

ECOLOGY OF COATI SOCIAL BEHAVIOR IN TIKAL NATIONAL PARK, GUATEMALA

By

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I studied the social organization and mating system of the white-nosed coati (*Nasua narica*) in Tikal National Park, Guatemala. Most previous socioecological information on coatis comes from studies of a single island population.

I conducted systematic behavioral observations of solitary males as well as band members for 12 consecutive months in 1995 and 1996. Additional information was obtained through radiotelemetry and opportunistic observations from June 1994 to November 1996. Microsatellite DNA analyses of blood samples were used to determine paternity of 50 cubs from 15 litters.

Invertebrates were the most common items in the diet of both males and females, with fruit second in importance; vertebrates rarely were consumed. Females experienced higher foraging success when they were solitary than when they were with bands; social condition did not affect male foraging success.

Size of study bands ranged from 28 to 162 individuals. Bands were not observed to split into small foraging groups. Females formed small groups upon bringing their new cubs down from the nests, and did not fully reaggregate into bands for several

weeks. Females were more than five times as likely to be killed by predators when they were solitary or in small groups as when they were in bands.

Bands were usually accompanied by an adult male; several different males associated with each band. Each male associated almost exclusively with one band. Males had friendly interactions with females at all times of year. Most interactions between males and cubs were not agonistic; males sometimes associated closely with very young cubs.

During the mating season many males aggregated around each band and vocalized from trees. Copulation took place when a female ascended to a male's perch. Males provided no resources or parental care. Most sampled litters were multiply sired. Most marked males fathered offspring.

I concluded that group living in coatis evolved as an anti-predation strategy. Males are not driven out of bands by females, nor do they apparently leave to avoid feeding competition. The differences between my results and the results of previous studies demonstrate the influence of ecological conditions on social behavior.

CHAPTER 1 INTRODUCTION

As in the rest of the world, the primary direct threat to vertebrate biodiversity in the Neotropics is habitat loss. Destruction of habitat affects animal populations not just by eliminating their living space, but also by dividing them up into small isolated subpopulations. Hunting, which is probably the second greatest threat to Neotropical diversity, directly reduces animal populations. The social organization and mating system of a species partially determine how sensitive it will be to reductions in population size. Some species, such as the passenger pigeon (*Ectopistes migratorius*) (Schorger, 1955) and white-lipped peccary (*Tayassu pecari*) (Kiltie and Terborgh, 1983), seem to require very large social groups to thrive. If these social groups become reduced in size, the remaining individuals suffer diminished reproduction and/or survival. Species in which a single male is able to control reproductive access to a large number of females, such as many pinnipeds (Le Boeuf, 1978), have smaller effective population sizes than species in which mating success is more evenly distributed among males. As a result, the former species require larger populations to maintain genetic viability (Lande and Barrowclough, 1987). Socioecological studies, therefore, while often not appearing directly relevant to conservation issues, can provide information that is valuable in interpreting threats to biodiversity and in devising conservation strategies (Creel, 1998; Komdeur and Deerenberg, 1997; Parker and Waite, 1997).

The white-nosed coati (*Nasua narica*) is a medium-sized procyonid that is found from the southwestern United States throughout Mexico and Central America to northwestern coastal South America (Gompper, 1995). It is considered a threatened

species by the IUCN/SSC Small Carnivore Specialist Group (Glatston, 1994). The designation was based on widespread habitat destruction throughout the species' range and high levels of mortality from hunting and trapping.

The coati is the most social carnivore of the Neotropics, and one of the very few group-living forest carnivores in the world. Sociality by terrestrial vertebrates is less common in forest habitats both because communication and coordination of behavior are restricted by dense vegetation and because animals in open habitats are more vulnerable to predation and therefore more likely to benefit from the protection of a group. In an analysis of ecological characteristics of group-living carnivores (Gittleman, 1989), coatis and dholes (*Cuon alpinus*) stand out as the only forest-dwelling species that live in large groups. As canids, dholes have phylogenetic inertia on the side of sociality, but coatis are the only group-living procyonids. Like cheetahs (*Acinonyx jubatus*), coatis are exceptional among carnivores in that only one sex is gregarious, whereas the other is solitary. Furthermore, the coati is the only social carnivore that is not territorial. Because of these unusual characteristics, a variety of evolutionary and ecological hypotheses have been proposed to explain the social organization of coatis.

Most field studies of coatis have been conducted on Barro Colorado Island (BCI) in Panama. BCI is a 15km² island that was created from a hilltop when the Panama Canal was flooded in 1910. The small size of BCI has led to local extinction of some species, notably large mammalian (Glanz, 1982) and avian (Robinson, 1999; Willis, 1974) predators. Other species, particularly medium-sized mammals, apparently attain higher population densities on BCI than at other Neotropical sites (Glanz, 1990). It has long been suggested that the ecological conditions and communities on BCI are rather unusual (Eisenberg et al., 1979; Terborgh and Winter, 1980; Willis, 1974), and the question continues to be debated (Glanz, 1990; Wright et al., 1994). The first coati study on BCI was conducted by Kaufmann (1962), who emphasized that extreme caution

should be used in generalizing his results to coati populations elsewhere. Such caution has not been used, however, and his excellent observations have been extrapolated even to the South American coati, *Nasua nasua* (Emmons, 1990). Recent studies of coatis in Costa Rica (Sáenz, 1994) and Mexico (Valenzuela and Ceballos, 2000) have not focused on social organization, but differences in parameters such as home range size suggest that coati socioecology in other locations may be very different from what has been described on BCI.

The basics of coati natural history are known primarily from BCI. Coatis are diurnal omnivores whose diet consists primarily of leaf-litter invertebrates and fruit (Kaufmann, 1962; Russell, 1982). They are largely terrestrial, but rest and sometimes forage in trees (Kaufmann, 1962; Russell, 1982). Adult males are predominantly solitary, but females and immatures live in bands (Kaufmann, 1962) consisting mainly, but not entirely, of closely related individuals (Gompper et al., 1997). Coatis breed during the dry season, with all breeding females in a population producing their litters in tree nests (or caves, in Arizona) within a period of a few weeks (Gilbert, 1973; Kaufmann, 1962; Russell, 1982). Females leave the bands to nest solitarily shortly before parturition, and rejoin them with their offspring when the young are about six weeks old (Kaufmann, 1962; Russell, 1982). Juveniles reach maturity in their second year, at which time males leave their natal band and become solitary (Kaufmann, 1962). Females generally remain in their natal band, but sometimes join other bands (Russell, 1983).

This dissertation presents the results of a 2-year study of white-nosed coatis in Tikal National Park, Guatemala. I believed that studying coatis in a non-island environment would result in a more accurate picture of their socioecology than had previously been available. My goal was to identify the selective forces responsible for the unusual social organization of the coati, and I hoped that comparing my results with

those from BCI would demonstrate how differences in ecological conditions can result in differences in social behavior.

CHAPTER 2 ECOLOGICAL DETERMINANTS OF GROUP LIVING IN COATIS

Introduction

Group living in carnivore species is generally thought to result from the increased ability of groups to either acquire food or defend themselves from predators (Gittleman, 1989). The latter factor is thought to be more important for smaller species, and the former for larger species that hunt larger prey (Gittleman, 1989). However, even in small species, feeding ecology may be important in permitting, rather than promoting, sociality. Frugivory and insectivory lead to smaller home ranges in carnivores (Gittleman and Harvey, 1982), and if conclusions from other taxa (Brown, 1964; Crook et al., 1976; Schoener, 1968) can be extrapolated, may also lead to a lack of territoriality. Furthermore, the availability of ample food or large clumps of food encourages aggregation in carnivores (Bekoff et al., 1984).

A number of explanations for group living in coatis have been proposed. Smythe (1970) put forth the group-selection argument that coati social structure evolved as a mechanism to reduce feeding niche overlap between males and females. He believed that males forage solitarily for harder-to-find vertebrate prey so that females face less competition for invertebrates, for which he claimed they forage cooperatively. Russell (1979) concluded that females band together to protect the juveniles from predation, but that females themselves receive no benefit. Burger and Gochfeld (1992) suggested that female gregariousness has evolved to protect all band members from predators. Gompper (1996) hypothesized that the coati social system results at least in part from an interaction between sexual dimorphism and frugivory, such that females band together in

order to defend fruit patches against competition from the larger males, whereas males, able to drive off solitary females or small groups, are still able to gain access to fruit patches without having to put up with intragroup competition.

The current study was conducted to evaluate the above hypotheses on group living in coatis by collecting data to test the following predictions:

- 1) Male coatis eat more vertebrate prey than do females, at least during times when fruit is scarce (from Smythe, 1970).
- 2) Band cohesion is greatest when juveniles are youngest and most vulnerable (from Russell, 1979).
- 3) Solitary coatis suffer higher predation mortality than coatis in groups (from Burger and Gochfeld, 1992).
- 4) Solitary females have a lower rate of success foraging on fruit than do females in groups (from Gompper, 1996).

Methods

Study Area

I studied white-nosed coatis in Tikal National Park, Guatemala, from June 1994 to November 1996. Tikal is located at approximately 17°N 90°W, at an elevation of 130 to 400m above sea level. The mean annual temperature is approximately 26°C, with the lowest monthly mean occurring in January and the highest in May. Rainfall averages 1300-1400mm per year, most of it falling between May and December (INSIVUMEH, 1989-1996). Geologically, the region is a limestone karst, which means that water drains away quickly; the only permanent water bodies in the park are reservoirs that were dug by the ancient Maya.

The dominant tree species in upland areas, where the canopy averages 21m, are *Pouteria* spp., *Brosimum alicastrum*, *Pseudolmedia oxyphyllaria*, *Trichilia* spp., and *Blomia prisca* (Schulze and Whitacre, 1999). *Sabal mauritiiformis*, *Haematoxylum campechianum*, *Croton pyramidalis* and *Aspidosperma cruenta* are the most common

species in wetter regions (Schulze and Whitacre, 1999). Tikal has an intact vertebrate fauna which includes top predators such as jaguars (*Panthera onca*), pumas (*Puma concolor*), and crested eagles (*Morphnus guianensis*). Threatened species such as ocellated turkeys (*Meleagris ocellata*) and black howler monkeys (*Alouatta pigra*) are locally abundant. Approximately 300 species of birds have been identified in the park (Nations et al., 1988).

Tikal was designated a national park in 1955, primarily to protect the ruins of one of the largest city/states of Mayan civilization during the Classic period (500-900 A.D.). Essentially the whole area was probably deforested during that period, except for trees that were used for food, but it has been virtually uninhabited for the past 1000 years, and the climax forest has been reestablished (Lundell, 1937). Tikal is a 576km² core area of the 15,000km² Maya Biosphere Reserve, which occupies most of northern Guatemala. In combination with adjoining areas in Mexico and Belize, this Reserve constitutes the largest tract of lowland forest remaining in Central America (Nations et al., 1988), and has been the focus of enormous interest by the conservation community. Approximately half of the Reserve is designated for sustainable use, whereas resource extraction is prohibited in the remaining areas, including Tikal (Reining et al., 1992).

Animal Handling

Some coatis were captured in 27cm x 32cm x 82cm Tomahawk live traps (Tomahawk Live Trap, Tomahawk, WI), but most were blow-darted using a handmade PVC blowgun. The darts, constructed from 3cc syringes, contained 6-10mg/kg Telazol (Fort Dodge, Fort Dodge, IA). Blood samples and data on tooth wear, weights, and measurements were collected while the animals were unconscious. Captured coatis were marked with either colored aluminum eartags (Jiffy poultry wing bands; National Band & Tag, Newport, KY) or 90g motion-sensitive radiocollars (Advanced Telemetry

Systems, Isanti, MN), as well as being tattooed (lip tattooer; Nasco, Fort Atkinson, WI) with a unique three-digit number on the inside of one thigh. Thirty males and 53 females were marked, of which 22 males and 43 females were radiocollared for at least a portion of the study. All released coatis were monitored during recovery from anesthesia until they were fully mobile.

Behavioral Observations

Whenever a coati or group of coatis was sighted, every effort was made to identify any marked animals present, both visually and by listening to all radio frequencies of transmitted animals. Whenever possible, I counted the total number of animals present, as well as the number in each sex and age class. Coatis <1 year old will be referred to as cubs; those that had passed their first birthday but not their second will be referred to as yearlings; those at least 2 years old will be referred to as adults.

I radiocollared females in four bands, but lost contact with Band 2 early in 1995 due to transmitter failure. By the end of the study I was monitoring five bands because Bands 1 and 3 had split in two. Band 4 was seen 1-5 times per month and Bands 1 and 3 were each seen 5-25 times per month. During the nesting season (mid-April to mid-June; Binczik GA, unpublished data), I attempted to locate each radiocollared female in Bands 1 and 3 every 2-3 days to determine whether she was still pregnant and whether she was alone, and to identify any other coatis that might be with her.

Systematic behavioral observations were conducted on five adult males and Band 1, which contained 14-24 adult females (the number varied as juveniles matured and individuals died). The band underwent periods of fission late in the study, and observations were conducted on the two halves alternately during these periods. Due to transmitter failures, only three or four males were under observation in any given month. Females were observed three to four times per month from October 1995 through

September 1996. Each male was observed twice per month from September 1995 through August 1996. Observation sessions began between 0600 and 0900 h (depending on the time required to locate the animals initially) and lasted 4 to 6 h. During observations of bands, a focal animal was selected opportunistically (rotating through age classes and avoiding sampling the same animal twice in a session) on each quarter-hour. For the next 5 min the duration of every behavior performed by that animal was recorded and every food item eaten was recorded and identified as specifically as possible. While one person was observing and recording behaviors and food items, another was using a tally counter to record the distance in meters being traveled by the focal animal. During observations of males and solitary nesting females, the same individual was the focal animal for each 5-min observation period. A total of 100 h of focal animal observations was conducted on males, and 41.25 h on females (31.75 h while with bands, 9.5 h while solitary).

Radiotelemetry

From March 1995 to September 1996 all collared coatis (range 17-44; mean=27) were radiolocated 10-12 times per month using receivers from Advanced Telemetry Systems and Wildlife Materials, Inc. (Carbondale, IL) and antennae from Advanced Telemetry Systems and Telonics, Inc. (Mesa, AZ). Compass bearings were taken from the tops of temples in the central ruins of Tikal, and only two bearings taken less than an hour apart were used to calculate an animal's location. To avoid autocorrelation, radiotracking sessions were always separated by at least 36 h, and were rotated through four time periods (0400-0800, 0800-1200, 1200-1600, and 1600-2000 h) so that locations were taken during each time period approximately three times per month. The approximate Universal Transverse Mercator coordinates of the sites from which bearings were taken were determined using a Global Positioning System receiver, and the

bearings were converted to animal locations using the LOCATE utility of the home range analysis program CALHOME (Kie et al., 1996). CALHOME was then used to compute 90% minimum convex polygon home ranges.

When a collared coati was suspected to have died, based on the lack of variation in its radiosignal or its absence from a band, an attempt was made to find the animal as quickly as possible. When the collar was found, the site and remains were examined for evidence as to the cause of death.

Data Analyses

Food items were grouped into four categories: fruit, invertebrate, vertebrate and other. "Other" consisted of food garbage taken from trash cans and dumps, and handouts obtained from tourists or their guides. For items in the "other" category, bites or mouthfuls were counted rather than items, in an attempt to make quantities more comparable. To obtain overall diet composition, the total numbers of items or bites taken in each category during all focal animal observations were calculated separately for adult females and adult males. To calculate foraging success, the numbers of fruits and invertebrates eaten per minute of foraging time were calculated for each 5-min observation period, and then averaged over the day's observation session. Observation sessions during April, May, June, August and September (the months when at least some females were solitary) were used to compare values for solitary females and females in groups. I did not include the data for females in groups from the remaining months of the year because I did not want the comparison to be confounded by seasonal differences in food availability.

To calculate relative mortality rates, I categorized each radiocollared female as either solitary or with a band for each month of the study, based on observations of her social status at mid-month. The small subgroups that formed after the cubs were

brought down from the nests but before the bands had fully reaggregated were included in the solitary category. I then used a chi-square test for goodness-of-fit to test whether mortality rates of females in each social category were different from what would be expected if mortality were unaffected by social status.

The distances traveled by the focal animals during each 5-min observation period were averaged over the day's observation session. Observation sessions during April, May, June, August and September were used to compare values for solitary females and females in groups.

Results

Coati bands in Tikal were large; thus, it was difficult to obtain exact counts. All band members could not be seen simultaneously in the forest, so they could be counted only when a band was seen crossing a road or large trail at a fairly slow pace. I was never able to obtain reliable counts of Bands 2 and 4, but estimated their numbers at about 30 and 50 individuals, respectively. Sizes of Bands 1 and 3, the ones I spent the most time with, ranged from 28 to 162 individuals, varying with fission events, birth, mortality, and dispersal (Figure 2-1).

Aside from major fission events, band composition was extremely stable for most of the year. Small foraging subgroups of one or a few individuals were never observed to split off from the study bands. By the end of 1995, all females in Band 1 that were at least 1 year old ($n=24$) were marked or individually recognizable. Only twice during the non-nesting season was a female missing when the band was observed. Once, the female had apparently sustained a spinal injury, but recovered sufficiently to rejoin her band after a few days. On the other occasion, a female and a yearling apparently got temporarily separated from the band when a female was killed by a predator. However, during the first month after cubs were brought down from the nests, females associated

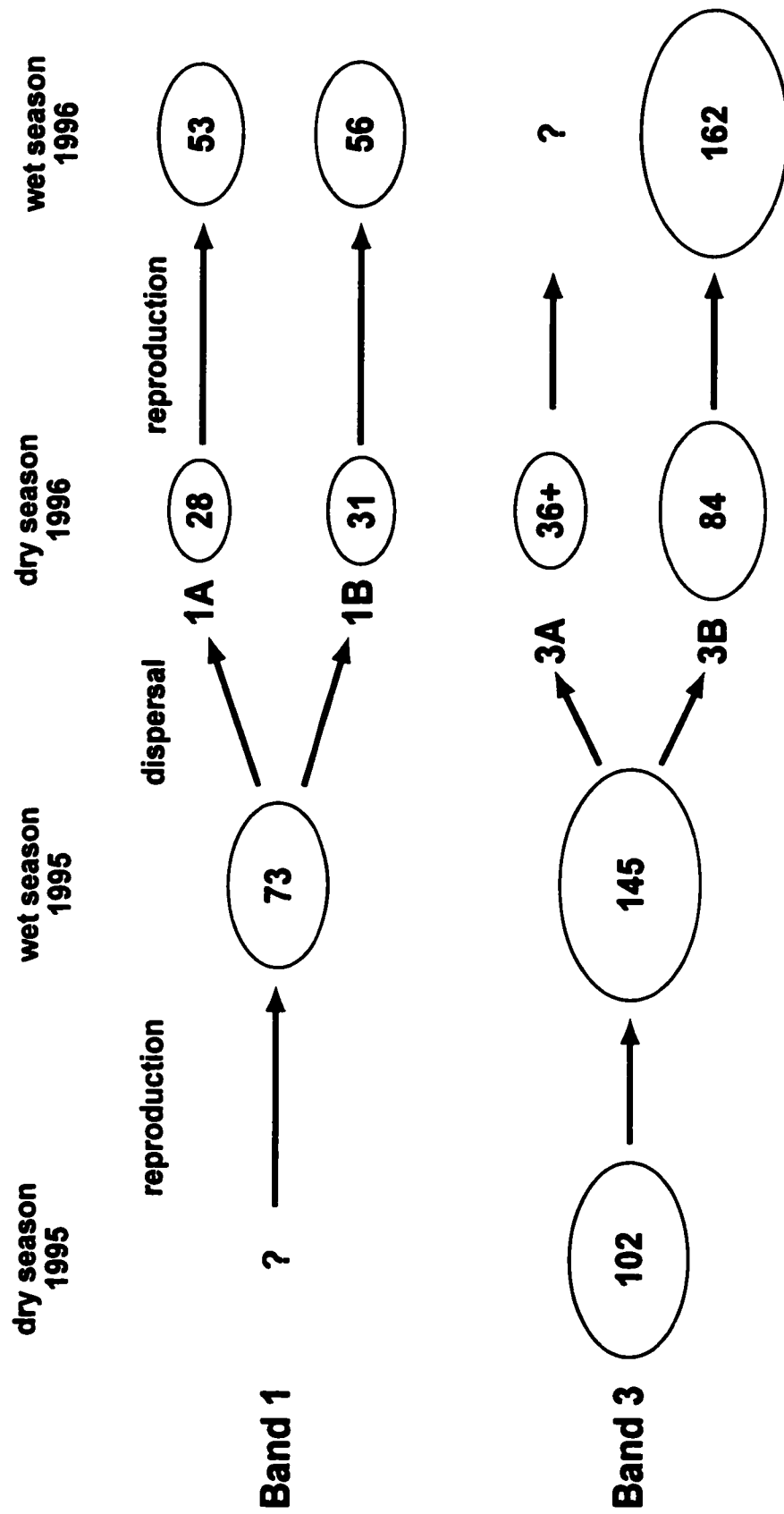


Figure 2-1
Population dynamics of two coati bands in Tikal National Park, 1995-1996. Numbers are maximum counts of band members obtained during the seasons indicated. Question marks signify that no count was obtained. The "+" signifies that the count was believed to be incomplete.

in much smaller groups. The small groups encountered each other repeatedly and joined temporarily, but did not stay together for more than a day. Every radiocollared female with young in Band 1 ($n=10$) went from being with a larger group to being with a smaller group at least twice during the month after nesting in 1996.

Most adult females were solitary during May and June, when they were nesting (Figure 2-2). A few females, who apparently lost their litters, resumed a solitary status when they nested again in August and September (Binczik GA, unpublished data). In all, 104 radiocollared female-months (29%) were spent solitary or in small groups and 251 radiocollared female-months (71%) were spent with a band. Of the 10 adult females known to have died during the study, seven died while solitary or in small groups (0.067 deaths/female-month) and three died while they were with bands (0.012 deaths/female-month). This distribution was significantly different (chi-square: $df=1$, $p<0.01$) from the three and seven, respectively, that would be expected if there were no effect of group living. The deaths during the nesting period do not represent parturition-related mortality; only one female died <1 month after giving birth. All known deaths of adult females were believed to be a result of predation, because the animals were never observed to be sick, injured, or in poor condition before death. Two of the females that died, one while solitary and one while with a band, were elderly, as evidenced by the worn condition of their teeth. Three females that died while solitary were known to be 24-25 months of age. I observed no instances of predation on coatis, although a jaguar did approach a band once in my presence, causing all the coatis to take to the trees in alarm. One of the radiocollared females had been killed by the next time the band was observed.

Solitary females ($n=3$) traveled an average of 15.8m during the 5-min observation periods, which was significantly less (two-tailed t -test: $df=6$, $p<0.05$) than the 24.3m traveled by females with bands ($n=5$). Band 1 used an area of 2.18km² during the time

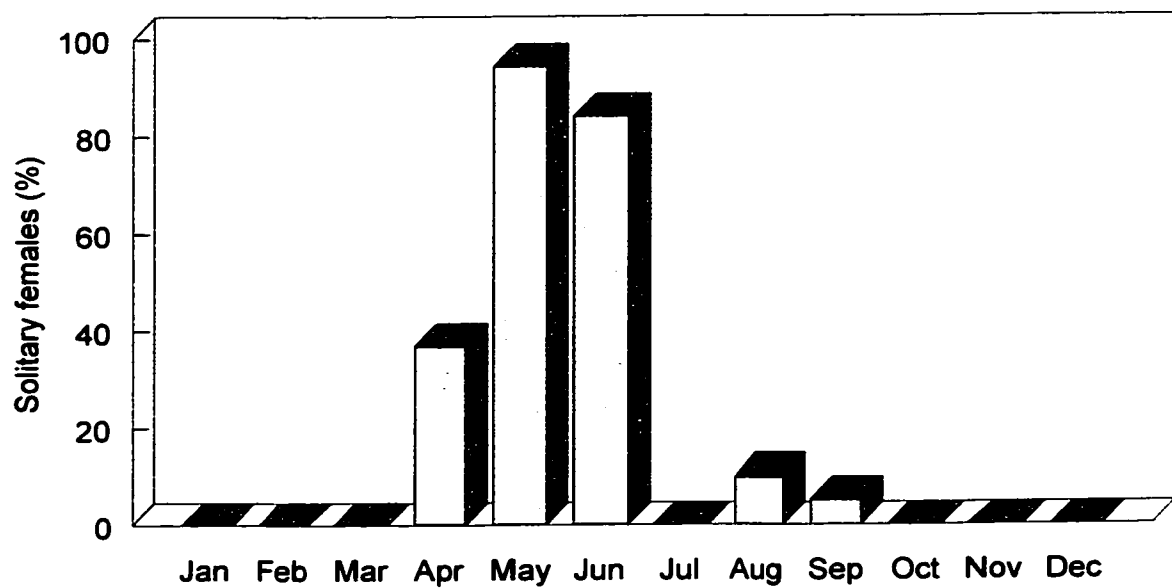


Figure 2-2

Percentage of radiocollared females that was solitary or in small groups each month. Data from 1994, 1995, and 1996 were combined. The number of females with functioning radiocollars fluctuated, with a mean of 13 and a high of 32.

(mid-February to mid-April) the females were pregnant in 1995. During the subsequent nesting season (mid-April to mid-June), four radiocollared females from Band 1 used areas that ranged only from 0.05km² to 0.17km².

Vertebrate prey comprised <1% of the diet of both males and females (Figure 2-3). Coatis captured and ate a wide variety of vertebrates, including amphibians, reptiles, mammals and birds, but all were rare occurrences. Invertebrates were the largest component of the diet of both sexes. From September 1995 through January 1996, females ate no fruit during focal animal observations, and neither males nor females ate any vertebrates. Males frequently made use of human sources of food, whereas females did not. Even with the "other" category removed, diet composition of males and females was significantly different (chi-square: df=2, $p<0.0001$).

Female coatis had higher foraging success for both fruit and invertebrates when they were alone than when they were with bands (Figure 2-4). However, probably due to small sample sizes, neither difference was significant. When the data on fruit and invertebrates were combined, foraging success of solitary females ($n=6$) differed significantly from when they were with bands ($n=7$) (two-tailed t -test: df=11, $p<0.05$). I saw no evidence of cooperative foraging among coatis in bands. There was little opportunity for cooperative foraging, or even for the sort of passive prey herding postulated by Kaufmann (1962), because most prey items were buried in the leaf litter, the soil, or rotting wood. They were detected by smell and dug out, and very rarely had to be chased. Groups of foraging coatis exhibited mostly scramble competition; whoever found a food item ate it. However, disputes over particularly attractive food items were observed. Such disputes sometimes took the form of chases and squabbles, but on other occasions were less agonistic. The coati attempting to steal the food item would back up to the owner and attempt to wedge himself between owner and food, often sitting on the food item. If the owner momentarily lost control of the food, the interloper

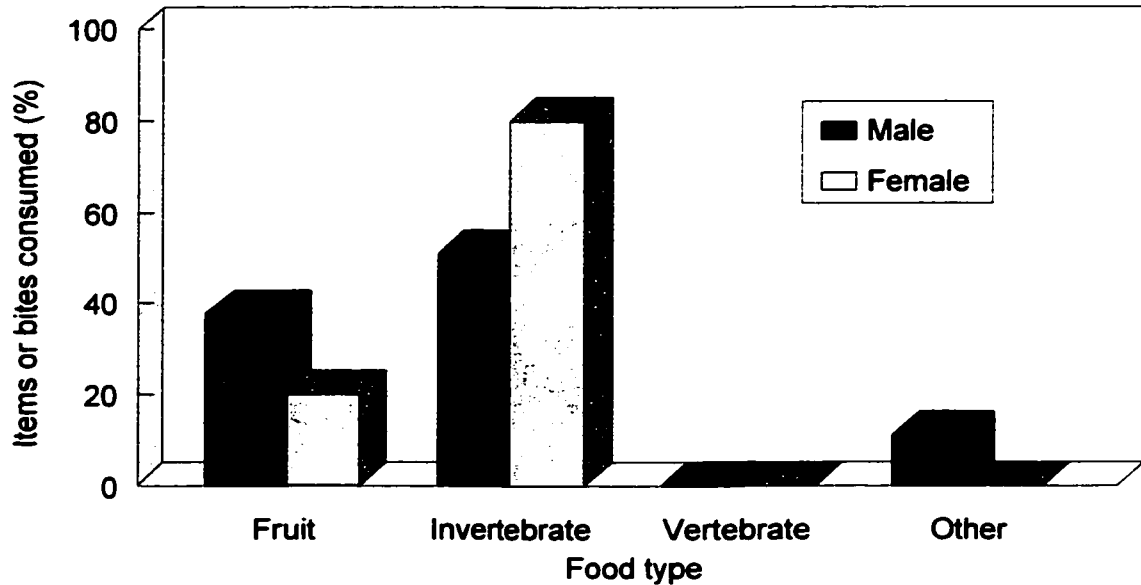


Figure 2-3

Diet composition of adult coatis, September 1995 - September 1996. The "other" category consists of handouts from tourists and items found in trash cans and dumps. All invertebrates, vertebrates, and fruits consumed during focal animal observations were counted; bites taken were counted for items in the "other" category. $n=2529$ for males and 1615 for females.

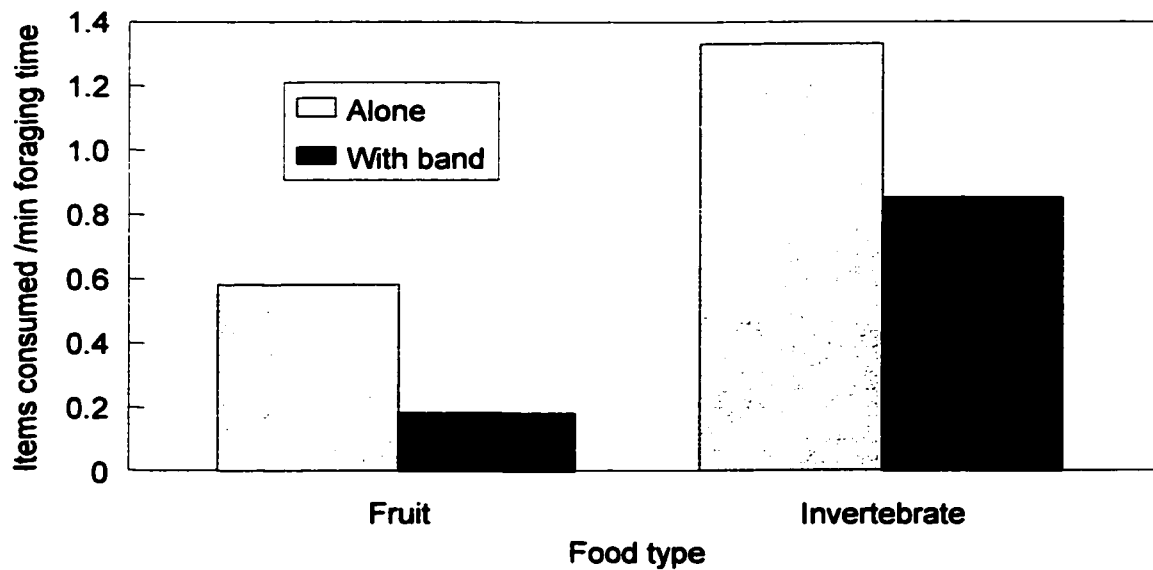


Figure 2-4

Foraging success of adult female coatis in different social situations, April-June and August-September, 1996. $n=120$ fruits and 478 invertebrates.

reached under with his snout and grabbed it. The owners rarely displayed any objection to such maneuvers, perhaps because presenting the back or rump was apparently a submissive or conciliatory posture.

Discussion

Coati band sizes in Tikal were much larger than those observed in other coati studies. Band sizes on BCI ranged from 2 to 26 individuals (Gompper, 1997; Kaufmann, 1962; Russell, 1979), and band sizes at Los Tuxtlas, Mexico, ranged from 10 to 25 individuals (Estrada et al., 1993). This difference may have been due in part to the availability of human sources of food in Tikal, but only Band 3/3B, the largest band, was known to make use of such food sources. Its range included the hotels, restaurants, and employee housing areas, virtually all of which engaged in illegal dumping of garbage in the forest. Band 1, which was the most intensively studied band and attained a maximum size of 73 individuals, was never observed utilizing unnatural food sources, and neither it nor Bands 2 and 4 inhabited areas that contained human dwellings. The consistently large size of bands in Tikal, therefore, must have been due to some factor other than garbage dumps. Abundant natural food resources (Binczik GA, unpublished data) may have made it possible for the coatis to forage in such large groups, but what would make it adaptive?

Protection from predators is one of the most common reasons for animals in any taxon to live in groups (Barash, 1982; Edmunds, 1974; Lott, 1991; Wilson, 1975). This study demonstrates that group living very likely serves to reduce the risk of predation for coatis, at least in Tikal. The more than four-fold increase in mortality when females left their bands represents strong selection against a solitary lifestyle. The fact that all previous long-term studies of coati social organization have been conducted on BCI probably explains why they did not reveal such selection. There may be no predators on

BCI capable of easily killing an adult coati. The island has not had any resident jaguars or pumas for many decades (Glanz, 1982; Kaufmann, 1962), nor do large raptors such as harpy eagles (*Harpia harpyja*) and crested eagles nest there (Robinson, 1999; Willis, 1974). Russell (1979), working on BCI, concluded that group living was important for the protection of juveniles, but that adult females received no anti-predation benefit. Burger and Gochfeld (1992), however, whose study consisted only of 5 days of observations of vigilance behavior in coatis drinking at a water hole in Costa Rica, suggested that all band members would benefit from the increased vigilance capabilities of a group. Apparently that is the case in Tikal. Tikal is home to both jaguars and pumas (personal observation; Kawanishi, 1995; Nations et al., 1988), as well as crested eagles (Beavers, 1982; Whitacre DF, personal communication). A study of jaguar and puma scats at Calakmul, Mexico, approximately 100km north of Tikal, found that coatis were the second most common item in the diet of both species (Aranda and Sánchez-Cordero, 1996).

There are many predators in Tikal (and on BCI) capable of killing juvenile coatis. During the first month after the young are brought down from the nests, females may behave so as to maximize the survival of their offspring rather than themselves. The fact that females did not reaggregate into bands as quickly as possible, choosing instead to remain in smaller groups, indicates that the adaptive value of living in large bands is not protection of juveniles. The cubs are not very coordinated when they first come down from the nests, and often lag behind the older animals, particularly if the group runs in alarm. The females do not attempt to keep track of them, going back for a cub only if it cries out. Cubs do cry frequently and quite loudly during those first weeks, often finding themselves alone or stranded on a tree branch. Presumably being with a larger group would increase both the likelihood that cubs would lag behind the group and the likelihood that predators would be attracted by the noise they made. The small groups

may represent a balance between the anti-predation benefits of grouping and the hazards of grouping with very young cubs. On BCI adult females are probably not at risk of predation, and they remain in small groups permanently. Group living there may serve only to protect the juveniles, as Russell (1979) concluded. In Tikal, however, females are at risk, and they receive more protection in large groups. Thus, they maintain large groups except when the cubs are too young to make it feasible. Similarly, female grey kangaroos (*Macropus giganteus*) are found alone or in small groups when they are accompanied by recently emerged joeys, and in larger groups at other times. Grouping appears to be an anti-predator behavior (Banks, 2001), and it has been hypothesized that recently emerged joeys are safer from predation away from large groups (Jarman and Coulson, 1989).

Not surprisingly, females experience costs as well as benefits from living in groups. The costs I observed were related to foraging. Like Kaufmann (1962), Russell (1979), and Gompper (1996), I saw no evidence of the cooperative foraging proposed by Smythe (1970). In the absence of cooperation, a cost associated with foraging in a group is to be expected. Surrounded by dozens of noses searching simultaneously, any individual coati will have access to fewer food items in a given area than if it were foraging alone. The effect of this competition is demonstrated by the fact that solitary females were able to find the food they needed not only in less time, but also while covering less space. Despite the high energetic demands imposed by nursing, lactating females were able to find enough food to support themselves and their litters in a very small area, compared to the area they used when they were with their band. Their energy expenditures related to foraging were thereby reduced, as well as their chances of encountering predators.

Gompper (1996) concluded that grouping confers a foraging benefit on females, even though he found that solitary females experienced significantly higher foraging

success on invertebrates than females with bands. However, he did not present data on their relative foraging success on fruit. His conclusion was based on observations of agonistic interactions over fruit patches between males and females or bands. I never saw such interactions in Tikal. The very few male-female agonistic interactions over food I observed were over food items, not patches. If anything, agonism seemed to be reduced at food patches. Several times during the nesting season I saw adult males feeding amicably next to single adult females in and under fruiting trees, whereas Gompper (1996) suggested that aggression from males prevented solitary females from gaining access to fruit patches. The differences in behavior between the two populations imply that food is an amply abundant resource for coatis in Tikal, but not on BCI.

The diet of coatis is similar in the two locations, although differences in data collection prevent direct comparison of the dietary results of this study to those of previous studies. Kaufmann (1962) and Russell (1982) found that coatis spent the majority of their time foraging for invertebrates, with fruit being a seasonally important component of the diet and vertebrates being taken only rarely. Approximately 44% of the coatis Gompper (1996) sighted were foraging on invertebrates and 55% were foraging on fruit, but because his largest sample sizes were from the months when the most foraging on fruit occurred, it is not clear how representative those percentages are of the diet as a whole.

Gompper (1996) found no vertebrate remains in 86 scats on BCI, including 24 from adult males. Vertebrate remains rarely were found in scats of males or band members in Costa Rica (Sáenz, 1994). Vertebrates were not an important food source for either sex in Tikal, even when fruit was unavailable. Thus, support for Smythe's (1970) argument concerning dietary niche separation between the sexes is lacking. The relative proportions of fruit and invertebrates in the diet differed between males and females, however, and the males in my study had a tendency to seek out food sources

of human origin. Kaufmann (1962) also commented on the greater propensity of males to pursue handouts and other non-natural food sources on BCI.

In contrast to their lack of cooperation in foraging, coatis do exhibit a variety of cooperative anti-predator behaviors, including shared vigilance (Burger and Gochfeld, 1992; Russell, 1979), alarm calls (Kaufmann, 1962; Russell 1979), and group defense (Janzen, 1970; Russell, 1979). These behaviors provide support for the conclusion that group living confers anti-predation benefits rather than foraging benefits. Coatis are similar in many ways to some species of mongooses, which live in groups, eat insects, and cooperate in vigilance and defense (Rood, 1986). Only the absence of adult males from coati social groups and the fact that coatis pursue this lifestyle in dense forest habitat are unusual. Although group living is certainly more common in open habitats, there are other species, such as dholes and peccaries, that maintain social groups in dense forests. Most forest-dwelling terrestrial insectivore-omnivores are nocturnal (e.g., armadillos, *Dasypodidae*; opossums, *Didelphis* spp.). By switching to a diurnal lifestyle, coatis may have avoided some resource competition with those species. Diurnality entails a higher likelihood of being detected by predators, however, and coatis minimized that risk by becoming social.

As in the *Herpestidae* (Rood, 1986), both feeding ecology and predation pressure have been important in the evolution of group living in coatis. Animals that live in groups or have overlapping ranges tend to require larger home ranges than animals with exclusive ranges, because the range must contain enough resources to support many individuals. The insectivorous/frugivorous diet of coatis allows many animals to share a home range, because the high density of food resources means that an individual can satisfy its resource needs in an area far smaller than that which it is physically capable of covering. This flexibility originally may have permitted philopatry in females, as Waser and Waser (1985) postulated for high-density populations of the

white-tailed mongoose (*Ichneumia albicauda*). Within the Procyonidae, raccoons (*Procyon lotor*) have been found to have a high level of female philopatry, with some related females continuing to associate closely as adults (Gehrt and Fritzell, 1998). Kinkajous (*Potos flavus*) show extensive home range overlap and associations among adults, although they forage solitarily (Kays and Gittleman, 1995). However, white-tailed mongooses, raccoons, and kinkajous are all nocturnal, whereas coatis, like the group-living mongoose species (e.g., *Helogale parvula*, *Mungos mungo*, *Suricata suricatta*) (Rood, 1986), are diurnal. The higher predation pressure inherent in a diurnal lifestyle supplied the selection necessary to move these latter species from home range sharing to group living.

CHAPTER 3 INFLUENCES ON THE SOCIAL BEHAVIOR OF MALE COATIS

Introduction

The social system of coatis is unique among the Carnivora. Adult female coatis live in stable social groups with their immature offspring, but adult males are essentially solitary (Kaufmann, 1962). In other social carnivores, such as canids, lions, hyenas, and mongooses, groups always contain at least one adult male. The behavioral differences might be expected to result from ecological differences, because coatis are forest-dwelling, partially arboreal insectivore/frugivores (Kaufmann, 1962). This suite of characteristics applies to none of the other group-living carnivores. It does, however, apply to many primate species, and one of the hallmarks of primate social organization is year-round associations between males and females (Pereira et al., 2000). The ecological similarities between coatis and primates do not, therefore, translate into similarities in social organization. Actually, the coati social system appears most similar to those of the African elephant (*Loxodonta africana*) (Moss and Poole, 1983) and the sperm whale (*Physeter catodon*) (Whitehead and Weilgart, 2000). As coatis have very little else in common with either elephants or sperm whales, interspecific comparisons seem to have little power to explain the unusual social system of the coati.

Several explanations for the solitary lifestyle of male coatis have been proposed. Smythe (1970) believed that they forage solitarily for vertebrates so as to reduce the competition females face for invertebrates. However, studies of coatis have revealed that vertebrates are rarely consumed by males (Chapter 2; Gompper, 1996; Sáenz, 1994), and invertebrates are the primary food of both sexes (Chapter 2). Russell (1981),

after observing infanticide by an adult male, concluded that adult females exclude males from bands to protect their young. No other coati researcher has seen any evidence of infanticide, but that does not eliminate the possibility that it may have been an important selective force in the past to which females have evolved an effective counter-strategy. Finally, Gompper (1996) hypothesized that, rather than being driven out, males leave the bands to avoid feeding competition and improve their foraging success.

The goal of this study was to identify the selective factors responsible for the predominantly solitary lifestyle of male coatis. I evaluated the infanticide hypothesis of Russell (1981) and the resource competition hypothesis of Gompper (1996), as well as the possible effects of other factors, particularly reproductive competition.

Methods

The study area, animal handling, behavioral observations, and radiotelemetry were as described in Chapter 2.

The social situation of the focal male (i.e., solitary or with a band) was recorded for each 5-min observation period. One-tailed *t*-tests were used to test the hypothesis that solitary males have higher foraging success. Data points used in the analyses were the averages of values from all observation periods in a given social situation in a day.

All observed encounters between bands and males were recorded and described. Data collected include time of day, location, who approached whom, what types of behavior were exhibited, and what the outcome of the encounter was. During behavioral observations, all direct interactions between adult males and any other individuals were recorded similarly. Interactions between males and females were classified as friendly, agonistic, or mixed, based on the behaviors displayed. Interactions between males and cubs were classified as friendly, avoidance by the male, agonistic/male defers, agonistic/cub defers or agonistic/inconclusive.

Results

It became clear early in the study that adult males were accompanying bands much more commonly than had been observed in previous studies. There was at least one adult male known to be present during 306 out of 458 (67%) encounters with coati bands in Tikal. Bands were accompanied by males most often (96% of encounters) during February, when mating occurred, and least often (20% of encounters) during May, the middle of the nesting season (Figure 3-1). The monthly presence of males with bands averaged 64%. Males accompanied bands less often during May than during the other non-mating-season months (chi-square: $df=1$; $p<0.001$).

Outside of the mating season, February 13-28 (Binczik GA, unpublished data), individual males spent from 18% to 52% of the time they were under observation with bands (Table 3-1). Sometimes a male spent a whole morning's observation session with a band, but more often he was with them for only a portion of the time. When a male was accompanying a band, he was usually on the periphery of the group, and in most cases it was clear that he was an outsider. Frequently, he would move to avoid approaching band members, and band members (particularly yearlings) often would behave aggressively toward him for no apparent reason. However, band members were not observed in lengthy pursuit of males, as though trying to drive them away from the band. In fact, males and band members often foraged quite peacefully alongside one another. When an allogrooming session with a male began, band members of all ages would come running eagerly to join in.

Each male tended to associate with a particular band, and it was not simply because they did not encounter other bands. Of 16 males that were seen at least five times with any band (mean=25 times seen with bands for these males), the average number of bands each male visited was two, and some males were seen with as many

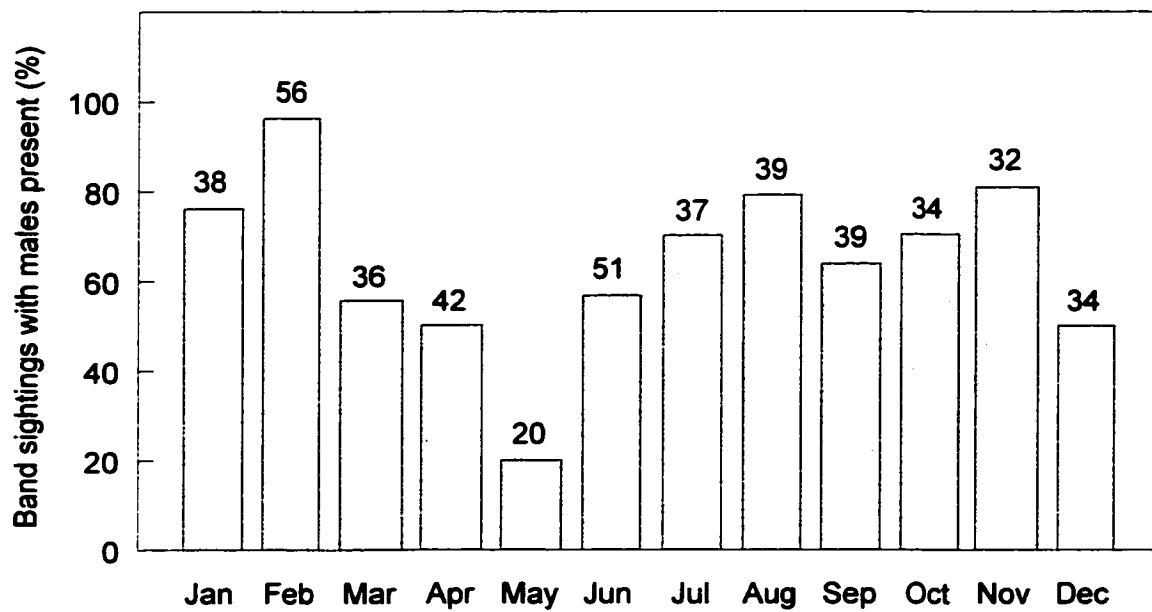


Figure 3-1

Percentage of coati band sightings for which at least one adult male was known to be present. Numbers above bars are total band sightings in each month for 1995 and 1996 combined.

Table 3-1

Association between individual males and bands in the non-mating season

| Male | Period of observation | Total observation time (hours) | Percentage of time spent with bands |
|------|-----------------------|--------------------------------|-------------------------------------|
| 03 | Sep 1995 - Sep 1996 | 98 | 36 |
| 32 | Nov 1995 - Aug 1996 | 45 | 52 |
| 43 | Sep 1995 - Aug 1996 | 91 | 18 |

as four different bands. However, each male had a primary band; on average 94% (range 83-100%) of the sightings of each male was with his primary band.

Females allowed males to be in close proximity to cubs, even very young ones. In June 1995, I was following a male when he encountered two females with five or six cubs on their first day out of the nests. There was no direct interaction between the male and the others. He made no attempt to pursue the cubs (which were still rather wobbly and uncoordinated and would have been easy to catch), and the females made no attempt to chase him away. A few days later I was with a female and her two cubs when a male joined them. Again there was no direct interaction; in fact, the male and the cubs actually meandered as a group toward other members of the band, leaving the female behind for a few minutes. Similarly, in 1996, I was observing a male when he joined a partially reaggregated band, including cubs who had probably been out of the nest only a few days. At one point I was with the male, six cubs, and about a dozen yearlings, with no adult females in sight, and the male completely ignored the cubs. These three observations involved different males and different females.

When I did see direct interactions between males and females they were most often agonistic (57%), but friendly interactions (usually allogrooming sessions) occurred at all times of year (Figure 3-2). Not surprisingly, agonistic interactions made up the lowest percentage of the total during February, when mating occurred. Most of the observed interactions also were friendly during July, August, and September, when cubs were still quite small and vulnerable. Although June, the month when cubs were brought out of the nests, had one of the highest percentages of agonism, three of the five agonistic interactions observed were with females that did not have cubs. Most male-female agonistic encounters were a result of males approaching females without overt aggression and being aggressively rebuffed. The quality of the male-female relationship differed among individuals, with some males involved in very few unequivocally friendly

interactions (Figure 3-3). One male's (43) relationship with the females in the band he regularly associated with seemed to improve throughout the time he was observed (Table 3-2).

Most direct interactions observed between males and cubs were either friendly on both sides, or characterized by male avoidance of a cub's attempt to allogroom or play (Table 3-3). When interactions were agonistic, the cubs "won" four times as often as the males did. Agonism was usually restricted to vocalizations and chases. Only once did I see a male actually make aggressive physical contact with a cub, and that was in March, when the cub was almost a year old. No male was ever observed to actually injure a cub, nor was there ever any reason to suspect that infanticide had occurred. Cubs only 2 to 3 months of age were seen attempting to play with and allogrooming males. In the weeks prior to the mating season, when males frequently pursued adult females aggressively, I sometimes saw cubs attempting to chase the males away from the females. The way males behaved toward cubs varied greatly according to the individual. One of my focal males spent a lot of time in the company of cubs, frequently playing and allogrooming with them, whereas most males ignored cubs or actively avoided interacting with them.

All observed interactions ($n=27$) between adult males, or between adult males and newly dispersed yearling males, were agonistic. When two males saw each other, the result was usually that one chased the other away, often for hundreds of meters. Actual fights were rare, except during and just prior to the mating season. As the mating season approached, males that were accompanying bands became less likely to leave when they were chased, so encounters would escalate. Once mating actually began, on the other hand, males seemed to focus more on the females, and several males could be calling simultaneously in neighboring trees without interaction (see Chapter 4). The only other occasions when two males were known to be in sight of each other without

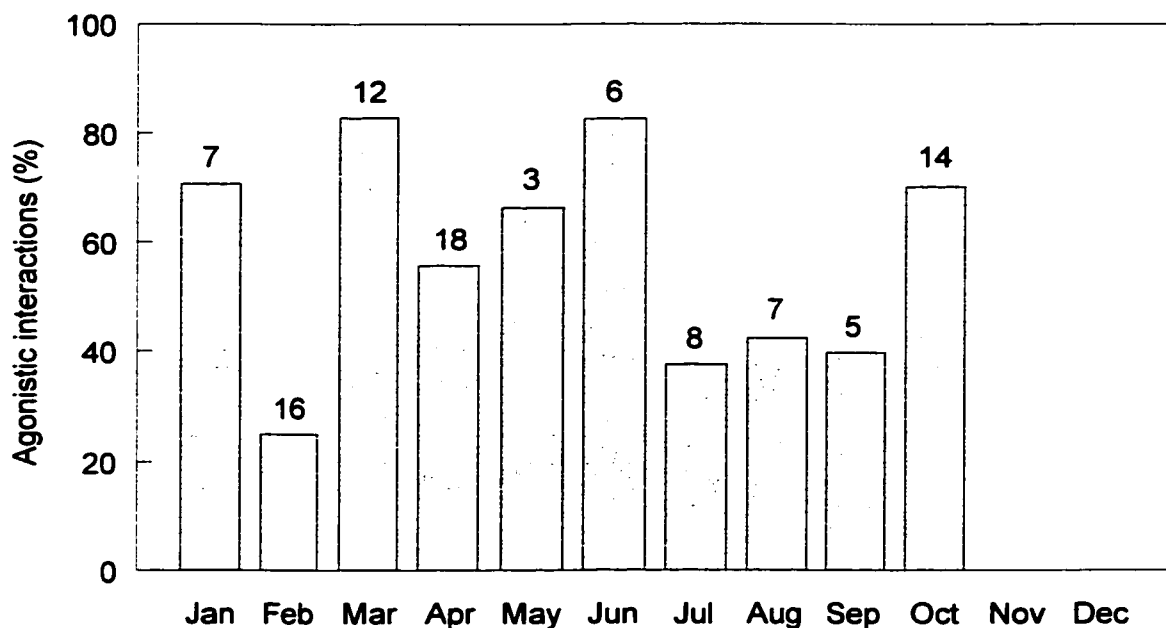


Figure 3-2

Percentage of interactions between male and female coatis that was agonistic, September 1995 - September 1996. Percentages were not calculated for November and December because fewer than two interactions were observed in those months. Numbers above bars are the total number of interactions observed in each month.

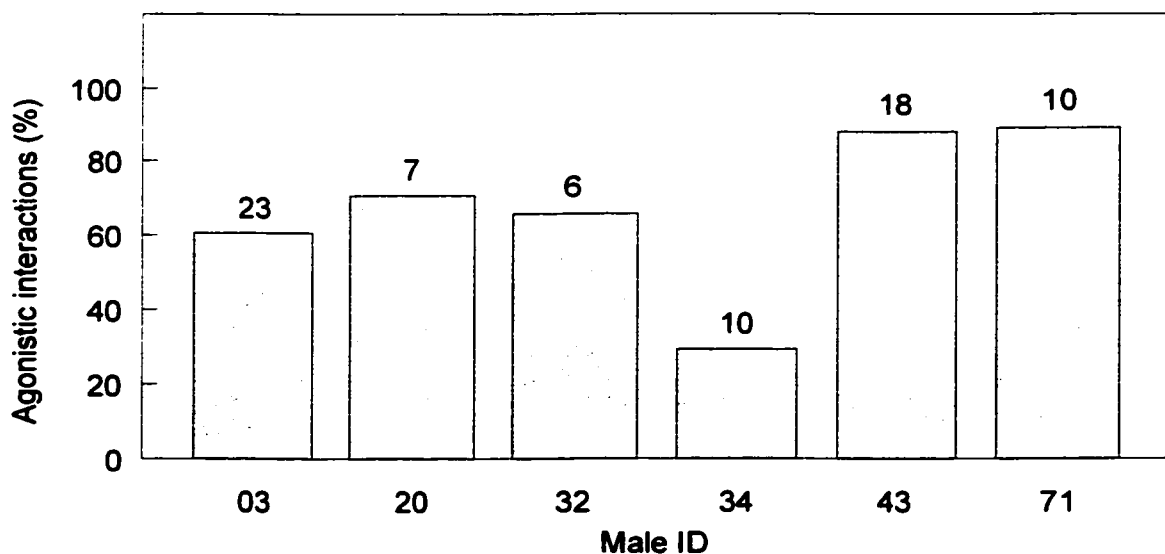


Figure 3-3

Percentage of interactions between females and individual males that was agonistic, September 1995 - September 1996. Numbers above bars are the total number of interactions with females observed for each male.

Table 3-2
Pattern of interactions between Male 43 (adult) and adult females

| | Agonistic | Mixed | Friendly |
|---------------------|-----------|-------|----------|
| Sep - Nov 1995 | 7 | 0 | 0 |
| Dec 1995 - Feb 1996 | 1 | 1 | 0 |
| Mar - May 1996 | 8 | 2 | 2 |

No interactions were observed after May 1996.

Table 3-3
Frequency of different types of interactions
observed between cubs and adult males,
September 1995 - September 1996

| Interaction Type | Number of Occurrences |
|-------------------|-----------------------|
| Mutually friendly | 12 |
| Avoidance by male | 7 |
| Agonism | |
| Male defers | 8 |
| Cub defers | 2 |
| Inconclusive | 5 |
| Total | 34 |

actually interacting were when one or both was eating at a rich food source, such as a fruiting tree.

Time of dispersal of eight yearling males in Band 1 ranged from early November 1995, when the yearlings were 18 months old, to early February 1996, when they were 21 months old. No yearling males remained with the band into the mating season. There was no sign of increased agonism from adult females as yearling males matured. The yearlings continued to behave like band members and be treated as band members until they left. There also was no indication that dispersal was stimulated by agonism from adult males. Interactions between adult males and yearling males still with their bands were frequently agonistic, but the adult male was the “winner” in only three of the eight such agonistic interactions observed.

Males did not experience higher foraging success when they were alone than when they were with bands. In fact, they tended to consume fruit at a higher rate when they were with bands (Figure 3-4), although the difference was not significant (one-tailed t -test: $df=85$; $p=0.20$). Solitary males had higher invertebrate foraging success, but again, the difference was not significant (one-tailed t -test: $df=85$; $p=0.15$).

Active (i.e., non-resting) males scentmarked an average of once every 2.7 minutes by rubbing their penises against tree buttresses, branches, or rocks. They scentmarked throughout the year, both when they were alone and when they were with bands. Scentmarking did not appear to function as territory demarcation *per se* because every male's home range overlapped extensively with those of several other males and there were no areas of exclusive use.

During the 1995 nesting season, when four nesting females used areas of 0.05 to 0.17km² (Chapter 2), the four radiocollared males whose ranges overlapped with those females' ranges used areas of 0.41 to 1.12km².

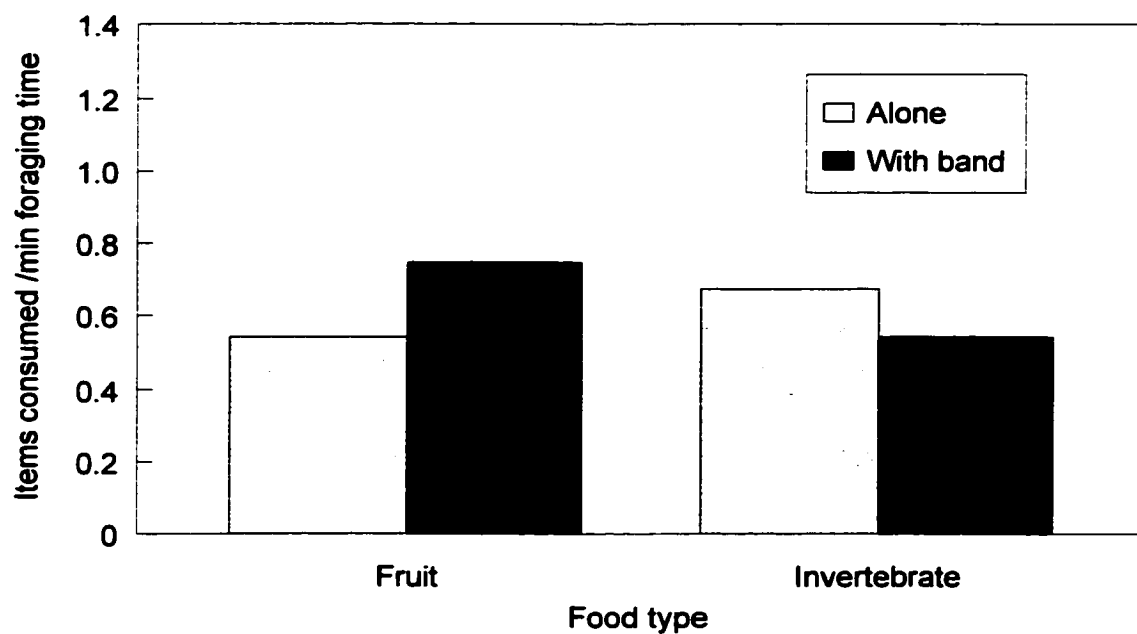


Figure 3-4

Foraging success of adult male coatis in different social situations, September 1995 - September 1996. $n=963$ fruits and 1283 invertebrates.

Discussion

Association patterns between males and bands in Tikal contrasted sharply with coati behavior on BCI, where researchers saw very little association between males and bands outside of the mating season (Kaufmann, 1962; Russell, 1981). Two relatively long-term associations were observed (Gompper and Krinsley, 1992), both probably involving 2-year-old males who delayed dispersal from their natal bands. It's possible that researchers on BCI were often unaware of males that were accompanying bands. Males in Tikal almost always stayed on the edges of the bands, and I often detected them only by listening for their radiosignals. Only four males were radiocollared during one BCI study (Gompper, 1997), and none during the others. However, bands on BCI are so much smaller than those in Tikal (see Chapter 2) that males with bands on BCI should have been relatively easy to detect. It seems more likely that differences in band sizes, home range sizes, or food availability between BCI and Tikal have led to differences in the frequency of association between males and bands. There are indications that males in Arizona (Gilbert, 1973) and Santa Rosa National Park, Costa Rica (Sáenz, 1994) also associate with bands more regularly than do males on BCI.

When Russell (1981) proposed that male coatids are excluded from bands because of their propensity for infanticide, he concluded that males must kill cubs solely for food, because he could find no other adaptive explanation. Coati reproduction is highly seasonal (Binczik GA, unpublished data; Kaufmann, 1962; Russell, 1982), so killing a female's dependent offspring ordinarily would not give the infanticidal male an earlier opportunity to mate with her than he would otherwise have. However, studies in Costa Rica (Sáenz, 1994) and Tikal (Binczik GA, unpublished data) have since shown that females who lose their litters shortly after birth do sometimes mate again and produce replacement litters. Therefore, infanticide potentially could be a viable strategy

for male coaties to increase their reproductive success, as it seems to be for lions (*Panthera leo*) (Pusey and Packer, 1994), brown bears (*Ursus arctos*) (Swenson et al., 1997), and a variety of primate species (Hiraiwa-Hasegawa and Hasegawa, 1994; Struhsaker and Leland, 1987).

However, there are a number of other factors that might influence the success of an infanticidal strategy. Female coaties are able to choose among possible mates (Chapter 4), and if they would avoid or at least not prefer to mate with a male that killed their offspring, such a strategy would not work. The fact that infanticide is much more common in single-male primate groups than in multi-male groups (Struhsaker and Leland, 1987) lends support to this idea. The high frequency of multiple mating by female coaties (Chapter 4) may also function to prevent infanticide, because it would be very difficult for a male to be sure that he was not killing his own offspring. Finally, coati cubs are hidden in nests for the first five to six weeks of life, and primate species that leave their infants somewhere are thought to be less vulnerable to infanticide than those in which mothers carry the infants with them (Pereira et al., 2000).

Bands were accompanied by males approximately two-thirds of the time in Tikal, so females were evidently not excluding males effectively. The fact that females and males had friendly interactions at all times of year suggests that females were not actually attempting to exclude males, contrary to Russell's (1981) hypothesis. The frequency of close contact between males and young cubs, the tendency of cubs to attempt friendly interactions with males, and the tendency of males to behave submissively when cubs were not friendly also support the idea that infanticide by males has not been a major selective force on coati behavior in Tikal. Similarly, other studies on BCI found no indication of infanticide (Gompper, 1994; Kaufmann, 1962), which suggests that what Russell (1981) observed was a rare event.

Like the infanticide hypothesis, the resource competition hypothesis (Gompper, 1996) does not seem to apply to coatis in Tikal. Males did not have higher foraging success when they were alone than when they were with bands. Logically, there must be competition among animals foraging in a group, and I did find an effect of such competition on the foraging success of females (Chapter 2). It may be that males minimize such effects by spending most of their time on the edges of bands, in areas where band members have not yet foraged. Gompper (1996) also found that females had higher success foraging on invertebrates when they were alone; however, he did not have data on the foraging success of males with bands. That males in Tikal spend such a high percentage of their time with bands supports the idea that they do not incur a high foraging cost by doing so. Perhaps more limited resources on BCI make the effects of competition in bands more severe, leading to the lack of association between males and bands. Gompper (1996) reported frequent agonistic interactions over fruit patches. I saw no apparent defense of food patches by coatis (Chapter 2). In fact, male-male aggression seemed to be reduced at food patches, which implies that competition for food is much less intense in Tikal.

The space-use patterns of coatis in Tikal also suggest that males do not leave bands simply to avoid foraging competition. If they did, one would expect the size of the area they use to be determined by their resource needs. However, nesting females were able to support themselves and their nursing litters on areas an order of magnitude smaller than those used by males during the same period. Clearly, males were using areas larger than they needed to find adequate food, so their movement patterns must be determined by something other than resource availability. The asynchronous dispersal of juvenile males implies that resource competition is not even a proximate stimulus for males to leave the bands. If decreased food abundance at a particular time of year led to juvenile males experiencing increased difficulty finding sufficient food and

resulted in dispersal, one would expect all juveniles to disperse at approximately the same time.

If males are not driven out of bands by females, and they do not leave to avoid foraging competition, then why do they leave? Or, more accurately, why do they not become integrated into another band once they have dispersed from their natal band? There are a variety of possible explanations that have not yet been tested. Females are safer from predation in groups (Chapter 2). However, females are constantly accompanied by cubs who both require their attention and attract the attention of predators by making noise. Males are more cryptic and better able to defend themselves than females are, and may actually be safer alone. Alternatively, it could be that frequent agonistic encounters with other males would make it too costly for a male to try to maintain a permanent presence in a band. Or, it may be that a male benefits more reproductively from maintaining a well-marked home range than he would from remaining with a band constantly. Of course, these explanations are not mutually exclusive, and doubtless no one cost or benefit is solely responsible for the solitary lifestyle of male coatis.

If there are selective forces that prevent the permanent integration of male coatis into bands, though, the question becomes: why do males in Tikal spend so much time with bands? They are obviously focused on females, because males accompany bands much less frequently when females are nesting. That reduces the viability of several possible explanations. If males associated with bands to help protect their offspring from predation, to reduce their own predation risks or parasite loads, or to improve their foraging success, then they would presumably continue to do so in the absence of females. Therefore, the benefits must relate to reproduction. Monitoring for estrous females would be an obvious reason for males to accompany bands, but the highly seasonal and predictable nature of coati reproduction makes this unlikely to be

important. Even when second litters have been observed they were restricted to a very brief season (Binczik GA, unpublished data; Sáenz, 1994), which means that there are mating opportunities during only 2 months of the year, at most. Associating with bands throughout the year, then, is apparently a way for males to increase their success during future mating seasons.

The tendency for males to associate almost exclusively with one particular band suggests that it is important for males to develop relationships with females. Females may be less willing to mate with a male with whom they are unacquainted, perhaps because they have not had an opportunity to assess his quality. Or they might fear that a strange male would be aggressive, and therefore not approach him to mate. While a male is accompanying a band to establish relationships with the females, he also could interfere with attempts by other males to establish similar relationships by driving the males away, thereby demonstrating his dominance to the females.

Nevertheless, it appears that in addition to spending time with females, establishing a strong presence in an area through scentmarking must somehow be important to male success. There is no other viable explanation for the high frequency of scentmarking in a male's daily activities. Every male's home range is shared with many other males, as well as bands of females, so scentmarking does not seem to be a way to control access to an area. Perhaps one way females assess the quality of a male is through the size of the area over which they regularly encounter predominantly his scentmarks. High quality males would presumably have more time and energy to devote to scentmarking and would be able to keep their marks fresher than those of their rivals.

There is abundant evidence from small mammal experiments that female behavior toward males can be influenced by exposure to scentmarks. Female rabbits (*Oryctolagus cuniculus*) exhibit a preference in laboratory choice experiments for males

whose odors have been deposited in the surrounding environment (Engel, 1990).

Female brown lemmings (*Lemmus trimucronatus*) (Coopersmith and Banks, 1983), pikas (*Ochotona princeps*) (Meaney, 1986), and golden hamsters (*Mesocricetus auratus*) (Tang-Martinez et al., 1993) exhibit higher levels of sexual behavior when paired with males to whose odors they have been previously exposed. Female meadow voles (*Microtus pennsylvanicus*) (Johnston et al., 1997) and house mice (*Mus musculus*) (Hurst and Rich, 1999), after being presented with environments containing overlapping scentmarks from two males, show a preference for the male whose marks were deposited on top.

The easiest way for a male to ensure that females regularly encountered his scentmarks, of course, would be to travel with a band, which brings up the original question: why are males solitary? Obviously, additional research is needed to examine the conflicting forces that shape male behavior. The balance between these forces, which apparently differs in different habitats, is what determines the degree of sociality of male coatis.

CHAPTER 4

LEK-LIKE MATING IN A CARNIVORE, THE WHITE-NOSED COATI

Introduction

Understanding the mating system of an animal is important for understanding many other aspects of its behavior and ecology, such as sexual selection, social organization, population dynamics, and population genetics. Mating systems have been classified in many ways and according to many different criteria, but the basic categories that are theoretically possible are monogamy, in which each individual has one mate; polygyny, in which males have more than one mate; polyandry, in which females have more than one mate; and polygynandry, in which individuals of both sexes have more than one mate. Polygyny, which has been traditionally considered the most common mating system among mammals (Clutton-Brock and Harvey, 1978), is commonly subdivided into resource-defense polygyny, female-defense polygyny, and male-dominance polygyny (Emlen and Oring, 1977).

Lekking is a form of polygyny or polygynandry that involves defense of neither resources nor females. Lekking males perform displays in aggregations to which females come for mating. Lekking has been described in a wide variety of taxa, including insects, fish, amphibians, birds, and mammals (Hoglund and Alatalo, 1995). There is some disagreement over exactly what should be classified as a lek, but the most commonly accepted definition is that of Bradbury (1981), who listed four criteria for identifying a lekking species: 1) males do not provide parental care; 2) males aggregate in an arena to which females come to mate; 3) males' display sites contain no resources; and 4) females can select their mates.

Lekking has been called male-dominance polygyny (Emlen and Oring, 1977), but in some species dominance rank does not seem very important in determining which males get to mate (Höglund and Alatalo, 1995). Because female choice seems to play a large role in determining male mating success in many lekking species, these species have been popular models for examining sexual selection. Much effort has been devoted to identifying the factors on which females base their choices (Harvey and Bradbury, 1991) and attempting to answer the question of why leks form (reviewed in Höglund and Alatalo, 1995). This research, most of which has been conducted on birds, has resulted in a wide variety of proposed explanations for the formation of leks. The evidence suggests that different factors are important for different species, and there are probably multiple ways for leks to evolve (Höglund and Alatalo, 1995).

In mammals, lekking has been described almost exclusively in ungulates, perhaps because they are more likely than most other mammals to have the high mobility and high population densities that are necessary for lekking to be feasible (Höglund and Alatalo, 1995). Here I describe the first lek-like mating system observed in a member of the Carnivora.

Methods

The study area, animal handling, and behavioral observations were as described in Chapter 2. Recording of interactions between individuals was as described in Chapter 3.

In addition to collecting blood samples from all captured adults, I located the nests of as many radiocollared females as possible during the nesting seasons of 1995 and 1996 and collected blood samples from the cubs. I succeeded in sampling 50 cubs from 15 litters in Band 1. Samples were preserved at room temperature in lysis buffer (100mM Tris-HCl, pH 8; 100mM EDTA, pH 8; 10mM NaCl; 1.0% SDS) until analysis.

DNA was extracted with a QIAGEN (Valencia, CA) DNeasy Tissue Kit and stored in sterile, distilled, deionized water at -20°C. I used four microsatellite primer pairs (Pfl3, Pfl4, Pfl8, Pfl9) that were developed for kinkajous (*Potos flavus*) (Kays et al., 2000), as well as one (Ma3) that was developed for American marten (*Martes americana*) (Davis and Strobeck, 1998) and one (G10H) for black bears (*Ursus americanus*) (Paetkau et al., 1998).

Amplification was carried out by polymerase chain reaction (PCR) in a Biometra (Gottingen, Germany) thermocycler. The PCR mix for the kinkajou primers contained 100ng DNA, 200µM dNTPs, 1µM primers, 1µM fluorescently labeled dCTP (PE Applied Biosystems, Foster City, CA), 1X PCR buffer, 1.5mM MgCl₂, and 1U DNA polymerase (buffer, MgCl₂, and polymerase from either Sigma-Aldrich, St. Louis, MO or Finnzymes Oy, Espoo, Finland) in a 25µl volume. The PCR mix for the bear primer set was the same, except that only 120µM dNTPs and 0.5U polymerase were used. The PCR mix for the marten primer set differed in containing 120µM dNTPs, 0.16µM primers, 2mM MgCl₂, and 0.3U polymerase. In all cases, cycling was as follows: 1 min at 94°C; four cycles of 30 sec at 94°C, 20 sec at annealing temperature (see Table 4-1), 5 sec at 72°C; followed by 34 cycles of 15 sec at 94°C, 20 sec at annealing temperature, 1 sec at 72°C; then 30 sec at 72°C; hold at 4°C. PCR products were run through a 5% denaturing acrylamide gel with Genescan 400HD size standard in each lane on an ABI 373 automated sequencer. Results were analyzed using GENESCAN and GENOTYPER software (size standard, automated sequencer and software all from PE Applied Biosystems). The number of alleles per locus in the sampled animals ranged from two to six (Table 4-1).

Paternity of cubs with known maternity was determined by exclusion. In cases where two males could not be excluded as possible fathers, half of the cub was assigned to each male in calculations of reproductive success. In cases where all

sampled males were excluded as possible fathers, the alleles that must be present in the father were determined, and all such cases from all litters were examined collectively to determine the minimum number of unsampled males that could have sired all of them.

Results

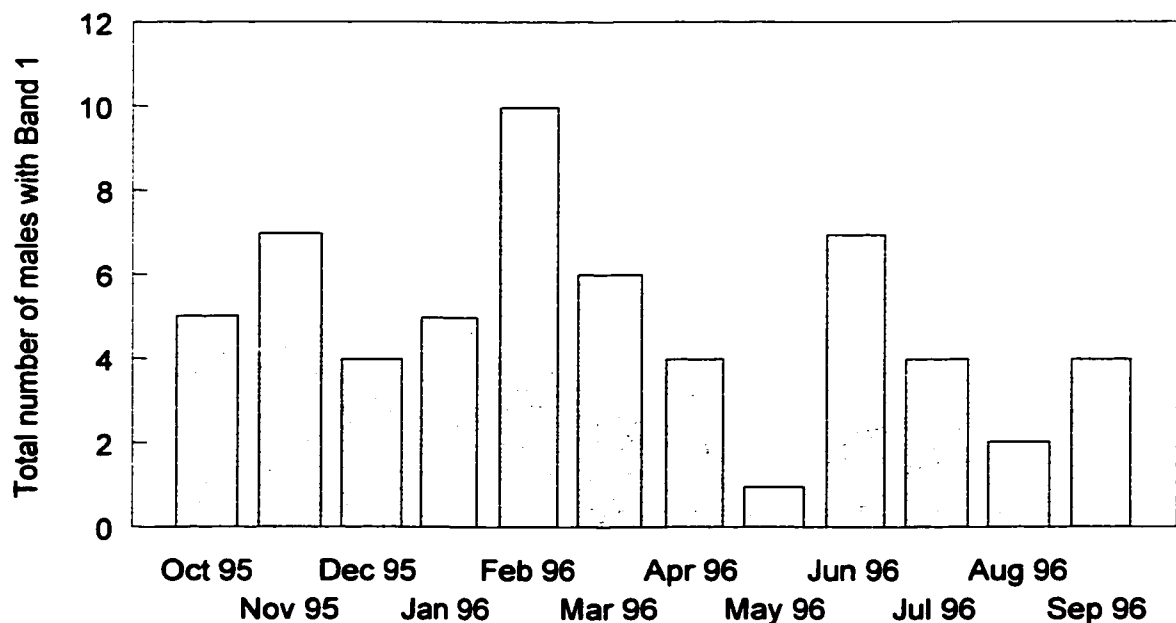
Many different male coatis associated with each band (Figure 4-1). Usually only one male was present at a given time, but during the mating season, February 13-28 (Binczik GA, unpublished data), males aggregated around bands (Figure 4-2). The mean number of males with a band during the non-mating season was 0.84 ($n=425$, 95%CI 0.77-0.91). However, during the mating season, when as many as nine males were seen with a band at one time (Figure 4-3), the mean was 3.7 ($n=33$, 95%CI 2.8-4.6).

Although male home ranges typically overlapped with the home ranges of several bands of females, and the mating period was slightly staggered between bands (Binczik GA, unpublished data; see also Figure 4-3), males showed mating-season fidelity to particular bands (Table 4-2). Only one of 16 marked males that were seen more than once accompanying bands of females during February was observed with more than one band. This band fidelity held true between years as well as within a single season; none of the four marked males that were observed with bands in both the 1995 and 1996 mating seasons switched bands.

Males displayed during the breeding season. They vocalized from perches high in the trees above and around the band, and as the band members moved along, foraging in the leaf litter, the males would descend and move with them, finding new trees from which to call. To the human ear these vocalizations were similar to the alarm calls given by coatis in bands, but they were repeated steadily for many minutes at a time, not given in short bursts as in alarm situations. Furthermore, band members did

Table 4-1**Characteristics of six microsatellite loci in coatis in Tikal National Park, Guatemala**

| Locus | Annealing temp (C) | Number of alleles | Size range (bp) | Frequencies | Number of animals analyzed |
|-------|--------------------|-------------------|-----------------|-------------------------------------|----------------------------|
| Pfl3 | 53 | 6 | 188-198 | 0.42, 0.28, 0.18, 0.10, 0.02, <0.01 | 100 |
| Pfl4 | 51 | 5 | 171-179 | 0.45, 0.32, 0.10, 0.07, 0.05 | 74 |
| Pfl8 | 56 | 2 | 187-191 | 0.95, 0.05 | 75 |
| Pfl9 | 57 | 6 | 198-212 | 0.67, 0.11, 0.09, 0.06, 0.05, 0.01 | 75 |
| Ma3 | 54 | 3 | 278-287 | 0.57, 0.25, 0.18 | 34 |
| G10H | 54 | 4 | 271-283 | 0.61, 0.19, 0.15, 0.05 | 75 |

**Figure 4-1**

Total number of identifiably different adult males seen with Band 1 in each month during which behavioral observations of the band were conducted. $n=195$ total band sightings.

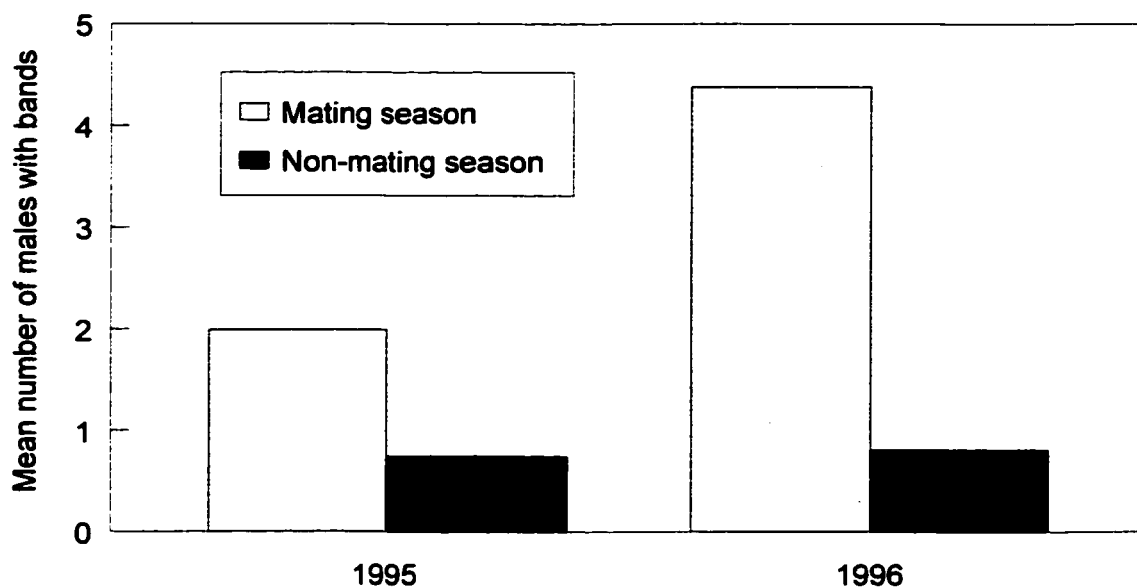


Figure 4-2

Mean number of adult males known to be present each time a band was encountered during mating seasons and non-mating seasons. $n=458$ total band sightings.

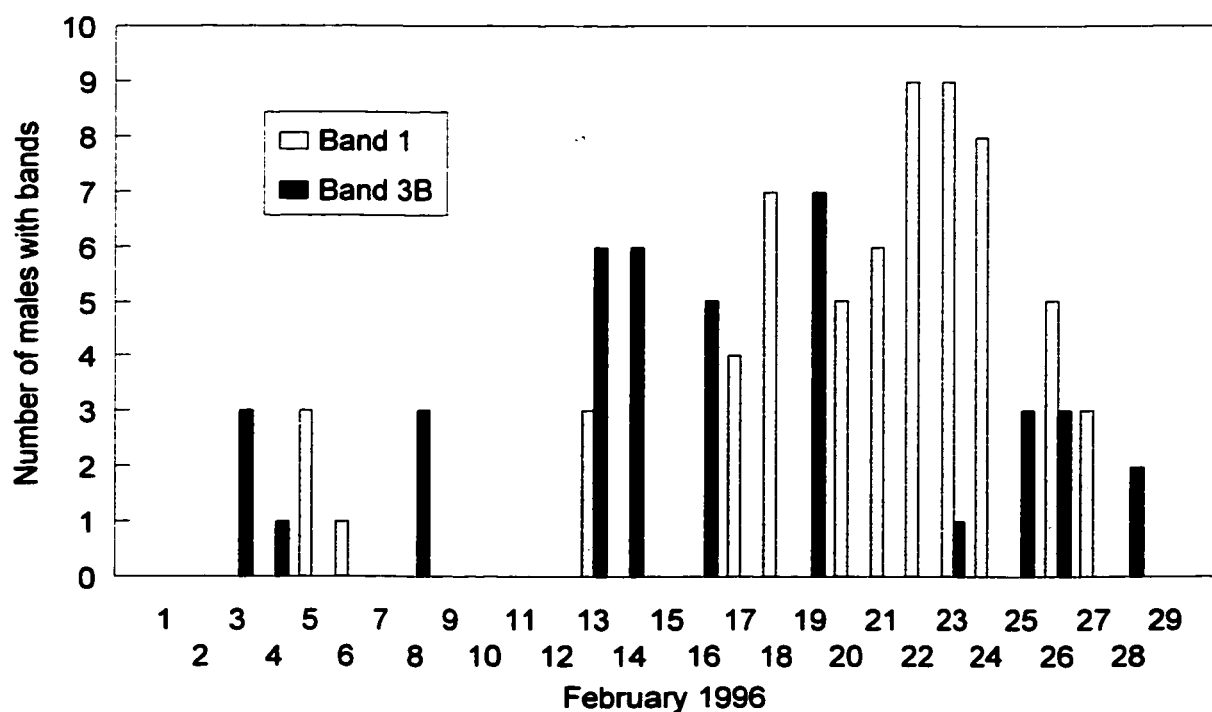


Figure 4-3

Number of adult males known to be present in two bands during February 1996. Absence of a bar means that the band was not encountered on that date; there were no zero values.

Table 4-2
Band fidelity among male coatis

| | M1 | M3 | M16 | M20 | M28 | M32 | M34 | M40 | M43 | M50 | M51 | M53 | M71 | M90 | M91 | M93 |
|---------|----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1995 | | | | | | | | | | | | | | | | |
| Band 1 | 4 | 3 | | 5 | | 0 | 2 | | | | | | | | | |
| Band 3 | 0 | 0 | | 0 | | 2 | 0 | | | | | | | | | |
| 1996 | | | | | | | | | | | | | | | | |
| Band 1 | | 11 | 10 | 12 | 0 | 0 | 9 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 6 | 0 |
| Band 3A | | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 4 |
| Band 3B | | 0 | 0 | 0 | 4 | 1 | 0 | 3 | 7 | 0 | 0 | 4 | 4 | 4 | 0 | 0 |

Values are numbers of times each male was seen with each band during February. Blanks indicate that the male was not marked, not adult, or not alive during that year's mating season.

not respond to these calls as they did to alarm calls. The focal males called during all five of the observations of males with bands in February, but never called during observations throughout the rest of the year. The vocalizations did not serve to repel other males, as several males could often be seen calling simultaneously in neighboring trees. During the period when females were receptive the males seemed to pay more attention to the females than to each other, but before the receptive period the sound of a calling male often would prompt another male to climb the tree and attack him.

Females appeared to be free to choose their mates, ascending to a male's perch when they were ready to mate. My research associates and I observed 11 copulations, eight of which were already in progress when first observed. In the three copulations that were observed in entirety, the females approached the males. Throughout the study, 42 instances of a male directly approaching and attempting to interact with an individual female were recorded. The female aggressively drove the male away on 52% of those occasions, demonstrating that females are quite capable of rebuffing unwanted advances from males. Male-male competition might interfere with female choice, but although coati copulations last up to an hour (Binczik GA, unpublished data; Hass and Roback, 2000), only one of the 11 observed copulations was interrupted by another male. In that instance the interrupting male returned to the female after chasing off the original male, but she ran away at his approach and he did not pursue.

Males provided no resources to females at the time of mating. Ten of the 11 observed copulations took place low in the tree canopy (the eleventh was on an elevated limb of a large fallen tree). Theoretically, the males might have been controlling access to some resource in the trees. However, 100% of the food items ($n=103$) consumed by females during behavioral observations in February were obtained on the ground. Furthermore, when a copulation ended the female usually descended precipitously and raced off to rejoin her band. Only three of the 11 copulations did not follow this pattern:

on one occasion the copulation was interrupted by another male and the males fell out of the tree fighting, leaving the female behind; on another, the female remained in the tree resting for approximately 2 min post-copulation before running down and away; on another, the female remained in the tree resting for about half an hour.

Males were not observed to provide any kind of parental care. Males, as well as band members, that attempted to closely approach nests were always driven off by the nesting females, even though they sometimes interacted quite amicably away from the nests just a few minutes before or after such chases. Males accompanying bands never responded to the distress calls of cubs in the band, although band members other than the cub's mother often did. Males also never gave alarm calls when they were with bands, responding to threatening situations simply by becoming alert or running away. Only two of the 16 marked males that accompanied bands during observation sessions were ever observed allogrooming cubs.

The behavioral observations suggested that male mating success was not highly skewed. Seven of the 11 observed copulations involved marked males, and six different males participated in those seven copulations. The highest number of copulations seen in any one band during a single breeding season was five, and four different males participated in those five copulations. Genetic analyses revealed a more pronounced skew in paternity of the sampled offspring in 1995 than in 1996 (Figure 4-4). In both years the majority of the sampled cubs was fathered by unmarked males (Table 4-3). At least three of the four marked males that accompanied Band 1 during the 1995 mating season sired cubs, and at least four of the seven marked males that accompanied them in 1996 sired cubs. The eight litters that were sampled in 1996 had a minimum of nine fathers, so more males than females contributed to those litters.

Multiple mating by females was common. At least seven of 11 litters in which all offspring were sampled, as well as two of three incompletely sampled litters, showed

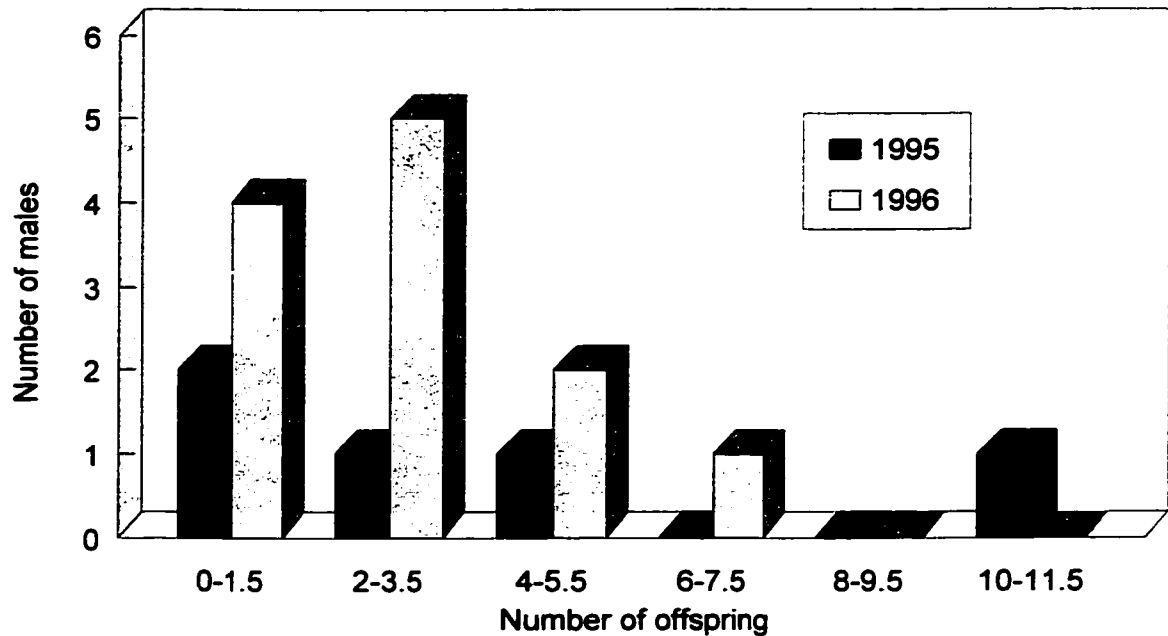


Figure 4-4

Frequency distribution of male reproductive success, based on seven litters sampled in 1995 and eight in 1996, all in Band 1. The number of males achieving the lowest level of reproductive success is doubtless an underestimate due to the presence of an unknown number of uncaptured males.

Table 4-3

Reproductive success of individual males

| Male | Number of Sampled Offspring Sired | |
|--------------|-----------------------------------|-----------|
| | 1995 | 1996 |
| 01 | 1 | |
| 03 | 0 | 1.5 |
| 16 | | 2.5 |
| 20 | 5 | 3 |
| 34 | 2 | 1.5 |
| 51 | | 6 |
| 89 | | 0.5 |
| 91 | | 0 |
| U1 | 10 | 4 |
| U2 | | 3 |
| U3 | | 3 |
| U4 | | 4 |
| U5 | | 3 |
| Total | 18 | 32 |

U1 - U5 were never captured. A blank indicates that that male was not known to be present in that year.

multiple paternity. Four litters (of four and five cubs) had three fathers. The mean number of fathers per litter was 1.4 in the 1995 sample and 2.6 in 1996. The number of fathers per litter was positively correlated with the number of offspring in the litter ($df=9$; $p<0.05$), but to some extent correlation is inevitable, because there cannot be more fathers than there are offspring. When the analysis was restricted to litters of at least three cubs, there was no significant correlation. Eight of the nine males that sired three or more of the sampled cubs in a given year had offspring in more than one of the sampled litters in that year.

Discussion

The coati mating system in Tikal appears to fulfill at least three of the four criteria suggested by Bradbury (1981) to identify a lek: lack of paternal care, lack of resources at display sites, and female choice. The fourth criterion is that there is an arena where males aggregate and females come for the sole purpose of mating. Coatis in Tikal did not have arenas *per se*, but they did have areas where males aggregated and displayed and females went to mate. The only difference is that those areas moved as the bands of females moved.

Leks are generally thought of as being tied to specific geographic locations, and there often is remarkable site stability across years, both for the lek as a whole and for the territories of individual males within the lek. However, variations in this pattern have been documented in other species. Male natterjack toads (*Bufo calamita*) display at the edges of ponds and return to the same pond night after night, but not necessarily to the same display site (Arak, 1988). Rather, they seem to choose sites based on environmental conditions, and seek to prevent other males from displaying within a certain distance of them. Sage grouse (*Centrocercus urophasianus*) normally have extremely stable leks, but on occasion they abandon their arenas to follow, display to,

and mate with females off the lek (Gibson and Bradbury, 1987). Buff-breasted sandpiper (*Tryngites subruficollis*) lek sites are not stable between years, or even within years; most leks last only a few days, after which the males move to another lek. Furthermore, as soon as nesting starts, some males follow the females and begin to display near nests, with up to four males aggregated around a single nest (Lancot and Weatherhead, 1997). Male ruffs (*Philomachus pugnax*) spend most of their display time off leks, frequently following foraging females. They follow both individually and in groups in which each male defends his immediate vicinity against other males (Lank and Smith, 1987).

The association patterns of buff-breasted sandpipers and ruffs have been called mobile leks (Lancot and Weatherhead, 1997), and it seems that coatis have been able to form lasting mobile leks, rather than ones that are continuously dissolving and reforming, because female coatis are group-living. Males in Tikal show a high degree of band fidelity, similar to the site fidelity found in classical lekking species. Rather than being tied to an arena, coati males simply aggregate around the already clumped females.

Leks have traditionally been thought of as resulting in extremely skewed male reproductive success, and this belief gave rise to the "paradox of the lek" (Borgia, 1979), which is that female choice among males is still exhibited, even though strong directional selection should have virtually eliminated male variability. This view of lekking was based on behavioral observations that seemed to show that each female only mated once and virtually all the females mated with the same few males, so that most males were excluded from mating. However, as the use of molecular methods to determine paternity has become widespread, it has become increasingly obvious that across all types of mating systems, multiple mating by females is the rule rather than the exception (Birkhead, 2000). Very few paternity studies of lekking species have been conducted,

but multiple paternity was found to be frequent in the buff-breasted sandpiper (Lanctot et al., 1997), the ruff (Lank DB, Smith CM, Hanotte O, Ohtonen A, Bailey S, Burke T, unpublished data), and a variety of cichlid species (Kellogg et al., 1995). Multiple paternity was not found in black grouse (*Tetrao tetrix*), but only 11 clutches were sampled (Alatalo et al., 1996). It is possible that the rate of multiple paternity in coatis is even higher than this study demonstrates, because I am assuming only the minimum number of unsampled fathers required to account for all the observed genotypes of the cubs.

Lacking information on the number of unmarked males present that did not sire cubs, I was not able to calculate the complete distribution of male reproductive success. However, if marked males are representative, it seems that most coati males do manage to reproduce. Very little skew was found in the reproductive success of buff-breasted sandpiper males; more males than females contributed to the clutches examined (Lanctot et al., 1997). If paternity studies of other lekking species reveal similar patterns, the lek paradox will be resolved and theories of sexual selection in lekking species will need to be thoroughly reexamined. Females of many lek-breeding bird species have been seen mating with multiple males (Lanctot et al., 1997), which suggests that genetic analyses would indeed reveal multiple paternity.

Widespread multiple paternity might also be relevant to theories of lek evolution. One pathway that has been proposed for the evolution of leks is that females prefer to mate with clustered males because it is faster and easier for them to compare the males and choose the best one (Alexander, 1975; Bradbury, 1981; Emlen and Oring, 1977). If multiple mating turns out to be common in lekking species, it may be that females prefer leks because it is faster and easier for them to find several males to mate with when the males are clustered.

There are numerous possible advantages to multiple mating (Birkhead, 2000), many of which are not relevant to lekking species because they involve direct benefits, such as resources or paternal care. That leaves a variety of possible indirect, or genetic, benefits (reviewed in Jennions and Petrie, 2000), and empirical evidence for some of these benefits is mounting. Female adders (*Vipera berus*) (Madsen et al., 1992), sand lizards (*Lacerta agilis*) (Olsson et al., 1994), and tree swallows (*Tachycineta bicolor*) (Kempnaers et al., 1999) all have lower embryo mortality when they mate with multiple males, apparently because they frequently have genetic incompatibility problems with a single mate. Most Mexican jay (*Aphelocoma ultramarina*) broods have multiple paternity, and small broods contain a higher proportion of extra-pair young (Li and Brown, 2000), suggesting that the social mate may be genetically incompatible with the female in those cases. Offspring of multiply mated females have higher survival in sand lizards (Olsson et al., 1994), yellow-toothed caviies (*Galea musteloides*) (Sachser et al., 1999), and possibly in Columbian ground squirrels (*Spermophilus columbianus*) (Murie, 1995), and are more skilled at predator-escape behaviors in guppies (*Poecilia reticulata*) (Evans and Magurran, 2000). Such increases in fitness indicate that multiple mating can be a way for a female to find a male with “good” genes.

There is one direct benefit of multiple mating that could be relevant to lekking species, and may be particularly relevant to coatis. That is assurance of fertility: increasing the likelihood that all of a female’s eggs will be fertilized. Breeding synchrony is so tight within a coati band (Binczik GA, unpublished data) that in a large band, many females must be in estrus each day, and a highly preferred male might have his sperm stores depleted. In captive hamadryas baboons (*Papio hamadryas*), synchronized estrus among the females in a male’s harem results in a lower probability of conception for each female (Zinner et al., 1994). Polygynous northern harriers (*Circus cyaneus*) have a higher percentage of unhatched eggs when females in a harem have overlapping

copulation periods (Simmons, 2000). In red-winged blackbirds (*Agelaius phoeniceus*), females in larger harems are more likely to have unhatched eggs, and broods with offspring resulting from extra-pair copulations contain fewer unhatched eggs (Gray, 1997). Female Gunnison's prairie dogs (*Cynomys gunnisoni*) that copulate with several males are more likely to conceive than those that only copulate with one or two males, and they also have larger litters (Hoogland, 1998). The author hypothesized that male prairie dogs experience sperm depletion when several females are in estrus on the same day.

Evidence that female fertility can be limited by temporary sperm shortages raises the possibility that multiple mating could be a consequence of a lek-like mating system, rather than a cause of it. It may be that female coatis would choose to mate with only one male, but if they all preferred the same few males, a sperm shortage would result. In this scenario, the females would have to mate with additional males to ensure that all their eggs would be fertilized. Female coatis were seen following and soliciting displaying males who did not respond to them, which may be an indication that the males were not capable of successfully copulating at that moment. Similarly, high-ranking, preferred male primates have been seen turning down female solicitations, forcing the females to resort to lower-ranking males (Boinski, 1987; Lindburg, 1983). Also, male Columbian ground squirrels are sometimes unresponsive to female solicitations, even though they have not previously mated with those females (Murie, 1995). If sperm is abundant, males should take every opportunity to mate and increase their reproductive success (Bateman, 1948; Trivers, 1972). The fact that they do not suggests that under some conditions sperm becomes a limiting resource. Female peafowl (*Pavo cristatus*) on leks are more likely to mate multiply if their first copulation is with a non-preferred male (Petrie et al., 1992), demonstrating that temporary unavailability of preferred mates can lead to multiple mating. My observations suggest

that such temporary unavailability occurs among coatis in Tikal. In addition to the unresponsive displaying males mentioned above, a female coati was observed sitting next to a copulating pair for more than 10 min as though waiting for the male to become available. The male left when the copulation ended, after which time the waiting female also left. I never saw a male copulate twice in quick succession.

So why has lek-like mating evolved in coatis? Nothing resembling lekking was observed in previous coati studies, and it may not be the mating system typical for this species. Researchers who conducted early observational studies on BCI believed that coati bands were accompanied by one male consort during the breeding season (Kaufmann, 1962; Russell, 1981). It was thought that the consorting male monopolized access to the females, although Kaufmann (1962) did see bands associating briefly with males other than their consorts. A later study on BCI involving both behavioral observations and genetic analyses found that some bands consorted with at least two males, and that four of the five offspring sampled were not fathered by the known consorting males (Gompper et al., 1997), which suggests that there were more males associating with these bands than the researchers were aware of. Nevertheless, as no male displays were reported in the BCI studies, and they are the most prominent feature of coati breeding season activity in Tikal, it seems clear that coatis in Tikal exhibit different mating behavior than those on BCI.

This difference demonstrates the powerful influence that ecological conditions can have on mating systems. The ecological conditions on BCI are unusual, in that it is a 15km² island with no resident large predators (see Chapter 2). Ecological conditions in Tikal may also be unusual, as it was a major population center of the ancient Maya civilization (ending around 900 A.D.) and the current forest composition may be a legacy of their silvicultural (Lundell, 1937; Puleston, 1982) or architectural (Lambert and Arnason, 1982) practices. As a result of these differences in predation pressure and/or

resource availability, coati ecology differs widely between the two sites (Table 4-4).

Coati bands are much larger in Tikal, and not surprisingly, band home ranges are also much larger. Because females in Tikal are so clumped, many more males compete for mating access to each band. The size of the bands means that no male is able to defend either the females or the amount of resources required by the females. The males' best option becomes displaying to attract the females, and a lek-like situation results.

Table 4-4

Differences in ecological conditions and coati social and mating behavior between two study sites: Barro Colorado Island, Panama (BCI) and Tikal National Park, Guatemala

| BCI | Tikal |
|--|--------------------------------------|
| Island | Mayan forest |
| Band size: 2-26 ^a | Band size: 28-162 ^b |
| Band home range: 0.3-0.4km ^{2c} | Band home range: 5-8km ^{2d} |
| 1-2 male consorts ^e | 5-12 male consorts ^d |
| No male display | Male display |

^aGompper, 1997; Kaufmann, 1962; Russell, 1979

^bChapter 2

^cGompper, 1997; Kaufmann, 1962

^dUnpublished data

^eGompper et al., 1997; Kaufmann, 1962; Russell, 1981

Lekking ungulates also show considerable intraspecific variation in mating systems, and lekking has been correlated with large overlapping female home ranges in a variety of taxa (Bradbury, 1981; Clutton-Brock, 1989; Höglund and Alatalo, 1995). It would be worthwhile to study the coati mating system at additional sites to determine whether it varies consistently with differences in ecological conditions and spacing patterns. In Los Tuxtlas, Mexico, coati band sizes ranged from 10 to 25 individuals and band home ranges were less than 1km² (Estrada et al., 1993), similar to BCI. Two bands in Santa Rosa National Park, Costa Rica, on the other hand, had home ranges of

4.3 and 5.4km² (Sáenz, 1994), and bands in the Chamela-Cuixmala Biosphere Reserve in Mexico had home ranges of 2.5-6.9km² (Valenzuela and Ceballos, 2000). Information on band sizes at the latter two sites is not available. Coatis show high ecological flexibility, occupying habitats ranging from dry temperate woodlands to lowland tropical rainforests to cloud forests (Gompper, 1995), and their mating system may be correspondingly flexible.

The current lek-like system in Tikal is not necessarily the final adaptation to the ecological conditions there, but may simply be a transitional step. Given time, coatis might evolve male-male coalitions that would cooperate in competing with other coalitions for control of reproductive access to a band of females, much as lions do (Bygott et al., 1979). Alternatively, coatis might develop stable dominance hierarchies among the males that associate with a band, with mating opportunities dependent on rank. This would limit male-male aggression and facilitate the permanent integration of males into bands, resulting in a social system similar to that of many primate species (Clutton-Brock, 1989).

How did male coatis in Tikal develop their lek-like displays? It seems possible that the display call evolved from the alarm call, as they sound very similar and band members frequently respond to alarm calls by climbing trees. The generalized tree-climbing response may have simply been refined into climbing to find a mate. Although copulations were not observed by coati researchers on BCI, Kaufmann (1962) noted that breeding season behaviors such as chasing, allogrooming and mounting generally occurred in trees, particularly when the band had gone up for the night. In a chance encounter, two other scientists on BCI observed two coatis copulating in a tree above a band that was moving along on the ground (Sunquist and Montgomery, 1973). In small bands, it may be that most copulations take place when the band is already up in the trees resting. In larger bands, with more females in estrus, there would not be sufficient

time for that, so males might give an alarm call when the band began to descend, hoping to induce the females to remain aloft. (Several times I observed females with young cubs employing a similar strategy to extend a resting/nursing session when the rest of the band was ready to move on.) If this strategy were successful, it could lead to the development of the display call as a reproductive signal.

Although it is possible that females are assessing some parameter of the males' calls, such as volume or duration, it seems likely that the calls function to help females locate males rather than evaluate their quality. Because males accompany bands sporadically throughout the year, females have ample opportunity to evaluate them based on more meaningful criteria, such as the quality and/or size of their home ranges, the intensity of their scentmarking, or the amount of time they spend with the band. It remains to be discovered which male characteristics influence female coatis' choice of mates.

In summary, coatis in Tikal have a polygynandrous mating system that can best be described as mobile lekking. Among the competing theories regarding the evolution of lekking, the "hotspot" hypothesis (Bradbury and Gibson, 1983; Emlen and Oring, 1977) seems most applicable to coatis. Males have taken the strategy of aggregating in locations that females frequent to an extreme by aggregating around the females themselves. Coatis also provide support for the idea that lekking is a default strategy, adopted when defense of females or resources is not feasible (Clutton-Brock, 1989; Emlen and Oring, 1977).

CHAPTER 5 CONCLUSIONS

This study has provided a variety of evidence for the influence of ecological factors on social behavior. Ecological conditions determine the social organization of female coatis, and therefore, indirectly, the mating system. Differing conditions in different habitats result in differences in social organization and mating system.

My results demonstrated that group living confers a substantial anti-predation benefit on adult female coatis. They were more likely to be killed while solitary than while they were with their bands. I found no support for other proposed benefits of group living, leading me to conclude that, as in other small carnivore species, coati sociality evolved as an anti-predation strategy. The lack of large predators on BCI apparently permits coati bands to be smaller and less cohesive.

The reasons for the solitary lifestyle of male coatis remain less clear. I found no support for the idea that infanticide is a factor, nor did I find evidence of a foraging cost to males from associating with a band. In fact, they did associate with bands quite frequently, which suggests that they gained some benefit therefrom. The lack of males with bands during the nesting season, when the females were absent, leads me to conclude that the benefit involves reproduction. However, how and why associating with a band enhances a male's reproductive success remains to be discovered.

The large size of coati bands on Tikal relative to BCI is probably due to higher predation pressure, more abundant food resources, or both. It has resulted in a different mating system. Males in Tikal are able to defend neither a band of females nor the

amount of resources required by a band, so they have adopted a lek-like mating system. Males aggregate around bands during the mating season and display to attract the females. Such behavior has not been observed on BCI, where the small bands may be defensible by individual males. These differences are testament to the importance of studying species at numerous sites and the danger of assuming that a species is well-known because it has been well-studied at one site.

These findings have mixed implications for conservation of coatis. In areas with healthy populations of large predators, coatis in small groups might have very low survival. Reducing group sizes through hunting, therefore, might result in local extinction of coati populations. On the other hand, multiple mating by female coatis apparently allows most males to father offspring. This mating system means that effective population sizes will be larger than might have been expected based on results from BCI.

Coatis fulfill a large and central role in the Tikal ecosystem. Recent studies have demonstrated the massive impact that hunting is having on coati populations around Tikal. Changes in the population density of coatis are likely to have effects at every trophic level. If conservation laws in Guatemala are not enforced and expanded upon, there will soon be little vertebrate biodiversity remaining in the Maya Biosphere Reserve. Before such laws can be enforced, however, rural people must be provided with means of support other than hunting and deforestation. And as in all parts of the world, human population growth must be controlled, or all efforts at conservation will be futile.

APPENDIX ECOLOGICAL ROLE OF COATIS AND CONSERVATION IMPLICATIONS

Introduction

Due to the desperate circumstances of much of the earth's biodiversity and the low rank of biodiversity on most people's list of priorities, wildlife conservation has become largely crisis management. The vast majority of effort and money is spent on rare, often virtually extinct, species. Too often, the resources necessary to conserve a species are not made available until it is teetering on the brink of extinction; only then does public outrage become sufficient to sway governments and powerful corporations. At that point, of course, the amount of resources required to restore a species is many orders of magnitude greater than what would have been required to safeguard it at an earlier point in its decline.

A corollary of this reliance upon crisis management is that a disproportionate amount of research also is focused on rare species, because the need is perceived as being greater and funding is easier to acquire. However, studying rare species may entail a variety of difficulties. The sample sizes that can be obtained may not be sufficient to generate scientifically meaningful results. The types of research that are allowed may be severely limited by concerns about detrimental effects on the animals. The factors that are endangering the species may also alter its behavior or ecology such that the data are compromised. Because of these difficulties, more common, related species are sometimes studied as models for rare species of interest, but the degree to which such results are transitive is obviously limited.

Clearly, more accurate and complete scientific information can be obtained if a species is studied before it becomes rare. More knowledge will be obtained not only about the species itself, but also about its ecological role. Such knowledge is vital because biodiversity conservation must encompass ecosystem processes as well as species. Furthermore, if common species, which represent a large proportion of the biomass and tend to be linked trophically with many other species, do become reduced in abundance, the impacts on ecosystem and landscape processes may be enormous.

Although coatis have the potential for high densities, their populations in many areas have been much reduced through hunting and habitat destruction (Glatston, 1994). As a result, they are legally protected in the state of New Mexico, and are listed on CITES Appendix III in Honduras (Glatston, 1994). I assessed the ecological role and conservation importance of coatis in the Tikal ecosystem by examining their functional relationships with other species through interactions such as predation and frugivory.

Methods

The study area, animal handling, and behavioral observations were as described in Chapter 2.

In order to estimate population density, I used data on sightings of animals in the forest to map the total area used by the study population. Radiotelemetry data, which were collected from temples in the center of the study area, were deemed to contain too much error at the far edges of the coatis' ranges. A strip one-half of the width of the area of overlap between study bands was then subtracted from the edge of the above area to account for presumed overlap with coatis unknown to me. The existence of such overlap was verified by occasional sightings of unknown bands in the outer portions of the study area.

To estimate the number of food items eaten by coatis during a day, I multiplied mean counts of food items consumed during behavioral observations by six. This conversion was used because my observation sessions occupied approximately one-half of the coatis' daily active period, and focal animal observations made up one-third of each observation session. These calculations undoubtedly resulted in very rough approximations, but the final numbers calculated are so large that a general idea of magnitude was all that was desired. To calculate the total amount of fruit consumed throughout a fruiting season, I multiplied means of daily consumption estimates by coati density and by the number of days from the first time focal animals were seen eating each fruit to the last time. Total consumption estimates were divided by production estimates (Binczik GA, unpublished data), which resulted in an estimate of the percentage of the crop of each fruiting species that was consumed by coatis.

Rate of travel, which was used in estimating seed dispersal distances, was calculated differently for adult males and coatis in bands. For males, the average number of meters traveled during 5-min observation periods was extrapolated to provide an estimate of the total number of meters traveled per hour. Animals in bands frequently circled around and moved back and forth in a small area, however, so this method could lead to an overestimate of seed dispersal distance for them. Instead, the average straight-line distance between where a day's observation session began and where it ended was divided by the average duration of observation sessions. This latter method was not deemed appropriate for males because their movements could be described as patrolling their home range; a male might travel several kilometers in a roughly circular pattern during an observation session, only to end up less than half a kilometer from where he started.

Results

In late 1995 and early 1996, the period during which the majority of counts of coati bands were obtained, the four bands with radiocollared females contained a total of approximately 250 animals. They occupied an area of 14km^2 , which also encompassed the home ranges of 19 marked males. Based on observations of males accompanying the bands during the mating season and the results of genetic paternity analyses (see Chapter 4), I believe that a minimum of 16 unmarked males also inhabited that area. (Because not all yearling males behaved as adults by following bands during the mating season, there were probably additional solitary males that remained undetected by me.) Using the conservative total of 285 individuals yields a population density estimate of 20 coatis/ km^2 in the study area. The age structure of the population was approximately 25% adults, 25% yearlings, and 50% cubs, which results in a coati biomass estimate of $62.5\text{kg}/\text{km}^2$, based on the mean weights of captured animals in each age class.

Coatis in Tikal were largely insectivorous (see Chapter 2), and during much of my study their primary prey was *Enema endymion*, a large scarab beetle. These beetles were found in the soil or on the forest floor, where, as larvae, they apparently fed on dead leaves. The adult beetles were present mainly in June, and the larvae in August-November. Between August 22 and November 30, 1995, 50% of all food items ($n=583$) consumed by focal coatis during behavioral observations were *E. endymion* larvae. Because these larvae were substantially larger than most other prey, their actual contribution to the diet was much greater than 50%. Focal animals consumed an average of 10 larvae during a day's observations, which resulted in an estimated 60 larvae/coati/day, or $1200\text{larvae}/\text{km}^2/\text{day}$, and a seasonal total of approximately 120,000 larvae/ km^2 consumed by coatis. Coatis did not feed as heavily on the adult beetles, consuming only an estimated 20 beetles/coati/day between May 30 and July 2, 1996.

Coatis were observed eating fruit of more than 30 plant species, but relatively few of them contributed significantly to the diet (Table 1). The amount of fruit in the diet fluctuated greatly throughout the year. From September 1995 through January 1996, a total of three pieces of fruit were consumed by focal animals during behavioral observations. In contrast, in August 1996, an adult male ate 130 *Pimenta dioica* fruits during a morning of focal animal observations, which extrapolates to almost 800 fruits in a day. Sufficient data on consumption rates and fruit production were available to permit calculation of the percent of fruit crop consumed by coatis for six species of trees (Table 2).

Table 1
Species of trees whose fruit formed a major part of the diet of coatis in Tikal

| <u>Family</u> | <u>Species</u> | <u>Common name</u> |
|---------------|---------------------------------|---------------------|
| Arecaceae | <i>Cryosophila stauracantha</i> | escobo |
| | <i>Sabal mauritiiformis</i> | botán, guano |
| Meliaceae | <i>Trichilia moschata</i> | cedrillo rosa |
| Moraceae | <i>Brosimum alicastrum</i> | ramón |
| | <i>Coussapoa oligocephala</i> | ? |
| Myrtaceae | <i>Pimenta dioica</i> | pimienta |
| Piperaceae | <i>Piper</i> spp. | cordoncillo |
| Sapindaceae | <i>Blomia prisca</i> | tzol |
| Sapotaceae | <i>Manilkara zapota</i> | chicozapote |
| | <i>Pouteria reticulata</i> | zapotillo hoja fina |

Table 2
Estimated percentage of total fruit crop of selected tree species consumed by coatis, September 1995 - September 1996

| <u>Species</u> | <u>Number of fruits eaten per km²</u> | <u>Percentage of crop eaten</u> | <u>Seeds swallowed</u> |
|----------------------------|--|---------------------------------|------------------------|
| <i>Trichilia moschata</i> | 89,000 | 12 | no |
| <i>Brosimum alicastrum</i> | 208,000 | 5 | no |
| <i>Pimenta dioica</i> | 189,000 | 3 | yes |
| <i>Blomia prisca</i> | 54,000 | 37 | yes |
| <i>Manilkara zapota</i> | 29,000 | 3 | no |
| <i>Pouteria reticulata</i> | 167,000 | 5 | yes |

Coatis cannot be considered seed dispersers of all the species whose fruit they eat; they swallowed the seeds of only three of the species in Table 2. When eating fruit of the others, they chewed off the pulp and spit the seeds out. Their effectiveness as dispersers of those seeds they do swallow depends on how long the seeds are retained in the digestive tract and how far the coatis have traveled during that time. My combined observations of feeding behavior and fecal content indicated that seeds passed through a coati's digestive tract in 1-3 h. Adult males traveled an estimated 250m/h, so they probably dispersed seeds 250-750m from the parent plant. Coatis in bands traveled an estimated 65m/h, so they could disperse seeds a distance of 65-195m.

Four males and ten females died while they were radiocollared. One male was hit by a car and two others died during the mating season, possibly from injuries sustained in fights with other males (Binczik GA, unpublished data). The rest of the deaths were believed to have been predation events, as the coatis were not observed to be sick or injured before they disappeared; however, I never saw an act of predation. Because I had evidence for additional sources of mortality affecting the males, predation rate was calculated for females only. I had yearling and adult females radiocollared for a total of 355 coati-months, which would be equivalent to having 30 coatis collared for one year. Ten of those females, or 33%, were killed. Observed sex ratios indicated that there were six adult and yearling females per km², so two of them, or approximately 8kg/km², would be taken by predators each year. I believe that many dispersing yearling males must also be taken by predators, creating the female-biased sex ratio, but I was unable to obtain mortality data for them.

Discussion

Population Density and Biomass

My estimate of coati density (20/km²) agrees with the only previously published density estimate for Tikal (Glanz, 1990), although the origin of the latter estimate is unclear. Glanz cited Cant (1977) as the source, but Cant did not provide a density estimate for coatis, nor did he provide sufficient information to calculate one. A recent transect-based study of wildlife populations in Tikal resulted in a density estimate for coatis of 9-10/km² (Polisar et al., 1998). The difference between my estimate and theirs could be due to the difference in methodologies, or it could reflect a higher density of coatis close to the central ruins area, where my study was conducted. A camera-trapping study in Tikal indicated that wildlife densities as a whole were indeed considerably higher close to the central ruins area (Kawanishi, 1995). These density differences could be caused by some avoidance of the central area by top predators, higher densities of fruit-producing trees there as a result of ancient Mayan silviculture, increased availability of food and/or water due to the activities of the humans currently occupying the Park, or the impacts of illegal harvesting in the outer portions of the Park.

There are numerous coati population density estimates available from BCI. Kaufmann (1962) reported that coati densities declined from approximately 40/km² to approximately 25/km² during his study. Later estimates ranged from 24/km² (Glanz, 1982) to over 50/km² (Gompper, 1997; Wright et al., 1994). Estimates reported from other locations include 2/km² in the Chiricahua Mountains of Arizona (Lanning, 1976) and 33/km² in southern Veracruz, Mexico (Coates-Estrada and Estrada, 1986). It seems that coatis are able to attain high densities throughout their range with the exception of the southwestern U.S., which is the very edge of their geographic distribution and doubtless provides only marginally suitable habitat. The relatively low density in Tikal

compared to other tropical sites may be due to the drier climate, higher predation pressure, or both.

The transect data of Polisar et al. (1998) suggest that among medium- to large-bodied terrestrial mammals in Tikal, coatis rank fourth in contribution of biomass (Table 3). If my density estimate were used, however, they would rank second. I know from experience that the distracting effects of many animals scattering through the underbrush make it difficult to estimate accurately how many there are. I suspect that the transect counts seriously underestimated the densities of group-living animals like coatis and peccaries, as Cant (1977) predicted would be the case. Polisar et al. (1998) recognized that this was likely for collared peccaries, and applied a correction factor in coming up with their estimate, but they did not do so for coatis. Because most of the peccary groups I sighted were several times larger than even their adjusted group size, I agree that their counts underestimated this species. Inasmuch as my coati bands were an order of magnitude larger than their reported mean group size of six (see Chapter 2), I believe that their density estimate for coatis needs adjusting also.

Table 3
Biomass estimates for selected medium- and large-bodied terrestrial mammals in Tikal, based on density estimates in Polisar et al. (1998)

| Species | Common name | Mass(kg) ^a | kg/km ² |
|-------------------------------|-------------------------|-----------------------|--------------------|
| <i>Odocoileus virginianus</i> | white-tailed deer | 40.0 | 111 |
| <i>Tayassu tajacu</i> | collared peccary | 17.5 | 52 |
| <i>Mazama americana</i> | red brocket deer | 26.1 | 47 |
| <i>Nasua narica</i> | white-nosed coati | 3.9 | 38 ^b |
| <i>Dasyprocta punctata</i> | Central American agouti | 3.6 | 8.2 |
| <i>Agouti paca</i> | paca | 8.2 | 7.8 |

^aFrom Robinson and Redford (1989).

^bBiomass estimate from this study is 62.5kg/km².

Using Kaufmann's (1962) density estimate of 40 coatis/km², Eisenberg and Thorington (1973) calculated that coatis contributed 2.7% of the total nonvolant

mammalian biomass on BCI, which they estimated at 4431kg/km². Mammalian biomass in Tikal may be more comparable to that in Guatopo National Park, Venezuela, which was estimated at 1500kg/km² (Eisenberg et al., 1979), because rainfall levels and patterns are very similar at the two sites. If it is, then my estimate of coati biomass would mean that coatis represent approximately 4% of the total nonvolant mammalian biomass in Tikal.

Frugivory and Seed Dispersal

Six of the fruit species on which coatis fed most heavily are among the dozen canopy species with the highest densities in Tikal (Schulze and Whitacre, 1999); two others are common understory species. Seed dispersal by coatis has not been studied on BCI. In Santa Rosa National Park, Costa Rica, males and bands were found to disperse seeds an average of 586m and 492m, respectively (Sáenz, 1994).

Frugivory by coatis may be beneficial even to species whose seeds are not swallowed in that it removes the fruit pulp from the seeds, which discourages pathogens (Howe, 1986). *Brosimum alicastrum*, which is not dispersed by coatis, may benefit in yet a different way. *B. alicastrum* seeds are extremely nutritious, and it has been hypothesized that reliance on them as a staple is what permitted the ancient Maya to achieve such high population densities in Tikal (Puleston, 1982). I observed arboreal species that are normally considered frugivorous, such as monkeys and parrots, consuming (and destroying) the seeds of *B. alicastrum* and letting the pulp fall to the ground. By doing the opposite, coatis may be reducing the opportunity for seed predation, leaving more seeds available for germination.

Coatis consumed more than a third of the total fruit crop of *Blomia prisca*. In studies of seed dispersal in the tropics, the proportion of a tree species' fruit crop that was removed by its primary disperser species ranged from 18% to 59% (Howe, 1980;

Howe, 1993; Howe and Vande Kerckhove, 1979). Coatis are probably the primary dispersers of *B. prisca* seeds in Tikal. Interestingly, *B. prisca* is the only upland tree species for which our survey plots produced a much higher density estimate (Binczik GA, unpublished data) than the plots of Schulze and Whitacre (1999), which were distributed over a larger area. If coatis are indeed more abundant around the central ruins area of the Park, perhaps they have increased the density of *B. prisca* in that area as well. Alternatively, it may be that the microhabitat produced by decaying limestone structures is particularly favorable to *B. prisca*, as has been proposed for *Brosimum alicastrum* (Lambert and Arnason, 1982). If that is the case, then coati population levels might be responding to *B. prisca* densities, rather than vice versa.

Blomia prisca seeds are the largest ones that are swallowed by coatis. There seems to be a tendency for some frugivores to selectively spit out large seeds (Corlett and Lucas, 1990; Feer, 1995). By occupying space in the digestive tract, large seeds that are swallowed may limit a frugivore's ability to take full advantage of pulses in fruit abundance. Because the fruiting season observed for *B. prisca* (19 days; Binczik GA, unpublished data) was shorter than that of any of the coatis' other major food sources, this could be a relevant issue. However, the short gut passage time of coatis should enable them to circumvent this problem by returning to a tree for repeated feeding bouts, resting nearby between bouts rather than searching for other food sources. I observed such behavior, as did Kaufmann (1962). I suspect that *B. prisca* fruits, which are extremely juicy, may be as important to coatis for their water content as for their nutritive value, so the seeds may be swallowed to prevent loss of juice while spitting them out. Tikal has no permanent natural bodies of water, and *B. prisca* fruits ripen at the end of the dry season, when females are supporting their new litters entirely through lactation (Binczik GA, unpublished data).

Predation

Jaguars and pumas are probably the only significant predators of adult coatis in Tikal. Valenzuela and Ceballos (2000) reported that five of the 17 coatis they radiocollared in Jalisco, Mexico, were killed by jaguars. Scat analyses at the same study site revealed that coatis were the third most important prey species of jaguars in terms of biomass, and fifth most important for pumas (Núñez et al., 2000). Based on the authors' estimates of cat densities and predation rates, big cats kill 1-1.25 coatis/km²/year at that site. I calculated a minimum predation rate of 2 coatis/km²/year in Tikal. There is no information on coati density at the Jalisco site, but as it receives approximately half as much rainfall as Tikal (Valenzuela and Ceballos, 2000), densities are likely to be lower there than in Tikal.

A study of 52 jaguar and puma scats in southern Campeche, Mexico, approximately 100km north of Tikal, found that coatis were the third most common prey type in the scats (Aranda and Sánchez-Cordero, 1996). Brouck deer and white-tailed deer were lumped together in the analysis, however, and combined, the deer ranked second in frequency, so coatis may have been the second most common species, after collared peccaries, in the scats of the two predators. The authors of that study cited Aranda (1994) as having concluded from a track study that collared peccaries were the most abundant medium- to large-bodied terrestrial mammal species in that area, followed by coatis. Other studies have found that jaguars take prey in proportion to their abundance (Emmons, 1987; Rabinowitz and Nottingham, 1986). Polisar et al. (1998) concluded that coatis were by far the most abundant species of those they surveyed in Tikal, so it seems likely that jaguars and pumas rely even more heavily on coatis in Tikal than they do in Campeche.

Conservation

Due to their high density and functional connections to many other species at a variety of trophic levels, coatis play a major role in the natural processes of the Tikal ecosystem. Unfortunately, they also are quite vulnerable to human-induced mortality.

The northern part of Guatemala, surrounded on three sides by Mexico and Belize, is called the Petén. Although the Petén represents about one third of Guatemala's land area, it has historically been extremely sparsely populated, and physically and culturally remote from the rest of the country (Mahler, 1993). However, that situation is changing. Centuries of ethnically-based inequity in land distribution led to several decades of civil war beginning in the 1950's (Schwartz, 1990). Relative peace finally has been achieved, but refugees, instead of being allowed to return to their fertile highland farms, were relocated to the Petén. Thus, the Petén has become the fastest-growing region in Latin America in terms of human population (The Nature Conservancy, 1993), and the slash-and-burn agriculture associated with population growth has led to massive deforestation (Reining et al., 1992).

Because much of the Petén lies within the Maya Biosphere Reserve (MBR) and is officially off-limits to settlers, and because most of its soil is too poor and thin to support agriculture (Nations et al., 1988), there is enormous pressure for people to make a living off the forest. More than 7000 Peteneros are employed in harvesting three non-timber forest products: *xate* (*Chamaedorea oblongata* and *C. elegans*), *chicle* (*Manilkara zapota*), and allspice (*Pimenta dioica*) (Salafsky et al., 1993). This industry brings in export earnings of approximately \$6 million per year (Nations et al., 1988). Several national and international conservation organizations are promoting the extraction of such products as a way for local people to benefit economically from the forest without destroying it, and numerous studies have been conducted to evaluate the sustainability

and ecological impacts of these activities (Dugelby, 1995; Gould, 1996; McNab, 1999; Reining et al., 1992). Most of these studies examined ecological impacts on the species being harvested, but McNab (1999) studied the impact of hunting by *xate* and *chicle* harvesters on wildlife populations.

Although coatis are considered a relatively undesirable game species, at least in the Petén (McNab, 1999), they are a major food resource for subsistence hunters throughout their range (Jorgenson and Redford, 1993; Redford and Robinson, 1991). Coatis were the mammal most commonly hunted by *xate* and *chicle* harvesters working immediately north of Tikal (McNab, 1999), representing 25% of the individuals and 14% of the biomass harvested. They also were by far the most commonly hunted mammal in a study of subsistence hunting in Quintana Roo, Mexico (Jorgenson, 1998), representing 43% of the individuals and 20% of the biomass. Coatis provided the greatest biomass of any game species in the diet of residents of a village adjacent to Chagres National Park in Panama (Samudio and Samudio, 1995).

McNab (1999) concluded, based on the hunting intensity he observed, that non-timber forest product harvesters are likely to have a high impact on coati population levels throughout the multiple use zone of the MBR. In addition to the subjects of his study, moreover, people involved in harvesting timber and petroleum, as well as the residents of villages within the MBR, contribute to hunting mortality of forest wildlife species. The impact that hunting by villagers can have is illustrated by the results of Polisar et al. (1998), who had a frequency of coati sightings on transects within 11km of the village of Uaxactún (which lies 8km north of the northern border of Tikal) that was <4% of the sighting frequency on Tikal transects. They did not attempt to calculate a population density for coatis around Uaxactún because they had so few sightings. Furthermore, the fact that all of the sightings in the Uaxactún area were of single animals (Polisar et al., 1998) suggests that there may be no resident coati population left in that

area. Subsistence hunting has also greatly reduced or eliminated coati populations in many areas of Mexico (Kaufmann, 1987), and probably in less-studied portions of the species' range as well.

In addition to direct mortality from hunting, human activities may impose substantial indirect effects on coati populations. Two of the coatis' main food species in Tikal, *Manilkara zapota* and *Pimenta dioica*, also figure prominently in the human economy of the region, through harvest and sale of the sap of the former (*chicle*) and the fruit of the latter (allspice). Approximately 1600-1900 men tap *chicle* in the MBR each year (Dugelby, 1998). *Chicle* tapping increases tree mortality and interferes with reproduction, because recently tapped trees do not bear fruit; field surveys of the MBR found fruiting *M. zapota* only in Tikal, where *chicle* tapping is prohibited (Reining et al., 1992). *Chicle* harvesting, therefore, reduces or eliminates a major food resource for coatis and other wildlife. *Chicle* has been harvested commercially in the Petén for more than a century (Schwartz, 1990), but harvesters have become less careful of the trees in recent years (Dugelby, 1998; Reining et al., 1992), so tree mortality and other impacts are undoubtedly increasing.

Allspice is not harvested on as large a scale as *chicle*, but where it is harvested, impacts may be even greater. Harvesters climb trees and cut off secondary branches while the fruit is still green, traditionally leaving one leaf-bearing branch for the health of the tree (Gould, 1996). Harvesting slows growth, increases mortality, and eliminates fruit production for 4 to 6 years (Reining et al., 1992). That food resource also, therefore, is made unavailable to wildlife. Sometimes harvesters fell trees or remove the entire crown (Gould, 1996), and these practices have increased in recent years as well (Gretzinger, 1998; Reining et al., 1992).

Enforcement of laws relating to wildlife and conservation in Guatemala is virtually nonexistent. A 1970 law delineating hunting seasons is completely ignored by

subsistence hunters, as are bans on the hunting of certain species (McNab, 1999).

Offering wild game in restaurants is illegal, but extremely common in the Petén. Not uncommonly, those responsible for upholding the laws, such as military officers or national park administrators, are actually directing operations violating them.

Even in Tikal, the jewel of the system of protected areas, the cessation of formerly regular border patrols has facilitated increasing exploitation of all types. *Xate* and *chicle* harvesters establish camps in the Park and even transport their harvests out on public buses (Polisar et al., 1998). The heavily hunted area (with virtually no coatís) surrounding the village of Uaxactún actually includes the northernmost portion of the Park (Polisar et al., 1998). During a 3-month camera trapping study in 1994, seven cameras were stolen out of the forest (Kawanishi, 1995). Even so, 27 out of 107 photographs recorded by the remaining cameras were of humans, and the majority of those were on the most remote transects, far from any known activities in the Park. These observations support the hypothesis that the trend Kawanishi (1995) reported of higher wildlife densities closer to the central ruins area could be a result of hunting in the more remote areas. In 1996, I saw *chicle* collection and artifact looting within 2km of the Park administration offices, and *xate* harvesting within 1km of the Great Plaza, the most-visited tourist site. Polisar et al. (1998) reported that heavy use by extractionists had rendered their transects nearly useless by 1997, and that the entire Park had become subject to such traffic.

Even if the level of exploitation does not progress to the point of clear-cutting, it seems that the MBR may be on the way to becoming an "empty forest" (Redford, 1992), as is happening in so many other parts of the world. Coatís are a small but important part of the big picture. Reduction in their numbers through human activities will reduce prey availability for jaguars and pumas and may affect forest composition. The fact that such an abundant species in Tikal could be virtually eliminated from an area of 511km²

(Polisar et al., 1998) by a village with only 681 inhabitants (McNab, 1999) should serve as a warning of the fragility of the Tikal ecosystem. Jorgenson and Redford (1993) predicted that hunting by humans in multiple-use reserves would cause declines in jaguar and puma populations as a result of competition for prey species. Both direct and indirect impacts on ecosystem processes of activities such as non-timber forest product extraction need to be evaluated before these activities are promoted as "sustainable development".

The solution to the plight of coatis and other wildlife in Guatemala will have to be political, rather than scientific. There is little governmental will for conservation, but even if there were, no real progress can be made without social reform. As long as the majority of the country's population is living in poverty, powerless and landless, they will continue to exploit the forest out of necessity.

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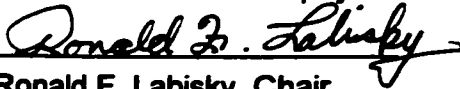
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BIOGRAPHICAL SKETCH

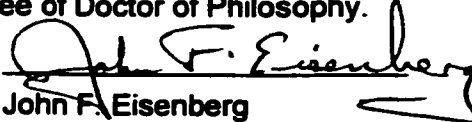
Susan Drummond Booth-Binczik was born on April 11, 1964, at Community-General Hospital of Greater Syracuse in Onondaga, New York. She attended Edward Smith Elementary School, T. Aaron Levy Junior High School, and William Nottingham High School in Syracuse. She then moved to Bethesda, Maryland, where she graduated from Walt Whitman High School in 1981. She received a B.S. in biology from Yale University in 1985 and an M.S. in wildlife conservation from the University of Minnesota in 1991. Her master's thesis research was on chemical communication in tigers.

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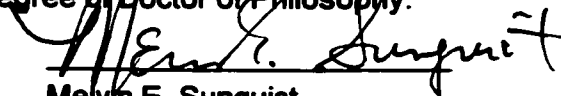
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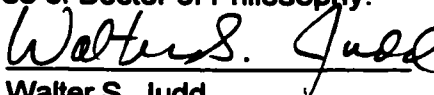
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This dissertation was submitted to the Graduate Faculty of the College of Agricultural and Life Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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