Janson 1985, 1990a, van Schaik & van Noordwijk 1986, Rayor and Uetz, 1990, Clifton 1991, Flynn and Giraldeau 2001, Krause 1994a, Ron et al. 1996). Janson (1985, 1990ab) emphasized that feeding ecology could drive these patterns. In many studies of frugivorous primates, centrality in the group often equates to being inside a fruit tree, while subordinates are often excluded from the patch (Vogel and Janson in press).

Hemelrijk (1998, 2000) noted that patterns of group geometry could arise from simple social processes. Using individual-based computer models, Hemelrijk (1998, 2000) found that dominants are predicted to be more central, and subordinate individuals peripheralized as a result of aggressive interactions. If spatial centrality of dominants can arise in the absence of predation and feeding competition effects, these computer models are an important insight into the origin and formation of within-group spatial preferences. However, it must be noted that the dominance relations that Hemelrijk modeled are typically driven by feeding competition, thus the two factors are often inexorably linked. Although the avoidance of dominants may be an important proximate factor in determining spatial position, the underlying cause in most cases is presumed to be feeding competition (but see: Ron et al. 1996).

The purpose of this study is to describe the spatial structure of ring-tailed coatis (Nasua nasua) in relation to their social status, and to determine how important these factors are compared to feeding and predation. In the companion paper, no front to back food depletion was recorded when coatis fed on small ground-litter invertebrates. During fruit feeding, feeding success declined from the front to the back of the group, and was not found to be highest in the center. This may be related to the fact that coatis do not typically monopolize food patches and exclude others.

In general, adult male ring-tailed coatis are the highest-ranking individuals in a social group (one per group), followed by juveniles, adult females and subadults. Because dominance in ring-tailed coatis is closely tied to age/sex class and not to matriline (Hirsch in press), spatial position preferences are described in relation to each age/sex class (e.g. Janson 1990a,b) and not by linking the dominance hierarchy to spatial centrality (e.g. Hall and Fedigan 1997). Of all age/sex classes, the subadults are most likely to be constrained in their choice of spatial position. Subadults are the most subordinate age/sex class, and receive large amounts of aggression from adult females. This pattern of agonism between adult females and subadults is particularly severe when juveniles are six months of age or less (November-April).

A previous study of white-nosed coatis (*N narica*) spatial position reported that adults tended to range on the periphery of the group during terrestrial invertebrate foraging, while juveniles were located in the center (Russell 1979). Russell concluded that this pattern was a response to predation because the most vulnerable individuals ranged in the center, particularly when juveniles are less than three months old. Because Russell (1979) did not record within-group spatial position with respect to group movement, it is difficult to further understand how feeding competition and predation may have shaped spatial patterns in white-nosed coatis. The predictions of how predation pressure affects ring-tailed coatis can be refined due to previous work on the Iguazu study population. Individuals at the front-edge of the group were found to spend significantly more time being vigilant than all other spatial positions, indicating a particularly high threat of predation at the front (Di Blanco and Hirsch 2006). These considerations lead to the following hypothesized patterns:

Hypothesis 1.

If predation was the principal factor driving spatial patterns, juveniles should be more central than other age/sex classes, and rarely be found at the front edge of the group. This pattern should decrease as juveniles grow older.

Hypothesis 2.

Individuals on the front edge of the group had higher feeding success on fallen fruit. If feeding success was the primary force driving individuals to choose a spatial position, it is predicted that juveniles and adult males would be found on the front edge of the group more often than other age/sex classes.

Hypothesis 3.

If spatial patterns were driven exclusively by social interactions, adult males and juveniles should have been centrally located in the group, while subadults were predicted to be the most peripheral.

Methods

The study was conducted at Iguazu National Park, Argentina between August 2002 and October 2004 (for details of the field site see: Brown and Zunino 1990; Di Bitetti

2001a,b). Coati groups used in the study ranged from 8-31 individuals (See Table 1 in Di Blanco and Hirsch 2006 for details). One-three adult females per group were fitted with radio-collars in order to locate the groups. Coatis were captured using Tomahawk or similar traps, anesthetized, and either fitted with radio-collars or given multi-colored plastic eartags for individual identification (Dalton Rototags). Eartags were placed on juveniles older than four months of age, and albeit was possible to individual recognize all group members older than four months of age. Groups of coatis were usually habituated within two to three weeks. Habituated coatis would allow observers to silently walk within 2m of a focal animal.

Individual focal samples were taken on known individuals from two groups (PQ and PSG) from August 2002 until October 2004. The group composition changed over time, and subadults were only present in the PQ group during 2003, and the PSG group during 2004. Focal samples were ten seconds in duration, and the same individual was not resampled within ten minutes. During the focal sample, I recorded the identity of the focal individual, within-group spatial position, individual and group activity (terrestrial foraging, rest, alert, travel), individual and group terrestriality (arboreal or terrestrial), group speed (ranked from 0-3 with 0 being no movement and 3 being rapid travel), the number and identity (when possible) of all individuals within 3m of the focal, and the number of food items ingested. Short focal samples were used because many of the associated variables recorded during the focal samples changed frequently (particularly neighbor density). Individuals were selected opportunistically. Due to poor overall visibility in the dense forest, it was not feasible to select individuals based on a pre-determined order. Adults were preferentially targeted over juveniles, especially during 2004 when both groups had large numbers of juveniles.

Spatial position of individuals was recorded in the same manner as Janson (1990a,b). The group spread was visually divided into three concentric circles: 1) center, 2) middle, 3) edge. The coatis location within these circles was then further subdivided into 12 positions based on the number of a clock, with 12 being the front most position and 6 representing the back of the group. These 36 spatial positions were then summarized into 5 spatial position categories (as in Di Blanco and Hirsch in press); 1) front edge, 2) front middle, 3) center, 4) back middle, 5) back edge (Fig. 1).

Statistical analyses

An unequal sample size was recorded for each age/sex class due to differences in the number of individuals in each age/sex class and opportunistic sampling. Unequal sample sizes were recorded for each within-group spatial position because the area of outer spatial positions was larger than inner spatial positions and because coati density varied by spatial position. All samples taken during periods of invertebrate foraging and fruit feeding were entered into a JMP dataset. In order to test whether age/sex class had a significant effect on spatial position, the focal samples were entered into a contingency table with four age/sex classes and five spatial positions (N= 20 cells). To test for changes over time, the dataset was divided into two seasons corresponding to the age of the juveniles, resulting in two contingency tables. The first season was when juveniles were 6 months of age or less (November-April), and the second when the juveniles were all at least 6 months of age (May-October). Both Chi^2 models were significant. Expected cell wise values were calculated for each age/sex class and spatial position, based on the total number of samples recorded for each age/sex class and the total number of samples recorded at each spatial position. The relative deviations from these expected values were calculated by subtracting the observed values from the expected values, and then dividing these by the expected values. These relative deviations were graphed separately for each age/sex class (Figures 2 & 3). To test whether different age/sex classes were more or less likely to be found in certain spatial positions, G-tests were used to determine if age/sex class spatial preferences differed from random, and if so, cell wise Chi^2 values were calculated for each age/sex class and spatial position combination. All significant values ($P=<0.05$) are noted on Figures 2 & 3.

To measure association patterns within and between certain age/sex classes, association indexes were created using data from the two group years when subadults were present (PQ 2003, PSG 2004). Association matrixes were constructed using individual focal samples where all individuals within 3m were identified. To summarize the age/sex class associations, individual ID data were pooled into their corresponding age/sex classes. Two matrices per year were constructed to test for changes over time (juveniles younger or older than 6 months of age). Because of a delay in trapping the PSG juveniles during 2004, the first PSG 2004 matrix does not include juveniles. The total number of near neighbors for each age/sex class was summed and divided by the total number of group members which could have been a neighbor to the focal (group size minus one). This number was then multiplied by the number of members of each age/sex class to determine the predicted number of samples with which each age/sex class should have been found within 3m. The distribution of samples recorded for each age sex class was then analyzed using G-tests to determine whether the distribution of associations deviated from random. Cell wise P values were then calculated, but only if the P value for the overall test for heterogeneity was 0.05 or less (for each age/sex class per time period).

Results

The spatial positions in which the four age/sex classes were recorded during terrestrial foraging were significantly different from random for both halves of the year (Nov.-April: total model R^2= 0.021, N= 1472, DF= 12, Chi^2= 95.187, P= <0.001. May-Oct.: total model R^2= 0.007, N= 1957, DF= 12, Chi^2= 44.546, P= <0.001). With the exception of adult males, the spatial distribution of each age/sex class was significantly different from random (G-test Chi^2 value >9.488, DF= 4). The spatial patterns of the four age/sex classes changed over time. During the period between November and April, when juveniles were 6 months of age or less, the differences between the observed and expected values were larger for adult females and subadults (Figures 2 and 3). When juveniles were young, adult females were significantly more likely to be central in the group, and less likely to be peripheral. The spatial distribution of subadults during the first period was the reverse of adult females. Subadults were significantly less likely to be in central spatial positions, and were more likely to be peripheral (Figure 2). During the latter half of the coati year when the juveniles were older, adult females and subadults were significantly more likely to be at the back edge of the group (Figures 2 and 3). Juveniles exhibited the reverse pattern throughout the year and were significantly less likely to be in the back of the group. When data from all 12 months was pooled, juveniles were found more frequently in the front-edge spatial position (front-edge deviation= 0.111, Chi^2=4.662, P=0.031). No significant results were found for adult males unless the results from both halves of the year were pooled. In this total dataset, males were significantly less likely to be in the front-middle spatial position (front-middle deviation= -.405, Chi^2= 5.510, p=0.019).

The groups were not spatially heterogeneous. The average number of neighbors within 3m was highest in the center compared to peripheral spatial positions, and the positions in the front had more neighbors than their corresponding positions in the back of the group (1. front edge= 1.50, 2. front-middle= 2.34, 3. center= 3.03, 4. back middle= 1.63, 5. back edge= 1.18). The number of neighbors within 3m differed by age/sex class (Kruskal-Wallis test, Chi^2= 56.00, DF= 3, P<0.001) and by time period (Chi^2= 59.00, DF= 1, P<0.001)(Figure 4). The most notable difference was that adult females had many more neighbors when their offspring were young compared to when they were six months of age or older (Chi^2= 96.00, DF=1, P<0.001).

The age/sex class composition of near neighbors of adult females, subadults, and juveniles were all significantly different from the expected values (Tables 2abcd). The age/sex class composition of near neighbors for adult males never differed from expected. Adult females and subadults were always found together less than predicted, with the exception of PQ subadult neighbors during the latter half of 2003. The average deviation from expected for adult females and subadults was greater during the period in which juveniles were 6 months of age or younger compared to the latter half of the year. In general, each age/sex class was found with other members of the same age/sex class more often than predicted. A seeming exception to the pattern of age/sex class cohesiveness was the pattern found during the latter half of 2004 in the PSG group, when subadults and adult females were found to be near neighbors less often than expected. In this case, an exceptionally large number of juveniles, which often clustered together, may have skewed the results from other age/sex classes.

Discussion

Hypothesis 1. Predation and spatial position.

There is little evidence to suggest that predation is the major factor shaping within-group spatial position preferences in ring-tailed coatis. If predation were a major factor juveniles should have been found on the front edge of the group less often than other age/sex classes. This hypothesis was not supported, and juveniles were found on the front-edge of the group more often than predicted. A previous study of white nosed coati spatial position in Panama found that juveniles were more often in the center of the group, especially during the first three months of life (Russell 1979). Because coati juveniles spend their first 6-7 weeks in their mothers nest, Russell's results presumably only apply to the first 5-6 weeks in which juveniles have entered their social group. Because juveniles in Iguazu were only ear-tagged after the age of four months no equivalent data are available here. Russell found the same pattern of juvenile centrality after 3 months, which is different from the pattern found in Iguazu. Russell (1979) claimed that the peripherality of adults and subadults functioned to protect juveniles from predators. In Iguazu adult females were found in the center of the group more often than predicted. In this respect, the patterns of age/sex class spatial preferences are the exact opposite found by Russell (1979).

The lack of juvenile centrality may have been a byproduct of low predation threat in Iguazu. A previous study of ring-tailed coati vigilance behavior in Iguazu found that levels of anti-predatory vigilance were much higher at the front of the group than all other spatial positions (Di Blanco and Hirsch 2006). Because juvenile coatis were frequently found in the front of the group, it might be concluded that the costs of increased predation risk in the front-edge were outweighed by foraging benefits.

Hypothesis 2. Feeding competition.

Higher feeding rates at the front edge spatial position have been found in a large variety of organisms (reviews: Krause and Ruxton 2002, Hirsch 2007). If feeding competition is the main factor determining within-group spatial position, juvenile coatis were predicted to be found at the front edge of the group more than lower-ranking age/sex classes. Juveniles were more likely to be found in the front edge of the group when data from throughout the year was used in the analysis. When juveniles were 6 months of age or less, subadults were also found at the front edge of the group more often than predicted. If there was a correlation between dominance rank and forward group positions, subadults should have been found at the front edge less than all other age/sex classes. The patterns found in this study may indicate that spatial position preferences were mostly driven by social factors, or a more complex mechanism of feeding competition (Hirsch 2007). In the companion study, a correlation was found between the front-edge spatial position and fruit intake rate. In the case of juveniles, they may have chosen front edge spatial positions to arrive at fruit resources before other age/sex classes. By arriving first, the juveniles are able to consume more and possibly higher quality fruit than those who arrive later. Subadults also appeared to use a similar strategy of ranging in the front of the group, but they differ from juveniles in their frequent use of the back edge spatial position. Subadults appeared to use a bimodal strategy of spatial position choice. They either ranged at the front of group or the back, and rarely the center. When at the front, they were sometimes able to arrive at fruit trees before others, but were often forced to leave when adult females arrived. Alternately, the subadults stayed at the back of the group where they ate the leftovers and avoided aggression.

Despite their high dominance rank, adult males were not found in the front edge of the group more than other age/sex classes. Adult males were found at fruit trees less frequently than all other age/sex classes. This avoidance of fruit trees may be the result of an active avoidance of concentrated food patches. In white-nosed coatis, adult females and their offspring have been found to form coalitions against adult males, and chase them from fruit tree shadows (Gompper 1996). This was also occasionally seen in ring-tailed coatis. If a similar threat of coalitionary aggression is present in ring-tailed coatis, adult males may be avoiding fruit trees, or other areas where several coatis are concentrated in a small area. Although the average number of near neighbors was not lower for adult males compared to other age/sex classes, they were found at fruit trees less often than other age/sex classes.

Hypothesis 3. Social effects on spatial position.

Patterns of spatial position preference by age/sex class appear to be heavily influenced by social effects. In particular, adult females and subadults were much less likely to be in the same spatial positions from November-April (Figure 2). This pattern was also reflected in the proximity data, wherein adult females and subadults occurred as neighbors less than predicted (Table 2A & 2C). These patterns indicate that subadults were actively avoiding adult females or were chased away by adult females when juveniles are six months of age or less. Patterns of dominance behavior are consistent with both of these conclusions (Hirsch in press). Although the precise ultimate mechanisms for juvenile dominance have yet to be determined, ring-tailed coatis exhibit a form of juvenile dominance or tolerated aggression unlike those found in other social mammals (Hirsch in press). In these groups, juveniles aggressively fought for food and won dominance interactions with older larger individuals. The ability of juveniles to win dominance interactions was probably linked to adult female support from. In particular, adult females are particularly aggressive towards subadults when their juveniles are six months of age or younger. This pattern of increased aggression when juveniles are young and vulnerable appears to influence the spacing and spatial position patterns as well. When juveniles first enter the group, the new subadults are chased from or actively avoid those areas where adult females are found. Once the levels of aggression subside, the subadults shift spatial position preferences as to no longer strictly avoid being close to adult females.

Conclusion

Ring-tailed coatis of different age/sex classes had distinct spatial position preferences. These preferences did not fit predictions conforming to anti-predation benefits of spatial position choice. It appears that feeding competition and social interactions were the key factors driving individual spacing decisions. Juvenile ranging at the front edge of the group was likely a strategy to increase fruit intake. This conclusion is further supported by fruit tree focal samples in which juveniles were more likely to feed during the first minute than other age/sex classes and had higher total fruit feeding levels than all other age/sex classes (Hirsch in prep). It appeared that juvenile ring-tailed coatis in Iguazu National Park located themselves based more on feeding competition than predation risk. Subadults were seen at the front or back of the group more frequently than the center. Given that aggressive interactions between adult females and subadults were more frequent during the first 6 months of the coati year, the spacing of subadults appeared to have been driven by aggression more than any other factors. This was evident during the latter half of the coati year when subadult avoidance of adult females seemed to have relaxed. Spacing patterns of adult males were generally not significant, and did not fit neatly into any strict pattern. Adult males were found at fruit trees less often than all other age/sex classes. Although adult males tended to be dominant to all other age/sex classes, the avoidance of concentrated food patches may have been a strategy to avoid contest competition from coalitions of related females (Gompper et al. 1997).

These results partially mirror the conclusions from Janson (1990 a,b) on capuchin monkeys, in which dominant individuals (the dominant male and female) chose spatial positions that maximized their feeding success, and the least tolerated individuals stayed in peripheral spatial positions despite higher predation risk and at best mediocre foraging success. However, in Janson's study, the most vulnerable individuals preferentially stayed close to the center of the group, unlike the case for ring-tailed coatis. The ring-tailed coati patterns also differed from white-nosed coatis, where juveniles were central and adult females peripheral (Russell 1979). In ring-tailed coatis, food acquisition and social competition appear to be the major factors driving spatial position preference and not predation.

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Table 9.1. Group membership for the PQ and PSG during the study period. Subadults are individuals between 12 and 24 months of age. Juveniles are between 2 and 12 months old.

Group	Year	Adult males	Adult females	Subadults	Juveniles	Total group size
PQ	2003	1	3	2	9	15
	2004	0-1	5	0	22-24	27-29
PSG	2003	0-1	3-5	0	6	9-12
	2004	1	5	6	15-17	27-29

Table 9.2. Deviations from expected summed pair wise associations for each age/sex class. Rows represent the focal individuals and columns represent the deviations from predicted pair wise associations. Each age/sex class was tested for heterogeneity for each time period (e.g. each row) using G-tests. With the exception of adult males, the distribution of neighbors for all age/sex classes differed from expected for all years (DF=3, G-test Chi^2 >7.815). In every year, adult males did not significantly differ from expected (DF= 2, G-test Chi^2 <5.991). The cell wise P values for adult males were not reported to reflect this lack of overall significance.

A. Group PQ, March-April 2003

	Adult Male		**Adult Females**		**Subadults**		**Juveniles**		**N**
	deviation	P	deviation	P	deviation	P	deviation	P	
Adult Male	-	-	-0.129	-	0.307	-	-0.025	-	75
Adult Females	-0.677	<0.001	0.085	<0.001	-0.624	<0.001	0.103	<0.001	735
Subadults	0.195	0.026	-0.175	<0.001	1.732	<0.001	-0.156	<0.001	164
Juveniles	-0.383	<0.001	0.532	<0.001	-0.244	<0.001	0.75	<0.001	672

B. Group PQ, May-October 2003

	Adult Male		**Adult Females**		**Subadults**		**Juveniles**		**N**
	deviation	P	deviation	P	deviation	P	deviation	P	
Adult Male	-	-	0	-	-0.25	-	0.056	-	28
Adult Females	-0.553	0.002	0.005	0.593	-0.181	0.003	0.1	<0.001	188
Subadults	-0.451	0.029	0.19	0.003	0.647	<0.001	-0.085	0.001	102
Juveniles	-0.563	<0.001	-0.114	<0.001	-0.192	<0.001	0.161	<0.001	416

C. Group PSG, December 2003-April 2004

	Adult Male		**Adult Females**		**Subadults**		**N**
	deviation	P	deviation	P	deviation	P	
Adult Male	-	-	0.074	-	-0.062	-	43
Adult Females	0.704	<0.001	0.214	<0.001	-0.26	<0.001	213
Subadults	-0.465	<0.001	-0.513	<0.001	0.606	<0.001	226

D. Group PSG, May-October 2004

	Adult Male		**Adult Females**		**Subadults**		**Juveniles**		**N**
	deviation	P	deviation	P	deviation	P	deviation	P	
Adult Male	-	-	-0.017	-	-0.058	-	0.021	-	83
Adult Females	-0.306	0.007	-0.289	<0.001	-0.151	<0.001	0.139	<0.001	346
Subadults	-0.568	0.01	-0.222	<0.001	-0.317	<0.001	0.173	<0.001	222
Juveniles	-0.339	0.023	-0.295	<0.001	-0.394	<0.001	0.244	<0.001	218

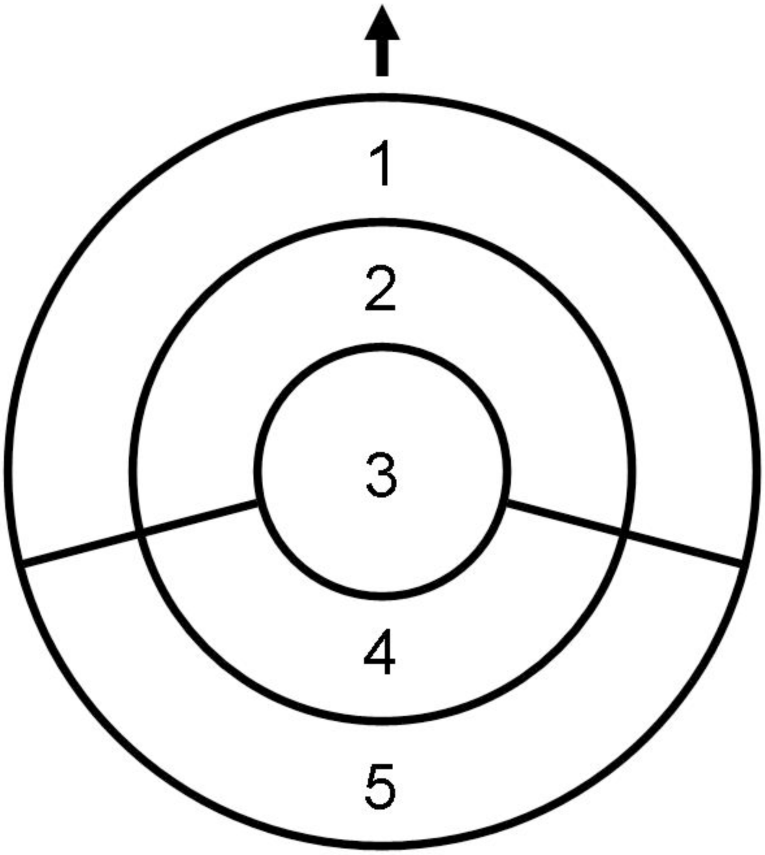


Figure 9.1. Spatial position categories with the top representing the direction of group movement. 1) Front edge, 2) front middle, 3) center, 4) back middle, 5) back edge.

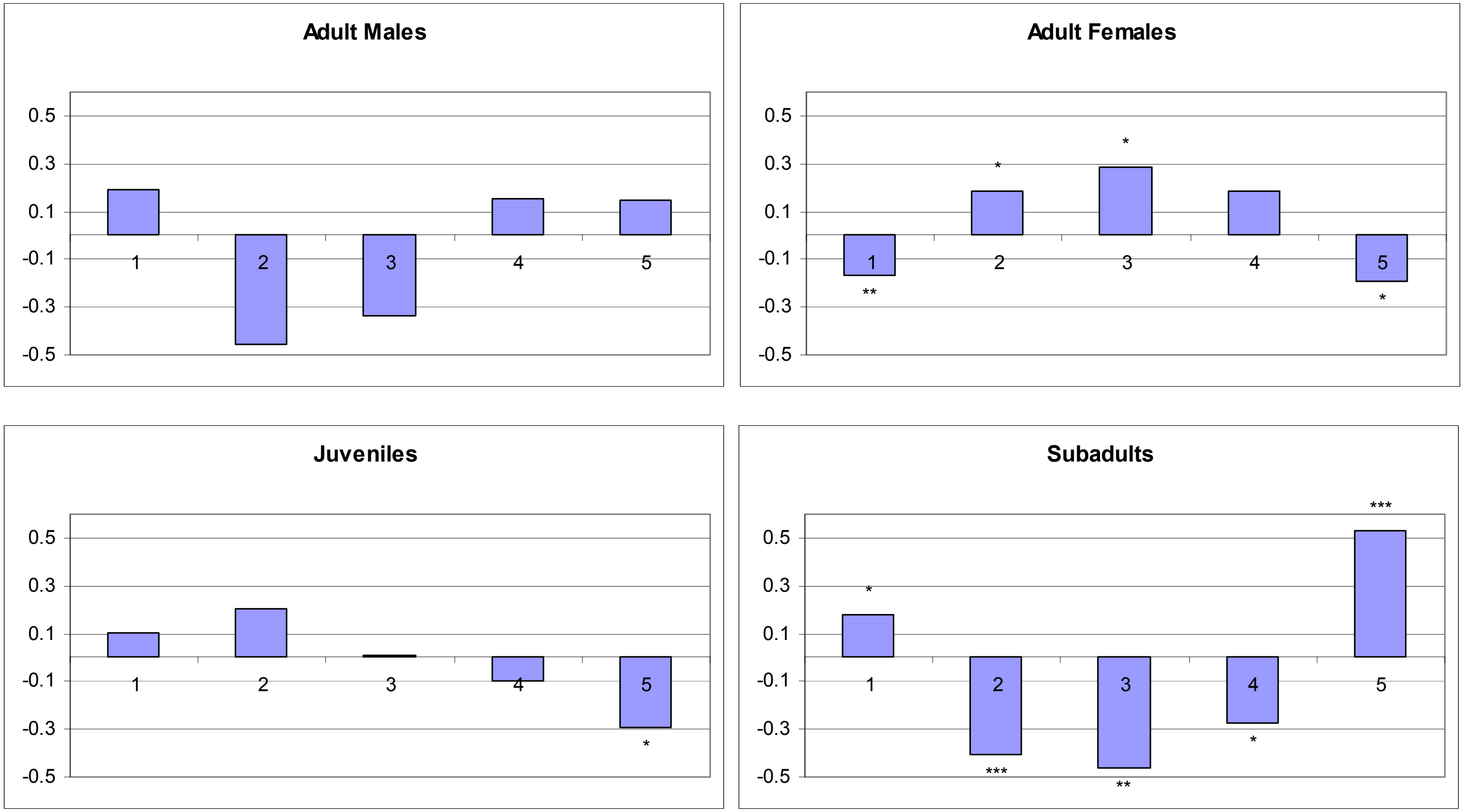
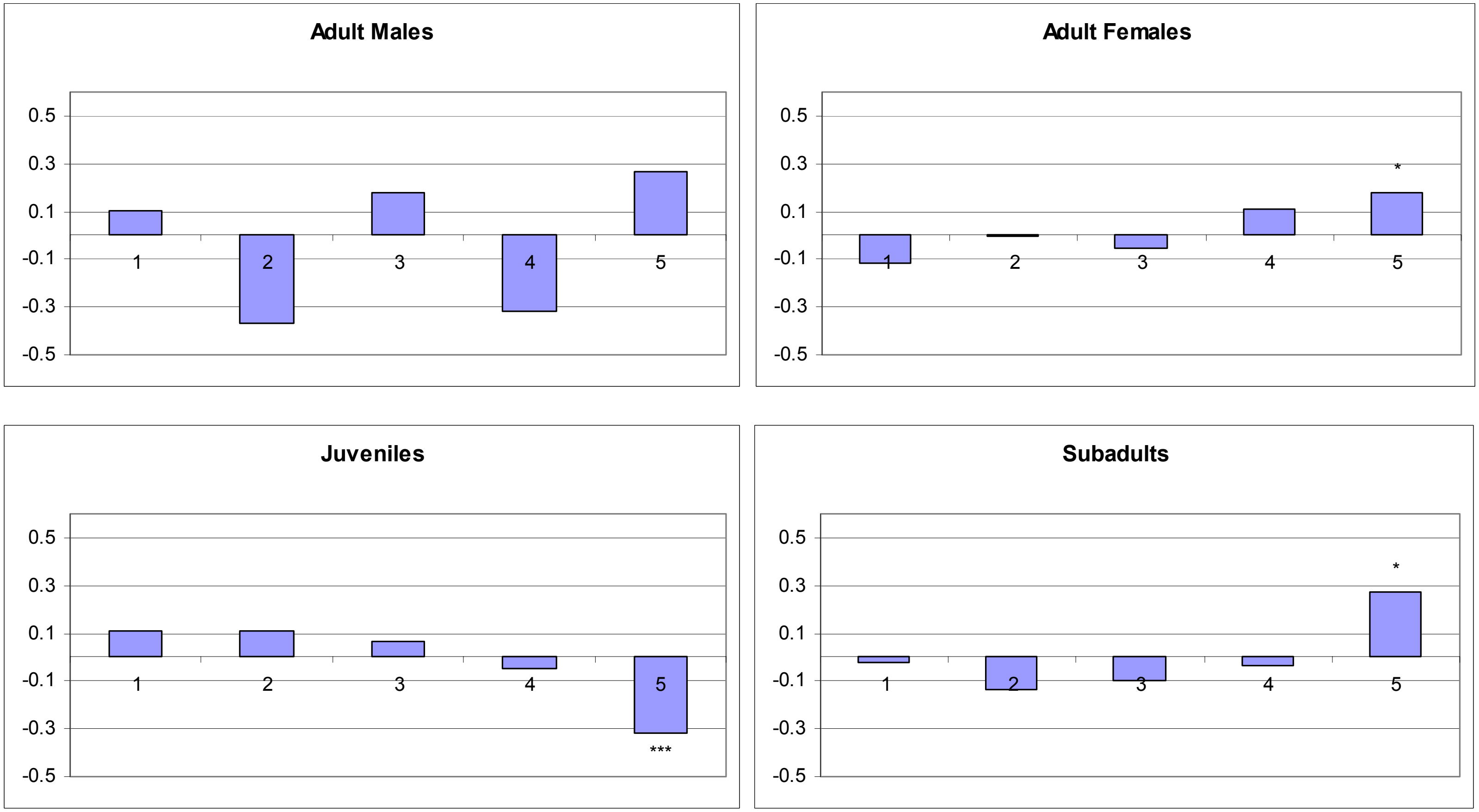


Figure 9.2. Deviations from expected values of within-group spatial position during November-April. Juveniles are 6 months of age or less during this period. Spatial positions correspond to positions 1-5 in figure 1. * P = <0.05, ** = <0.01, *** = < 0.001. Total model R^2= 0.021, DF= 12, Chi^2= 95.187, P= <0.001, N=1472.



Adult Males

Adult Females

Juveniles

Subadults

Figure 9.3. Deviations from expected values of within-group spatial position during May-October. Juveniles are at least 6 months during this period. Spatial positions correspond to positions 1-5 in figure 1. * P = <0.05, ** = <0.01, *** = < 0.001. Total model R^2= 0.007, DF= 12, Chi^2= 44.546, P= <0.001, N= 1957.

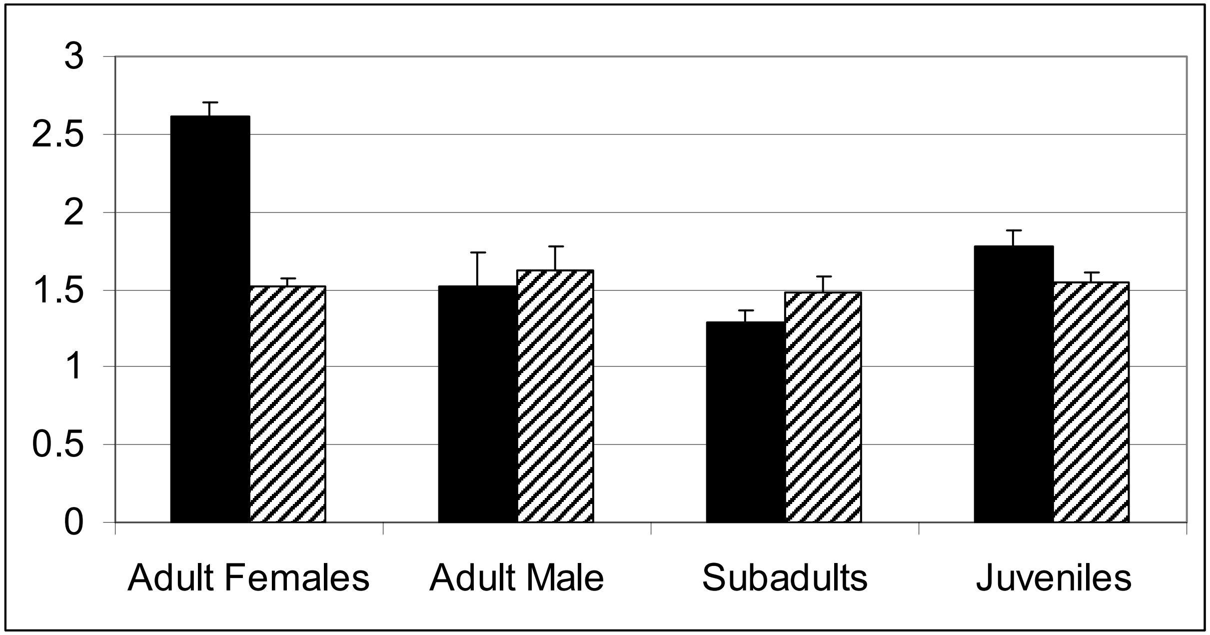


Figure 9.4. Average number of neighbors within 3m of each age/sex class. The black bars correspond to November-April, and May-October stripped bars. Errors bars represent the standard error.

Chapter 10

Summary and Conclusions

Within-group spatial position is affected by a variety of factors. In the first chapter, I developed several predictions about how dominance, food size, number of food items within the group, prior knowledge of resources, and predation threat should lead individuals to choose spatial positions which increase their personal fitness. Much of this model was based on observational and experimental studies conducted by Charles Janson and Mario Di Bitetti on brown capuchin monkeys (*Cebus apella*). Because brown capuchins are sympatric with ring-tailed coatis in Iguazu, comparing the two species may lead to important conclusions. In this summary chapter I will outline the major conclusions of the thesis, synthesize disparate sections of the previous chapters, and compare the behavior of ring-tailed coatis to other species such as brown capuchin monkeys. By writing this summary I hope to clear up some unanswered or unclear topics present in the thesis, discuss where this study relates in the larger picture of mammalian social behavior, and address what needs to be done in the future to answer some of the unanswered questions about ring-tailed coati social behavior.

Predation is an important determinant of spatial choice in most social mammals (Krause 1994, Krause and Ruxton 2002, Caro 2005), yet this topic has mostly been excluded from this thesis. I highly encourage the reader to read Di Blanco and Hirsch (2006) if they have not already done so. That paper is an important piece of the puzzle addressed in this thesis, but was not included because it was primarily the work of my coauthor, Yamil Di Blanco. One of the most important results of that work is that within-group spatial position was found to be a stronger determinant of vigilance levels than inter-individual spacing and group size. This contrasted with one of my previous publications where I found that inter-individual spacing may be the strongest determinant of vigilance levels in capuchin monkeys (Hirsch 2002). What is clear from both of these studies is that social mammals in Iguazu perceive a significant predation risk when on the ground. This perception is probably a good reflection of true predation threat because Iguazu has low raptor densities combined with an intact terrestrial predator community. In 2004, a study measuring felid abundance was undertaken in Iguazu by Mario Di Bitetti, Agostin Paviolo, and Carlos De Angelo (2006ab, and in preparation). The results from these studies indicated that predation abundance in Iguazu was low compared to other Neotropical forests, including other coati field sites. Although the comparatively low density of predators drives vigilance behavior in a manner which was consistent with a significant threat of predation (e.g. vigilance levels were highest at the front edge of the group), there was little evidence indicating that predation was an important factor driving spatial preferences.

Low predator densities in Iguazu were partly responsible for the high coati survivorship. The two other major factors responsible for high coati survivorship were the presence of tourists, and the coatis' use of steep cliffs. A sharp increase in predation on the GR group during 2004 supported the hypothesis that the use of steep cliffs was the major factor preventing predation in the coati groups. This high survivorship had marked impacts on the demography and population biology of coati groups in Iguazu. The coati groups which were followed during this study increased in size every year, and these groups were not demographically stable. This local population growth may have produced something akin to a source-sink population dynamic in which growing groups gradually dispersed from the main study area, only to encounter much higher predation rates in areas further away. Observations by Agustin Paviolo and his field assistants reported that the population density of coatis appeared to be much lower outside the main study area, and it has been noted that high coati densities are often found in areas with access to human refuse (Alves-Costa et al. 2004).

The patterns of coati survivorship in Iguazu may have played an important role in shaping social behavior. It appeared that nest mortality occurred in an all-or-nothing pattern, with most cohorts surviving more or less intact until weaning, while about 10% of nest cohorts disappeared. By having all-or-nothing juvenile survivorship, coatis often had companion littermates in their group throughout development, and often into maturity. The presence of these close relatives appeared to be a consistent phenomenon in Iguazu coati groups. For example, the PQ group was composed of one large matriline, and all adult females had either mother-daughter, sister-sister, or aunt-niece, relationships during the study. This high degree of relatedness may exceed that of manyother female philopatric social mammal species. Determining the degree of relatedness, and the maternity and paternity of coati offspring during the course of this study is a major priority for future work. Fortunately, an extensive collection of tissue samples was taken during the ear tagging procedure. It was hypothesized that the high degrees of relatedness between group members could have helped drive juvenile dominance or tolerated aggression. If so, this tolerated aggression is basically an altruistic act on the part of older individuals (i.e. giving up food to younger individuals).

On its face, high degrees of relatedness alone probably could not result in the type of juvenile dominance found here. If competition is intense, as it often is in coati groups, the costs of competition should outweigh the inclusive benefits of altruism, and thus not lead to the juvenile "dominance" found here (West et al. 2002). In other words, inclusive fitness may play an important role in shaping juvenile agonistic patterns in coatis, but it likely that this is not the sole explanation.

Along with growing group sizes, coati groups in Iguazu often had high juvenile: adult female ratios (often 5:1). It visually appeared that the large number of juveniles in these groups had an effect on dominance relations, but juveniles with high dominance ranks were found in groups with low ratios as well. The demography and life history of coatis in Iguazu appeared to influence agonistic interactions in other important ways. Compared to primate species, coatis have very fast life histories, with females maturing at the age of 22 months and giving birth to as many as six offspring per year. Young juvenile coatis gained weight rapidly, which should have been energetically costly. In order to grow so rapidly, juvenile coatis need to have relatively high food intake. One possible way to increase food intake is to increase the time spent foraging. Although comparative levels of time spent foraging were not recorded, it appeared that juvenile coatis spent less time foraging than older individuals, and more time playing. Another way to increase food intake is through an increase in foraging efficiency. No significant differences were seen in invertebrate foraging intake rates between juveniles and older individuals. In addition, intake rates at the front edge of the group, where juveniles were located more often, were not higher than other areas of the group. It appeared that juveniles had similar invertebrate food intake rates as older individuals.

The foraging patterns found in pindo tree focal samples indicated that juveniles ate more fruit than other age/sex classes. Given that a significantly higher proportion of agonistic interactions occurred at pindo fruit trees compared to all other food sources, and that pindo was the single most important fruit resource used by coatis at Iguazu, successful agonism during pindo foraging was likely to be particularly important in permitting rapid juvenile growth. The "dominance" or "tolerated aggression" of juvenile coatis is one of the more interesting findings of this study, as well as one of the most difficult to reconcile with studies of other social mammals. Although the fighting ability of juvenile coatis was presumably less than subadults and adults, juveniles regularly won dominance interactions. These interactions were typically, but not always, during foraging. It appears that the combination of high degrees of relatedness and the greater need for food in juveniles may have combined to be a major factor driving patterns of juvenile agonism. If a juvenile receives a higher benefit from eating an individual food item than older individuals, the benefit/cost ratio of fighting over the item may shift towards the juvenile (cf. Parker and Rubenstein 1981). Because juveniles and older individuals are likely to be closely related, the benefits to older individuals of winning food items may be completely offset by inclusive fitness gains if juveniles, who value the item more, win the item.

A shift in the relative value of foods for different age classes combined with high degrees of relatedness between group members was not the only thing driving juvenile agonistic patterns. Although these factors may be important, the presence of adult female support for juveniles appeared to play a major role in enforcing deference to juvenile agonism. Adult females supported all juveniles in the group, not just their own offspring (although the genetic analyses needed to confirm this are still not available). It appeared that even if an older individual wanted to fight a juvenile over food, adult female support for juveniles generally enforced compliance and tolerance for juvenile aggression.

Because juveniles were the highest-ranking age/sex class (behind adult males), they should have been able to choose any within-group spatial position, and were predicted to conform to the model outlined in the first chapter. Juveniles were regularly found at the front edge of the group more often than other age/sex classes. In the original model, this pattern would have been predicted based on invertebrate foraging benefits. Because invertebrate foraging efficiency was not highest at the front-edge of coati groups, invertebrate foraging could not have been responsible for this pattern. Instead, it appeared that quickly depleted fruit trees, such as pindo, were driving juveniles to range in the front-edge spatial position. During the first four minutes of pindo fruit feeding, juvenile coatis were found foraging on fruit proportionately more than all other age/sex classes.

The total time spent feeding on pindo fruit was highest for juveniles as well. In the original model, it was not predicted that pindo would drive these spacing patterns. In brown capuchins, pindos were depleted more slowly, and generally led to spatial strategies consistent with producer-scrounger relationships (Di Bitetti and Janson 2001). So why are capuchins and coatis utilizing this fruit species differently?

When capuchins consume pindo fruits, only one or two monkeys typically feed in a tree at a given time. When coatis eat pindo, an average of four coatis was found per tree, and often times, more than 15 coatis would forage at a pindo simultaneously. So why was there a difference in pindo usage? The major explanation is that capuchins have much wider group spreads than coatis. Capuchins in Iguazu had an average group diameter of 96.5m (Macuco group 1999, Hirsch unpublished data) while the average group length and width of coatis was 22.3m, and 14.3m respectively. Because of this, capuchin groups often contained several pindo trees at the same time. Multiple fruit trees were also observed inside coati groups, but to a much lesser extent. Coati groups foraging on fruit typically had 1.45 fruit trees within the spread at the same time, whereas the number for capuchin groups was about 4 (Janson, pers.comm.). Because of the greater number of fruit trees inside capuchin groups, the opportunity costs of feeding in a pindo were much lower in capuchins, and thus they avoided aggression by spreading out over multiple resources at a time (cf. Vogel and Janson 2006), reducing the number of individuals per pindo. The higher numbers of co-feeding animals at a pindo in coati groups may have led to a greater need to fight for pindo resources, thus helping to favor juvenile dominance.

Substrate use was another likely reason why more coatis simultaneously foraged at pindo than capuchins. Capuchins ate pindo inside the tree, while coatis ate fruits both inside the tree and on the ground. The maximum number of coatis which were observed arboreally foraging on one pindo frond was 5 individuals, and typically, only 2-3 could fit in one frond. Because most of the coatis ate on the ground, many more coatis could forage at a pindo tree compared to capuchin monkeys. In addition, there appeared to be major differences in the ability of coatis and capuchins to monopolize fruit resources. Dominant capuchins were able to exclude individuals from fruit patches at distances up to 10m (Janson 1996). This was not the case for coatis. During the 100 grape feeding experiments, dominant coatis were not able to exclude others from areas as small as 30cm^2. It also appeared that coatis rarely attempted to do so. In one case, an adult male attempted to monopolize a 70cm^2 fruit feeding plot, but was unable to without having other coatis sneak behind it and steal fruit. It appears that different social mammals have different "monopolization" distances. Some species are able to exclude others from large areas, while other species are unable to exclude others, even from small food patches. The ability to monopolize resources has been well studied in fish in laboratory conditions by James Grant (Grant *et al.* 2000, 2002, Dubois *et al*. 2003), but little work has been done comparing different species in these types of controlled conditions.

Capuchins and coatis not only differed in how they use pindo fruits, but they also differed in time spent foraging on pindo. Capuchins typically visited pindo fruits during 5% or less of their fruit tree visitations (April-January), with a seasonal peak of 38% of visits during February-May (Janson unpublished data). Coatis spent 30% of fruit foraging time at pindo trees (April-January), with a seasonal peak of 60% of fruit foraging time during February-May. This is a major difference in fruit usage for these two conspecific frugivorous mammal species. It appears that coatis specialized on pindo, while capuchins specialized on larger fruit sources with slower depletion times. In the winter months, when only pindo fruits were available in areas without exotic species, capuchins spent a major fraction of their feeding time using the growing shoots of a common viny bamboo (*Chusquea ramosissima*). This resource required great manual dexterity to use efficiently and was rarely eaten by coatis (N= 1 observation).

This heavy reliance on pindo fruits resulted in different costs and benefits of spatial position with respect to feeding competition than predicted. Because coatis exploited pindo so frequently, and because the pindo were depleted so quickly (partly because greater numbers of coatis fed on each pindo compared to capuchins), pindos were a “quickly depleted” food source for coatis, while they were a “medium depletion time” resource for capuchins. The use of pindos by coatis also appeared to be clumped in space (Hirsch unpublished data). Coatis would often travel to clumps of pindo trees where several trees were found within 10-50m of each other, and group members would “ping-pong” between these various trees. In many cases, coatis visited the same tree several times a day, although repeated visits were often undertaken by only a handful of individuals and not the whole group. Although detailed ranging data was recorded, the complete results and analyses of this data were not completed in time for inclusion in this dissertation. Because coatis used pindo trees in a repeated, quickly depleted manner, the best way for individuals to increase their fruit foraging success was not by monopolizing individual fruit trees (as happened in capuchins), but to locate themselves at the front of the group.

Juvenile coatis were found in the spatial positions one would predict if feeding competition was the primary determinant of spatial choice. The odd aspect of this pattern is that the front-edge spatial position was also the area of the group with the highest perceived predation risk. For juvenile coatis, which are the most vulnerable to predation, to seemingly ignore this risk of predation in favor of foraging benefits is rather remarkable. In most animal species, juveniles and infants are found in the center of the group more often, thus the coatis were spaced contrary to the general mammalian pattern (Hirsch in press). Why would juveniles seemingly "ignore" predation in favor of more food? Although the levels of predation were not high, the threat of predation exists (Di Blanco and Hirsch 2006). Maybe the drive for food was so strong in this species, that the benefits of increased food intake outweighed the (small) risk of predation. This same drive for food also led to an unusual system of juvenile tolerated aggression. What is needed for future research is additional data on the impact of feeding rates. It would be ideal to have detailed measures of coati weight gain per month (which could possibly be recorded in a similar manner as Clutton-Brock and colleagues work on meerkats). It would also be informative to study these groups during periods of very low food availability. Because the presence of exotic fruits near the tourist areas provided a "fallback food" during the period of lowest invertebrate and natural fruit abundance, there appeared to be no period during the year when coatis were particularly food stressed. After this study ended (December 2004), the National Park toughened up their program to eradicate exotic fruit species. It would be interesting to study these groups now to see if the removal of exotic fruits had an impact on the behavior of these coatis.

Ultimately, there are still many unanswered questions from this study. First and foremost, what is the genetic relatedness of group members? Secondly, how important is human disturbance on the behavior and ecology of coatis? It would be advantageous to study ring-tailed coatis in other study areas that have less human disturbance and better visibility for observers. Third, if the coati populations had higher predation threats and were not expanding every year, what impact would this have on the social structure of these groups? Fourth, if adult female coatis occasionally transferred to other groups, how would this impact the system of adult female support for all juveniles? Fifth, if coatis fed on resources of different size and depletion time, how would this impact the relationship between spatial position and feeding success, and would the coatis adjust their behavior in the hypothesized manner? The behavior of ring-tailed coatis in this study was different from expected, but generally seemed to fall into explainable patterns. Nonetheless, the unusual dominance structure described here may depend on an overlap of low predation rate mostly concentrated on nests, high female relatedness, and small food patch size. Changing any one of these may cause marked changes in the observed social structure of ring-tailed coatis. What is needed to test the explanations suggested here is a greater number of studies on this species under different ecological situations.

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Appendix

Group home range maps and detailed map of the waterfalls area

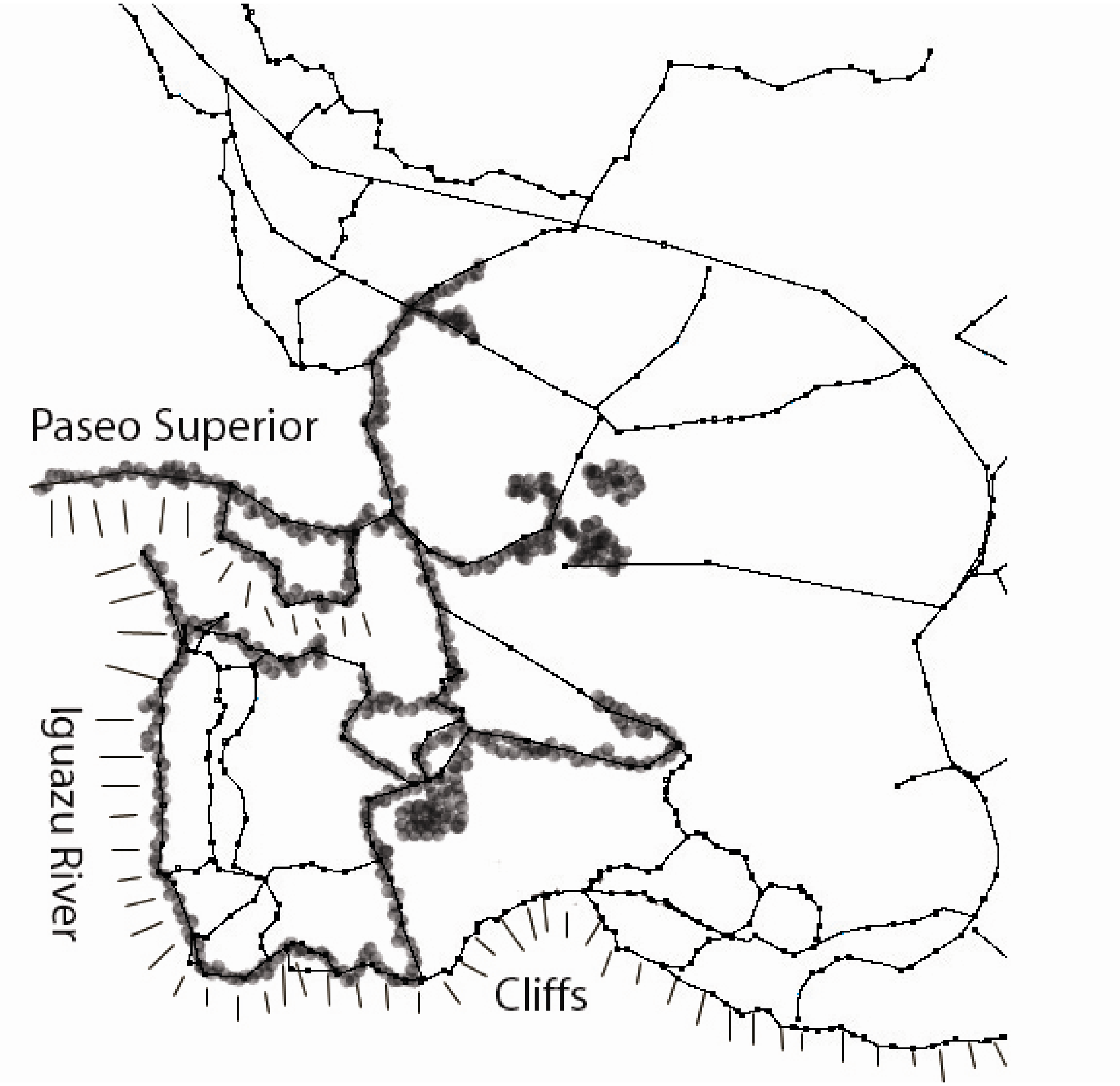

Figure A.1. Detailed map of the trail system near the waterfall area. Blotched black dots indicate areas where coatis potentially had access to human foods. Cliffs are denoted by parallel lines around the cliff areas. These cliff areas are bordered by the Iguazu river.

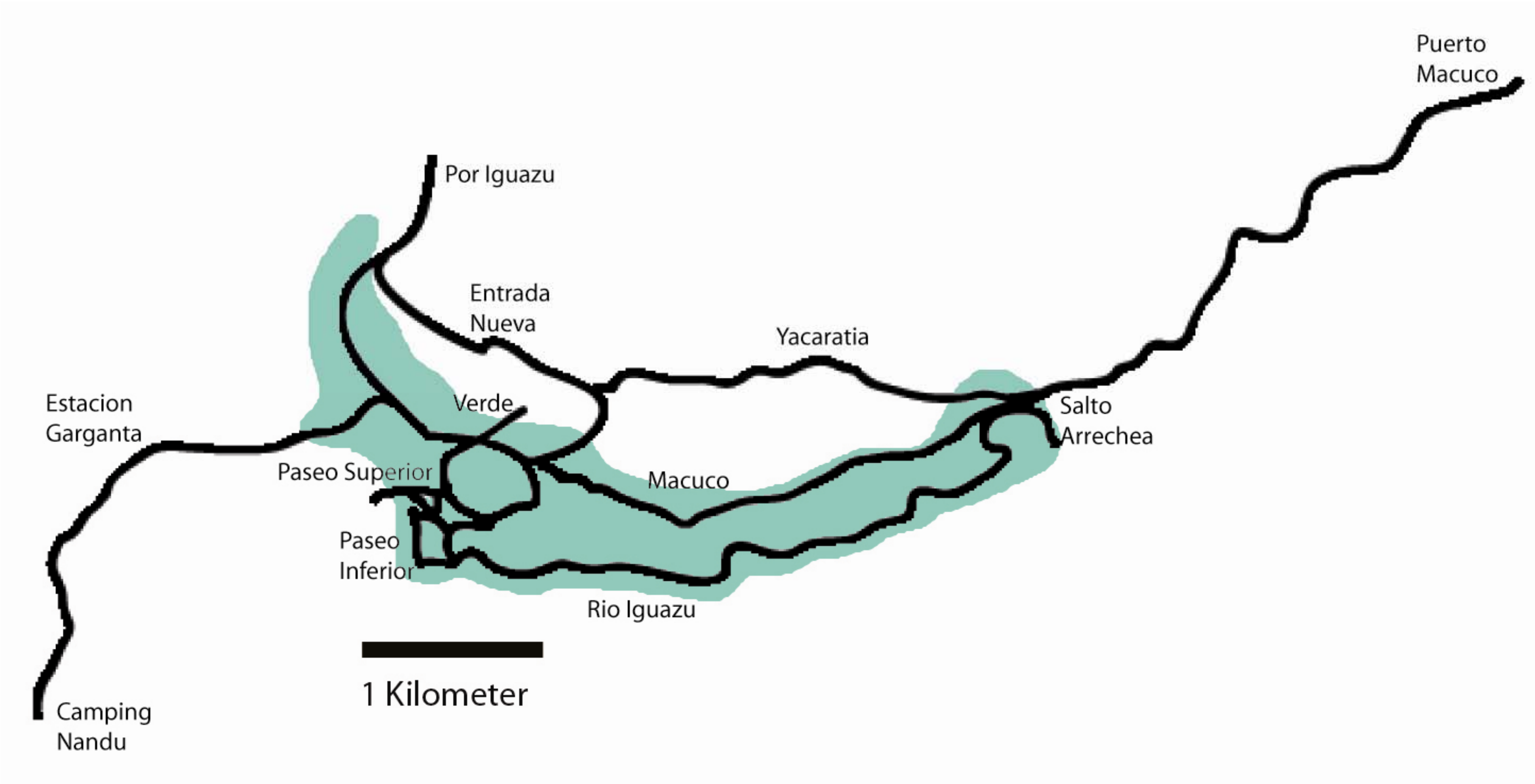

Figure A.2. Home range of group PQ.

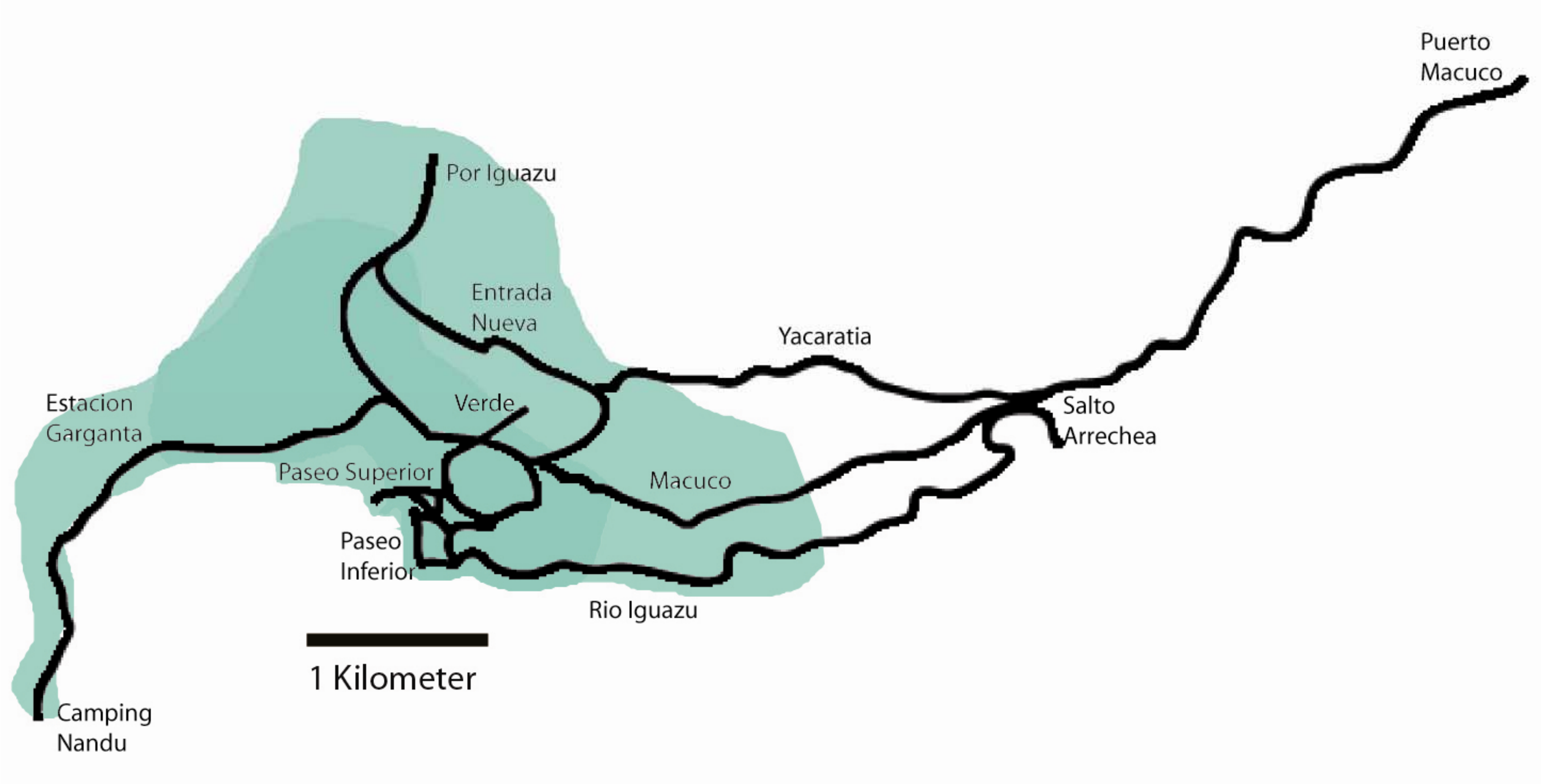

Figure A.3. Home range of group PSG.

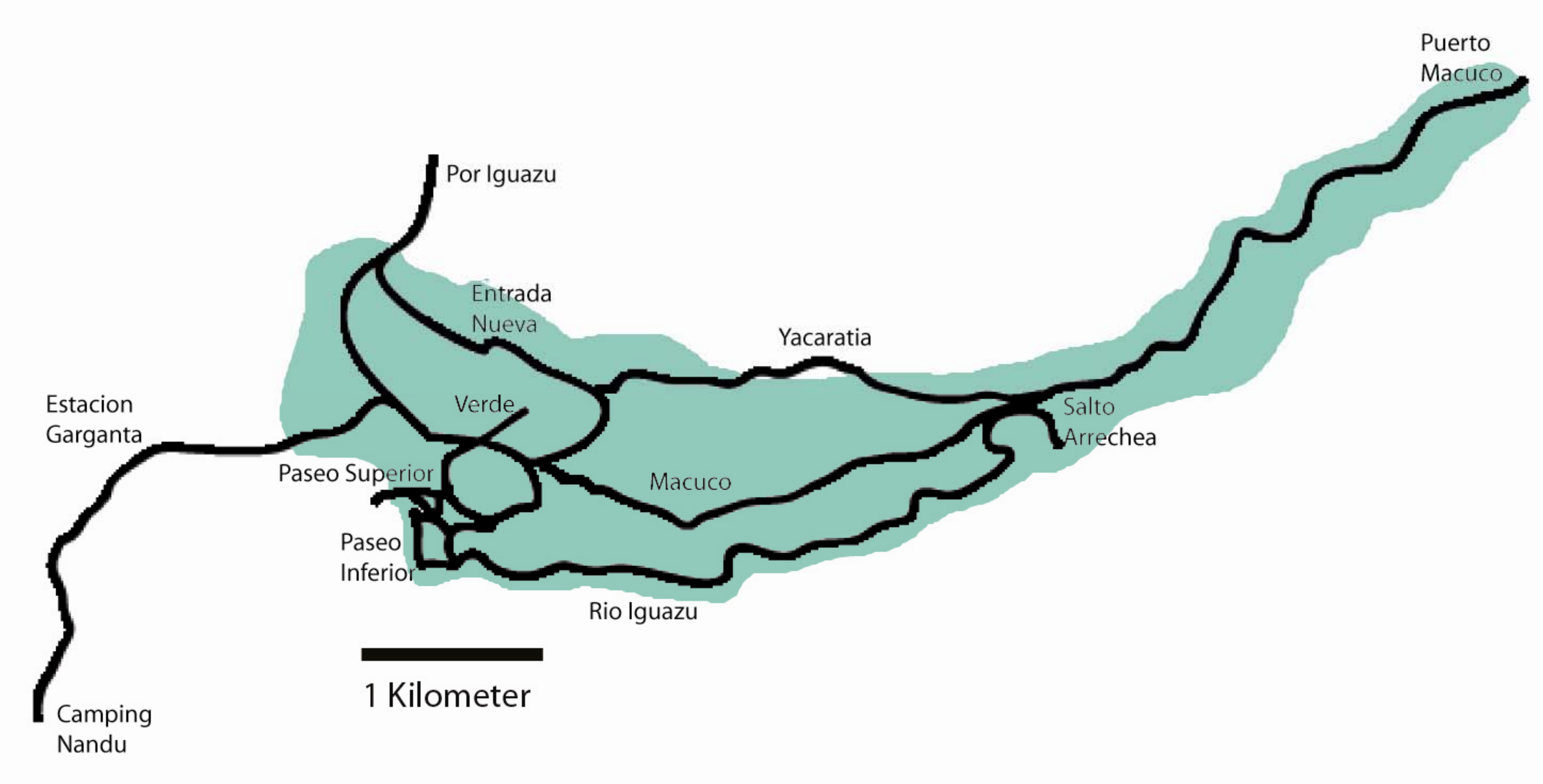

Figure A.4. Home range of group SF.

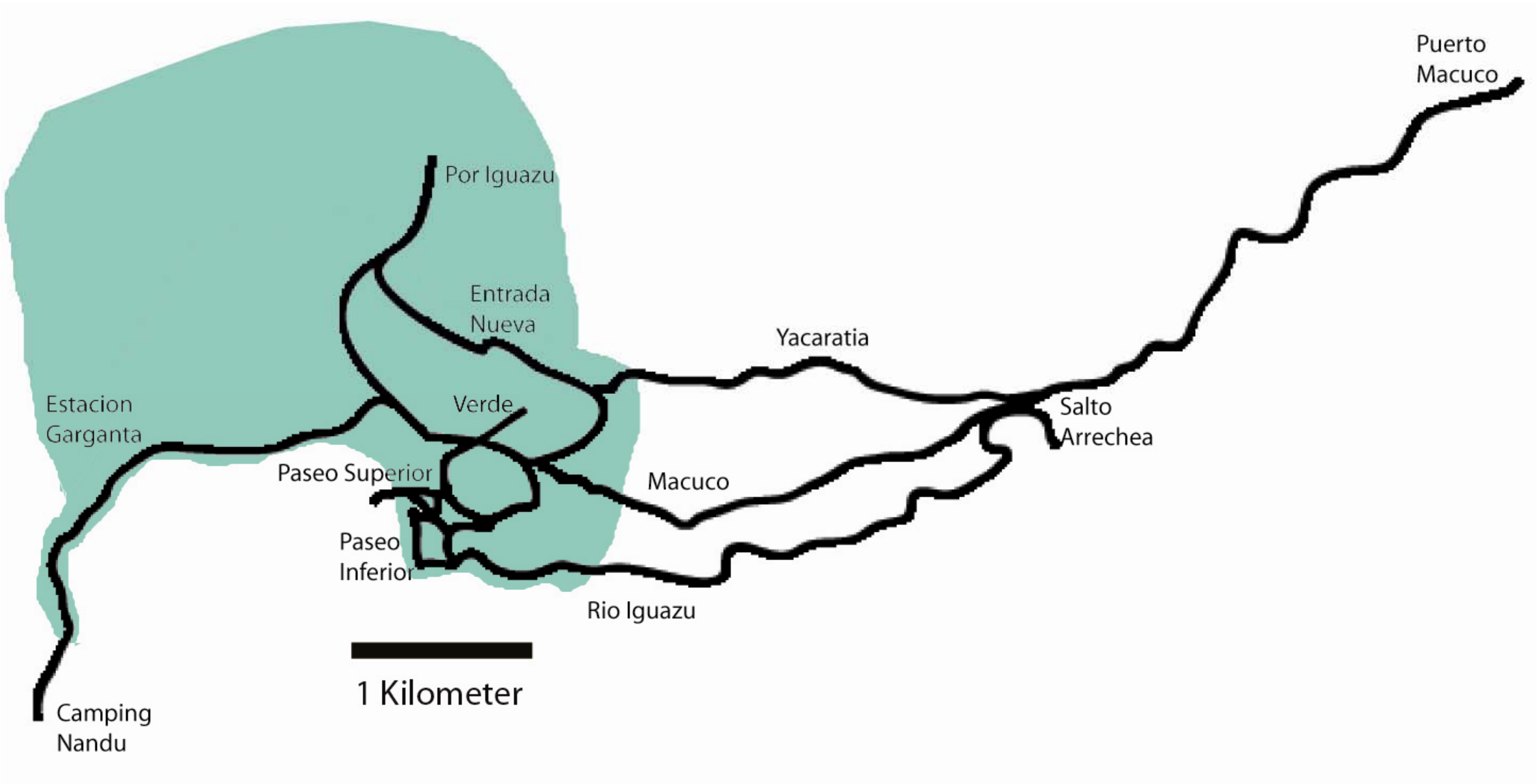

Figure A.5. Home range of group GR.