

REPRODUCTIVE BIOLOGY OF A TROPICAL PROCYONID, THE WHITE-NOSED COATI

By

GERALD ALLEN BINCZIK

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I tarried in producing this document, and as a result two of the people I most wanted to share it with did not live to see its completion. I offer my dissertation in their memory...

My mother, Rosemary Binczik

Professor John F. Eisenberg

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Abstract of Dissertation Presented to the Graduate School  
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REPRODUCTIVE BIOLOGY OF A TROPICAL PROCYONID, THE WHITE-NOSED COATI

By

Gerald Allen Binczik

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Chair: Louis J. Guillette, Jr.  
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Some 80% of the world's mammals reside in the tropics, but few—and almost no long-lived—species there have been subjects of reproductive research. This study contributes detailed information on the reproduction of a long-lived procyonid carnivore, the white-nosed coati (*Nasua narica*), in Tikal National Park, Guatemala.

Whereas most tropical mammals display broad reproductive seasonality (*e.g.*, producing offspring within a six-month period) or reproduce year-round, the coati exhibits extraordinarily tight timing in reproductive events. In Tikal mating took place within about two weeks in the middle of the dry season, births occurred in a comparably short period at that season's end, and young emerged from nests and began foraging alongside adults early in the wet season. When the timing of parturition was examined in more detail, the interquartile range (*i.e.*, middle 50%) for females from three social groups spanned only five and six days in consecutive years, and the mean birthdates in those years differed by only six days. The male coati has responded to reliable clustering of female receptivity by evolving a rut more akin to that of many ungulate species than to the pattern of any other carnivore species yet examined.

Coati reproduction is timed such that the young are weaned over an extended period coincident with the season of greatest food availability. Leaf litter invertebrates and fruits figure prominently in the coati diet, but the former are evidently most important. Notable among these are insects, and in Tikal especially the scarab beetle *Enema endymion*; adults and larvae of this one species accounted for 8.6% of all invertebrates consumed by coatis over the course of this study. Communal care and predator swamping were explored as alternative explanations for the coati's remarkable reproductive pattern, but these hypotheses were rejected.

Exactly how the coati achieves such tight reproductive seasonality remains unknown, but a prediction based on the hypothesis that sociality plays a role was upheld. Social cues exchanged among associates are presumably used by the coati to augment the weak environmental cues (*e.g.*, photoperiod) upon which seasonally reproducing tropical species must otherwise rely.

## CHAPTER 1 BACKGROUND

Although the white-nosed coati (*Nasua narica*) is a wide-ranging, locally abundant and readily habituated diurnal carnivore, the most detailed studies to date have been of a single island population. The majority of what is known and believed about coati ecology and reproduction is based upon extensive behavioral observations by Kaufmann (1962), Russell (1979) and most recently Gompper (1994) of a small group of animals on Barro Colorado Island (BCI), Panama.

The species is primarily insectivorous/frugivorous (Kaufmann, 1962), with some small vertebrates taken opportunistically. Adult females are highly social, living with their immature offspring in cohesive bands most of the year (except for a brief nesting period encompassing birth and early lactation), and adult males are chiefly solitary (Kaufmann, 1962; Booth-Binczik, 2001). Russell (1982; 1983) reviewed various hypotheses put forth to explain female sociality, and asserted that it functions to protect juveniles from predation, most notably by cannibalistic adult males (see also Russell, 1981), and ectoparasitism. Gompper (1996), however, concluded that group living is a way for females to increase their foraging success on patchy resources, whereas several studies at other sites have provided evidence that group living in coatis is an anti-predator adaptation (Burger and Gochfeld, 1992; Booth-Binczik, 2001; Hass and Valenzuela, 2002).

The coati has received considerable attention for its unusual social system, but it is even more notable among tropical mammals for its remarkable degree of reproductive seasonality. Kaufmann (1962) and Russell (1982) addressed the timing of coati reproduction on BCI. The species displays a strongly seasonal pattern at this locale, with apparently only one finely timed birth period per year. The proportion of adult females reproducing can vary dramatically from year to year; they are capable of delaying their first reproduction (which usually occurs at two

years of age) by one or two years, perhaps due to food availability, but generally reproduce every year thereafter. Males mature later than females, and most probably do not reproduce until one or two years after their first opportunity. It is unclear whether reproductive senescence occurs, but Kaufmann (1962) observed one and Russell (1982) two older females (estimated to be at least seven years of age) that did not produce young. Animals have lived to be more than 17 years old in captivity; Poglayen-Neuwall, 1990.

A few reports (*e.g.*, Gilbert, 1973; Hass, 2002 for Arizona; Valenzuela and Ceballos, 2000 for Jalisco, Mexico) suggest that coati reproduction may be patterned similarly at other locations as well, but these have not been confirmed by thorough study. Moreover, even the abundant behavioral/spatial ecological data for BCI fall short of satisfying the lack of basic knowledge about coati reproductive biology. Many questions remain: Does the portrait described for BCI apply elsewhere in the species' range? Where it is seasonal, is this largely tropical mammal pursuing an obligate or facultative (*i.e.*, opportunistic) strategy? What evolutionary pressures drive seasonality, and what environmental cues are used in timing it?

This study addresses these questions by extending beyond prior research in four important ways. It is the first intensive study of reproductive patterns in any coati population, focusing on animals at a site that is distant from but ecologically similar to BCI. It is also the first to examine male reproductive biology at any level. A much greater level of detail is presented on certain environmental stresses confronting the coati with an eye toward resolving specific issues left ambiguous by previous workers. Perhaps most important, this research provides the first information on the reproductive physiology of the species.

The focus of the study is the free-ranging coatis in Tikal National Park, Guatemala. The Park protects approximately 600 km<sup>2</sup> of tropical moist forest in the seasonally dry "Mayan" forest of northeastern Petén, and constitutes the centerpiece of Central America's largest remaining tract of lowland rainforest (Nations *et al.*, 1988). Unlike BCI (Willis, 1974; Glanz, 1982; Robinson, 1999) where ecological conditions could be considered somewhat artificial (Willis, 1974;

Eisenberg *et al.*, 1979; Terborgh and Winter, 1980), Tikal retains a full complement of large predatory species. The disagreement among studies regarding the adaptive value of coati group living provides an example of the risks of extrapolating from data obtained on BCI to the species as a whole. Studies at sites such as Tikal should be more useful for identifying selective pressures important in coati evolution.

## CHAPTER 2 REPRODUCTIVE SEASONALITY

### **Introduction**

Mammals display two basic patterns in the timing of their reproduction (Bronson, 1989): opportunism, in which they reproduce as often as conditions permit, and obligate seasonality, in which one or more predictable environmental factors in combination with other life history aspects compel them to follow a seasonal reproductive schedule. Evolutionarily, these are better thought of as tendencies than rigid choices, and a single species may employ both strategies under different conditions (*e.g.*, the purple-faced langur, *Presbytis senex*; Rudran, 1973).

Obligate seasonality appears to be the strategy adopted by most long-lived mammals (*i.e.*, those with lifespans of more than one year) inhabiting seasonal environments, especially species with a substantial investment per offspring, specialized diet or extreme seasonal survival mechanism such as migration or hibernation (Bronson, 1989). Ovarian function in such species is regulated by the appearance of reliable proximate cues—especially photoperiodic changes—thereby setting a schedule for sexual receptivity, ovulation and/or embryonic development. The most environmentally sensitive phase of the species' reproductive pattern is timed to coincide with the most favorable conditions for offspring survival (Lancaster and Lee, 1965; Sadleir, 1969).

Ultimate factors postulated to account for mammalian reproductive seasonality (summarized in Sadleir, 1969; Bronson, 1989; Di Bitetti and Janson, 2000) include food availability (both in terms of energy and essential nutrients), rainfall, ambient temperature, predation pressure and competition. Of these, food availability (most notably energy intake) is widely believed to be the strongest determinant of seasonality; other factors may modify a pattern but are considered unlikely to override it (Bronson and Heideman, 1994).

There is an obvious logic to seasonal reproductive patterns among mammals at temperate latitudes, where annual fluctuations in insolation profoundly affect temperature and the availability of free water, factors critical at the base of essentially all food chains. But strong seasonal weather patterns, particularly in rainfall, can also promote reproductive seasonality in the tropics (Bronson, 1985). Tropical rainfall patterns have pronounced effects on the abundance of all manner of terrestrial and arboreal food items, and climatic fluctuations could conceivably also affect competition, predation and/or parasitism pressures on a tropical species. Unfortunately, despite the fact that some 80% of all mammalian species reside in the tropics, relatively few species and very few locations in the lower latitudes have thus far been examined (O'Brien, 1993; Bronson and Heideman, 1994; Dubost *et al.*, 2005).

In this respect, the lowlands of the Panama Canal Zone may have received more attention than any other tropical site. In his review of the literature, Fleming (1973) found that half of the species studied at this locality (23 of 45) were known to be seasonal breeders, with a strong tendency toward birth or weaning occurring at the beginning of the wet season. This pattern is exemplified by the region's best-studied carnivore, the white-nosed coati (*Nasua narica*).

Observations by Kaufmann (1962) and Russell (1979; 1982) indicate that coati reproduction on Barro Colorado Island (BCI), Panama, is strongly seasonal: mating activity there appears to take place early in the four-month dry season, litters are born late in that same season, and young emerge from the nest and are gradually weaned beginning early in the eight-month wet season. Scattered observations suggest reproductive events may also be seasonal at other sites (*e.g.*, southern Arizona: Gilbert, 1973; Hass and Roback, 2000; Costa Rica: Sáenz, 1994).

Fruit and leaf litter invertebrates are the principal foods of coatis on BCI (Kaufmann, 1962; Russell, 1982; Gompper, 1996) and elsewhere (Delibes *et al.*, 1989; Sáenz, 1994). Smythe (1970) examined fruit-fall on BCI in correlation with Kaufmann's (1962) data on coati life history stages and concluded that the period encompassing parturition and first emergence of young from their nests matches the time of greatest fruit supply. Russell (1982) compared coati

intake rates of fruit and animals, and concluded that reproduction is timed to allow juveniles to begin foraging at the onset of a long-lasting peak in the availability of invertebrate prey; he believed the concurrent availability of a major fruit crop was "perhaps fortuitous" (p. 428).

This discrepancy stems from the fact that on BCI the seasonal peak in size and abundance of forest floor arthropods (at the onset of the wet season; Levings and Windsor, 1982) overlaps substantially with one of two annual peaks in fruit availability (Foster, 1982b). Fruit availability in neotropical forests often peaks at the onset of the wet season (van Schaik *et al.*, 1993; Sakai, 2001). As arthropod abundance in tropical forests commonly varies positively with moisture levels (Levings and Windsor, 1984; Burgess *et al.*, 1999), such overlap is likely widespread.

Tikal National Park, Guatemala, is similar to BCI in that it is characterized by fairly uniform temperatures and strongly seasonal rainfall (Fig. 2-1); there is a marked four-month dry season from January through April and a six-month wet season from June through November, with May and December being transitional periods. In contrast to BCI, however, the forests of northern Guatemala are believed to have been significantly altered by the ancient Maya (Lundell, 1937; Puleston, 1982), whose horticultural practices likely favored species which produce plentiful, nutritious fruit and tend to do so at what would otherwise be times of scarcity. For example, the highly nutritious *Brosimum alicastrum* (*ramón*, a.k.a. breadnut), a tree which has been reported to undergo three heavy, evenly-spaced fruit sets per year (February-March, June-July and October-November; Puleston, 1968; in Coelho *et al.*, 1976), is unusually dense throughout the region (Lundell, 1937; Puleston, 1982).

Given the above, it was anticipated that coati reproduction in Tikal would be highly seasonal as it appears to be elsewhere, but that Mayan efforts there might have resulted in sufficient temporal separation between peaks in fruit and invertebrate abundance to aid in determining the relative importance of these foods to the timing of coati reproduction. Even if peak overlap was found to occur in Tikal, it was believed that a more rigorous exploration of

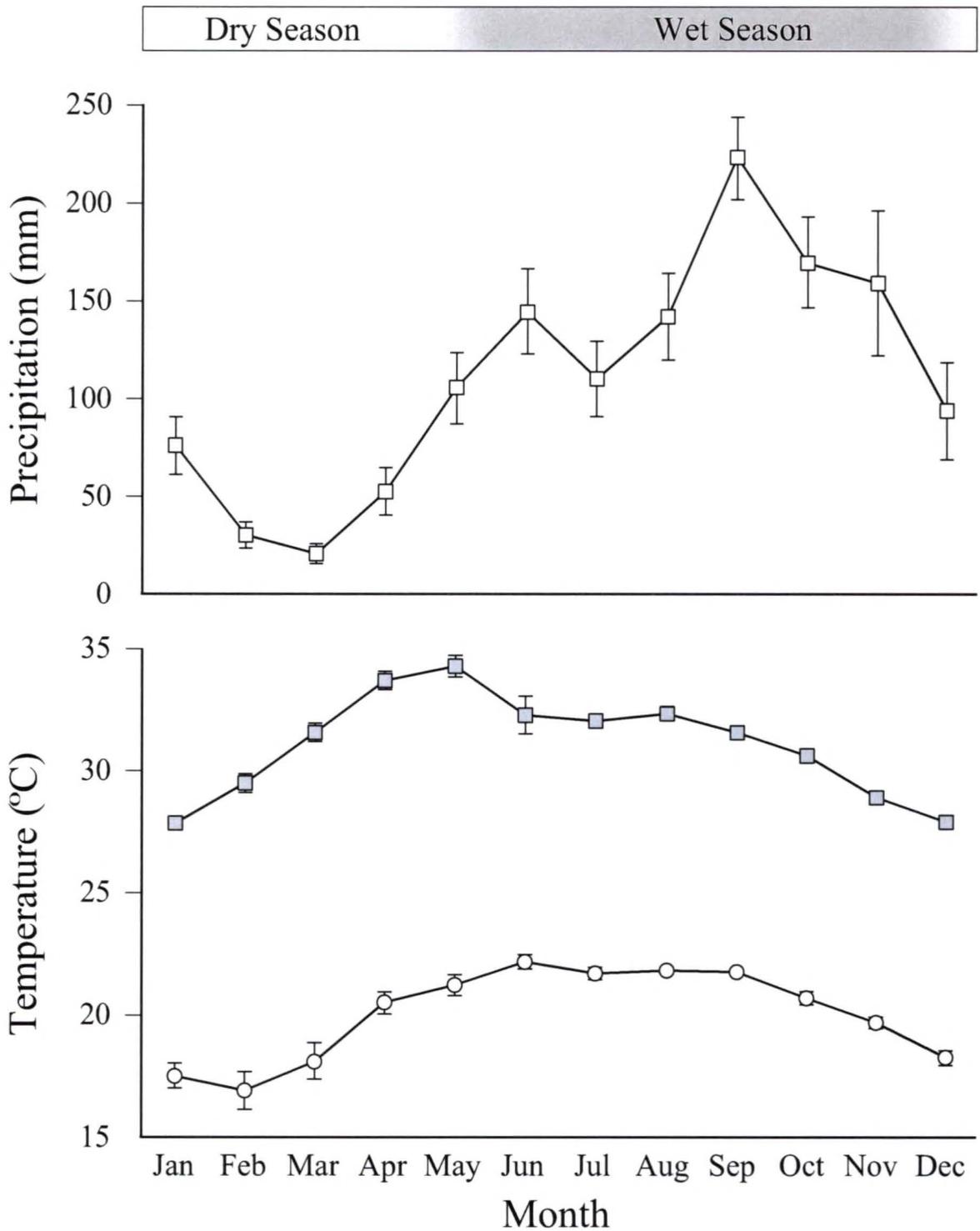


Figure 2-1. Mean ( $\pm$  SEM) monthly rainfall and maximum (filled squares) and minimum (open circles) temperature in Tikal National Park, Guatemala, January 1984 through April 1998. Number of years contributing to each mean ranges from 10 to 13 depending on availability of complete month's data from the Instituto de Sismología, Vulcanología, Meteorología e Hidrología (Guatemala City, Guatemala).

coati foraging habits accompanied by consideration of nutritional matters might clarify this issue.

The purpose of the present study was therefore twofold:

1. Coati reproductive phenological events were monitored year-round at Tikal to document—and provide greater detail on—the species' reproductive seasonality at this new tropical forest site.

2. The abundance and quality of potential coati food items and also coati foraging behavior and body condition were monitored year-round to clarify the relationship between the species' reproductive pattern and food availability.

### **Methods**

Free-ranging white-nosed coatis were studied from June 1994 into November 1996 over an area of approximately 20 km<sup>2</sup> at the center of Tikal National Park (17°N, 89°W). The Park protects nearly 600 km<sup>2</sup> of forest that has at various times been identified as subtropical moist or tropical semi-deciduous (Schulze and Whitacre, 1999; based on the classification schemes of Holdridge *et al.*, 1971, and Pennington and Sarukhan, 1968, respectively), tropical dry (Walker and Cant, 1977; based on Holdridge, 1957), and quasi-rainforest (Lundell, 1937). Total annual rainfall averages 1285 ± 80 mm (based on the eight complete years of data between 1984 and 1998 available from the Instituto de Sismología, Vulcanología, Meteorología e Hidrología, Guatemala City, Guatemala). Located in the "Mayan" (*i.e.*, ancient Maya-modified; J.F. Eisenberg, pers. comm.) forest of northeastern Petén, Tikal constitutes the centerpiece of Central America's largest remaining tract of lowland rainforest and retains a full complement of the region's wildlife species (Nations *et al.*, 1988).

Rainfall in the park during the study was recorded at a uniform time daily via a government-operated weather station. From these data monthly totals were calculated for comparison to various phenological data.

Fifty-five adult female coatis resident to four bands (females of this species live in groups with their maturing young except to nest, whereas males are largely solitary; Kaufmann, 1962)

were utilized in this study. Animals were initially captured by live-trap or (more often) blowgun and chemically immobilized by intramuscular injection of approximately 7 mg/kg Telazol (Fort Dodge Laboratories Inc., Fort Dodge, IA). Anesthetized animals were tattooed and eartagged for identification, weighed, visually examined to determine general physical condition and measured as described below. Forty-three of the coatis were additionally fitted with 90 g motion-sensitive radiocollars (Advanced Telemetry Systems, Isanti, MN) to enable subsequent location and recapture, and to confirm death if such occurred. Individual females were recaptured by blowgun (never more often than monthly) for resampling; the average number of immobilizations per female was  $2.6 \pm 0.2$ . All animal handling procedures were conducted as per protocol #4084 approved by the University of Florida's Institutional Animal Care and Use Committee.

In order to monitor reproductive state, size indices for the vulva and right anteriormost teat were obtained during each female's immobilization. For each body part, the longest dimension ( $L$ ), the widest perpendicular dimension ( $W$ ) and the highest dimension above the surrounding body surface ( $H$ ) were measured to the nearest 0.1 mm via calipers and then combined in the formula  $V = L \times W \times H$  to produce an approximation of volume. One person was responsible for taking these measurements throughout the study. Indications of pregnancy and lactation were also noted. (Originally serum and fecal reproductive steroids were to be monitored as well, but samples obtained for this purpose were rendered useless by a catastrophic freezer failure after fieldwork was completed and before radioimmunoassays could be conducted.)

As a measure of body condition, an index of each coati's body fat level was also determined at the time of immobilization. Following Hossler *et al.* (1994), a fold of the animal's skin (*i.e.*, excluding muscle) was pinched at the back of each rear leg midway between knee and hip, and calipers were used to measure the thickness of this fold to the nearest 0.1 mm. Measurements for the left and right thighs were averaged to produce the index reported for that coati/immobilization. One person took all such measurements throughout the study.

The animals in three coati bands were habituated to the close presence of investigators, who simply visited the bands frequently over several weeks and briefly baited the coaties at the beginning of each encounter until the animals allowed themselves to be accompanied (without additional feeding) for several hours thereafter. By the end of the habituation period it was possible to follow animals so closely that at times investigators had to be careful not to kick or step on them, and sometimes the coaties even had to be gently shooed a short distance away to allow investigators sufficient room to process immobilized animals during captures.

Thereafter, the reproductive activities of habituated females were monitored *ad libitum* (Altmann, 1974) one to three times per week (as often as their bands were visited) during the period of detailed behavioral observations (see below) or as close to daily as possible during periods of particular interest. Data on six reproductive phenomena were recorded.

**Copulation** was either directly observed or presumed based on the presence of mating wounds (see Results for description of latter).

**Pregnancy** was generally identified by the midpoint of gestation, when an increase in a female's girth became visually apparent.

**Nesting** was defined as beginning when a female departed from its band prior to giving birth, and ending when the infants first accompanied the female down from the nest.

**Parturition** was determined to have occurred when a female showed a sudden pronounced reduction in girth followed by continued nesting behavior, and was ultimately confirmed by observation of young still in the nest or shortly after their emergence from the nest.

**Reaggregation** was operationally defined as the rejoining of a postpartum female and its young with at least three other such females and their young.

**Nursing** was either directly observed or inferred from evidence of lactation noted during a female's immobilization.

During nesting, 20 nest trees were climbed and nests examined to verify the presence and count the number of young. Ages at which young were examined varied from approximately one

to five weeks after birth, depending on when nests were initially located and how soon thereafter opportunities occurred to examine the nests without the females nearby.

Systematic observations of female coati foraging behavior were conducted from August 1995 through September 1996. Observation sessions were scheduled two to three times per week, and in each case began as soon after first light as the target animals could be located (typically by 08:30) and continued for several (typically four) hours thereafter. All-day (up to 10 hr) observation sessions were conducted once each month to confirm that activity patterns did not change such that mornings were no longer appropriate for monitoring normal foraging behavior. In each session, one 5-minute block of focal animal sampling (Altmann, 1974) was conducted each quarter hour, rotating through focal animals opportunistically selected for that session; during the nesting period each session instead focused on a single female (reducing sample sizes during this period). In the selection of target animals for systematic behavioral observations, priority was placed on distributing observation effort across females without respect to their band membership, such that no individual coati served as a focal animal in more than one block per hour (except in the nesting period), nor in more than one session per week.

During each sampling block, the amounts of time spent by the focal animal foraging in, under and away from potentially relevant fruiting trees were recorded. Also recorded were the type and number of food items consumed in each of these three areas, as well as the time spent consuming the items; foraging time and time of food consumption were mutually exclusive categories. The identities of animal prey were determined to the lowest taxonomic levels possible, and fruits eaten were identified to species.

As bases for calculating monthly rates of foraging success, the three foraging areas were used thus: The leaf litter invertebrate zone was the combination of under and away from fruiting trees. The fruit zone was the combination of in and under fruiting trees. A given female's monthly foraging success rates were then calculated as both number of items consumed per minute foraging and number of seconds spent consuming the items per minute foraging, using

monthly totals for each zone. To eliminate evident outliers caused by undersampling of specific individuals in specific months, females with fewer than 300 seconds spent foraging in a leaf litter invertebrate zone or 20 seconds in a fruit zone in a given month were not included in analyses; the monthly rates for the remaining females were averaged to produce the reported values.

Leaf litter and associated invertebrates were sampled on approximately the 5<sup>th</sup>, 15<sup>th</sup> and 25<sup>th</sup> of each month from September 1995 through September 1996. On each collection date 10 samples were obtained. Each sample was collected by placing a bottomless tub, the area of which was 1 m<sup>2</sup>, on the forest floor and quickly scooping the litter and invertebrates therein into a bag; the soil thus cleared was then dug to a depth of three to four inches (as the substrate allowed) and any additional animals found thereby were added to the bag. Exact sample locations and times were determined by accompanying a foraging band of coatis for two to four morning hours and placing the tub at the front edge of the band at random intervals (skipping any preselected times at which the animals were not foraging).

Each sample bag was weighed fresh and then hand-sifted to harvest visible invertebrates. Animals thus obtained were identified to the lowest practical taxonomic level and weighed to the nearest 0.1 g; animals individually weighing less than 0.1 g were grouped by type and the total weight for the group was used to calculate an average weight per individual. Voucher specimens were occasionally preserved to aid species identifications, but otherwise invertebrates were bagged by sample date and then frozen in liquid nitrogen and stored in an ultracold freezer for subsequent nutritional analyses (see below). Finally, each sample's leaf litter was dried in the sun for a minimum of two days (or more, as weather dictated) and again weighed to obtain dry litter mass and litter moisture content. Monthly means were calculated for total invertebrate mass, litter mass and litter moisture content. The individual contributions of various invertebrate classes to monthly totals were examined by calculating their monthly numbers and masses on a percentage basis.

Fruiting tree phenology was monitored from June 1995 through September 1996. Ten 10 m x 50 m plots were established at random intervals along 1 km of (and also at random directions and distances up to 50 m from) each of three forest paths traversing the entire home range of one coati band as well as parts of the ranges of three other bands. In each plot, all trees measuring at least 10 cm diameter at breast height at the onset of data collection were tagged and identified to species. Every month, each plot was randomly assigned to a group of 10 which was then surveyed on approximately the 5<sup>th</sup>, 15<sup>th</sup> or 25<sup>th</sup> of that month. During surveys, tagged plants were checked for the presence and percentage of immature and ripe fruit, and when fruit was present in a tree it was quantified via the visual count method (Chapman *et al.*, 1992). Samples of ripe fruits were also collected to aid species identifications and frozen/stored as described for invertebrates to provide material for later nutritional analyses (see below). One person was responsible for determining fruit counts and percent ripe fruit in almost all months; a second person trained under and performed calibration runs with the first person repeatedly throughout the study before replacing the first person in the final month.

Using the above methodology, data were obtained on many more tree species than appeared in the coati diet. Only those species which were ultimately seen being eaten by coatis and/or appeared in their scat on at least 15 separate dates were selected for analysis and presentation in this paper. The percentage of trees with fruit and the mean number of fruits and ripe fruits per tree were calculated on a monthly basis for each of these species.

After field work was completed, proximate nutritional analyses were conducted on monthly (*i.e.*, mixed) leaf litter invertebrate collections and also on individual invertebrate and fruit species deemed of particular relevance to the coati diet (as described above). Each sample, consisting of either whole invertebrates or the edible portions of fruits, was first thawed, weighed, dried for two days at 60°C, allowed to equilibrate to room temperature overnight before being weighed again, then finely ground and homogenized by use of a Wiley Mini-Mill equipped with a 20-mesh Monel screen (both Thomas Scientific, Swedesboro, NJ) prior to additional processing.

Crude fat and energy content were determined in nutrition laboratories of the University of Florida's Animal Science Department following procedures outlined in Helrich (1990). To obtain crude fat, samples were weighed, dried 3 hr at 102°C, equilibrated to room temperature under desiccation and then extracted four times in ethyl ether using a Soxhlet apparatus. Extracted samples were subsequently dried 12 hr at 102°C before being equilibrated under desiccation and weighed once more; the amount of fat was calculated as the difference in mass between pre- and post-extraction samples. Energy content was obtained by bomb calorimetry using a 1261 Isoperol Calorimeter (Parr Instrument Co., Moline, IL) after samples had been weighed into crucibles, dried at 65°C for 24 hr, equilibrated under desiccation and weighed again.

Crude protein, ash-free neutral detergent fiber (NDF<sub>af</sub>) and ash content were determined in the Forage Evaluation Support Laboratory of the University of Florida's Agronomy Department. Samples were first weighed, dried for 15 hr at 105°C and weighed again, and then organic matter was determined by ashing for at least 4 hr at 500°C. Total nitrogen (N), and from it crude protein (as N × 6.25), was obtained by a modification of the standard Kjeldahl procedure (Helrich, 1990). Samples were digested using a modification of the aluminum block digestion procedure by Gallaher *et al.* (1975); sample weight was 0.25 g, the catalyst used was 1.5 g of 9:1 K<sub>2</sub>SO<sub>4</sub>:CuSO<sub>4</sub>, and digestion was conducted for at least 4 hr at 375°C using 6 ml of H<sub>2</sub>SO<sub>4</sub> and 2 ml H<sub>2</sub>O<sub>2</sub>. Digestate nitrogen was then determined by semiautomated colorimetry (Hambleton, 1977) via a Technicon Autoanalyzer (Technicon Instruments Corp., Tarrytown, NY). Neutral detergent fiber (NDF) was determined by the procedure of Golding *et al.* (1985), consisting of boiling 1 g of sample in a neutral detergent solution for 1 hr, filtering, extracting with acetone and then drying; NDF<sub>af</sub> was obtained by correcting NDF for the amount of ash in the sample.

The moisture content of an initial sample was calculated by combining the results of the relevant drying steps outlined above. Crude protein, crude fat, NDF<sub>af</sub>, ash and energy content were calculated on a dry matter basis. (It must be noted that the invertebrate and fruit samples were subjected to the same storage freezer failure as were frozen serum and fecal samples,

although unlike the latter samples they appeared to take little or no harm from it. This topic is addressed further in the Discussion.)

Sokal and Rohlf (1981) guided all statistical efforts, and SPSS 8.0 (SPSS, Inc., Chicago, IL) aided computations. Correlational analyses were conducted to examine the relationships between environmental variables, resource availability and foraging behavior. Pearson correlations ( $r$ ) were tested where scatterplots of the data appeared consistent with bivariate normality, and Spearman rank correlations ( $\rho$ ) were instead tested where this assumption appeared to be violated or where samples were deemed too small for proper visual evaluation. Because multiple comparisons were involved and there are numerous arguments against the more elaborate methods that are often employed to adjust for such comparisons (Moran, 2003), a conservative  $P_{\alpha} \leq 0.01$  was adopted as the level of significance.

## Results

Ordinarily each female underwent only one complete reproductive cycle (*i.e.*, succeeding at least to the point of rejoining a band with recently born young in tow) each year, but rarely a female underwent a second cycle if pregnancy, nesting or early emergence was unsuccessful. Accordingly and unless otherwise indicated, the following data pertain only to females' lone/first yearly cycles.

Part or all of 11 copulatory events were observed; three of these (in two coati bands) occurred from 13 to 16 February 1995, and eight (in four bands) from 14 to 28 February 1996. Another 40 females (in four bands) were presumed to have copulated from 13 to 27 February 1996 based on the appearance of fresh mating wounds (see below).

In each of the three copulatory events observed in entirety, the female initiated mating by leaving its band foraging on the ground, approaching one of the males perched in the tree canopy above the foraging band (see Booth-Binczik *et al.*, 2004, for a detailed description of the coati mating system in Tikal) and standing beside the male with hindquarters oriented toward the male

and tail bent upward and to the side. The male briefly sniffed at and then mounted the female, clasped its forelegs around the female's midbody and presumably intromitted (intromission could not be visually confirmed). In all observed copulatory events, coitus included bouts of rapid, quivery thrusting alternating with bouts of apparent stillness by the male, accompanied throughout by soft grunting or panting. It often appeared as if the female was attempting to leave during the longer moments of copulatory stillness but was held fast by the male. Typically the female ultimately broke free from the grip of the male's claws during such a bout—leaving long, deep parallel scratches on the sides of the female's body in the process—then turned on the male with loud squealing vocalizations and feinted or actual bites and paw swipes (events occurred too rapidly to confirm the extent of physical contact) before fleeing down or even falling from the tree and racing back to its band. On one occasion the female was instead simply released by the male, walked away and then lay down and rested on the tree limb about a meter from where the male remained perched. Complete copulations lasted 16, 19 and 48 minutes from intromission until separation, although it should be noted that the first of these was concluded by the male in coitus being attacked by another male (Booth-Binczik *et al.*, 2004). The eight copulations already underway when first observed continued for 2-29 minutes thereafter.

Eleven pregnant females (from two bands) were confirmed to have established nests in 1995, and 28 (from four bands) in 1996. In 1995, the first of these females that was observed to depart its band to begin nesting did so on 12 April and the last did so on 24 April. In 1996 the onset of nesting among females under observation ranged from 12 April to 30 April.

In almost every case a nest was occupied by a solitary female, but on three occasions it appeared that pairs of females shared a nest at least temporarily. Nests were usually situated in large, living trees, either in their crotches or in tangles of lianas hanging free from or lying against their trunks, at a measured height of 9.8-30.2 m above the ground. They were constructed primarily of interwoven slender, leafy branches and vines bitten off of living plants. Nests varied in size and shape; most often they were approximately 0.5-0.7 m-diameter hollow spheres with

one or two entrances just large enough to accommodate a female, but occasionally they were much more simply constructed open bowls/platforms up to about 1.5 m in diameter. In any event the nest cavities/floors were lined with approximately 5-20 cm-deep carpets of small loose leaves, tiny branches and bromeliad tufts into which the infants burrowed.

Females often stayed out of sight in their nests for a few to several days surrounding parturition, making precise dates of birth seldom identifiable and in turn likely resulting in an overestimate of birth period duration. Bearing that in mind, the earliest and latest that parturition could have occurred among nine nesting females (from two bands) in 1995 were 16 April and 29 April, respectively, and 23 females (from two bands) gave birth in 1996 from 22 April to 9 May. Despite the fact that a substantial effort was made to pinpoint the timing of reproductive events, copulation and parturition could both be narrowed down to reasonably tight spans of time for only one female; it gave birth 71 to 74 days after mating. For 18 litters examined while still in the nest, average litter size was  $4.0 \pm 0.3$ .

Late in the nesting period it was common for a female to move its young from one nest to another, but the infants were not considered to have emerged (and the female to have concluded nesting) until they followed their dam down to the ground and began foraging; thereafter the female was rarely seen on foraging excursions without its young alongside. Eight females (from two bands) brought their young down from the nest 27 May to 4 June 1995, and 15 (from four bands) did so from 23 May to 19 June 1996. The process of reaggregation began so soon after emergence that it was possible on only three occasions to determine with certainty how many young individual females emerged with; these females (the nests of which had not been examined) brought down four, five and six young.

Complete band reintegration was in some instances a lengthy process even though females with infants reaggregated into small groups rapidly after nesting. The earliest and latest points at which any of 14 females (from two bands) reaggregated in 1995 were 5 June and 29 June, respectively, and 20 females (from two bands) reaggregated from 31 May to 19 June 1996.

Nursing was almost never observed, presumably because it most often occurred in various tree canopy roosts used by the coatis for taking brief siestas during the day and sleeping at night. Incidences of nursing on the ground (in brush piles) were seen on 4 August 1995 and 27 July 1996. On 13 September 1996 a female was observed evading attempts by an infant to suckle, and twice on 27 September 1996 (in a single band) infants were observed investigating but not suckling from females' teats, suggesting that nursing concluded in the middle or last half of this month.

Three females (in two bands) in 1995 and one in 1996 underwent interrupted reproductive cycles followed by second, successful cycles; one more female in 1995 was believed to be in the midst of a second cycle when initially encountered, and another female in 1995 died while nesting in a second cycle. It was never possible to identify the specific cause(s) of reproductive failure, but information on the point at which it was evident may be instructive. Females returned to their bands (presumably soon) after reproductive failure, and dates on which this phenomenon was observed were 30 April 1995 (*i.e.*, at the end of the observed parturition period) for three females, 23 May 1996 (late in the nesting period), and on or shortly after 5 June 1995 (soon after reaggregating with several other females; the exact date could not be identified because it quickly became unclear which young belonged to which females).

Although much less information was obtained on second cycles, they appeared to proceed similarly to lone/first cycles. Late mating was not observed. Pregnant females departed their bands to nest from 30 July to 18 August 1995 and by 7 August 1996. Parturition could be narrowly attributed for only one female, on or shortly before 12 August 1996; this animal's litter contained four young when it was examined while still in the nest on 5 September. Females concluded nesting and rejoined their bands from 3 September to 6 October 1995 and by 20 September 1996. The 1996 female brought to its band all four offspring that had been found in the nest; three other second-cycling females brought one, one and two young to their bands.

Nursing by females undergoing second cycles was observed on 13 November 1995 and 24 September and 8 November 1996.

Reproductive morphometric changes exhibited by females throughout the study (Fig. 2-2) were revealing of physiological events underlying the coati reproductive cycle despite the unfortunate lack of hormonal data (see Methods). Sudden, pronounced vulval swelling—presumably an estrogenic effect—was observed in immobilized females from 7 February to 19 February, *i.e.*, beginning shortly before the mating period and ending about midway through that period; a much smaller secondary increase in vulva size occurred in late March to early April, within a couple of weeks before parturition and roughly coincident with the beginning of a prolonged increase in teat size. Teat size—presumably reflecting estrogen, progesterone and prolactin levels in turn—rose fairly rapidly from March through the parturition period to a peak in late May to early June, then declined more slowly until it again reached baseline around the end of September, about the same time that lactation/nursing apparently concluded. (Note: The greatest teat size observed in the study actually occurred on 5 September, but this data point was unique in that it belonged to a female that was in the midst of a second reproductive cycle and therefore out of step with its cohorts.)

The amount of leaf litter varied seasonally in strong positive correlation to rainfall ( $r_{[11]} = 0.81, P = 0.001$ ), as did the overall mass of litter invertebrates (Table 2-1), falling from highs at the onset of sample collection in September 1995 to lows in February and March 1996 before rising again to moderately elevated levels that essentially held steady from June 1996 until the conclusion of sample collection in September 1996 (Fig. 2-3). Leaf litter moisture content (Fig. 2-3) varied less from month to month, and although it too resembled the rainfall pattern in some ways (*e.g.*, rising gradually from a low reached in March 1996), the correlation between these was not significant ( $r_{[11]} = 0.41, P = 0.17$ ). Rainfall over the course of sample collection (Fig. 2-3) resembled the typical year (Fig. 2-1) except that rains were somewhat heavier than usual in the middle of the 1995 wet season and unusually light in the middle of the 1996 wet season.

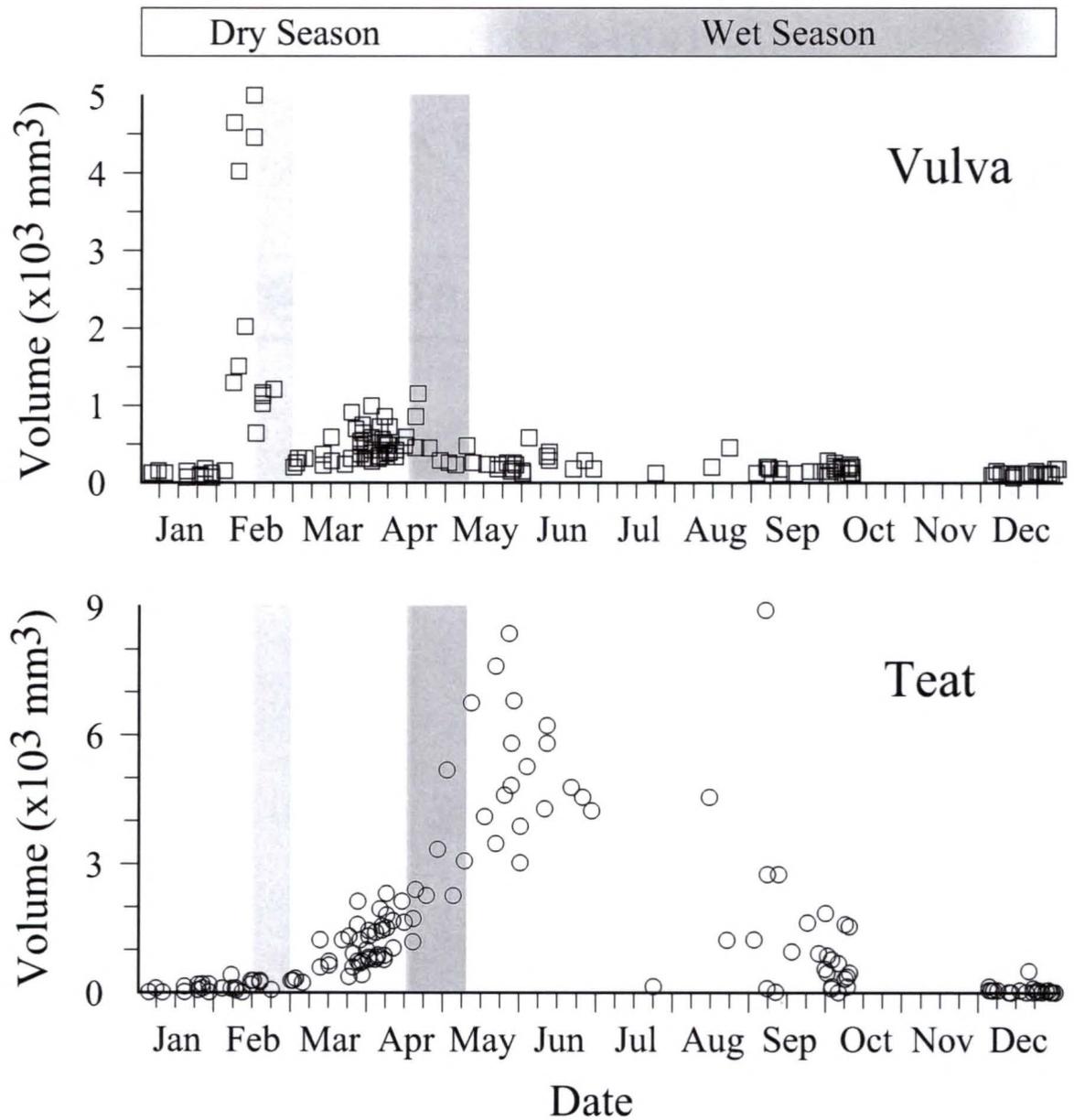


Figure 2-2. Annual vulva and teat size profiles exhibited by adult female white-nosed coatis in Tikal National Park, Guatemala, July 1994 through October 1996. Mating period (13 Feb - 28 Feb) indicated by lightly shaded background and period of parturition (16 Apr - 9 May) more darkly shaded. Based on measurements obtained during 139 immobilizations of 55 animals.

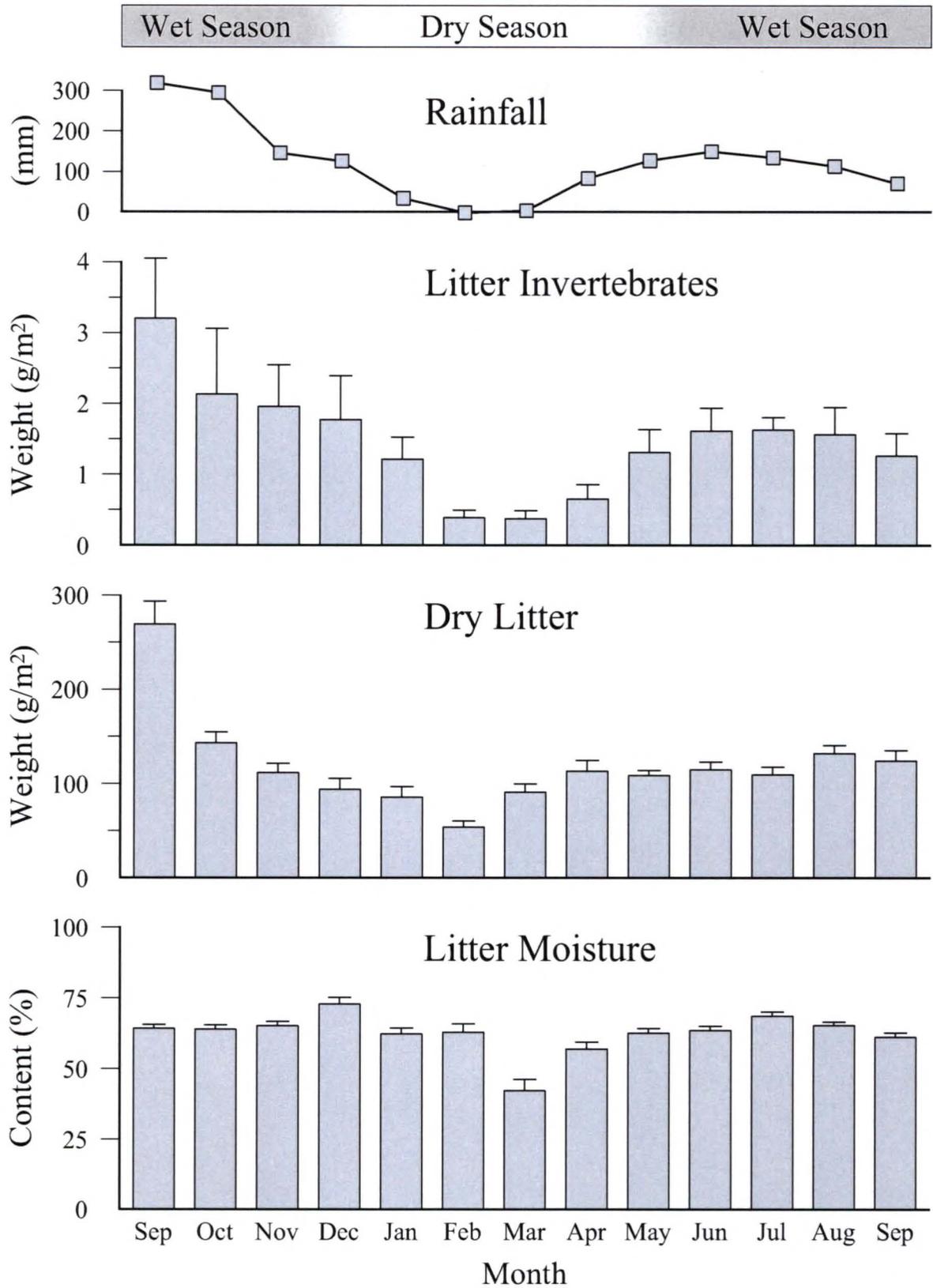


Figure 2-3. Monthly total rainfall and mean ( $\pm$  SEM) leaf litter characteristics in Tikal National Park, Guatemala, September 1995 through September 1996. Thirty 1-m<sup>2</sup> quadrats sampled each month.

Table 2-1. Correlational statistics for relationships between monthly leaf litter invertebrate data and rainfall, dry litter weight and litter moisture content in Tikal National Park, Guatemala. Thirteen consecutive months compared except where otherwise indicated; significant findings indicated in bold.

Invertebrates	Rainfall	Litter Weight	Litter Moisture
Total Mass	$r = \mathbf{0.91}$ , $P < \mathbf{0.001}$	$r = \mathbf{0.82}$ , $P = \mathbf{0.001}$	$r = 0.55$ , $P = 0.05$
Nutrient Content			
water	<sup>a</sup> $r = 0.48$ , $P = 0.08$	$r = 0.36$ , $P = 0.22$	$r = 0.32$ , $P = 0.29$
crude protein	<sup>a</sup> $r = 0.54$ , $P = 0.05$	$r = 0.34$ , $P = 0.26$	$r = 0.05$ , $P = 0.88$
crude fat	<sup>a</sup> $r = \mathbf{0.67}$ , $P = \mathbf{0.008}$	$r = 0.48$ , $P = 0.09$	$r = -0.05$ , $P = 0.87$
energy	<sup>a</sup> $r = 0.56$ , $P = 0.04$	$r = 0.36$ , $P = 0.23$	$r = -0.03$ , $P = 0.93$
Snails and Slugs			
number	$r = 0.52$ , $P = 0.07$	$r = \mathbf{0.66}$ , $P = \mathbf{0.01}$	$r = 0.20$ , $P = 0.50$
mass	$r = 0.14$ , $P = 0.64$	$r = 0.06$ , $P = 0.83$	$r = 0.36$ , $P = 0.22$
Earthworms			
number	$r = 0.65$ , $P = 0.02$	$r = 0.33$ , $P = 0.28$	$r = 0.64$ , $P = 0.02$
mass	$r = 0.36$ , $P = 0.23$	$r = 0.12$ , $P = 0.70$	$r = 0.65$ , $P = 0.02$
Centipedes			
number	$r = -0.38$ , $P = 0.20$	$r = -0.08$ , $P = 0.80$	$r = -0.25$ , $P = 0.41$
mass	$r = 0.47$ , $P = 0.10$	$r = \mathbf{0.81}$ , $P = \mathbf{0.001}$	$r = 0.12$ , $P = 0.69$
Millipedes			
number	$r = 0.02$ , $P = 0.94$	$r = 0.14$ , $P = 0.66$	$r = 0.38$ , $P = 0.20$
mass	$r = -0.10$ , $P = 0.75$	$r = 0.03$ , $P = 0.92$	$r = 0.23$ , $P = 0.45$
Arachnids			
number	$r = 0.57$ , $P = 0.04$	$r = 0.59$ , $P = 0.03$	$r = 0.42$ , $P = 0.16$
mass	$r = 0.12$ , $P = 0.68$	$r = 0.17$ , $P = 0.58$	$r = 0.23$ , $P = 0.46$
Insects			
number	$r = \mathbf{0.68}$ , $P = \mathbf{0.01}$	$r = \mathbf{0.85}$ , $P < \mathbf{0.001}$	$r = 0.34$ , $P = 0.25$
mass	$r = \mathbf{0.85}$ , $P < \mathbf{0.001}$	$r = \mathbf{0.82}$ , $P = \mathbf{0.001}$	$r = 0.25$ , $P = 0.42$

<sup>a</sup> based on comparison of 14 consecutive months

Leaf litter invertebrate groups varied considerably from one another in their temporal patterns of number and mass (with spiders and insects even differing within their own groups), as reflected in their contributions to monthly totals of these measures of abundance (Figs. 2-4 to 2-6). Examination of the relationships between invertebrate class numbers and masses (not proportionate numbers and masses) and environmental variables (Table 2-1) reveals that insects

were principally responsible for the correlations of overall invertebrate abundance with rainfall and litter mass.

Insects (Fig. 2-6) dominated the leaf litter fauna in overall abundance, but there were a few monthly exceptions: Earthworms (Fig. 2-4), the second most prevalent group overall, were slightly more numerous in October and December 1995 and weighed more in July and August 1996. Millipedes (Fig. 2-5) were slightly more numerous in February 1996. Snails and slugs (Fig. 2-4) were most prevalent by weight in May 1996. Spiders (Fig. 2-6) were always fairly abundant but never contributed much weight to samples, and were never predominant in either regard. Centipedes (Fig. 2-5) were generally scarce and contributed negligible weight even when modestly abundant in March 1996.

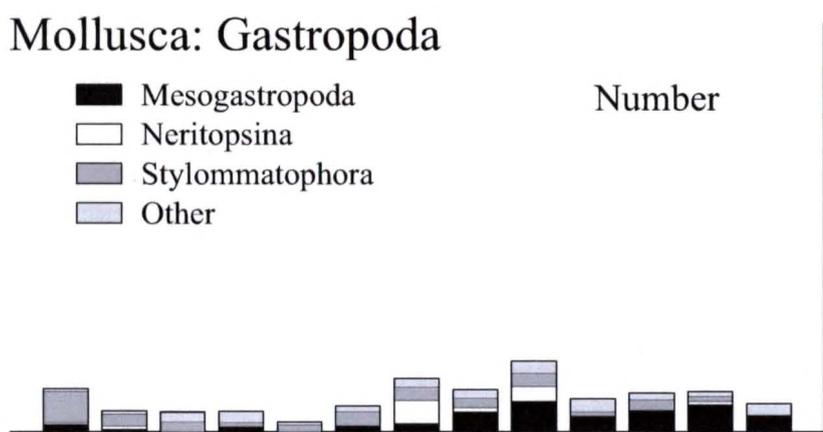
Within Insecta (Fig. 2-6), beetles and their grubs were notable in that they were always among the most abundant orders and contributed substantially more weight than any other order in every month except April 1996, when orthopterans dominated. The contributions of a single large scarab beetle species, *Enema endymion*, figured most prominently. The adults and larvae of this species were so common in the vicinity of the park that they were known by unique names (*ronrones* and *gallinas ciegas*, respectively) by the local people, and were at certain times of the year extraordinarily abundant atop or in the leaf litter or at shallow depths in the soil beneath it. By weight, adults constituted 34.2% of the June 1996 invertebrate sample, and larvae amounted to 60.4% in September, 69.9% in October and 51.3% in November 1995 samples, and 6.3% in August and 22.0% in September 1996 samples. Adults appeared in the coati diet (more on this below) or scat or were noted to be abundant in general observations made aside from leaf litter invertebrate sample collections from 8 June to 16 July 1994, 15 June to 4 July 1995 and 12 May to 17 July 1996. Larvae were similarly recorded from 17 August 1995 to 13 January 1996 and 17 July to 8 November 1996 (when field work concluded).

Six species of fruiting trees (Fig. 2-7) were selected for detailed examination based on the coati's reliance upon them over the course of the 16-month survey of tree phenology as well as on

### Mollusca: Gastropoda

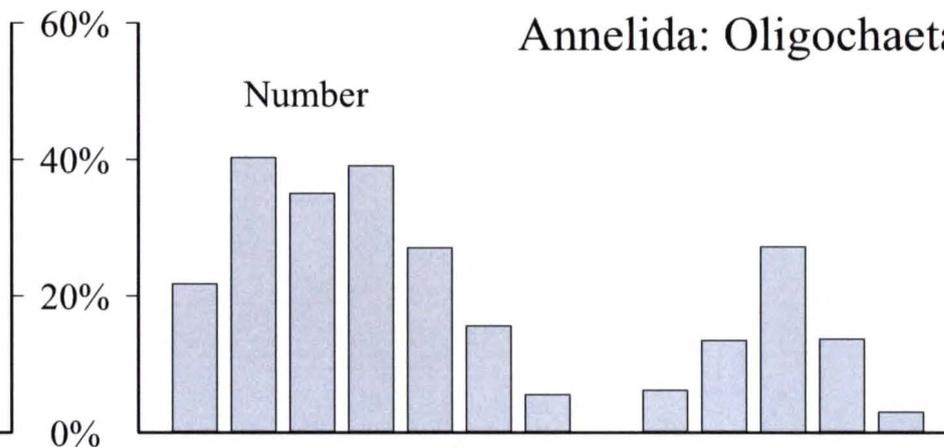
- Mesogastropoda
- Neritopsina
- Stylommatophora
- Other

Number

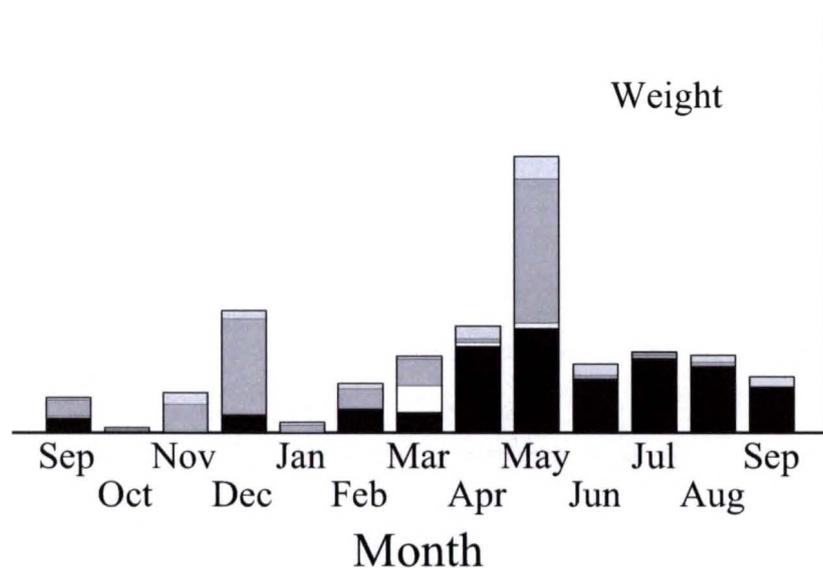


### Annelida: Oligochaeta

Number



Weight



Weight

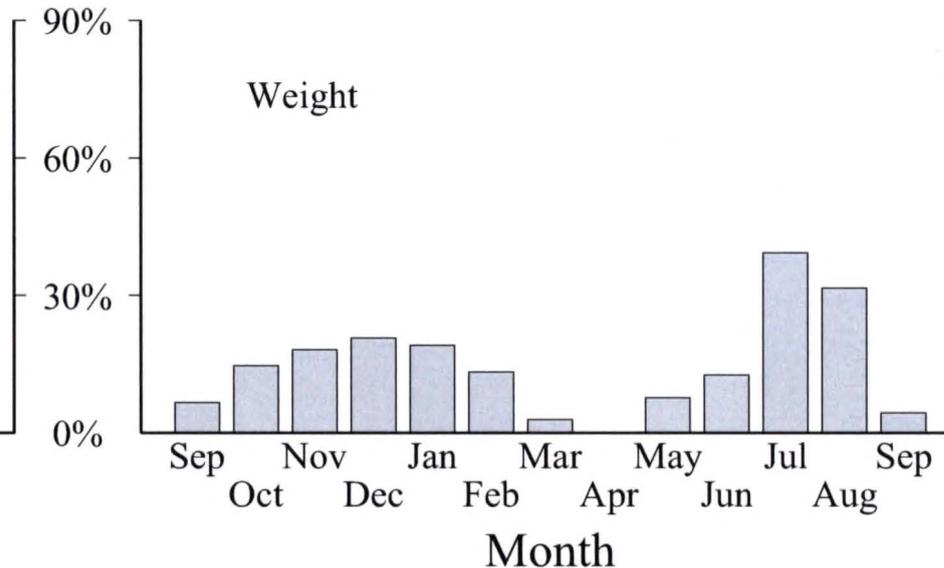
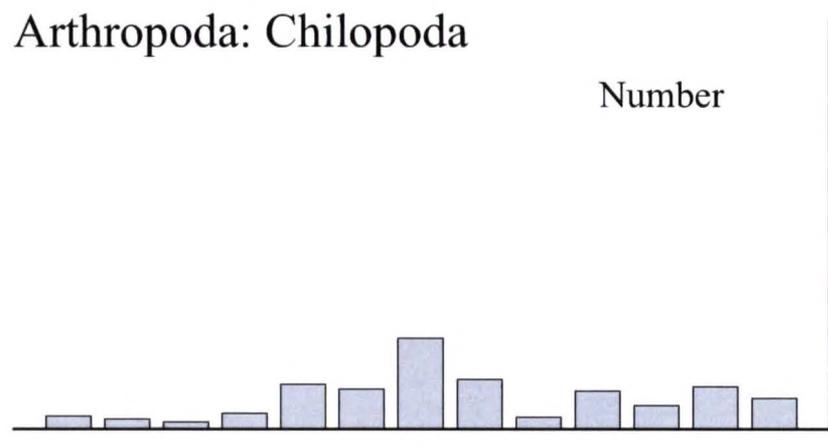
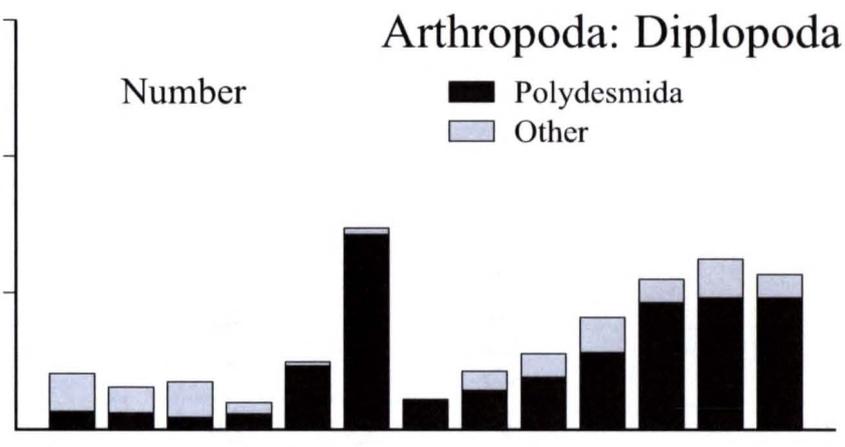


Figure 2-4. Monthly number and weight of mollusks and annelids as percentage of all leaf litter invertebrates sampled in Tikal National Park, Guatemala, September 1995 through September 1996. Based on 30 1-m<sup>2</sup> leaf litter samples per month.

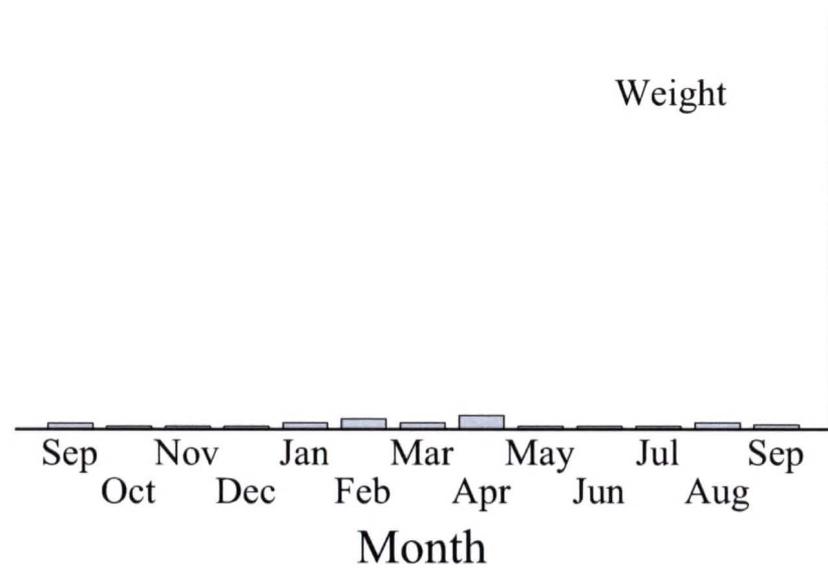
### Arthropoda: Chilopoda



### Arthropoda: Diplopoda



### Weight



### Weight

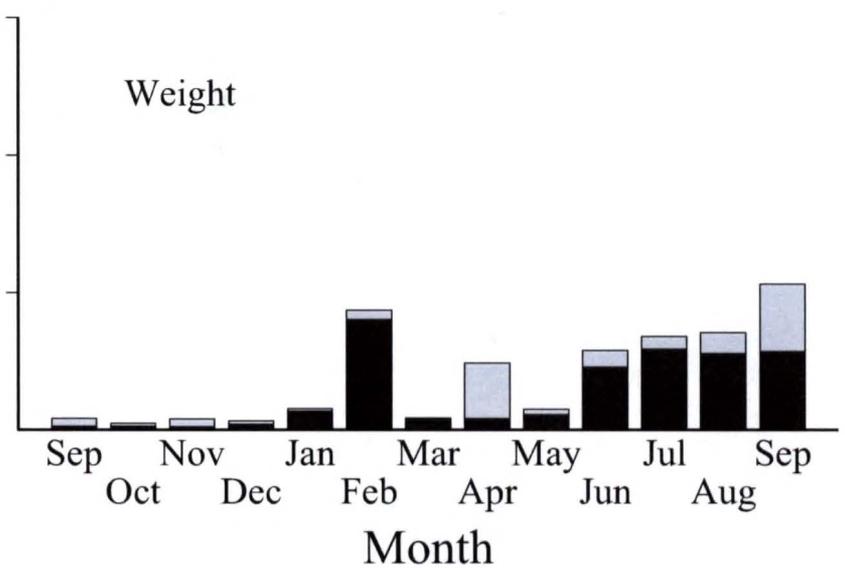


Figure 2-5. Monthly number and weight of centipedes and millipedes as percentage of all leaf litter invertebrates sampled in Tikal National Park, Guatemala, September 1995 through September 1996. Based on 30 1-m<sup>2</sup> leaf litter samples per month.

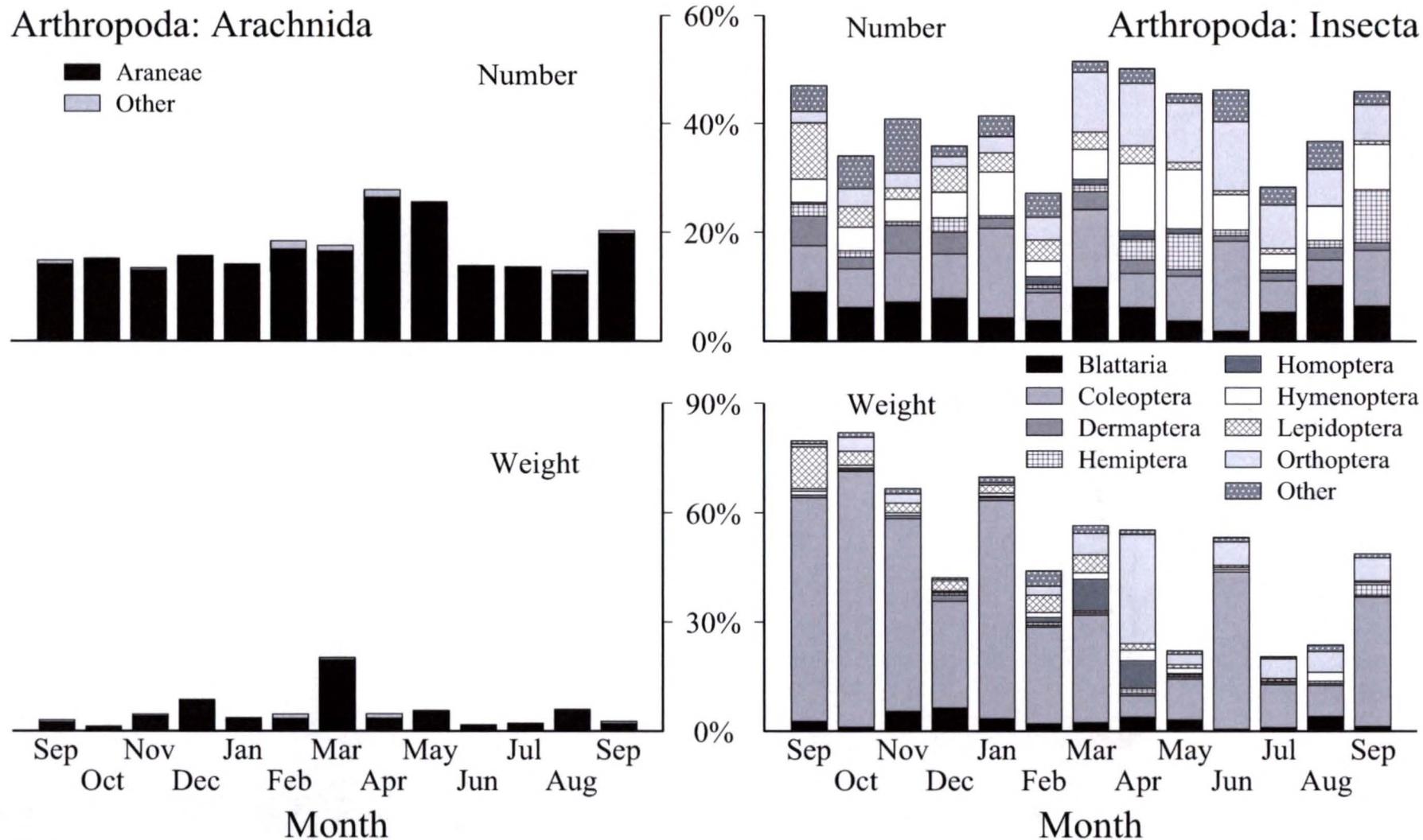


Figure 2-6. Monthly number and weight of arachnids and insects as percentage of all leaf litter invertebrates sampled in Tikal National Park, Guatemala, September 1995 through September 1996. Based on 30 1-m<sup>2</sup> leaf litter samples per month.

the species' abundance in forest plots. Aspects of some species' fruiting patterns appeared seasonal as noted below, but neither of the measures of fruit production (mean number of fruits per tree and percent of trees in fruit, which mostly but not in all ways varied together) was more than marginally correlated with rainfall for any species (Table 2-2). Ripe fruit was not observed in large enough numbers (presumably because coatis and other frugivores were eating it as it became available) to warrant depicting it in species' graphs.

*B. alicastrum* fruit (Fig. 2-7) was present and usually abundant in virtually every month of the survey, with a brief peak in August 1995 and a broad peak centered around February 1996, *i.e.*, in the middle of those years' wet and dry seasons, respectively. Ripe fruit was recorded March-September 1996, *i.e.*, from the last half of that year's dry season to the middle of the wet season. *B. alicastrum* was seen being eaten by coatis and/or was found in their feces on 94 dates between 7 March and 30 September 1996, demonstrating significant correlation with ripe fruit availability (Table 2-2). (It also appeared in the coati diet outside of the survey period three times from 30 December 1994 to 27 January 1995, and on 3 October and 8 November 1996.)

*Manilkara zapota* (*chico zapote*, a.k.a. *sapodilla*) fruit (Fig. 2-7) was also present and abundant much of the year, and displayed peaks timed similarly to *B. alicastrum*. There were lulls in fruit production in June and July, *i.e.*, early in the wet season, in both 1995 and 1996. Ripe fruit was recorded only in May 1996, coincident with the normal onset of rains, but distinguishing ripe from unripe fruit was particularly difficult in this species due to its lack of a pronounced color change; possibly only the most mature fruit specimens were recognized as ripe. This likely explains why the correlation between ripe *M. zapota* availability and the appearance of the fruit in the coati diet did not achieve significance (Table 2-2). This species was recorded eaten/defecated by coatis on 52 dates between 11 January and 27 June 1996 (and also 16 dates between 7 January and 3 May 1995).

Fruit production in *Trichilia moschata* (*cedrillo rosa*) (Fig. 2-7) was observed only during the last four months of the survey, June to September 1996, beginning early in the wet

season and increasing as the season progressed and the survey concluded. Ripe fruit was recorded only in the last month, September 1996. In contrast, *T. moschata* appeared in the coati diet in two bouts: 14 times from 11 April to 2 July 1996, and 10 times from 22 August to 29 September 1996 (and also on 3 and 10 October 1996)—indicating that a survey sample size greater than the 19 trees available would have been preferred for this species. Accordingly, fruit consumption was not significantly correlated with ripe fruit availability (Table 2-2).

*Blomia prisca* (*tzol*) fruited (Fig. 2-7) twice during the survey: for an indeterminate period including the first two wet season months examined, June and July 1995, and in April and May 1996 when rains resumed after that year's dry season. Fruits were very low in number during the latter of these periods, but ripe fruit was recorded in every month of fruit production except April 1996, correlating significantly with consumption by coatis (Table 2-2). *B. prisca* appeared in the coati diet six times from 2 June to 6 July 1995 and 10 times from 22 April to 18 May 1996 (and also six times from 23 April to 31 May 1995, and on 7 and 8 November 1996).

*Pouteria reticulata* (*zapotillo hoja fina*) fruit (Fig. 2-7) was present for five months beginning with the onset of rains in April 1996. Ripe fruit was noted in the last two months of fruit production, July and August 1996, *i.e.*, toward the middle of the wet season. This species was recorded in the coati diet on 23 dates from 13 June to 30 July 1996. The correlation between ripe fruit availability and fruit consumption was marginal (Table 2-2).

*Pimenta dioica* (*pimienta*, a.k.a. allspice) fruited (Fig. 2-7) in the same wet season months as *T. moschata*, June to September 1996. Unlike the latter species, however, fruit production in *P. dioica* peaked early in its appearance and was waning as the survey concluded. Ripe fruit was recorded in the last two months of the survey, August and September 1996. Fruit was similarly recorded eaten/defecated by coatis 20 times from 24 August to 29 September 1996 (and also five times from 1 to 10 October 1996), correlating significantly with ripe fruit availability (Table 2-2).

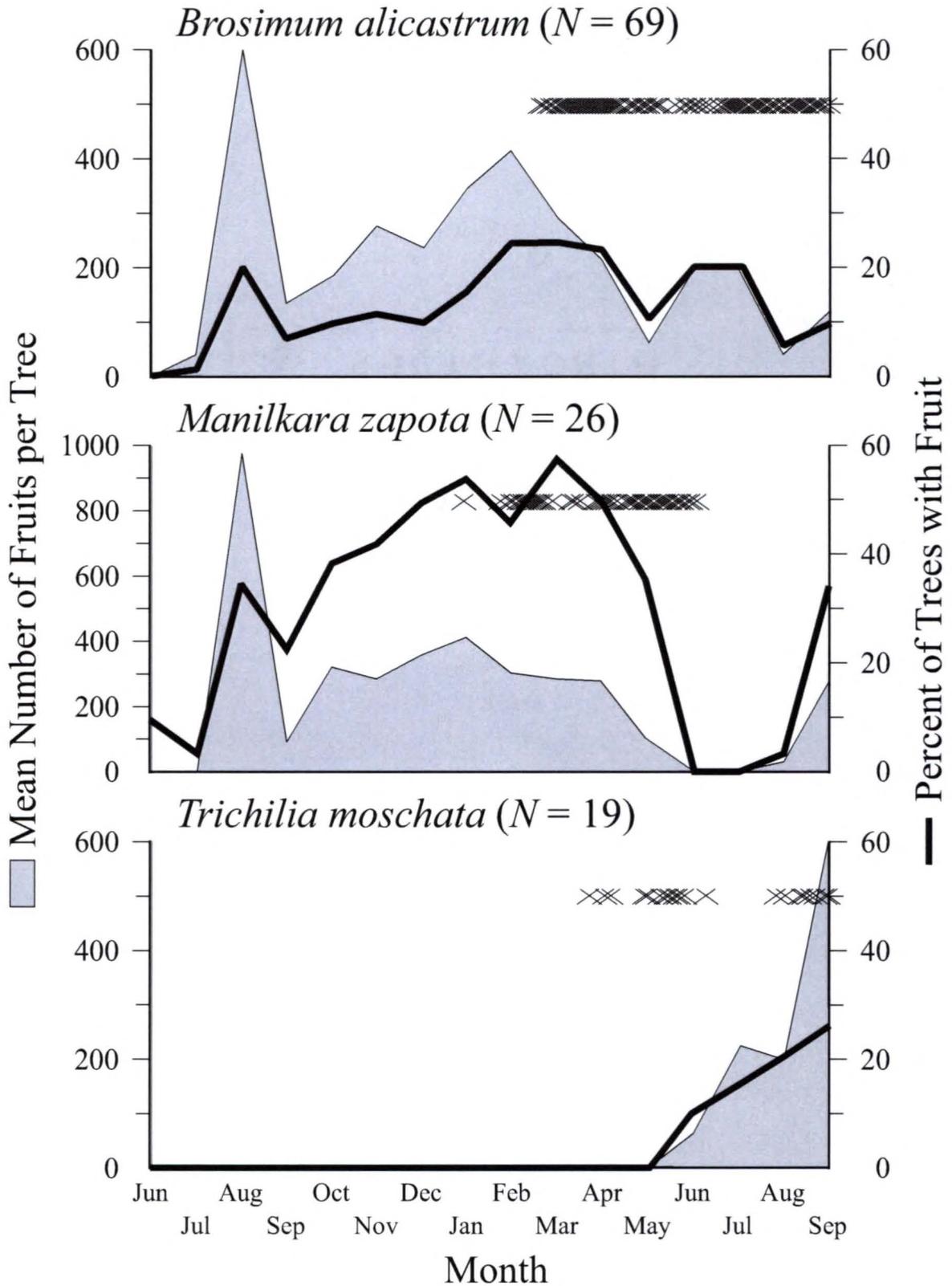


Figure 2-7. Fruiting phenology of and reliance upon tree species important to white-nosed coatis in Tikal National Park, Guatemala, June 1995 through September 1996. Dates fruit seen eaten and/or in feces indicated by Xs. Number of trees surveyed each month ( $N$ ) indicated parenthetically after species name.

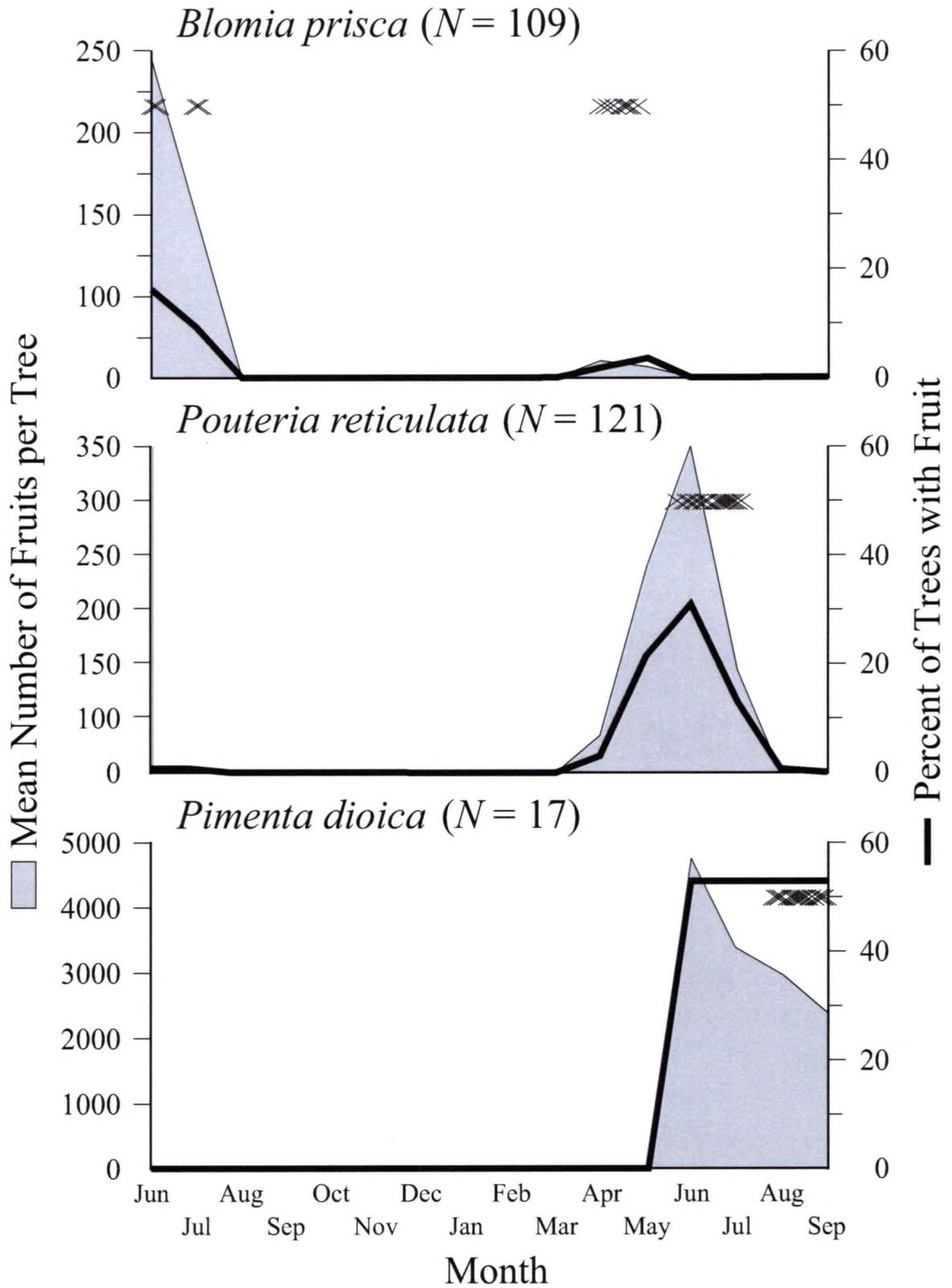


Figure 2-7 (Continued). Fruiting tree phenology and coati fruit consumption.

Table 2-2. Correlational statistics for relationships between monthly fruit availability and rainfall and between monthly ripe fruit availability and fruit consumption by white-nosed coatis in Tikal National Park, Guatemala. Sixteen consecutive months compared; significant findings indicated in bold.

Fruiting Tree Species	Rainfall	Coati Consumption
<i>Brosimum alicastrum</i>		
number of fruits / ripe fruits per tree	$\rho = -0.49, P = 0.05$	$\rho = \mathbf{0.94}, P < \mathbf{0.001}$
percent of trees in fruit	$\rho = -0.53, P = 0.03$	
<i>Manilkara zapota</i>		
number of fruits / ripe fruits per tree	$\rho = -0.40, P = 0.12$	$\rho = 0.48, P = 0.06$
percent of trees in fruit	$\rho = -0.54, P = 0.03$	
<i>Trichilia moschata</i>		
number of fruits / ripe fruits per tree	$\rho = -0.01, P = 0.96$	$\rho = 0.48, P = 0.06$
percent of trees in fruit	$\rho = -0.03, P = 0.92$	
<i>Blomia prisca</i>		
number of fruits / ripe fruits per tree	$\rho = 0.12, P = 0.65$	$\rho = \mathbf{0.78}, P < \mathbf{0.001}$
percent of trees in fruit	$\rho = 0.14, P = 0.60$	
<i>Pouteria reticulata</i>		
number of fruits / ripe fruits per tree	$\rho = 0.26, P = 0.34$	$\rho = 0.50, P = 0.05$
percent of trees in fruit	$\rho = 0.32, P = 0.23$	
<i>Pimenta dioica</i>		
number of fruits / ripe fruits per tree	$\rho = 0.09, P = 0.74$	$\rho = \mathbf{1.00}, P < \mathbf{0.001}$
percent of trees in fruit	$\rho = 0.03, P = 0.91$	

Considering coati food item nutrient composition (Table 2-3), a few general patterns were evident.

Among monthly leaf litter invertebrate samples (Table 2-3), protein, fat and energy content per gram were all highest from September to November 1995, in the latter half of that year's wet season and during and immediately after the months of highest rainfall recorded in the sample collection period. All three nutritional measures then dropped to low levels during the transition into the following dry season in December 1995, rose briefly and modestly as the dry season progressed, then declined again as rains resumed in April 1996 leading into the next wet season. All again began rising from August to September 1996, albeit at lower levels overall than

Table 2-3. Proximate nutrient composition of white-nosed coati dietary items in Tikal National Park, Guatemala. Nutrients other than water reported on a dry matter basis.

Sample	Water (%)	Crude Protein (%)	Crude Fat (%)	Ash-Free Neutral Detergent Fiber (%)	Ash (%)	Energy (kcal/g)
<i>Leaf Litter Invertebrates</i>						
August 1995	71.7	35.9	11.2	12.0	7.7	3.33
September 1995	78.3	50.4	19.1	18.6	2.1	4.61
October 1995	75.9	58.6	24.6	17.6	0.5	5.61
November 1995	77.5	61.6	14.9	19.9	1.5	5.02
December 1995	72.4	38.3	11.1	9.6	10.2	3.13
January 1996	74.4	35.3	11.2	11.2	2.5	3.37
February 1996	72.6	40.9	8.7	23.3	3.5	3.52
March 1996	70.5	39.8	12.3	11.9	1.5	3.58
April 1996	64.6	35.0	10.2	15.9	14.5	3.02
May 1996	70.0	35.9	7.1	13.3	12.7	2.89
June 1996	66.3	34.3	8.6	14.6	12.4	2.61
July 1996	74.3	33.1	6.3	10.6	12.5	2.67
August 1996	70.8	30.3	5.4			2.42
September 1996	67.4	40.2	6.6	16.3	10.7	2.57
<i>Enema endymion</i>						
larva	88.7	62.3	12.1	30.5	0.5	4.83
adult	62.5	67.5	20.3	51.5	4.1	6.03
<i>Brosimum alicastrum</i>	83.1	11.6	1.8			4.03
<i>Manilkara zapota</i>	80.0	4.0	5.9	61.8	2	4.80
<i>Trichilia moschata</i>	77.1	12.0	25.2			5.27
<i>Pouteria reticulata</i>	86.3	9.7	4.8			4.37
<i>Pimenta dioica</i>	74.6	5.1	2.2	31.6	1.1	4.07

in the previous year. Only fat, however, was significantly correlated with rainfall (Table 2-1), the other nutrients being at most marginally so. The contributions of *E. endymion* beetles and especially grubs (Table 2-3) figured as prominently in the above pattern as they did in leaf litter invertebrate samples. Adults provided the greatest amount of protein and energy per gram of any food item analyzed, and the third greatest amount of fat; larvae were particularly high in protein and energy and less so in fat, and had the highest moisture content of all food items.

No sample of *B. prisca* fruit was analyzed, but of the other five important fruit species (Table 2-3), *T. moschata* was highest in protein, energy and especially fat content; indeed, gram-for-gram this species achieved the highest fat level of any food item analyzed. The results for other fruit species were variable except that *P. dioica* was at or near the bottom of the group in every category.

All of the invertebrate samples contained higher protein levels than any of the fruit samples (bearing in mind that the latter consisted only of edible portions, therefore excluding seeds) (Table 2-3). With the aforementioned notable exception of *T. moschata*, invertebrates also typically provided more fat per gram. Fruits equaled or slightly bested the mixed leaf litter invertebrate samples in terms of energy content, and usually held more moisture as well.

In terms of foraging effort, coatis spent more—generally much more—time foraging in the leaf litter invertebrate zone than in the fruit zone at all times of year (Fig. 2-8). As noted above, ripe fruit was essentially unavailable for the five months of September 1995-January 1996, *i.e.*, the latter part of the 1995 wet season. However, even during the greatest months of overall ripe fruit availability, April and May 1996—*i.e.*, at the end of that year's dry season and during the transition into the following wet season—coatis were never observed to spend more than 6.6% of their foraging time in the canopy of fruiting trees. The animals searched for food under fruiting trees somewhat more, spending 22.8% of their foraging time in such areas in April, 24.6% in May and 24.5% in September 1996, *i.e.*, the early to middle wet season of that year, but these were areas of overlap in which not only ripe fruits but also leaf litter invertebrates could be found.

Examining invertebrate and fruit foraging success (Figs. 2-9 and 2-10, respectively) more closely, fewer invertebrates were consumed and fewer seconds were spent consuming them per minute relevant foraging time than was true for fruits in almost every month in which both food types were eaten; March and April 1996 were exceptional in that invertebrates and fruits were consumed at comparably low rates. With respect to time spent consuming items, however, it should be noted that coatis used some undetermined portion of that time processing fruits of

*Brosimum alicastrum*, *M. zapota*, *T. moschata* and *Blomia prisca* in order to discard various presumably inedible or distasteful portions (husks, skins and/or seeds).

Over the 14 months of systematic behavioral observations, the coatis' consumption of leaf litter invertebrates (Fig. 2-9) displayed a clear pattern in terms of number of invertebrates consumed and time spent consuming them. Overall, invertebrate consumption decreased from the beginning of the study in August 1995 through April 1996, *i.e.*, through the last half of the 1995 wet season and all of the 1996 dry season, then rose sharply in May 1996 with the onset of that year's wet season and peaked a month or two later (depending on the measure under consideration) before again declining. Neither measure of foraging success was significantly correlated with total invertebrate mass in monthly samples (number consumed:  $r_{[11]} = 0.26$ ,  $P = 0.39$ ; time spent consuming:  $r_{[11]} = 0.38$ ,  $P = 0.20$ ). In accordance with previously presented data, beetles and grubs—again, especially *E. endymion*—predominated. Only 19.4% of the invertebrates coatis preyed upon during observations could be positively identified (with an obvious bias favoring larger or more agile species); 96.2% of these were insects, and 81.9% various Coleoptera. *E. endymion* alone accounted for 44.4% of identified invertebrate prey, or 8.6% (6.5% larvae, 2.1% adults) of all invertebrates consumed by coatis over the course of the study.

Fruit consumption (Fig. 2-10) followed a similar pattern (aside from the several months in which ripe fruit was unavailable, of course). A notable exception resulted from the animals' early reliance upon *M. zapota*, the first tree species with ripe fruit in the 1996 dry season, causing a brief spike in consumption rates in February of that year. That species and also *Brosimum alicastrum*, which ripened soon after, continued to be consumed at much lower rates throughout the remainder of the dry season. Fruit consumption increased again in May 1996 when ripe fruit of various species appeared with the onset of wet season, as noted previously. It was not possible to look for correlations between fruit foraging success and total fruit availability because phenological data were lacking for several of the fruit species which were consumed by coatis.

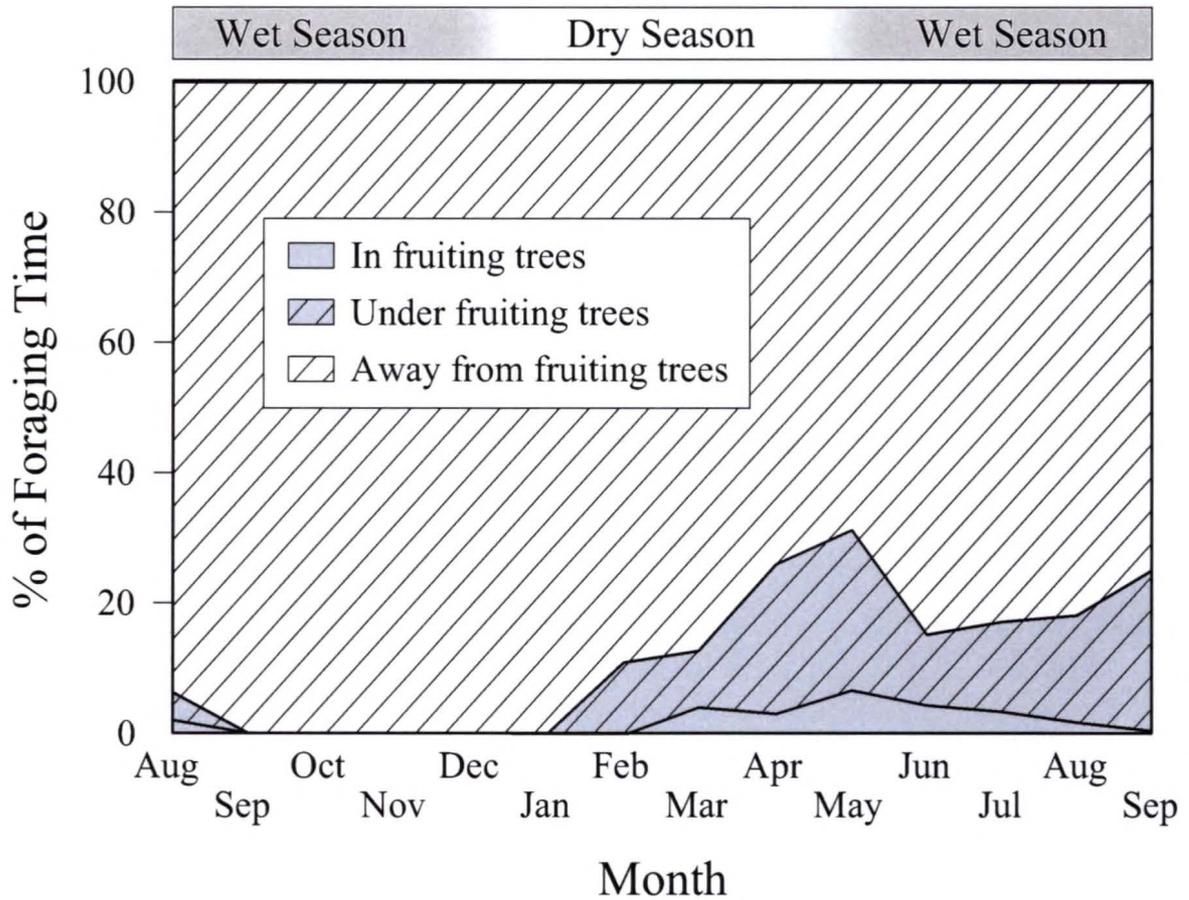


Figure 2-8. Mean percentage of time foraging adult female white-nosed coatis spent in areas where ripe fruit was present and absent in Tikal National Park, Guatemala, August 1995 through September 1996. Based on a total of 76.1 hours observation of foraging by 37 animals.

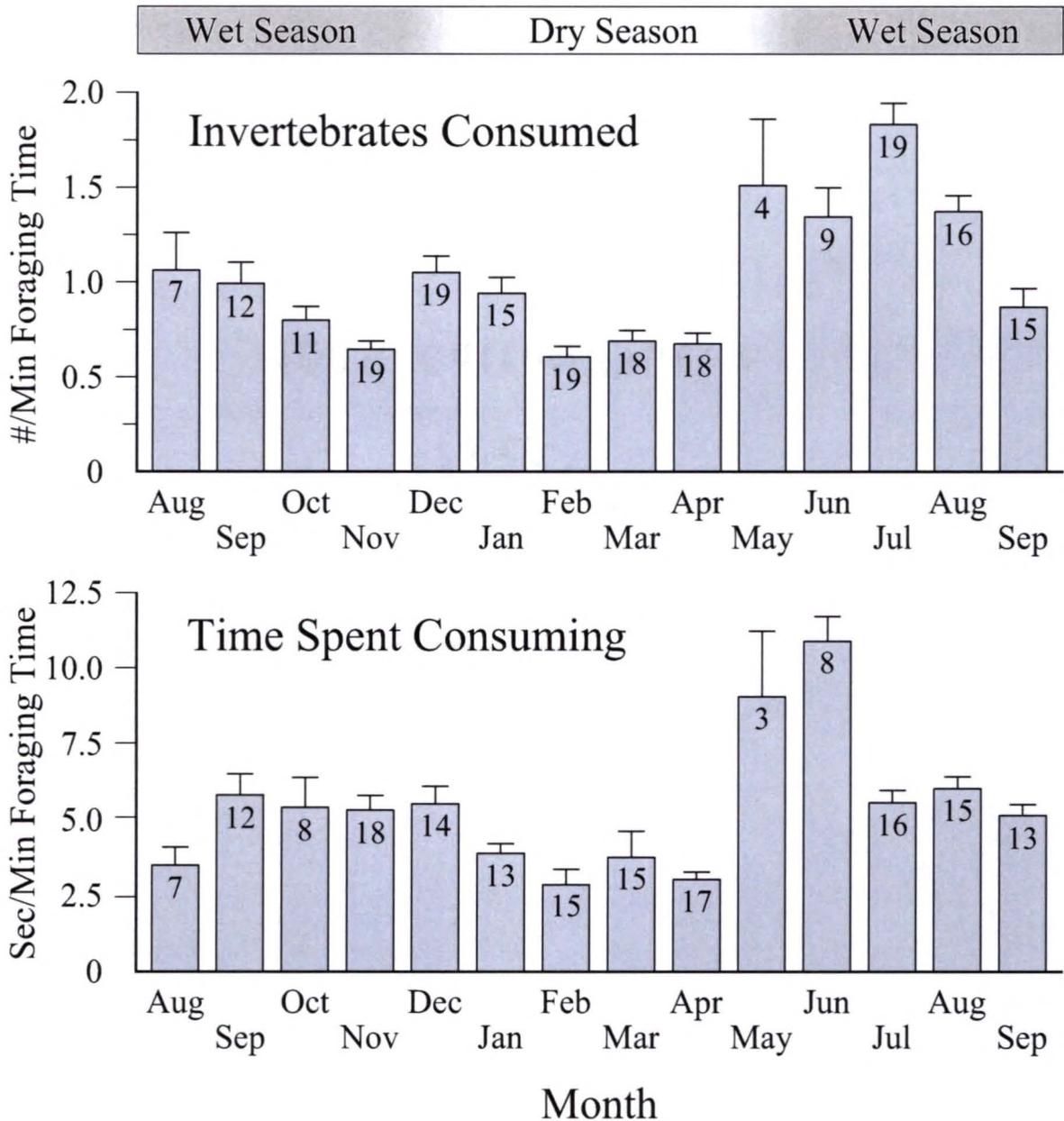


Figure 2-9. Mean ( $\pm$  SEM) number of invertebrates consumed and time spent consuming them by foraging adult female white-nosed coatis in Tikal National Park, Guatemala, August 1995 through September 1996. Number of females sampled in each month indicated on bars. Based on a total of 93.7 hours observation of invertebrate foraging by 32 animals and 73.0 of 29 animals, respectively.

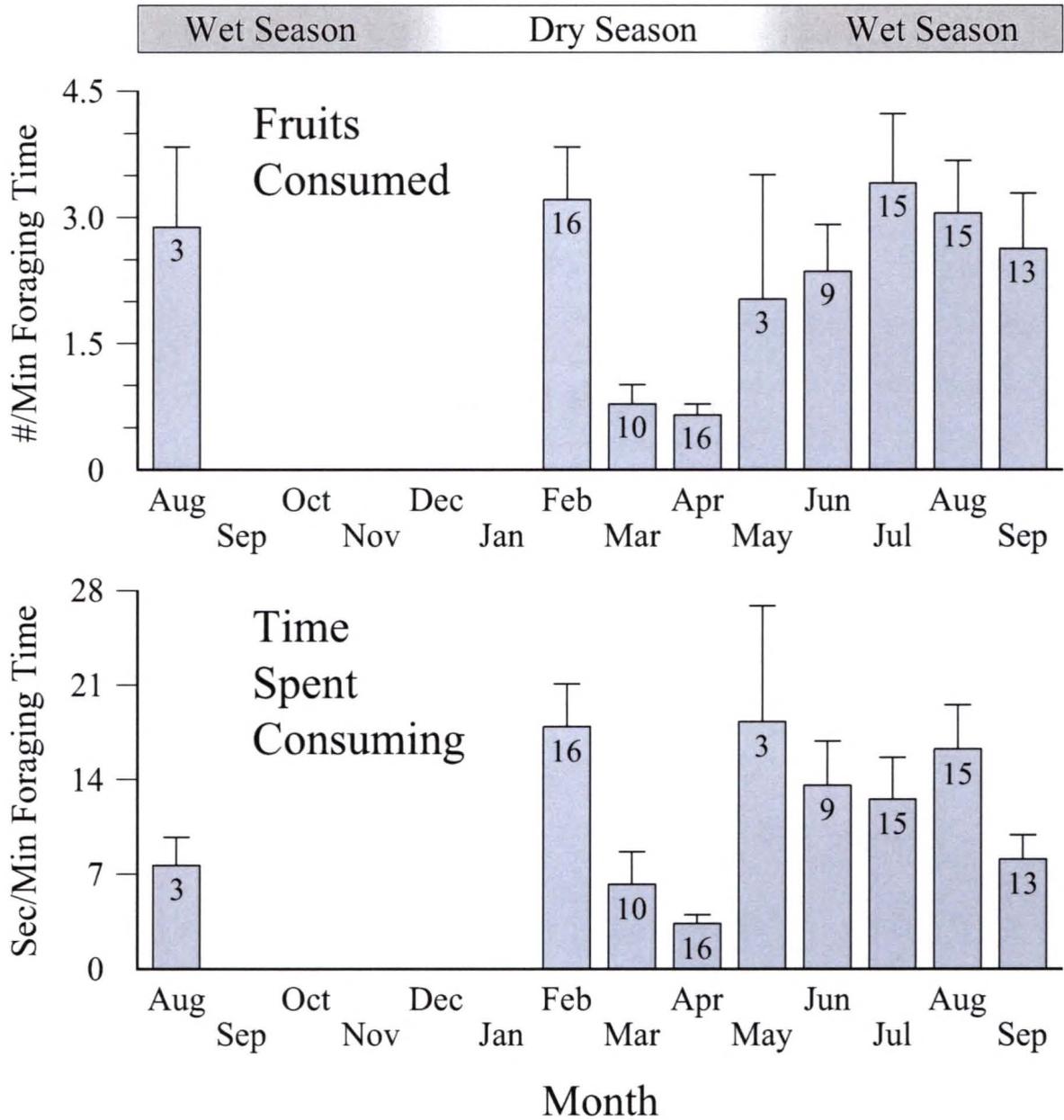


Figure 2-10. Mean ( $\pm$  SEM) number of fruits consumed and time spent consuming them by foraging adult female white-nosed coatis in Tikal National Park, Guatemala, August 1995 through September 1996. Number of females sampled in each month indicated on bars. Based on a total of 10.4 hours observation of fruit foraging by 23 animals.

Adult female coati body fat profiles (Fig. 2-11), presumably indicative of how well energy availability met energetic demands, displayed a clear seasonal pattern. Body fat declined rapidly from its high point at the beginning of the dry season in January to the mating period in the last half of February, leveled off or slightly rose thereafter until just before the parturition period began in the last half of April, then resumed its decline through the parturition period and well into the wet season. Fat stores appeared to reach nadir in the vicinity of July to early August (a time of sparse data), *i.e.*, shortly before the middle of the wet season, and then rose presumably steadily (discounting another gap in the dataset from mid-October through November) through the remainder of the wet season and until the end of the year.

### Discussion

Behavioral and morphometric data reveal that coatis in Tikal National Park normally reproduce only once per year, with relevant events occurring across the population in narrow, consistent periods: Mating takes place over an approximately two-week period in the middle of the dry season. Birth occurs over a comparable period at the end of the dry season, about 10 weeks after mating. Solitary nesting, which lasts 1½-2 months, begins shortly before birth occurs and ends with the emergence of young at the beginning of the wet season; the band reunites within the month following nesting. The young begin foraging alongside their dam as soon as they are brought down to the ground, but are not fully weaned until months later, in the middle of the wet season. A second reproductive cycle with similar timing but delayed by approximately four months may be initiated if the first is unsuccessful, but second cycles rarely occurred in Tikal and appeared to result in smaller litters. Taking into account seasonal differences in different parts of the coati's range, the reproductive pattern in Tikal fits well with previously published information on coatis at other locales.

Based primarily on observations of increased female-male affiliative behavior and male-male agonism from late January to mid-March 1959 and throughout January 1960, Kaufmann (1962) identified a month-long period of sexual activity among coatis on BCI; because it appears

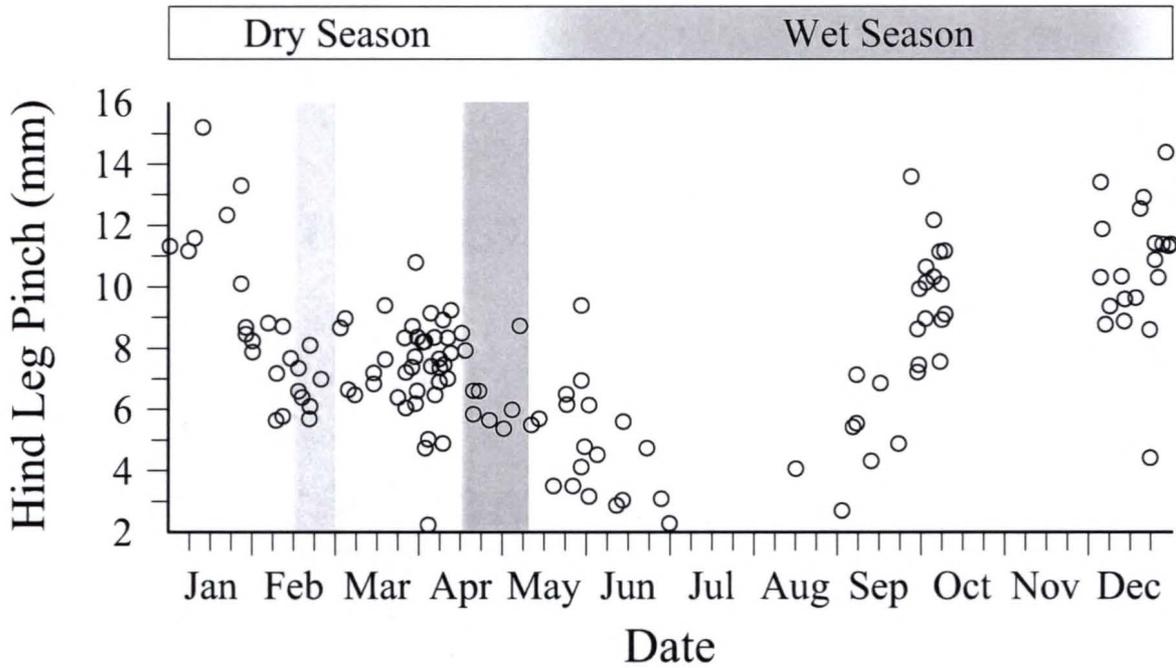


Figure 2-11. Annual body fat profile exhibited by adult female white-nosed coatis in Tikal National Park, Guatemala, July 1994 through October 1996. Mating period (13 Feb - 28 Feb) indicated by lightly shaded background and period of parturition (16 Apr - 9 May) more darkly shaded. Based on measurements obtained during 135 immobilizations of 54 animals.

that actual copulation was not observed (see below), however, the mating period could not be defined. Based on similar observations and the timing of nest emergence, Russell (1979; 1982) concluded that the coati mating period on BCI lasted one to two weeks in early February, shifting slightly from year to year. Sunquist and Montgomery (1973) observed a pair of coatis in coitus on the island on 5 March 1971. Gilbert (1973) believed that the coatis in southern Arizona, at the northernmost edge of the species' range, mated in March and early April. Hass and Roback (2000) observed two coati copulations (excluding a possible third; see below) there on 6 April 97 and 5 April 98, and also stated without providing further details that the mating period in their population lasted from late March to mid-April. Studying captive animals in southern Arizona, Smith (1980) reported that copulations took place on 28 and 30 March 1976.

Previous detailed descriptions of mating activity among free-ranging coatis include mounts lasting only a few seconds (Kaufmann, 1962; Gilbert, 1973; Hass and Roback, 2000). Kaufmann (1962) referred to these as attempted copulations, whereas the later authors considered them to be copulations. However, Gilbert (1973) also believed that more lengthy periods of mating activity probably occurred out of sight of observers, when a male and a female would depart from the band together, and Hass and Roback (2000) additionally observed two copulations lasting approximately 60 minutes each between coatis who were out of sight of other band members. The coatis found already engaged in copulation (most similarly to copulations observed in the current study, in the tree canopy over a foraging band) by Sunquist and Montgomery (1973) continued for seven minutes after being discovered. Smith described two copulations among captive coatis: one lasted one minute in total and another continued for 23 minutes after being discovered in progress. The numerous observations of prolonged copulatory events in the present and earlier studies suggest that Kaufmann (1962) was correct in describing brief mounts as merely attempted copulations.

Prolonged copulation could be interpreted as an indication that coatis are induced ovulators, as has been suggested by Hass and Roback (2000), but it may also be a form of mate

guarding by males. Litters examined in Tikal exhibited a high rate of multiple paternity (Booth-Binczik, 2001), indicating that female coatis commonly mate with more than one male.

Observations in the current study and by Smith (1980) of females attempting to break away from but being restrained by males suggest that prolonged copulation is more advantageous to the male than to the female. The closely related raccoon (*Procyon lotor*) was demonstrated by Sanderson (1961) to ovulate spontaneously (after initially being reported to be an induced ovulator by Llewellyn and Enders, 1954—an erroneous finding that unfortunately persists in the literature), but the review of carnivore ovulation by Larivière and Ferguson (2003) demonstrates that it is unsafe to base assumptions in this regard on phylogenetic relationships.

Coatis were not radiocollared for Kaufmann's (1962) BCI study, so he was able to keep track of only one female during the 1960 nesting period; that animal left its band on 1 April, gave birth on 10 April and brought its young out of the nest and joined other females with young on 20 May. Without providing any foundation, Russell (1979) stated that coati births occurred on the island during the second week of April in 1977 and the fourth week of April in 1978, and (Russell, 1982) that the nesting period there took place in April and May. Russell (1982) also said that coati bands on BCI reaggregated in late May. Based on animal movements monitored by radiotelemetry, Sáenz (1994) reported that female coatis in the dry forest of Santa Rosa National Park, Costa Rica, left their bands to nest in April. Also based on telemetry data, Ratnayeke *et al.* (1994) reported that females in southern Arizona were solitary for at least a month before parturition in early July. Gilbert (1973) stated that females there disbanded in the third week of June, and estimated that all females in the band he was observing gave birth between 16 and 23 June. Hass (2002) said that females in Arizona left their bands in mid-June and reaggregated in early August when the young were five to six weeks old.

There are as yet few data available on the length of coati gestation against which to compare the 71- to 74-day pregnancy seen in a single female in the current study. The most concrete of these come from Smith's (1980) Arizona captive animal study, in which one female

gave birth 71 days and another 76 days after being observed copulating. Average gestation lengths can be approximated for the two coati bands from which most data derive for the 1996 mating and parturition periods of the present study, bearing in mind that parturition periods (which are presented and discussed in greater detail in Chapter 3) were likely overestimated; the differences between the midpoints in the mating and parturition periods in these bands are 66 and 68 days. Kaufmann (1962) reported that three coati litters were born approximately 70 days after the period in which he observed heightened sexual activity on BCI. The relative consistency of these data across divergent locales—as well as the tightness and consistency of the mating period at the start of the coati reproductive cycle—suggest this species undergoes direct development.

Understandably little information is available concerning coati lactation. Kaufmann (1962) reported that in 1958 nursing was seen on BCI as late as 16 September. Inexplicably, Russell (1983) put forth that young there were nearly weaned by the time of reaggregation, months earlier. Smith (1980) noted that young born to a captive female first began eating solid food at 45 days of age. Smith also reported that the female began moving away at the approach of its young when the latter reached 74 days of age, and that the female's teats appeared greatly reduced in size at that time; she observed no nursing as of 80 days postpartum.

Prior to this study, nesting behavior and parturition outside of the usual narrowly defined coati nesting season had been observed only in Santa Rosa, where Sáenz (1994) found that females quite commonly underwent second reproductive cycles after losing their first litters to nest predation by white-faced capuchins (*Cebus capuchinus*); second litters were born there in late July or early August. Second litters have also been documented in the procyonid *P. lotor* in south Texas after failed reproductive attempts were made during the normal breeding season (Gehrt and Fritzell, 1996), and the phenomenon has been seen in many other mammals as well.

The data on food availability provide a ready ultimate explanation for coati reproductive seasonality in Tikal, but leave some details yet to be clarified. In the present study, infants emerged from their nests at the start of the wet season when (in at least one year) both leaf litter

invertebrates and fruit were increasing in abundance. Are these patterns in food availability consistent, though? Taken by itself, this ecologically brief study suggests that the invertebrate pattern may be consistent but the fruit pattern is not; placing the current results into the context of the literature provides much keener insight into the question of pattern (in)consistency.

Populations of leaf litter invertebrates in the tropics are strongly dependent on moisture levels (Levings and Windsor, 1982), as is evidenced by the high correlation between invertebrate abundance and rainfall in Tikal. As occurred in the present study, overall litter invertebrate abundance on BCI was lowest during the dry season and highest in the early wet season (Levings and Windsor, 1982). Nine of thirteen arthropod taxa examined there individually showed population maxima in the early wet season (Levings and Windsor, 1985). *E. endymion* adults congregate around lights at night in huge numbers (pers. obs.), and should therefore be considered night-flying insects as well as litter insects. Night-flying insect abundance (and large beetle abundance in particular) also peaked in the early wet season on BCI (Smythe, 1982), and night-flying insects were most abundant in the late dry season and early wet season at the Cocha Cashu Biological Station in Peru's Manu National Park (Terborgh *et al.*, 1986; cited in Goldizen *et al.*, 1988). Moreover, differences in rainfall patterns among years affect litter arthropod population levels but do not obscure seasonal trends in abundance (Levings and Windsor, 1985).

In contrast, seasonal patterns of tropical fruit production vary greatly from year to year not just in Tikal but at other sites as well (Foster, 1982a; Bullock and Solís-Magallanes, 1990; van Schaik *et al.*, 1993; Chapman *et al.*, 2005). None of the tree species that were most important in the coati diet in Tikal showed the same pattern of fruit availability in June-September 1995 as in June-September 1996 (at the beginning and end of the phenological survey). Rains were heavy at the height of the 1995 wet season and even more unusually light in the middle of the 1996 wet season; leaf litter fall and invertebrate and fruit availability all showed associated patterns. The climatic fluctuations may have been due to the occurrence of an El Niño event in 1994 (based on information from the U.S. National Oceanic and Atmospheric Administration, Washington, DC);

the El Niño Southern Oscillation tends to create a pattern in which dry sunny years alternate with wet cloudy years in Central America (Wright *et al.*, 1999). Unusually rainy dry seasons, particularly following an El Niño year (Wright *et al.*, 1999), apparently result in failure of the fruit crop in many species that normally produce fruit in the wet season, including the ordinarily prolific *B. alicastrum* (Foster, 1982a). Even in the absence of obvious rainfall anomalies, however, many tropical tree species exhibit non-annual rhythms in fruit production and/or high intraspecific variability in phenology (Milton, 1991; Newstrom *et al.*, 1994; Hemingway and Overdorff, 1999). It has been reported that *B. alicastrum* trees in Tikal produce fruit three times per year: February-March, June-July, and October-November (Coelho *et al.*, 1976). The phenology data in the present study do not support this contention, but do indicate non-synchronous fruit production by this species, as fruit availability continued and even increased during a lengthy period of heavy consumption by coatis and other frugivores (pers. obs.).

The data are scant but suggest consistent seasonal patterns exist in food nutrient content as well as food availability. In the present study virtually all leaf litter invertebrate nutrient levels rose and fell in parallel to rainfall, although only fat content correlated significantly. Fruit nutrient levels were examined herein at only a single point in time per species, but Schaefer and Schmidt (2002) reported that fleshy fruits in Venezuela rose steadily in caloric value throughout the dry season, and Worman and Chapman (2005) found that the fat content of ripe fruits of a single tropical species varied tremendously within a year, being much higher during periods of high rainfall. This is clearly an area of tropical ecology warranting further study.

There is also the matter of the freezer failure and its potential effects on the present study's nutritional analyses to consider. Few nutritional data are available in the literature that are useful for comparison, but those are encouraging. Analysis of an unknown species of dung beetle from Tanzania (Pennino *et al.*, 1991) produced values remarkably similar to those found in the present study for adult *E. endymion* for water content (58.3%), fat content (20.6%), NDF (51.6%) and ash (7.4%), but completely different for protein (7.8% versus 67.5% in the current

study). Previously published values (Coelho *et al.*, 1976) for *B. alicastrum* fruit (84% water, 15.6% protein, 3.1% fat, 3.50 kcal/g) and *M. zapota* fruit (75% water, 2.0% protein, 4.4% fat, 3.76 kcal/g) are likewise similar to those obtained in this study.

The relative importance of leaf litter invertebrate versus fruit availability to the timing of coati reproduction remains uncertain, but the findings of the present study appear to support Russell's (1982) assertion of the primacy of invertebrates. Tikal's coatis clearly focused their foraging efforts on invertebrates more than on fruit at all times, though seasonal patterns are somewhat difficult to assess due to the high degree of interannual variation in fruit availability during this study. For example, the animals ate no fruit during the second half of the wet season in 1995 because no fruit was then available, but data from September and anecdotal observations made in October and November 1996 suggest that foraging patterns late in that year's wet season might have looked quite different. Coatis spent the highest percentage of their foraging time in fruit zones at the end of the dry season, but it was still much less than the time they spent foraging for invertebrates; the time they spent consuming invertebrates was actually higher than at any other time, too, suggesting that both fruit and invertebrates were abundant at that time. An evolutionary argument also exists for invertebrates being more important than fruits as determinants of coati reproductive timing, namely that consistent annual peaks in invertebrate availability are much more capable of driving seasonal adaptation than are profoundly less consistent peaks in fruit availability.

In any event, the present study adds to the growing body of literature demonstrating the importance of leaf litter invertebrates and their phenology to coatis. Kaufmann (1962) reported that BCI's coatis spent more than 95% of their active time foraging for invertebrates, and that fruit was eaten more during the dry season than the wet season. Russell (1982) estimated that coatis on BCI spent 89% of their foraging time in the wet season and 54% in the dry season foraging for invertebrates. He also reported that scats he collected consisted mostly of beetle parts. Contrasting somewhat to the patterns in Tikal and BCI, Sáenz (1994) found approximately

equal frequencies of invertebrates and fruit in the scats he collected throughout the year in Costa Rica; as in Tikal, though, Coleoptera was the dominant invertebrate group in the diet (followed closely by Orthoptera). A heavy reliance upon beetle prey is clearly a common facet of coati ecology at a variety of sites, but no previous study has found as strong a relationship between this procyonid and a single prey species as was evident in Tikal between it and *E. endymion*.

Coati reproductive seasonality in Tikal appears to be driven not by restrictive effects of food availability on female physiology (reproductive or otherwise), but rather by its direct effects on the survival of offspring. Specifically, reproduction there is timed such that gradually weaning young (arguably the most vulnerable life stage; Russell, 1982) can capitalize on a surfeit of food resources which first appears at the beginning of the wet season and continues through the first half of that season. As others have pointed out, predatory species are unlikely to suffer shortages of particular nutrients (Stephens and Krebs, 1986; Bronson and Heideman, 1994; Galef, 1996), so when such species are timing reproduction to match food availability they are likely doing so with regard to more purely energetic constraints. Female coatis do lose energetic stores (*i.e.*, fat) during nesting and early weaning (the most energetically expensive part of reproduction for many mammals; Rutberg, 1987) even as males are rapidly rebuilding theirs after the mating period (see Chapter 4) by relying upon the same foods (Booth-Binczik, 2001), but females apparently have sufficient reserves to get them through. Unlike on BCI where deferment of reproduction was common (Kaufmann, 1962; Russell, 1982), virtually all mature females reproduced each year in Tikal (unpublished data). The fact that some females in Tikal were able to successfully complete second reproductive cycles after failing in their first provides additional evidence of ample energetic reserves in these animals. Reviewing reproductive seasonality among neotropical primates, DiBitetti and Janson (2000) concluded that very small species time reproduction so that peak food availability coincides with lactation, whereas species large enough to store sufficient energy reserves—*i.e.*, those similar in size to the coati—time reproduction so that peak food availability coincides with weaning.

To more fully assess the importance of birth season to offspring survival, it would be useful to compare survivorship among young born during second cycles to that among young born at the normal time of year. However, the few litters that were produced during second cycles in this study do not provide adequate data for such a comparison. One infant that was born in August 1995 and the four that were born in August 1996 were known to survive to the end of the study; the fates of the other out-of-season infants were unknown (as is the cause of whatever difference in litter size exists between first and second litters).

Beyond energy availability, a few related ultimate factors might contribute to the observed pattern of seasonal reproduction. For example, protein content of invertebrates peaked in the middle of the wet season, so birth might be timed such that infants are fully weaned when the most protein is available to support their continued growth. Also, the fact that birth occurs at the end of the dry season means that juveniles have as much time as possible to grow, learn and build energetic reserves before they have to deal with the dry-season low in invertebrate availability (Russell, 1982). The only other factor that appears at all likely to promote strong coati reproductive seasonality in Tikal is water availability. The region's pronounced dry season and lack of natural permanent surface water (due to underlying permeable limestone) create the possibility that lactating females might be restricted in milk production by a shortage of water. However, this is not likely to be a factor in most parts of the species' range, and the fact that females in Tikal give birth before the dry season ends suggests that water stress is not relevant to the timing of their reproduction.

Reproductive seasonality such as the coati displays would not be remarkable in a long-lived mammal inhabiting the higher latitudes; indeed, such patterns are the norm there (Sadleir, 1969; Bronson, 1989). Despite the paucity of studies on long-lived tropical species, reproductive seasonality is increasingly known from the lower latitudes, too. The coati is extraordinary among that latter group, however, in the narrow, consistent timing of its reproductive events. Looking past species which appear to display no seasonality whatsoever, such as the sun bear (*Helarctos*

*malayanus*) in Borneo (Schwarzenberger *et al.*, 2004), seasonal reproductive events among tropical mammals are better thought of as indistinct statistical phenomena rather than clearly demarcated ecological events. Spotted hyena (*Crocuta crocuta*) populations distributed across very low latitudes reproduce throughout the year, but often with modest population-specific seasonal peaks (Holekamp and Smale, 2000). Acouchies (*Myoprocta exilis*), agoutis (*Dasyprocta leporina*) and pacas (*Agouti paca*) at 6°N latitude similarly give birth throughout the year, albeit with apparent seasonal peaks (Dubost *et al.*, 2005). White-lipped peccaries (*Tayassu pecari*) at 8°N latitude and saddle-back tamarins (*Saguinus fuscicollis*) at 12°S latitude both display birth peaks coincident with greatest food availability in the first half of the wet season, as does the coati, but the peccary's mating period has been documented to last at least eight months (Altrichter *et al.*, 2001) and the tamarin's parturition period spans a similar length of time (Goldizen *et al.*, 1988). A population of the Ethiopian wolf (*Canis simensis*) times reproduction somewhat more finely at 7°N latitude, displaying a parturition period of about four months (Sillero-Zubiri *et al.*, 1998). Extremely few studies have as yet been conducted on or in the very near vicinity of the equator, but at least one species there has already been found to display seasonal reproduction: mandrills (*Mandrillus sphinx*) exhibit a 6-month mating period (Abernethy *et al.*, 2002).

Wherever it is found, reproductive seasonality for most long-lived mammals appears to be a strategy of optimization. As such, the degree of variation seen in the timing of specific reproductive events should reflect the selective pressures that favor those events taking place at the most advantageous times. So why is the same adaptation so often expressed so differently in the tropics than it is at the higher latitudes?

Two related arguments that have been posited are that optimal conditions occur over a longer time period or selective pressures favoring seasonality are otherwise weaker in the tropics than at higher latitudes because of the less variable/more benign climates generally thought to exist in the former region. However, many (perhaps even most) tropical locales fail to live up to

such rosy expectations (Foster, 1982a; Bronson and Heideman, 1994). Even setting that fact aside, selective pressures weak or strong are still selective pressures. Given an evolutionary timeframe, species—or more accurately, their populations—should respond to those pressures as best they are able.

Bronson and Heideman (1994) have argued persuasively that reproductive seasonality is generally less well-defined in the tropics because animals residing there have less reliable or distinct proximate cues upon which to rely. Photoperiod, the most universally relied upon *zeitgeber* for long-lived mammalian reproduction (Sadleir, 1969; Bronson, 1989), obviously diminishes in degree of both annual and daily change as one proceeds from the poles to the equator. Tropical rains and their innumerable effects on food availability, although often apparently consistent enough over history to promote the evolution of reproductive seasonality, generally vary too much from year to year to serve as predictive cues for timing specific reproductive events. Other possible cues appear even less reliable.

It is unknown at what point photoperiodic changes become too slight for animals to use them to time or fine-tune the timing of their reproduction (Bronson and Heideman, 1994), but of course such timing depends on the extent of both the photoperiodic changes themselves and the genetic variability of the populations subjected to them. One prediction based on this premise in combination with the assumption that there are no latitudinally based differences in population genetic variability is that long-lived seasonal species (or even closely related groups of species) should display a broadening and perhaps ultimately a disappearance of peaks in reproductive events in populations at increasingly low latitudes, and this has been amply demonstrated to occur (Bronson, 1985; Di Bitetti and Janson, 2000). Bronson (1989) also suggested that social species should be able to time their reproduction more finely than would otherwise be possible at low latitudes by using interactive cues to augment environmental cues, *i.e.*, the reproductive responses of the most environmentally sensitive individuals in a population could socially trigger like responses in the population's remainder. In accordance with this prediction, the tropical

mammals that have thus far been found to exhibit relatively narrow reproductive seasonality are indeed social species (*e.g.*, ring-tailed lemurs, *Lemur catta*; Jolly, 1967; impalas, *Aepyceros melampus*: Murray, 1982; greater spear-nosed bats, *Phyllostomus hastatus*: Porter and Wilkinson, 2001; red ruffed lemurs, *Varecia rubra*: Vasey, 2005). The coati may simply be one of the most extreme examples of such found to date. (This subject is examined in greater detail in Chapter 3).

The discussion does not end there, however. As O'Brien (1993) emphasized, lamentably few long-lived tropical mammals have so far been examined for the possibility—let alone the extent—of reproductive photoresponsiveness and, with the exception of Nile grass rats (*Arvicanthis niloticus*: Sicard *et al.*, 1992), all of the short-lived tropical species that have so far demonstrated any photoresponsiveness whatsoever in the laboratory have displayed continuous or opportunistic reproduction (*i.e.*, free from predictive cues) in the wild. Looking farther abroad taxonomically, spotted antbirds (*Hylophylax n. naevioides*) at 9°N latitude in Panama show reproductive physiological responsiveness to the very slight natural changes in daylength found at that latitude (Hau *et al.*, 1998). If tropical mammals possess similar capabilities, that of course merely begs the question of why they do not utilize them more often. To the delight of the curious, scientific endeavors invariably raise more questions than they answer.

## CHAPTER 3 BIRTH SYNCHRONY

### **Introduction**

In the absence of extraordinary selective pressures, reproductive seasonality is a strategy of optimization. As such, it often allows for considerable variation in the timing of specific reproductive events, even within a single population of an obligate seasonal species. This is especially true in the tropics, where annual variation in photoperiod is slight and other potential environmental predictors may be patchy or may shift somewhat from year to year in response to climatic conditions (*e.g.*, rainfall; Rand and Rand, 1982). For example, as Russell (1982) pointed out, birth peaks among Panama's seasonally reproducing mammals are largely probabilistic events; birth periods for most species span at least a few months (summarized in Fleming, 1973).

The white-nosed coati is unusual in this regard, with all parturition on Barro Colorado Island (BCI), Panama—the only population previously well-studied—seemingly occurring within a 1- to 2-week period each year (largely inferred from observations of first emergence of young from nests; Kaufmann, 1962; Russell, 1979; 1982). This pattern prompts consideration of ecological pressures favoring a high degree of birth synchrony in the species. [Note: The terms reproductive seasonality and synchrony have sometimes been used interchangeably (*e.g.*, Boinski, 1987), leading to confusion about the nature and causes of these phenomena. The author has adopted Ims' (1990b) definition of reproductive synchrony: "a phenomenon caused by biological interactions operating to produce a tighter clustering of reproductive events than would have been imposed by environmental seasonality alone" (p. 135).]

Adult female coatis are also highly social, living in cohesive bands with their young most of the year and becoming solitary only to nest (Kaufmann, 1962). Russell (1982; 1983)

emphasized the importance of cooperation among adult females to minimize losses of young to predation and parasitism, and (1982) suggested that a high degree of both intra- and interband birth synchrony exists to facilitate this strategy. Other possible explanations more generally offered for birth synchrony include predator swamping (Pianka, 1976), dependence upon an ephemeral food or other resource (*e.g.*, the need of some desert anurans for breeding ponds), or utilization of social mechanisms to supplement inadequate environmental predictors (*e.g.*, photoperiod at low latitudes) employed in a seasonal reproductive strategy (Bronson, 1989).

None of these explanations has yet been rigorously examined for the coati, nor has birth synchrony even been established as a general phenomenon in the species (although a handful of reports suggest that coati reproduction may be patterned similarly at other locations, *e.g.*, in southern Arizona: Gilbert, 1973; in Costa Rica: Sáenz, 1994; in Jalisco, Mexico: Valenzuela and Ceballos, 2000). It seems reasonable to rule out transitory requirements as an explanation for birth synchrony in this long-lived, tropical forest-dwelling mammal, however, and no such requirements were discovered during the extensive observations of BCI's coatis by Kaufmann (1962), Russell (1979) and Gompper (1994).

Accordingly, this study examines data on the timing of coati reproductive events at Tikal National Park, Guatemala, to provide details on birth synchrony at this new locale and to test specific predictions about the phenomenon based on the following hypotheses:

*H<sub>1</sub>: Coati birth synchrony minimizes juvenile mortality by facilitating communal care of young.*

The five- to six-week nesting period (Chapter 2) is the least social time in the lives of female and juvenile coatis, so communal care cannot become a relevant factor until the animals have reaggregated into bands after the young have emerged from the nest. Birth synchrony would be relatively useless for facilitating communal care if subsequent reaggregation is too asynchronous. It was therefore predicted that within a band of coatis, the variance in the timing of reaggregation is no greater than in that of parturition.

*H<sub>2</sub>: Birth synchrony minimizes juvenile mortality by predator swamping.*

Even the largest bands of coatis do not include more than about a score of reproductive females in a given year (Booth-Binczik, 2001; Chapter 2), and predators are capable of consuming an entire litter of newborn coatis in short order (*e.g.*, Rose, 1997). There is also much home range overlap among neighboring coati bands (Kaufmann, 1962; Gompper, 1997). To swamp predators rather than merely prompt them to shift their focus from band to band, then, birth synchrony would have to exist across as well as within bands. Hence it was predicted that the variance in the timing of parturition between bands is equal to that within bands.

*H<sub>3</sub>: Birth synchrony results from the coati's reliance upon social mechanisms to enhance reproductive seasonality.*

If coatis are relying upon social mechanisms to augment weak environmental cues for timing reproduction, it is reasonable to assume that this process will result in a greater degree of birth synchrony within than between bands. In opposition to the prediction of *H<sub>2</sub>*, therefore, this hypothesis generated a prediction that the variance in the timing of parturition between bands is greater than that within bands.

It should be noted that the aforementioned three hypotheses are in fact independent rather than mutually exclusive alternatives; more than one may pertain. Further, whereas the first two hypotheses directly address possible ultimate causes of birth synchrony, the third instead addresses a proximate mechanism by which the ultimate factor of seasonal food availability (see Chapter 2) may contribute to the coati's tight clustering of birth.

## **Methods**

From June 1994 through October 1996, various data were collected on a population of free-ranging white-nosed coatis in Tikal National Park, Guatemala (17°N, 89°W) as part of a broad study of the species' reproductive biology. (An overview of the coati's reproductive pattern at this locale appears in Fig. 3-1.) This chapter specifically examines data on the timing of parturition in 1995 and 1996, and the reaggregation of parous females after nesting in 1996.

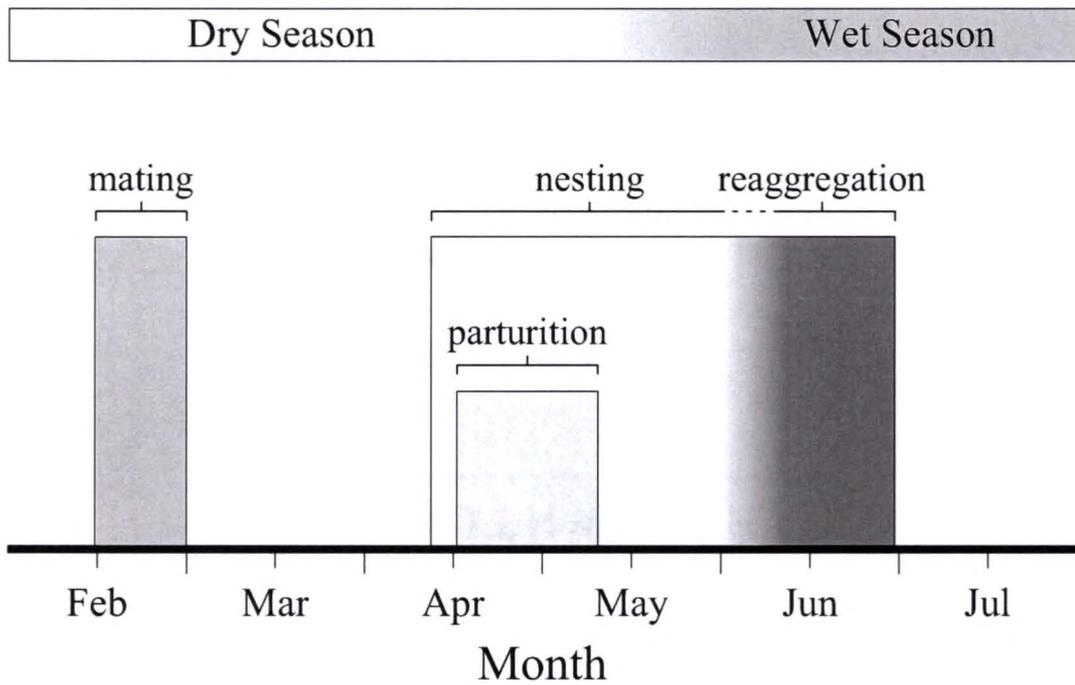


Figure 3-1. Timeline of white-nosed coati reproductive phenological events in Tikal National Park, Guatemala (see Chapter 2).

In all, reproductive events occurring among 28 females from three bands contributed to the study. Each female was initially captured by live-trap or (more often) blowgun and chemically immobilized by intramuscular injection of approximately 7 mg/kg Telazol (Fort Dodge Laboratories Inc., Fort Dodge, IA). Anesthetized animals were tattooed and eartagged for identification and fitted with 90 g motion-sensitive radiocollars (Advanced Telemetry Systems, Isanti, MN) to enable monitoring thereafter. The animals were subsequently habituated to the close presence of observers (as described in Chapter 2), and the status of each female was checked daily (as possible) during the time periods when parturition and (in 1996) reaggregation took place. All animal handling procedures were conducted as per protocol #4084 approved by the University of Florida's Institutional Animal Care and Use Committee.

**Parturition** was determined to have occurred when a female showed a sudden pronounced reduction in girth followed by continued nesting behavior, and was ultimately confirmed by observation of young still in the nest or shortly after emergence from the nest. Parturition dates could not usually be pinpointed because the females tended to give birth while remaining out of sight within their nests for days at a time. In this circumstance the scoring of a female's parturition was distributed over an appropriate span of time (*e.g.*, one-third of the female's parturition was ascribed to each of three possible days). Data on females of indeterminate status for two weeks or longer were not utilized.

For the purpose of this study, **reaggregation** was deemed to have occurred when a postpartum female and her young were observed to have reunited with at least three other such females. In most cases reaggregation dates could not be pinpointed and were scored as described above for uncertain parturition dates.

Sokal and Rohlf (1981) guided all statistical efforts, and a  $P_{\alpha} \leq 0.05$  level of significance was utilized in all tests. In order to assess whether the variance in the timing of parturition was greater than or equal to that of reaggregation, *i.e.*, to test the communal care prediction, a one-tailed test for equality of two variances was conducted for each of the two coat bands that

contributed almost all of these data in 1996; data on a single female from a third band were included in the descriptive statistics presented for this year. An ANOVA was conducted to compare the variances in the timing of parturition between and within the two primary bands in 1996, *i.e.*, to test the predictions for predator swamping and social facilitation of reproductive seasonality. Insufficient data were obtained for the 1995 parturition period to include in such analyses, and these data were therefore used only for comparison with the 1996 parturition period via descriptive statistics. To aid in comparing the annual birth pulse of the coati in Tikal to that seen at other locales and/or in other species, the interquartile range (*i.e.*, middle 50%) was also calculated for each year's data.

### Results

Coati parturition was both narrowly timed within each year and consistent between the years of the study (Table 3-1). The nine births recorded in 1995 occurred in a slightly flattened but normally distributed peak of 14 days duration, and the 24 births recorded in 1996 occurred in a similar peak lasting 18 days. These peaks were centered six days apart late in the dry seasons/at the beginning of the wet seasons (see Chapter 2) of their respective years.

There was a discernible difference in the timing of parturition between the two primary bands under observation in 1996 (Fig. 3-2), with Band 1 females giving birth over a 14-day span that began four days after the start of the 12-day span in which Band 2 females did so. Mean birthdates in the two normally distributed birth peaks were 2 May and 27 April, respectively. The variance in the timing of birth between Bands 1 and 2 was significantly greater than that within the bands ( $F_{[1,21]} = 24.21, P < 0.001$ ).

Reaggregation in 1996 occurred relatively quickly after females first brought their young down from their nests between the early and middle wet season (see Chapter 2). Eleven females with young from Band 1 found at least three other such families within a 20-day span beginning 31 May, and nine females with young from Band 2 accomplished it in 16 days beginning 4 June. Comparing parturition to reaggregation within each band: The variance in the timing of

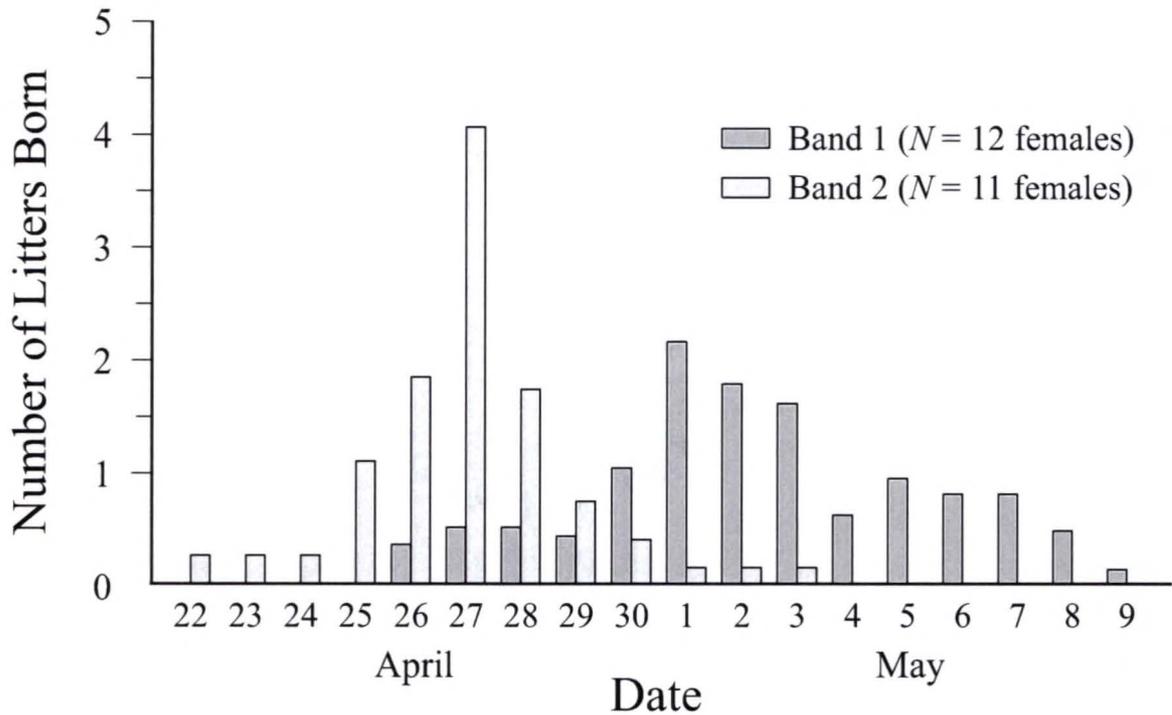


Figure 3-2. Timing of births in neighboring white-nosed coati bands in Tikal National Park, Guatemala, in 1996. Scoring of a female's parturition distributed over appropriate span of time when date not pinpointed (e.g. 1/3 of female's parturition ascribed to each of three possible days); mean ( $\pm$  SEM) span for all females  $3.9 \pm 0.6$  days, range 1-10 days.

reaggregation was significantly greater than in that of birth in Band 2 ( $F_{[8,10]} = 8.77, P = 0.001$ ). Band 1 displayed the same tendency, but it was not significant ( $F_{[10,11]} = 2.28, P = 0.10$ ).

### Discussion

The communal care hypothesis for coati birth synchrony assumes that the presence of multiple females at the same reproductive stage is important to the survival of young. Certainly, evidence suggests that coati sociality is employed in group defense, including of offspring. Russell (1983) found that BCI's coati bands adopted a formation that was optimal for protection of young rather than foraging efficiency when moving through the forest. He further reported that juveniles spent more time vigilant when unaccompanied by adults, and adults were more vigilant in smaller groups. This latter finding was also confirmed by Burger and Gochfeld (1992) in Costa Rica. However, the presence of the band may actually be more important to the survival of adult females than of juveniles, as mortality rates of females are higher when they are alone than when they are in groups (Booth-Binczik, 2001; Hass and Valenzuela, 2002) and female mortality is lower in larger groups, whereas juvenile mortality is not (Hass and Valenzuela, 2002). There are no published data on relative mortality rates of juveniles before and after band reaggregation, and direct observations of predation are few. During the course of the present study a pair of crested eagles, *Morphnus guianensis*, was observed taking five coati infants to its

Table 3-1. Descriptive statistics for observed white-nosed coati birth periods in two years in Tikal National Park, Guatemala.

Statistic	1995	1996
Number of Females / Bands	9 / 2	24 / 3
Parturition Period	16 - 29 April	22 April - 9 May <sup>a</sup>
Mean Birthdate	24 April	29 April <sup>a</sup>
Interquartile Range (days)	5	6
Degree of Kurtosis (- 3)	-0.62	-0.69

<sup>a</sup> calendar dates not strictly comparable because 1996 was a leap year

nest in a couple of weeks' time at about the end of the coati nesting period in Tikal, and other raptor species were occasionally observed preying upon nestling coatis as well (D.F. Whitacre, pers. comm.). Rose (1997) documented heavy predation on nestling coatis—principally within their first few weeks of life—by white-faced capuchins (*Cebus capuchinus*) in Santa Rosa National Park, Costa Rica, and Sáenz (1994) reported that this resulted in as much as 100% nestling mortality in some bands. Russell (1982) reported heavy juvenile mortality on BCI in the first three months following reaggregation, and Hass and Valenzuela (2002) estimated 43-75% mortality in the first 3-5 months of life in southern Arizona and Jalisco, Mexico. It appears likely that the risks faced by a young coati do indeed diminish in the company of its band, but the anti-predation benefits of group living do not depend on females being at the same reproductive stage.

Certain aspects of coati biology and two historical observations of coati behavior (albeit perhaps of a single animal) prompt special consideration of the adult male as a potential predator of young. The subject of infanticide by male coatis has been dealt with more fully by Booth-Binczik (2001), but brief mention in the course of this discussion of birth synchrony and communal care seems appropriate. Female coatis have been documented to undergo successful second reproductive cycles shortly after losing litters born at the normal time (Sáenz, 1994; Chapter 2), making sexually selected infanticide a possibility (Bertram, 1975; Hrdy, 1979). The fact that males are predominantly solitary has also been interpreted as a result of exclusion by females for the protection of their young (Russell, 1981). In support of his interpretation, Russell (1981) reported an apparently secondhand observation of an adult male coati on BCI consuming an infant near a biological laboratory animal feeding station, and another of an adult male (possibly the same animal) attacking and carrying an infant away from the same site on the following day. However, in Tikal most coati litters are multiply sired (Booth-Binczik, 2001), resulting in paternity confusion which would discourage sexually selected infanticide (Wolff and Macdonald, 2004). Male coatis are also not excluded from bands in Tikal, and in fact they frequently associate with bands there (Booth-Binczik, 2001) as well as in Arizona (Gilbert, 1973)

and Costa Rica (Sáenz, 1994). Moreover, despite several hundred–possibly thousands of–hours of field observations by several biologists at a few sites, no one other than Russell (1981) has uncovered any evidence of infanticide in the species. To the contrary, in Tikal adult male coatis were often seen in the near vicinity of young of all ages with neither the young nor their dams displaying any alarm or other defensive behavior (Booth-Binczik, 2001).

In addition to cooperative defense, other forms of communal care of offspring have been documented in the coati. Nest sharing has been observed both in the wild (Russell, 1979; 1983; Chapter 2) and in captivity (Smith, 1980). In some instances it involved a female that had lost a litter helping to care for another female's litter (Russell, 1979; Smith, 1980), and in one case two females pooled their litters and both nursed all infants (Russell, 1979). There have also been frequent observations of allogrooming by non-parents once bands have reunited after the nesting period (Russell, 1983; pers. obs.).

As important as communal care of whatever form may ultimately be to coati offspring survival, however, it does not appear to explain the species' remarkable birth synchrony, as a rather basic prediction arising from the communal care hypothesis failed testing in the current study. It is suspected but as yet unknown whether coatis undergo direct development (Chapter 2), but females are presumably able to exert at least as much control over the timing of reaggregation as parturition. Nonetheless, births were clustered significantly more than were reaggregation events. Selective pressures for being in a group are evidently not the driving forces behind coati birth synchrony.

Considering the aforementioned nest raiding by predators on coatis, the predator swamping hypothesis might at first look somewhat more attractive. The effectiveness of this anti-predation strategy, however, is determined not only by the degree of synchronization of a vulnerable prey stage but also by the nature of the predators and their methods. That is, if neighboring groups of prey differ somewhat in their timing and their predators are sufficiently mobile, the predators will simply respond by shifting their focus from group to group accordingly

(Ims, 1990a). Considering the mobility of coati nestling predators (especially raptors) and given the significantly greater variance in the timing of births between than within bands found in the present study, shifting predators appear to pose a real threat to coati young. The predator swamping hypothesis for birth synchrony is unsupported.

At least until new hypotheses and/or evidence are examined to account for coati birth synchrony, then, the most likely explanation appears to be that this phenomenon is merely an extreme example of a tropical animal using social cues to supplement the relatively weak environmental predictors it relies upon for timing reproduction. Some support for this argument is found in the results of the comparison of intra- and inter-band synchrony mentioned above.

Additional support can be found in a closer consideration of the coati's annual birth pulse. As mentioned, both the 1995 and 1996 overall peaks in parturition were slightly platykurtic, perhaps only differing from completely normal curves due to the method used for estimating uncertain birthdates, *i.e.*, attributing portions of each of these births to more than a single day. The coati has ample cause in terms of food availability to have developed the adaptation of reproductive seasonality (Russell, 1982; Chapter 2), which—barring severe climatic curtailment (*e.g.*, at very high latitudes) or protraction by variable response to weak environmental cues (*e.g.*, at low latitudes)—should produce a normally distributed biological response. That is, if the coati's annual birth pulse is driven purely by seasonal considerations, it should be normally distributed or flattened depending on the environmental predictors available to the species and its ability to respond to them. Accordingly, most seasonally reproducing tropical mammals studied to date display long, modestly peaked birth pulses (Fleming, 1973; Bronson, 1989; Di Bitetti and Janson, 2000; Chapter 2), and the notable exceptions are highly social species (Chapter 2). In contrast, the evolutionary forces that promote synchrony do so by acting against either tail of a response curve (*e.g.*, Findlay and Cooke, 1982), creating a leptokurtic distribution. The coati's normally distributed parturition peaks suggest that birth synchrony in and of itself is not adaptive in this species.

Given the likelihood of direct development in this species (Chapter 2), it is also possible that the coati's unusually tight clustering of births is simply the result of selection for mating synchrony. Synchrony of estrus among females should make it less possible for one male to monopolize mating access to a group of females (Emlen and Oring, 1977; Gehrt and Fritzell, 1999a). It could therefore be advantageous for females to synchronize their receptivity if it gives them access to more than a single male, enabling mate choice. However, some studies have failed to find a relationship between degree of synchrony in female receptivity and degree of monopolization by males (Poston *et al.*, 1999; Widdig *et al.*, 2004), and it has also been suggested that synchronized receptivity would limit rather than enhance females' opportunity for mate choice (Pereira, 1991; Schank, 2001). The nature of the relationship between mating synchrony and mate monopolization/mate choice undoubtedly depends upon the degree of overlap among females' periods of receptivity, which is not yet known for the coati.

Of course, it could be argued that to be most useful, the term "birth synchrony" should be reserved solely for situations in which selective pressures are acting directly on the clustering of births. From this viewpoint, the tight clustering of births exhibited by the coati would not qualify as birth synchrony *per se* if it results from such phenomena as reproductive seasonality and mating synchrony.

Left wholly unexplored is the question of precisely how the coati achieves such extraordinarily tight reproductive seasonality. Assuming social facilitation of environmental cues as appears to be the case, numerous possibilities exist. Among Mammalia social mechanisms for timing reproduction have primarily been investigated in rodents. Although in most cases the presence of chemical cues from reproductively active females inhibits ovarian cycling in others (reviewed in Bronson, 1989), in some situations it has instead been found to trigger (Drickamer and Hoover, 1979) or synchronize (McClintock, 1978) such cycling. Males have also been shown to use both chemical and tactile means of initiating and/or synchronizing female reproductive cycling (Whitten, 1956; Marsden and Bronson, 1964; Bronson and Maruniak, 1975;

Carter *et al.*, 1986), and in the case of red deer (*Cervus elaphus*), even to use auditory signals (McComb, 1987). On that last bit of information, it is perhaps worth noting that the coati is the first carnivore to be identified in which males undergo a rut (Chapter 4), and that a hallmark feature of this male adaptation is an advertising call. With opportunity, this will be a focus of future research.

## CHAPTER 4 RUT

### **Introduction**

Long mistaken for a separate species due to its larger size and markedly different habits (*e.g.*, Sanderson, 1941), the male white-nosed coati (*Nasua narica*) has received far less attention than has the female from researchers. This disparity in scientific effort is perhaps a result of the chiefly solitary nature of adult males (Kaufmann, 1962; Booth-Binczik, 2001) and the problems it poses to one wishing to work with these diurnal, semi-arboreal, medium-sized carnivores in their primarily dense, tropical forest habitat (general ecology reviewed by Gompper, 1995). Previous discussions of coati reproductive ecology addressed only the timing of reproductive events and possible benefits of seasonality to females and young (Kaufmann, 1962; Smythe, 1970; Russell, 1982). This paper focuses instead on reproductive patterns displayed by the male of the species.

Environmental influences act on females in determining a species' timing of birth, and males can be expected to respond to female imperatives or (in some instances) the environment which shaped them with reproductive adaptations of their own. Males of many species are opportunists, maintaining full reproductive readiness at all times for whatever mating chances occur, but many other species have evolved temporal variation in male reproductive capabilities in ways that reflect patterns of female receptivity. This variation seems designed both to maximize the males' ability to capitalize on mating opportunities when they exist and to minimize the costs associated with that ability when they do not. One such temporal pattern seen among male mammals involves rut.

The term "rut" has often been used to describe a seasonal, principally or wholly behavioral phenomenon displayed by males of some species or populations (*e.g.*, the "fall rut" of

several high latitude North American ungulates; Spomer, 1996). Sometimes it has even been used simply as shorthand for the mating period of any seasonally reproducing species (*e.g.*, Genovesi *et al.*, 1997). From an evolutionary perspective, however, rut might more properly be thought of as an attribute of individual males rather than of seasons, species or populations as a whole. Accordingly, the author defines rut as a brief annual period of dramatically enhanced male reproductive capability that likely arose in response to tight female reproductive seasonality in combination with the intense male-male competition such seasonality sometimes fosters, and that therefore tends toward synchrony within a population. It differs from other forms of male reproductive seasonality not only in the brevity and magnitude of the changes rutting males undergo, but also in the nature of those changes. Specifically, males in rut display a fugue of behavioral, physiological and anatomical characteristics that—despite some seeming maladaptive at first glance—act in concert to temporarily maximize competitive ability and thus likely reproductive success.

Besides being interesting in their own right, male reproductive adaptations can also provide insight into a species' overall reproductive strategy. One example is presented in the case of mammals in which the males undergo seasonal aspermatogenesis. Of interest in studies of species displaying seasonal reproduction is whether the pattern is a (relatively) rigid evolutionary result of historical climatic rhythms or merely an opportunistic response to prevailing conditions, *i.e.*, whether it is an obligate or facultative strategy (Negus and Berger, 1972; Bronson, 1989). Because spermatogenesis takes longer to complete than does ovulation after a period of reproductive quiescence, and because males are evolutionarily impelled to have mature sperm available whenever females might be ready to receive such, healthy adult male mammals have generally evolved to produce mature sperm over time periods that more than encompass periods of female receptivity (Bronson, 1989). Seasonal aspermatogenesis is thus *prima facie* evidence that a species has adopted obligate reproductive seasonality, as such an extreme male adaptation

would be expected to arise only where females have a highly predictable pattern of receptivity, especially where the potential costs of male reproductive capability are great.

The coati certainly fulfills the first part of this evolutionary scenario, being exceptional among tropical mammals (Fleming, 1973) for its high degree of reproductive seasonality at the few locales thus far examined (Kaufmann, 1962; Russell, 1982; Chapter 2). The pattern seen in Tikal National Park, Guatemala, may be typical in this respect. There, virtually all copulation occurs within an approximately two-week period near the middle of the January-April dry season and parturition occurs in a similarly brief period beginning shortly before the onset of the rains in May (Chapter 2).

There is also reason to hypothesize high costs of reproduction for male coatis. Unlike males, female coatis are highly social, living in cohesive bands with their young most of the year and becoming solitary only to nest and give birth (Kaufmann, 1962; Chapter 2). Combined with the species' brief mating period, the result is a temporal and spatial clustering of receptive females that could be expected to foster intense competition among males. Indeed, anecdotal observations of male coatis by previous researchers suggest such competition exists. Chapman (1938) and Kaufmann (1962) noted marked seasonal changes in male body condition. They and Gilbert (1973) also attributed a seasonal proliferation of serious injuries among males to intrasexual agonism during the mating period.

This study was undertaken to determine the extent and results of male reproductive competition in the coati and to evaluate the hypothesis that male coatis have evolved adaptations to maximize their competitive ability and minimize their associated costs. Specifically, year-round data on male behavior, physiology and anatomy were collected to test the prediction that male coatis exhibit periods of enhanced and reduced reproductive capability in a pattern which reflects that of female receptivity.

## Methods

### General

As part of a broader study of white-nosed coati reproductive biology in Tikal National Park, Guatemala (17°N, 89°W), behavioral, morphometric and endocrinologic data were collected on 24 free-ranging adult male coatis (plus one found freshly road-killed) from June 1994 through October 1996 (except as noted below). A male was considered adult once it dispersed from its natal band, which typically took place 1-2 months prior to the mating period in its second year of life (*i.e.*, at 20-21 months of age).

Each male was initially captured by live-trap or (more often) blowgun and chemically immobilized by intramuscular injection of approximately 7 mg/kg Telazol (Fort Dodge Laboratories Inc., Fort Dodge, IA). Anesthetized animals were tattooed and eartagged for identification, weighed, measured and subjected to blood collection. Each male was also visually examined to determine general physical condition, giving particular attention to the nature and abundance of any injuries. Identified injuries were fresh scars, open wounds and missing body parts. Eighteen of the coatis were additionally fitted with 90 g motion-sensitive radiocollars (Advanced Telemetry Systems, Isanti, MN) to enable subsequent location and recapture, and to confirm death if such occurred. Individual males were recaptured by blowgun (never more often than monthly) for resampling. The research was conducted under Institutional Animal Care and Use Committee protocol #4084 from the University of Florida. All animal handling procedures were conducted in accordance with National Institutes of Health standards.

### Behavior

Four radiocollared males were habituated to the close presence of observers (see Chapter 2) and then utilized for behavioral data collection from September 1995 through August 1996. Observation sessions were scheduled twice monthly for each available male (although frequent radiotransmitter failures often resulted in fewer males being available at any given time), and in each case began as soon as possible after locating the focal animal in the morning (typically

06:00-09:00) and continued for the next 4-6 h thereafter. Two observers were always present, one of whom was responsible for monitoring and recording behavior and the other for estimating the distance traveled by the focal animal via a tally counter as well as assisting in keeping the animal in sight. The same people performed the same observational tasks throughout the study, except that on eight occasions substitutes filled in for the second observer after cross-training and calibration sessions were conducted to ensure uniformity in coati travel distance estimation.

During each observation session, the amount of time spent by the focal male with a coati band versus alone was recorded, and the nature and duration of all interactions involving the male were recorded. A male was considered to be with a band if the observer following him could see any band member, typically less than 30 m distant. The frequency and/or duration of other behaviors were recorded during the first 5 min of every quarter hour. The following states and behaviors were utilized in the analyses: Active - doing anything other than sitting or lying down. Interaction - two or more animals apparently altering their behavior in response to one another. Agonism - aggressive or defensive interaction. Fight - agonistic interaction involving chasing, knocking each other out of trees, or actual or attempted biting and/or clawing. Approach - one individual orienting toward and moving to within touching distance of another. Scentmark - briefly (approximately 1 sec) rubbing the genital region against some substrate. Forage - bringing the nose into close proximity or manipulating various substrates in apparent search of invertebrates or fallen fruit, or similarly investigating fruit-bearing portions of plants. Groom - manipulating one's own body parts with mouth or paws. Travel - moving from one place to another with the head not oriented toward any substrate, *i.e.*, not apparently foraging. Rut call - producing a rhythmic, staccato, low-pitched vocalization which appeared to fall into Kaufmann's (1962) "grunting" (p. 123) classification; distinguishable from similar vocalizations (*e.g.*, grunting in alarm) by the combination of its slower cadence, greater loudness and much longer duration (typically several minutes at a time) as well as by the situation in which it was produced.

## Morphometry

Each male's teeth were visually examined for damage (such as broken tips) during each immobilization, and intact lower canines were measured from gum line to tip with calipers. If both teeth were undamaged, lengths (to the nearest 0.1mm) were averaged; otherwise only the length of the intact tooth was obtained. For comparative purposes, these same data were obtained for the teeth of females immobilized during a companion study.

An index of each male's body fat level was determined at the time of immobilization. This was accomplished in the manner of Hossler *et al.* (1994) by pinching a fold of the animal's skin at the back of each rear leg midway between knee and hip, and using calipers to measure the thickness of this fold to the nearest 0.1 mm. Measurements for the left and right thighs were averaged. One person was responsible for taking these measurements throughout the study.

Testis size was also measured during each immobilization, and from the measurements an index of testis size was determined. The scrotal skin was pulled taut around each testis and three axes were measured with calipers to the nearest 0.1 mm: the longest dimension ( $L$ ), the widest perpendicular dimension at midlength ( $W_1$ ), and the midlength dimension perpendicular to both of these ( $W_2$ ). One person took all measurements. Opportunistic dissections of two freshly road-killed coatis (one radiocollared, the other previously uncaptured) revealed a layer of fat surrounding the testes ranging from scarcely visible on 7 June 1995 to as much as 5 mm thick on 9 January 1996. To compensate for this in approximating an animal's actual testis size, a correction factor  $Y = 0.77X - 2.23$  was subtracted from each of the aforementioned dimensions, with  $X$  being the fat level index of the animal at the time of examination. (For this purpose, the fat level index of one coati for which leg pinch measurements were lacking was approximated from a regression of all available fat data on time of year.) The above equation represents the line connecting two points which were obtained by assigning the minimum and maximum fat level indices recorded in the course of the study  $Y$ s of 0 and 10 (*i.e.*, representing fat layers of 0 and 5 mm thick present on each side of a measured testis), respectively. This likely resulted in a

conservative correction of testicular dimensions, as 5 mm may have been a low approximation of the maximum possible scrotal fat layer. The adjusted testicular dimensions were then plugged into the formula for calculating the volume of an ellipsoid,  $V = L \times W_1 \times W_2 \times \pi/6$ , and the left and right testis volumes so obtained were averaged to produce the testis size index reported. (The raw data on coati testis size are presented in the Appendix.)

### **Endocrinology**

Five to 10 ml of venous blood were drawn from a foreleg of each immobilized coati. Blood was kept in an ice bath from the time of collection until the serum could be separated by centrifuge 2-4 h later and then frozen. Fecal samples were also collected whenever possible during immobilizations, and additional samples were obtained opportunistically from males under observation. In either case, an entire fecal deposit was collected within 5 min of defecation and maintained at ambient temperature for 2-6 h, after which it was homogenized and a sample of up to 10 ml was frozen. All serum and fecal samples were first held in liquid nitrogen and then at the completion of the fieldwork were transferred to a  $-70^{\circ}\text{C}$  laboratory ultracold freezer for storage until they were analyzed *en masse* by testosterone radioimmunoassay (RIA).

Prior to analysis, a malfunction of the ultracold freezer resulted in all serum and fecal samples thawing for a period estimated to have been 1-2½ weeks. The effect of this thawing on the androgen content of the samples is not known. The endocrinologic data presented herein should therefore be considered representative of the pattern but not necessarily of the actual testosterone levels circulating in or excreted by coatis.

**Serum Testosterone RIA.** Serum testosterone concentrations were determined via an RIA procedure (Guillette *et al.*, 1996) utilized previously for a wide variety of species and validated for coati serum. Duplicate 50 µl aliquots of serum were extracted twice with 2.5 ml -  $30^{\circ}\text{C}$  ethyl ether, dried under filtered air and reconstituted in 100 µl borate buffer (0.5 M, pH 8.0). To these were added 100 µl bovine serum albumen solution (0.75% BSA in borate buffer),

200  $\mu\text{l}$  testosterone antiserum (T3-125 at a final concentration of 1:18,750; Endocrine Sciences, Calabasas Hills, CA) and 100  $\mu\text{l}$  [1,2,6,7- $^3\text{H}$ ]-testosterone radiolabel (TRK-921 diluted in borate buffer to approximately 13,000 cpm/100  $\mu\text{l}$ ; Amersham Life Science, Inc., Arlington Heights, IL). Assay tubes were then vortexed briefly and incubated overnight at 4°C. Bound-free separation was achieved by adding 500  $\mu\text{l}$  5% charcoal/0.5% dextran in phosphate-buffered saline and then centrifuging the tubes for 30 min at 2000 g, 4°C. The supernatant was decanted, diluted with 5 ml scintillation cocktail (Scintiverse BD, Fisher Scientific, Fair Lawn, NJ) and counted on a scintillation counter (Beckman LS 5801, Beckman Coulter, Inc., Fullerton, CA).

Counts-per-minute were averaged for each pair of duplicates, and these were subjected to Rodbard and Lewald's (1970) logit transformation. Testosterone concentrations were determined by comparison of transformed data to a logit-log plot of 10 standards, ranging from 3.125 pg to 1600 pg hormone per assay tube, which were also run in duplicate in each assay. Naturally low, medium and high testosterone concentration serum pools were also run in duplicate in each assay as a check on inter-assay variance. Final testosterone concentrations were calculated as ng/ml serum, and are reported without correction for assay accuracy.

Two assays were conducted to analyze samples, and three more to complete validation. For all sample pairs, the mean ( $\pm$  SEM) duplicate coefficient of variance (CV) was  $3.5 \pm 0.4\%$ , and  $r > 0.99$  for the standard curve fit in all assays. Non-specific binding averaged  $2.6 \pm 0.6\%$ . Inter-assay CVs in low, medium and high pools of serum were 17%, 7% and 12%, respectively. The minimum detectable concentration of testosterone, based on the mean - 2SD percentage of bound radiolabel observed in five pairs of charcoal-stripped serum, was 0.04 ng/ml. A standard curve prepared by spiking charcoal-stripped serum (four pairs at each standard concentration) was parallel to that made using borate buffer (test for homogeneity of slopes  $F_{[1,16]} = 0.14$ ,  $P > 0.75$ ); assay accuracy as determined by spike-recovery was 102%. Serial dilutions (one pair each at 30  $\mu\text{l}$ , 50  $\mu\text{l}$  and 70  $\mu\text{l}$ ) of low, medium and high pools produced flat lines with CVs of 13%, 8% and

4%, respectively. Intra-assay CVs in low, medium and high pools (five pairs of each pool) were 6%, 6% and 7%, respectively. Cross-reactivities greater than 1% reported by the antiserum's manufacturer were: dihydrotestosterone 44.0%,  $\delta$ -1-testosterone 41.0%,  $\delta$ -1-dihydrotestosterone 18.0%,  $5\alpha$ -androstan- $3\beta$ , $17\beta$ -diol 3.0%, 4-androsten- $3\beta$ , $17\beta$ -diol 2.5%,  $\delta$ -4-androstenedione 2.0% and  $5\beta$ -androstan- $3\beta$ , $17\beta$ -diol 1.5%.

**Fecal Testosterone RIA.** Fecal testosterone concentrations were determined much as described for serum, except fecal steroid extraction was accomplished via a slightly modified version of the "short method" described in Wasser *et al.* (1994), and this procedure as well as the subsequent assay were validated for coat feces. Fecal samples were lyophilized at  $-55^{\circ}\text{C}$  under vacuum exceeding  $100 \times 10^{-3}$  mBar and then ground to fine powder (removing discernible extraneous material such as seeds, insect parts, etc.). For each sample, 0.1 g of powder was lightly boiled for 20 min first in 5 ml and subsequently in 2.5 ml of 90% ethanol, and the supernatant was dried under filtered air and reconstituted in 1 ml absolute methanol. The methanol suspension was diluted 100  $\mu\text{l}$  to 7.4 ml borate buffer, and 100  $\mu\text{l}$  of the resulting solution were pipetted into duplicate tubes and treated as per reconstituted serum extract in the RIA described above. The 10 standards utilized in the fecal RIA ranged from 1.5625 pg to 800 pg hormone per assay tube. Final concentrations were calculated as ng/g dried feces, and are reported without correction for assay accuracy.

Samples were analyzed in two assays, and validation was completed in another four. The mean CV for sample duplicates was  $1.8 \pm 0.2\%$ , and  $r > 0.99$  for the standard curve fit in all assays. Mean non-specific binding was  $0.6 \pm 0.1\%$ . Inter-assay CVs in low, medium and high fecal pools were 7%, 9% and 8%, respectively. The minimum detectable concentration of testosterone, based on the mean - 2SD percentage of bound radiolabel observed in six pairs of a naturally very low testosterone fecal pool, was 17 ng/g. A standard curve prepared by spiking the very low pool (four pairs at each standard concentration) did not differ statistically from that

made using borate buffer (test for homogeneity of slopes  $F_{[1,16]} = 0.58$ ,  $P > 0.5$ ); spike-recovery accuracy was 111%. Serial dilutions of a medium pool (one pair each at 50  $\mu\text{l}$ , 75  $\mu\text{l}$ , 100  $\mu\text{l}$ , 125  $\mu\text{l}$  and 150  $\mu\text{l}$  methanol suspension diluted in borate buffer to a total of 7.5 ml solution) produced a flat line with a CV of 8%. Intra-assay CVs in low, medium and high pools (five pairs of each pool) were 3%, 6% and 1%, respectively.

### Statistical Analyses

Observations obtained in companion studies of female coatis conducted over the entire 2  $\frac{1}{2}$ -year sojourn in Tikal (Booth-Binczik *et al.*, 2004; Chapter 2) were used to delineate three distinct annual periods to aid in data presentation and analysis:

- The *non-rut period* comprised the nearly 11 months of the year that occurred outside of the pre-mating and mating periods, from 29 February or 1 March (depending on year) through 22 January.

- The *pre-mating period* comprised the three weeks leading up to the mating period during which multiple male coatis (as opposed to one or none) were regularly detected accompanying a given band at a given time, from 23 January through 12 February.

- The *mating period* comprised the 16 days during which copulations were noted, from 13 February through 28 February.

In some analyses data for the pre-mating and mating periods were combined into a single rut period which was then compared to the non-rut period.

Whenever possible, each male was sampled repeatedly within each period every year, but was in general represented by only a single data point per period in a given statistical test. This was accomplished by averaging a male's subsamples where collection effort was equal (*e.g.*, in the case of multiple immobilizations) and adding subsamples where it was not (*e.g.*, in the case of multiple observation days of varying lengths). The exception was in evaluating the correlation between serum and fecal testosterone concentrations, in which all sample pairs (*i.e.*, serum and

feces collected from the same animal at the same time) were treated as independent; individual contributions to this dataset ranged from one to five sample pairs per represented male.

Sokal and Rohlf (1981) guided all statistical efforts, and STATGRAPHICS Plus 5.1 software (Manugistics, Inc., Rockville, MD) aided computations. Datasets for comparing the three periods first underwent a battery of tests for homoscedasticity and normality (using a conservative  $P_\alpha \leq 0.10$  level of rejection), and were subjected to standard transformations if such were indicated. When raw or transformed data met parametric assumptions, two-way ANOVAs were conducted treating period and male as main effects (male effects were never found to be significant and are not discussed further); otherwise the data were analyzed via Kruskal-Wallis tests. Fisher's Least Significant Difference procedure was used to distinguish among periods when overall significance was detected. Two-tailed  $t$ -tests were conducted instead of ANOVAs in the few cases where only two groups were compared. A  $P_\alpha \leq 0.05$  level of significance was utilized in all reported statistical tests.

## Results

Males interacted on 26 (90%) of the 29 occasions when they came within sight of one another during scheduled observations. All male-male interactions quickly escalated into relatively brief but intense physical altercations with few or no apparent preliminaries. Male coatis fought sporadically throughout the year, but the frequency of such contests increased during the pre-mating period and peaked during the mating period (Fig. 4-1). The frequency of male-male agonism in the three defined periods of non-rut, pre-mating and mating could not be statistically distinguished ( $H_{[4,4,3]} = 4.66, P = 0.097$ ). However, focusing instead simply on a comparison of non-rut to rut (the latter being pre-mating and mating combined) revealed fighting to be significantly more common during rut ( $0.41 \pm 0.18$  fights/hr versus  $0.04 \pm 0.01$  fights/hr during non-rut; paired  $t_{[3]} = 3.63, P = 0.036$ ).

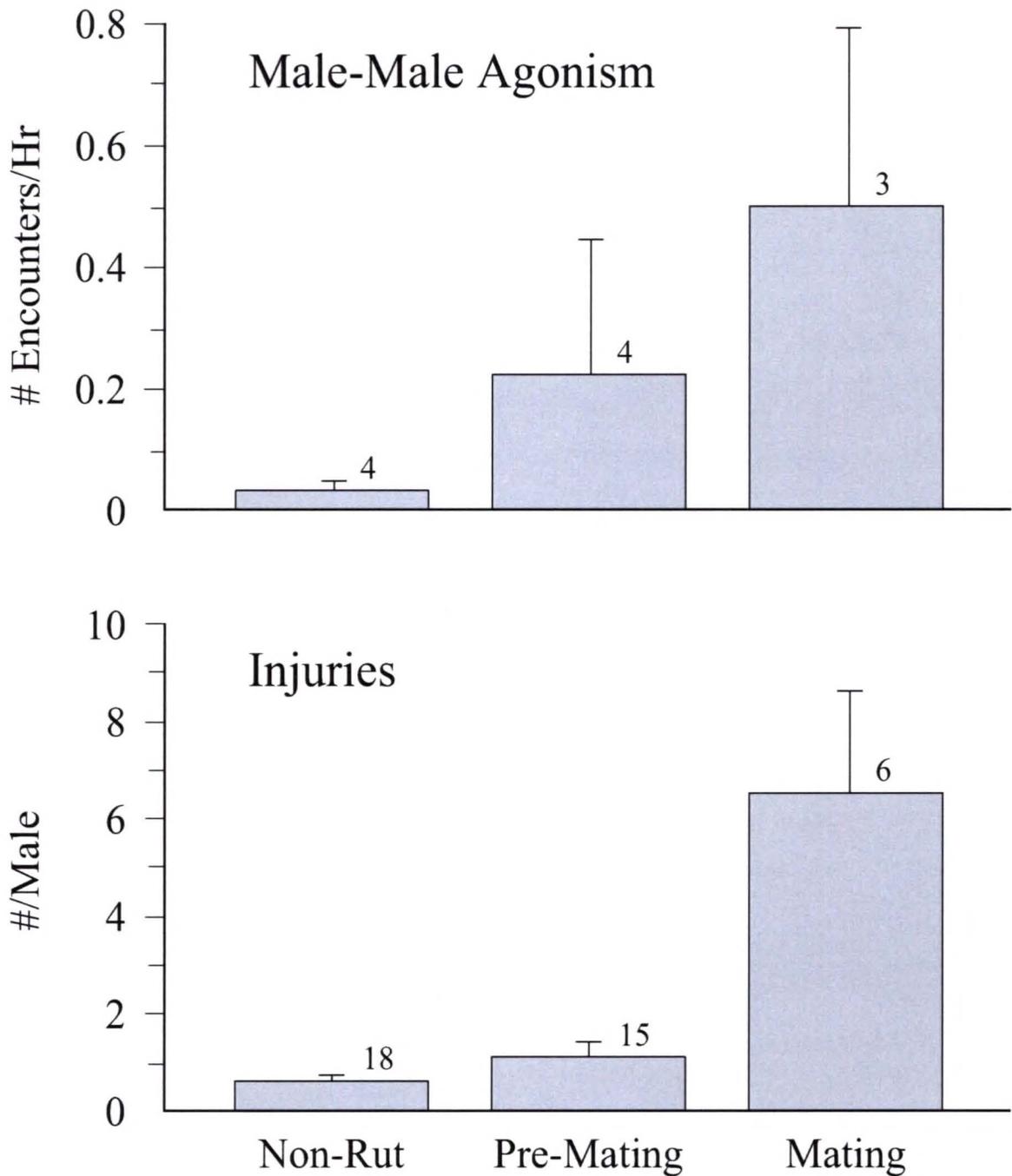


Figure 4-1. Mean ( $\pm$  SEM) frequency of intrasexual agonistic interactions and injuries observed among adult male white-nosed coatis in Tikal National Park, Guatemala, September 1995 - September 1996 and June 1994 - October 1996, respectively. Number of males sampled in each of the three defined periods (non-rut: 29 Feb/1 Mar - 22 Jan; pre-mating: 23 Jan - 12 Feb; mating: 13 Feb - 28 Feb) indicated on bars.

The incidence of injuries noted during immobilizations rose sharply during the mating period (Fig. 4-1;  $H_{[18,15,6]} = 8.74$ ,  $P = 0.013$ ). Injuries most often affected the head, chest or forelimbs and were frequently severe, including badly broken or missing teeth (especially canines) and missing claws or entire toes, as well as a variety of deep flesh wounds. Remarkably, none of the examined animals died as a direct consequence of such injuries, but two of the three natural deaths recorded among radiocollared males during the course of the study occurred in February 1995, *i.e.*, during rut of that year; the third death occurred in August 1996. Unfortunately it was not possible to reach the carcasses quickly enough to determine the exact timing or cause(s) of death.

A comparison of male and female coati dentition revealed the males' lower canine teeth to be substantially longer ( $15.5 \pm 0.4$  mm for 22 males versus  $8.7 \pm 0.2$  mm for 49 females;  $t_{[69]} = 18.40$ ,  $P < 0.001$ ).

Males spent significantly more time with bands during the mating period than at other times of the year (Fig. 4-2;  $F_{[2,5]} = 6.16$ ,  $P = 0.045$ ). Periods did not differ in terms of males approaching females either quantitatively (Fig. 4-2;  $F_{[2,5]} = 0.57$ ,  $P = 0.618$ ) or qualitatively; regardless of time of year such approaches were most often rebuffed—sometimes violently. Occasionally females allowed brief perineal sniffing by males, however, or less often investigated the males in a similar fashion themselves. Females also sometimes initiated or reciprocated allogrooming with males. These affiliative behaviors were infrequent and sporadically distributed throughout the year.

Males scentmarked at a high rate throughout the year against the base of a living or fallen tree or on a log or some other relatively low-lying feature of the terrain being traversed; they also occasionally climbed into and traveled through the forest canopy seemingly just to repeatedly scentmark the large, lower branches along some distance before returning to the ground. Although scentmarking was highest during the mating period, no time of year could be statistically distinguished from another (Fig. 4-3;  $F_{[2,5]} = 2.60$ ,  $P = 0.168$ ).

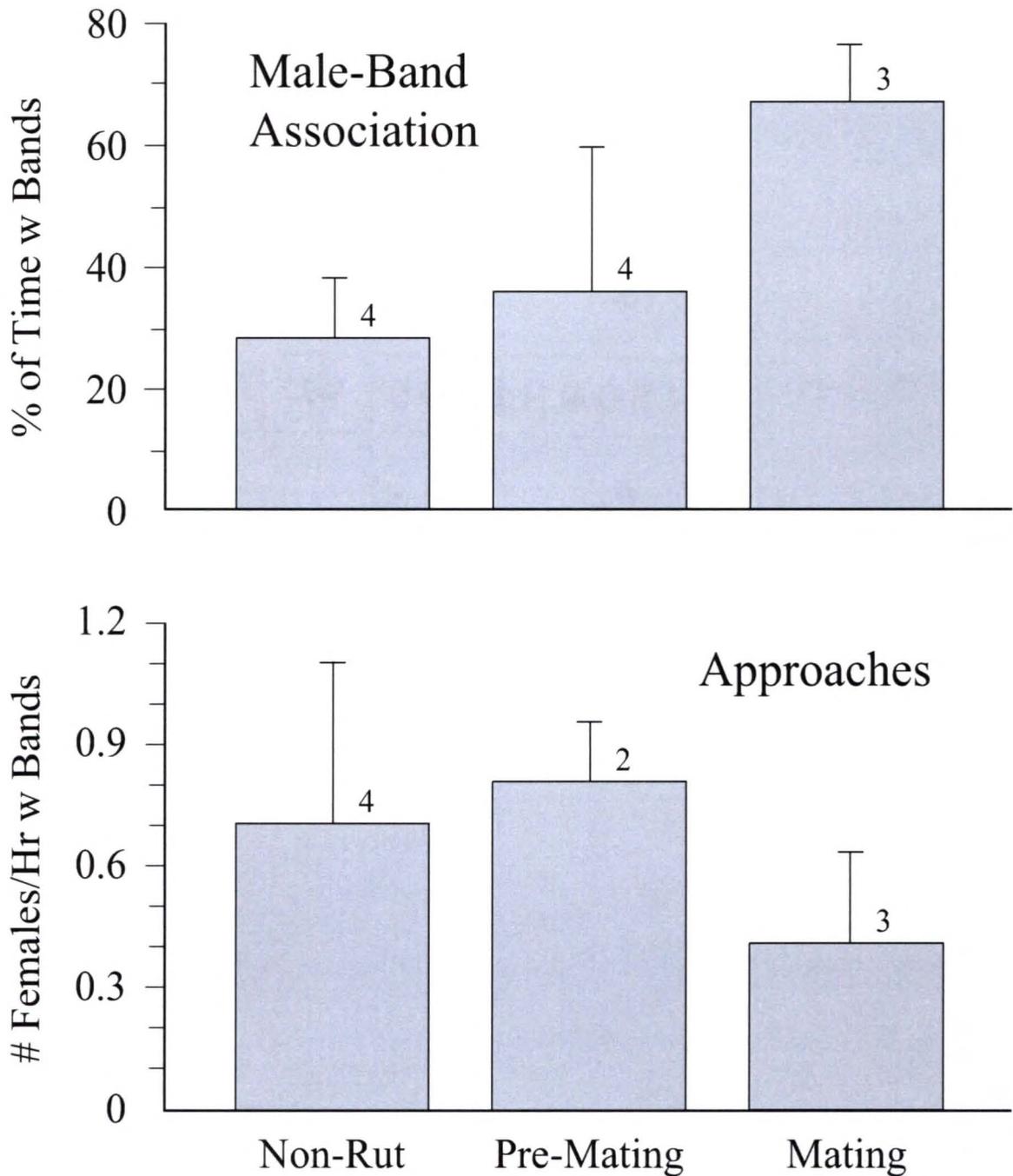


Figure 4-2. Mean ( $\pm$  SEM) percentage of time adult male white-nosed coatis spent with bands and frequency with which males approached females in Tikal National Park, Guatemala, September 1995 - September 1996. Number of males sampled in each of the three defined periods (non-rut: 29 Feb/1 Mar - 22 Jan; pre-mating: 23 Jan - 12 Feb; mating: 13 Feb - 28 Feb) indicated on bars.

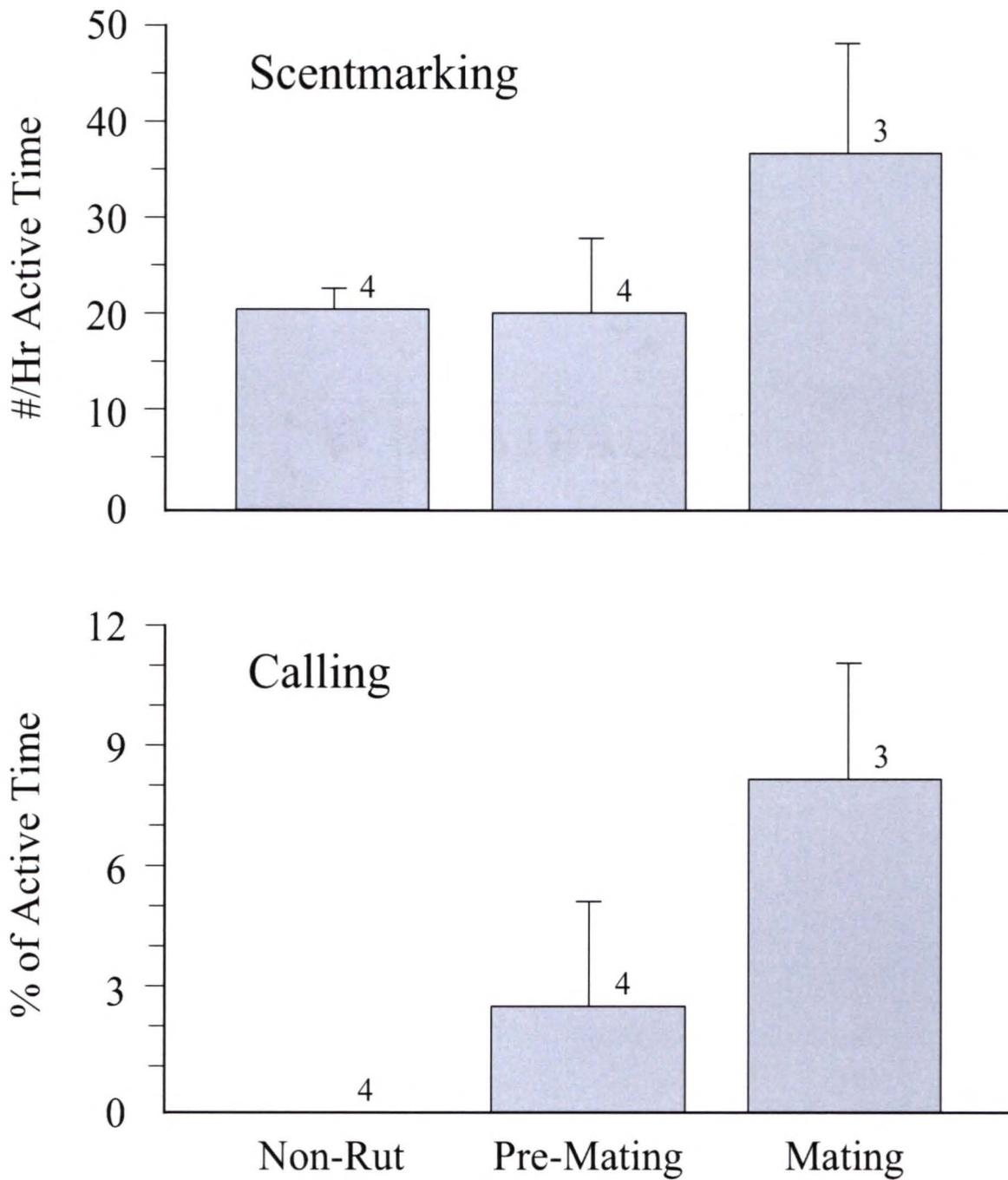


Figure 4-3. Mean ( $\pm$  SEM) frequency of scentmarking and percentage of active time spent calling by adult male white-nosed coatis in Tikal National Park, Guatemala, September 1995 - September 1996. Number of males sampled in each of the three defined periods (non-rut: 29 Feb/1 Mar - 22 Jan; pre-mating: 23 Jan - 12 Feb; mating: 13 Feb - 28 Feb) indicated on bars.

The rut call was heard only during the pre-mating and mating periods (especially the latter; Fig. 4-3;  $H_{[4,4,3]} = 6.14$ ,  $P = 0.046$ ) and elicited close investigation by both females and males. The area occupied by Tikal's large bands (up to 162 females and maturing young; Booth-Binczik, 2001)—and thus also the males accompanying them—as the animals moved through the forest precluded two human observers quantifying many aspects of the mating pattern, particularly when those observers were concentrating primarily on the behavior of a single focal animal. However, it was evident that up to several males (at least four could be conclusively identified in one instance) were calling at the same time from individual perches in the lower canopy directly or peripherally over a given band foraging on the ground below, changing their perches as necessary to keep up with the movements of the band. On at least six occasions individual females were seen leaving their bands and going to calling males, and at least three times the females stayed with the males to copulate. Calling males usually appeared to ignore one another, but on at least two occasions individual males were also seen briefly leaving their calling stations to chase or fight with others calling nearby; most recorded fights occurred when males were not calling.

Males in Tikal spent significantly less time grooming during the mating period than at any other time of year (Fig. 4-4;  $H_{[4,4,3]} = 6.66$ ,  $P = 0.036$ ). Periods did not differ appreciably in terms of time males spent foraging or distances males traveled (Fig. 4-4; for foraging  $H_{[4,4,3]} = 2.64$ ,  $P = 0.268$ ; for traveling  $F_{[2,5]} = 3.36$ ,  $P = 0.119$ ).

Body fat levels measured in immobilized males rose steadily throughout most of the year but fell sharply at the beginning of the pre-mating period, ultimately reaching a low at the end of the mating period that was only 20-25% of the peak achieved at the end of the non-rut period (Fig. 4-5). Fat levels were significantly lower during mating ( $3.8 \pm 0.6$  mm versus  $7.8 \pm 0.7$  mm and  $7.7 \pm 0.8$  mm during non-rut and pre-mating, respectively;  $H_{[18,15,6]} = 11.27$ ,  $P = 0.004$ ).

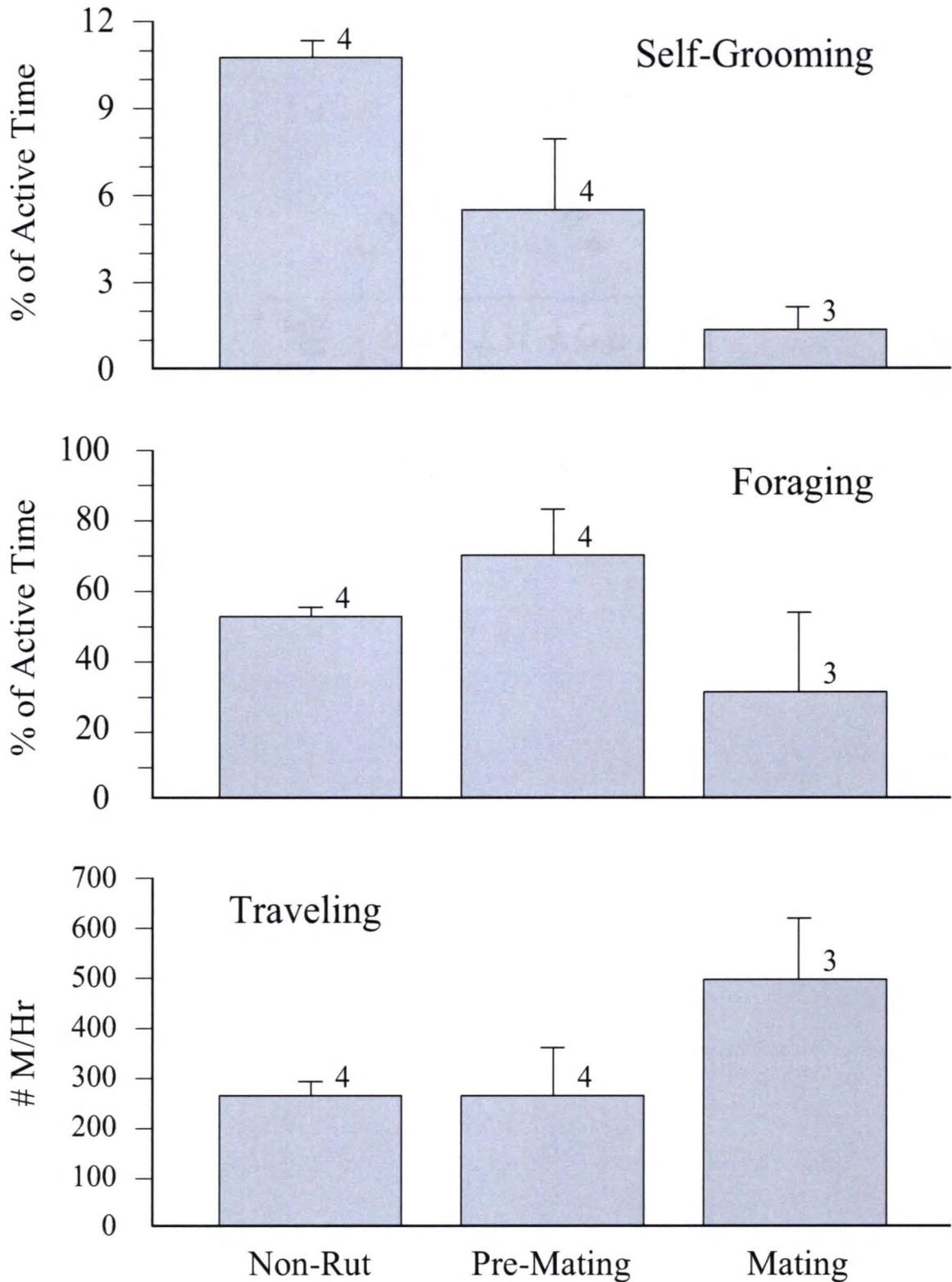


Figure 4-4. Mean ( $\pm$  SEM) percentage of active time adult male white-nosed coatis spent grooming themselves and foraging, and their rate of travel in Tikal National Park, Guatemala, September 1995 - September 1996. Number of males sampled in each of the three defined periods (non-rut: 29 Feb/1 Mar - 22 Jan; pre-mating: 23 Jan - 12 Feb; mating: 13 Feb - 28 Feb) indicated on bars.

The testes of immobilized males increased rapidly in volume with the beginning of the pre-mating period, peaked late in pre-mating or early in the mating period, decreased nearly as rapidly throughout the remainder of mating and then continued decreasing more slowly well into the non-rut period (Fig. 4-6). The males' testes were significantly smaller during non-rut ( $1.8 \pm 0.2 \times 10^3 \text{ mm}^3$  versus  $2.9 \pm 0.3 \times 10^3 \text{ mm}^3$  and  $3.3 \pm 0.2 \times 10^3 \text{ mm}^3$  during pre-mating and mating, respectively;  $F_{[2,13]} = 8.85$ ,  $P = 0.004$ ). Histological examination of testicular parenchyma obtained from road-killed males on 7 June 1995 and 9 January 1996 revealed the presence of all cell types—including mature spermatids—in the seminiferous tubules at both times of year.

Serum and fecal testosterone concentrations were highly correlated ( $r = 0.86$  for 28 sample pairs from 16 males;  $t_{[26]} = 8.42$ ,  $P < 0.001$ ) and displayed a clear circannual pattern (Fig. 4-7). Specifically, testosterone levels rose gradually beginning several months prior to the pre-mating period, spiked suddenly to a peak near the end of pre-mating and then fell even more suddenly back down to baseline by the end of the mating period. The three periods of the year differed significantly whether serum and fecal testosterone values were treated separately or combined (for combined data in which serum values ( $T_s$ ) were converted to fecal equivalents ( $T_f$ ) via the regression formula  $T_f = 52.97T_s + 51.07$ , non-rut was  $172 \pm 19 \text{ ng/g}$ , pre-mating  $549 \pm 63 \text{ ng/g}$  and mating  $358 \pm 106 \text{ ng/g}$ ;  $H_{[19,16,8]} = 16.66$ ,  $P < 0.001$ ).

## Discussion

### Male-Male Agonism

Lacking the showy weaponry seen in many rutting species (such as antlers, horns and tusks), the male coati nonetheless appears well-equipped for intrasexual combat. Both sexes rely on their teeth as well as their powerful forelegs and long, sharp claws when fighting, but the male's dentition may be specially designed for this purpose given the degree of lower canine tooth sexual dimorphism observed in the present study.

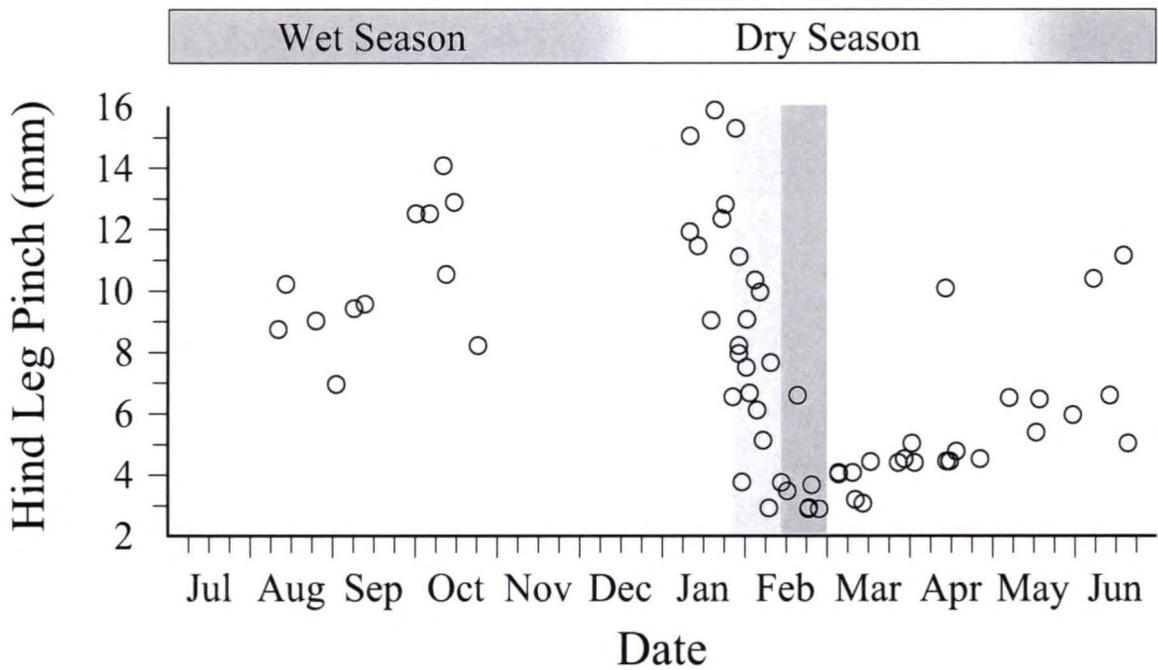


Figure 4-5. Annual body fat profile exhibited by adult male white-nosed coatis in Tikal National Park, Guatemala, July 1994 through October 1996. Based on hind leg pinch thickness measured in 42 immobilizations of 18 animals during non-rut period (unshaded background; 29 Feb/1 Mar - 22 Jan), 16 of 15 animals during pre-mating (lightly shaded; 23 Jan - 12 Feb) and 6 of 6 animals during mating (more darkly shaded; 13 Feb - 28 Feb).

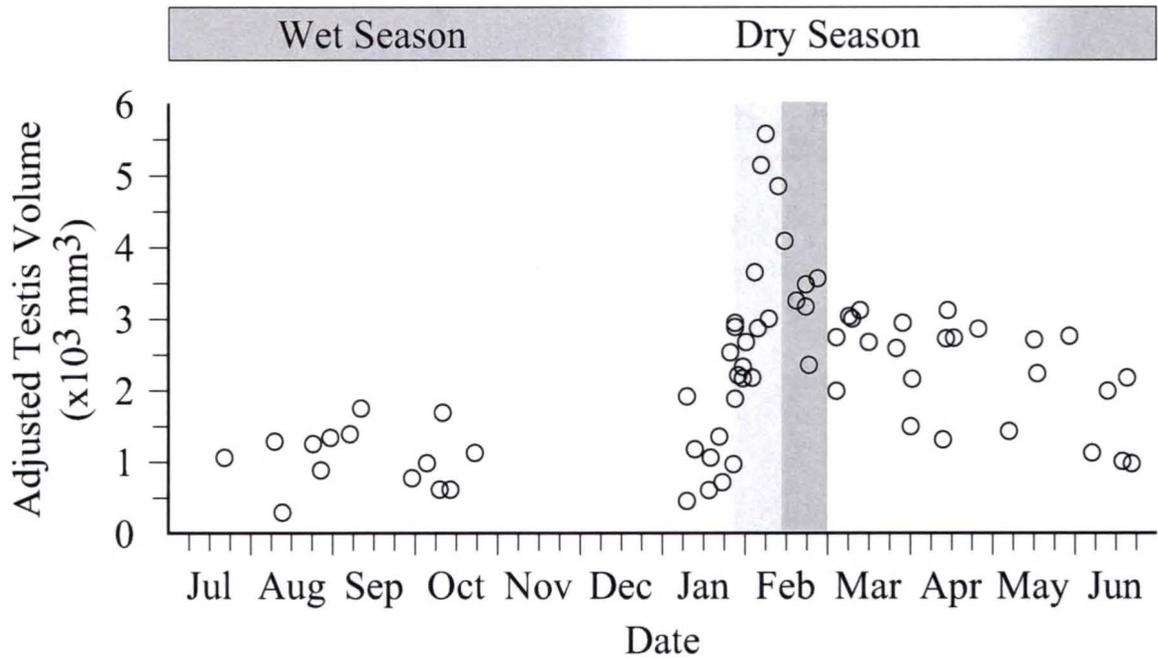


Figure 4-6. Annual profile of testicle size exhibited by adult male white-nosed coatis in Tikal National Park, Guatemala, June 1994 through October 1996. Individual testis measurements were corrected for the animal's estimated testicular fat layer (see Materials and Methods) prior to ellipsoid volume calculation. Profile based on 45 immobilizations of 19 animals during non-rut period (unshaded background; 29 Feb/1 Mar - 22 Jan), 16 of 15 animals during pre-mating (lightly shaded; 23 Jan - 12 Feb) and 6 of 6 animals during mating (more darkly shaded; 13 Feb - 28 Feb).

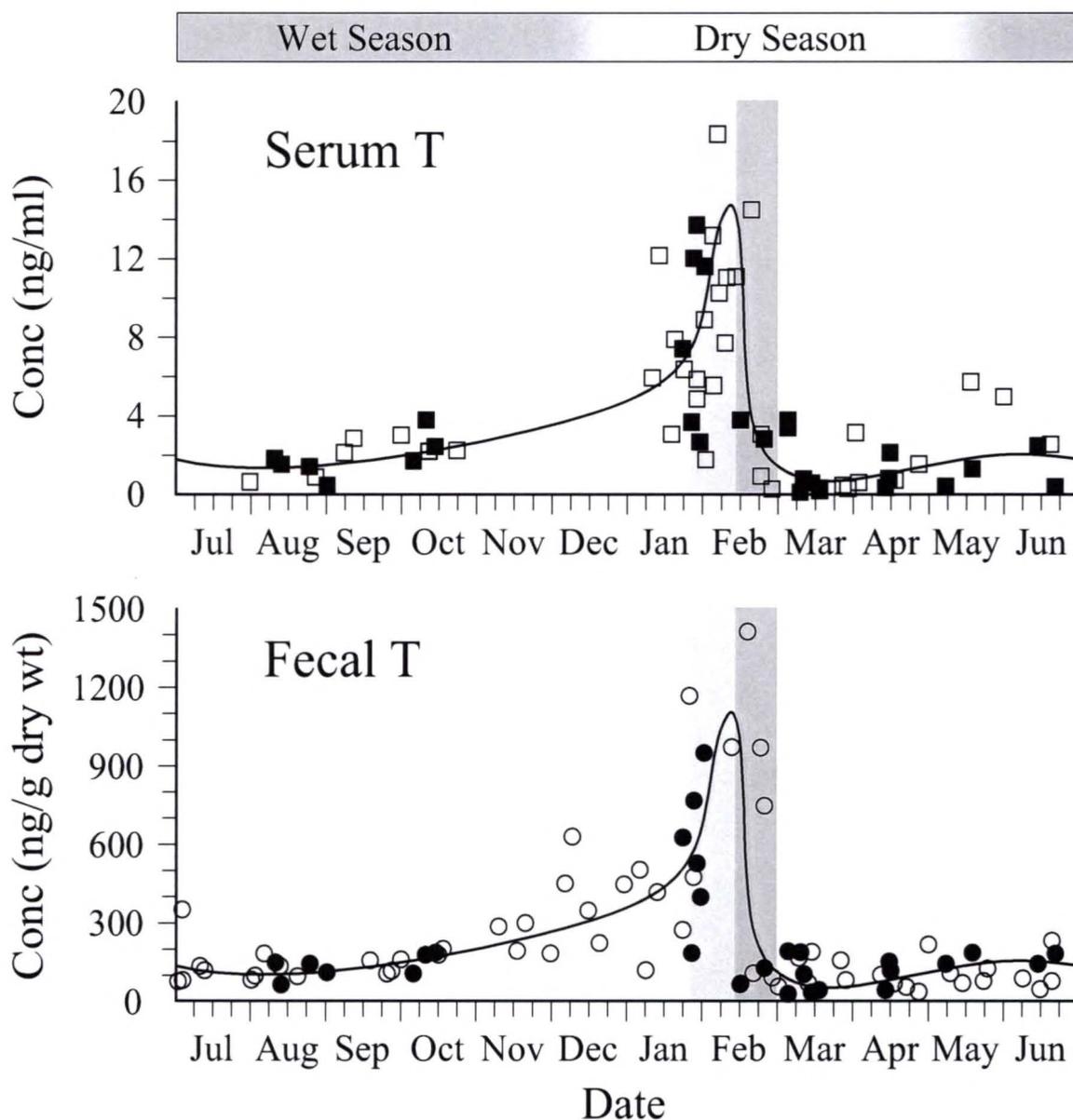


Figure 4-7. Annual serum and fecal testosterone (T) profiles exhibited by adult male white-nosed coatis in Tikal National Park, Guatemala, July 1994 through October 1996. Non-rut period (29 Feb/1 Mar - 22 Jan) indicated by unshaded background, pre-mating (23 Jan - 12 Feb) lightly shaded and mating (13 Feb - 28 Feb) more darkly shaded. Serum profile based on 42 samples from 18 animals during non-rut, 16 from 15 animals during pre-mating and 6 from 6 animals during mating; fecal profile based on 70 samples from 13 animals, 8 from 8 animals and 8 from 5 animals, respectively. Twenty-eight paired samples (i.e. serum and feces collected from same animal at same time) from 16 animals represented by solid symbols. Curve visually fitted to all combined and smoothed data.

Other than their potential usefulness in combat, no explanation for the male coati's enlarged canines is apparent. Although Smythe (1970) speculated that males on Barro Colorado Island (BCI), Panama, might pursue larger prey than females, this idea was not borne out in subsequent studies at that locale (Gompper, 1996) nor did it appear to pertain in Costa Rica (Sáenz, 1994) or Tikal (Booth-Binczik, 2001). In a comparative analysis of sexual dimorphism in carnivore dentition, Gittleman and Van Valkenburgh (1997) likewise found that dietary differences between the sexes were reflected in the size of the carnassials rather than the canines.

Instead, Gittleman and Van Valkenburgh (1997) determined that carnivore canine tooth dimorphism correlated with mating system, with more polygynous species exhibiting greater dimorphism. Such species likely experience particularly intense competition among males for mates (Emlen and Oring, 1977), suggesting the enlarged canines' principal role lies therein. It may be relevant in this respect to note that the ratio of male:female lower canine size found among coatis in the present study (1.78) exceeded that displayed by any of the 45 carnivore species Gittleman and Van Valkenburgh (1997) examined, and that the highest ratio they discovered (1.62) belonged to *Nasua nasua*, a South American congener of the white-nosed coati which has been much less studied but is believed to be similar in many respects (Emmons, 1990).

Based on the frequency with which Tikal's coati males were observed fighting and the frequency and severity of the injuries they sustained presumably as a result, it appears that males of this species do indeed face considerable and costly intrasexual competition. All male-male interactions observed in the present study were agonistic. Most male-male agonism occurs during the rut and, judging from the data on injuries, is most violent during the mating period.

Kaufmann (1962) reported that all male-male coati encounters he saw while conducting observations of females on BCI were similarly agonistic, but stated that actual physical contact was uncommon outside of the mating period, when most fights occurred. Chapman (1938) and Kaufmann (1962) attributed a seasonal proliferation of injuries among BCI's male coatis to intrasexual agonism associated with mating, and Gilbert (1973) reported a similar phenomenon

among male coatis in Arizona. Chapman (1938) and Kaufmann (1962) also detailed the severity of the animals' injuries, noting their prevalence on the heads and forelimbs, and remarked upon the animals' exceptional recuperative powers. Such healing ability notwithstanding, Chapman (1938) reported the permanent partial blindness of a semi-tame male under his casual observation after one such season, and believed the animal's ultimate disappearance two years later may have been the result of it succumbing to injuries obtained in a subsequent mating period.

Male-male combat is also common—and often results in the injury or death of combatants—in rutting species. Indeed, it might even be considered a hallmark of this reproductive pattern. As in the present study, fighting among males of such species generally spikes shortly before and during their brief annual mating periods (Wilkinson and Shank, 1976; Clutton-Brock *et al.*, 1982; Komers *et al.*, 1994), and in some cases appears to cause a substantial proportion of adult male mortality (Leslie and Jenkins, 1985; Hall-Martin, 1987; Poole, 1989). In contrast, male-male agonism in carnivore species other than the coati tends to be centered on territory establishment (*e.g.*, tigers, *Panthera tigris*, Smith, 1993) or acquiring control of a social group (*e.g.*, lions, *Panthera leo*, Bygott *et al.*, 1979; Packer and Pusey, 1982) before mating opportunities arise, and conflicts during the mating period itself are less common.

### **Male-Female Affiliation**

Bands of female coatis were typically the focal points of male-male encounters in Tikal, and to some extent the greater incidence of fighting among males during the mating period might simply reflect their increased opportunity to engage in such activity at that time. The present study revealed that males spend more time in the company of bands during the mating period than at other times of the year, and the number of males accompanying a given band at a given time varies accordingly; whereas bands were usually seen with only one (but not necessarily the same one) or no male in attendance throughout most of the year, during the mating period as many as nine males have been simultaneously observed with a single band (Booth-Binczik *et al.*, 2004).

Kaufmann (1962) also noted an increase in male-band spatial affinity at about the time of reproduction among coatis on BCI, but with some differences. He believed that males there only rarely associated with bands outside of what he considered to be the coatis' month-long mating period (essentially a combination of the pre-mating and mating periods of the present study), and that one particular male remained with each band almost constantly throughout that time, perhaps copulating with all females therein. (It is unclear whether he ever observed successful copulation; Chapter 2.) Kaufmann (1962) acknowledged, however, that unobtrusive males might have come and gone undetected because only the bands were habituated to his presence and served as the foci of his observations. That admonition was later borne out by Gompper *et al.* (1997), who found that the males most commonly seen with bands on BCI during the mating period nonetheless did not sire most of the young subsequently produced by females in those bands. Booth-Binczik (2001) further demonstrated multiple paternity not only within bands but also within individual females' litters in Tikal.

One might expect that male coatis would capitalize on their closer association with bands during the mating period by directly initiating interaction with the females therein more frequently, but this appeared not to be the case in Tikal. There, males approached females least during the mating period, and their approaches were generally rebuffed then just as they were at other times of the year.

This finding contrasts somewhat with Kaufmann's (1962) report that males in association with bands during the coati mating period on BCI spent much of their time pursuing females, and were more often amicably received by females then compared to other times of year. He described almost all close male-female encounters occurring outside of the mating period as hostile. Intersexual perineal sniffing and allogrooming were reportedly especially common at the beginning of the mating period. Russell (1981) observed less agonism and more allogrooming between the sexes not only during BCI's mating period but also for two months prior, which he called a period of courtship, and reported friendly male-female encounters at other times of year

as well. In Arizona, Gilbert (1973) believed that males required acceptance by bands in a social context prior to the mating period, simply approached and mounted receptive females during that period (though it is unclear whether any successful copulations were actually observed; Chapter 2), and remained with bands for months thereafter.

It is well established that males of rutting species spend more time with females while rutting than at other times of year (ungulates reviewed by Main *et al.*, 1996; Ruckstuhl and Neuhaus, 2000; African elephants, *Loxodonta africana*, by Poole, 1987). They are quite variable, however, in the strategies they employ to secure access to receptive females. Some maintain harems (Struhsaker, 1967; Clutton-Brock *et al.*, 1982; Lovari and Locati, 1991), others follow and defend individual females (Lent, 1965; Lott, 1981; Lovari and Appollonio, 1994), and others defend territories and wait for females to enter (Jarman, 1979; Miura, 1984; Schuster, 1976).

### **Advertising**

At least in Tikal, the male coati appears to depend more on advertising than on directly pursuing receptive females. Whether its scentmarking behavior exemplifies this strategy remains as yet unclear. Although the frequency of scentmarking behavior did not vary over the course of the year, the true significance of this behavior may lie in its quality rather than quantity. An unusually strong odor was incidentally noted during some male immobilizations and observations during the mating period. The author therefore believes that scentmarking may yet be found to be an important component of the male coati's rut.

Lending some support to this contention, Kaufmann (1962) remarked upon male coatis on BCI "urine-rubbing" (p. 130) at the base of or in trees, especially as the males approached bands of females during the mating period. Technically speaking, though, it should be noted that it has not yet been determined whether males of this species employ urine, some other product(s) or a combination thereof in scentmarking. Indeed, the procyonids have been studied far less than some other carnivore families in this regard, but males of the coati's congener *N. nasua* reportedly

behave similarly (B. Hirsch, pers. comm.) and have sebaceous preputial glands that are believed capable of producing copious secretory material (Shannon *et al.*, 1995).

Scentmarking is considered ubiquitous among terrestrial mammals (Gosling and Roberts, 2001), but an accentuated form/degree of it may be another hallmark of rut. Typically, specialized glands suddenly proliferate or activate in the rutting male (*e.g.*, the poll glands of the camel, *Camelus dromedarius*, Rai *et al.*, 1996; temporal glands of the Asian elephant, *Elephas maximus*, Eisenberg *et al.*, 1971; a variety of glands in cervids, reviewed by Müller-Schwarze, 1987), and the animal anoints itself and/or various natural signposts with the glands' redolent products. Urine is similarly used by rutting males of many species (Poole and Moss, 1981; Clutton-Brock *et al.*, 1982; Miura, 1984), and at least in the case of the fallow deer (*Dama dama*), its particularly strong odor appears to be due to the contribution of preputial glands that activate at that time (Kennaugh *et al.*, 1977).

More readily detected by an observer in Tikal than any coati odor is the male's rut call. This behavior features prominently in the species' mating pattern there, which has been described as a kind of mobile lek (Booth-Binczik *et al.*, 2004). Nothing resembling such has yet been reported for coatis outside of Tikal. However, Kaufmann (1962) noted that males interacting during BCI's mating period often emitted a "loud, rapid grunting" (p. 125), and on one occasion during that period he witnessed a male following and similarly vocalizing from a variety of perches near a band. Hass and Roback (2000) also reported that the male of a copulating pair of coatis in Arizona made what they interpreted as "alarm grunts" (p. 329) toward an approaching female. These observations notwithstanding, it seems unlikely that such a flamboyant phenomenon would have thus far been overlooked, particularly on BCI where so much time has historically been invested in studying this and other species' behavior. It may be that lekking by male coatis in Tikal represents a behavioral extreme compared to other populations which have been examined.

Plasticity in mating patterns may be the rule among ungulates that lek. Fallow deer, for example, utilize at least seven different mating systems under different ecological conditions (Langbein and Thirgood, 1989), and topi (*Damaliscus korrigum*; Gosling, 1991) and blackbuck (*Antelope cervicapra*; Isvaran, 2005) show almost equal flexibility.

Advertising calls may be the single characteristic most strongly identified with rutting mammals. In fact, the word “rut” originates in the Latin *rugire*, meaning “to roar”. Accordingly, such calls have been widely reported and are evident in all types of mating systems: territoriality (Estes, 1969; Miura, 1984), harem-holding (Struhsaker, 1967; Lovari and Locati, 1991), and following (Poole, 1987; Berger and Cunningham, 1991).

It is a matter of debate to what extent either olfactory or auditory signals are directed at potential mates versus rival males. Most researchers have concluded that both rut calls and scentmarks serve to notify rivals of a male’s physical condition and the attendant risks of challenging him (*e.g.*, Clutton-Brock and Albon, 1979; Bowyer and Kitchen, 1987; Berger and Cunningham, 1991). Conversely, Hurst and Rich (1999) argued that the primary function of scentmarking is to advertise quality to potential mates. There is evidence supporting both points of view. McElligott and Hayden (1999) found that the vocalization rate of rutting fallow deer was affected by whether other males were nearby, but not by whether the calling male was about to copulate or had just done so. In studies of elephants (which display an asynchronous rut known as musth), however, female African elephants preferred to mate with musth males (Moss, 1983) and apparently used both urine trails and musth rumbles to locate them (Poole and Moss, 1989), and female Asian elephants were able to identify males in musth from the males’ urine (Schulte and Rasmussen, 1999), and the age and musth phase of males from the males’ temporal gland secretions (Greenwood *et al.*, 2005). Additionally, both olfactory (Coblentz, 1976) and auditory (McComb, 1987) signals from rutting males have been shown to bring females of some species into estrus. Of course, whether the proximate function is to attract receptive females or repel competing males (or both), male advertising ultimately functions to increase mating

success; for example, of the many factors considered by McElligott *et al.* (1999), the amount of time rutting fallow deer spent groaning was most highly correlated with mating success.

### **Self-Maintenance Costs**

In addition to the risk of injury and death from combat, the male coati may pay a variety of less apparent costs to support its activities during rut. Coati males in Tikal spend less time grooming themselves during the mating period than at other times of year. The other relevant activities monitored in the present study (foraging, traveling) did not differ with time of year, but year-round male body fat profiles demonstrate a clear negative shift in the animals' energy balance during the rut. Female coatis display a similar shift at that time (Chapter 2), however, and the respective roles of reproductive activities and resource availability remain unclear.

No relevant data are available on male coatis at other locales. Profound variation in body fat or weight is seen in the coati's northern temperate relative, the raccoon (*Procyon lotor*), but tends to be more gradual; it is unknown as yet what if any influence mating period may have on the male raccoon's circannual pattern (Mech *et al.*, 1968; Dunn and Chapman, 1983; Moore and Kennedy, 1985; Davison, 1993; Gehrt and Fritzell, 1999b).

The indirect costs of rut are well documented in many ungulate species (see the partial albeit lengthy list of examples provided in Mysterud *et al.*, 2004). Looking at such costs individually, the effects of rut *per se* on grooming behavior have not previously been examined, but Mooring *et al.* (1996) found that territorial male impalas (*Aepyceros melampus*) groomed less while rutting than did females or males that were not holding territories, and the territorial males hosted more ticks as a result. Typically, rutting males sharply decrease or eliminate foraging (Mitchell *et al.*, 1976; Miquelle, 1990; Perez-Barberia *et al.*, 1998; Pelletier, 2005) while increasing their general activity levels (Clutton-Brock *et al.*, 1982; Flint and Krzywinski, 1997). As a result they experience a sudden decline in body weight and fat levels (Mitchell *et al.*, 1976; Dunham and Murray, 1982), in some cases even as a season of food scarcity approaches (Miquelle, 1990; Kollé *et al.*, 1993).

## **Testicular Activity**

The male coati is obviously engaging in a seasonal pattern of reproduction complementary to that of the female, but how committed is it to that strategy? Changes in gonadal tissue are clearly involved, as demonstrated by the circannual pattern males displayed in testis size. The finding that mature sperm are being produced both soon before and several months after the mating period, however, suggests that at least some level of fertility persists over a prolonged period if not year-round. Male reproductive capability beyond rut was also demonstrated by the fact that at least five females that lost their litters not long after parturition were apparently fertilized again more than three months after rut's conclusion, resulting in them giving birth to second litters (Chapter 2). Testicular data are lacking for coatis outside of Tikal.

Circannual cycles of testicular regression and recrudescence are normally observed in rutting species (included in mammalian review by Lincoln, 1989). In most species thus far examined these cycles include a period of cessation in spermatogenesis and a brief period of maximal sperm production coincident with rut (Robinson *et al.*, 1965; Lincoln, 1971; Chaplin and White, 1972; West and Nordan, 1976; Marchlewska-Koj and Kruczek, 1988; Reyes *et al.*, 1997). In other (typically lower latitude) species the males remain more or less competent year-round (Abdel-Raouf *et al.*, 1975; Brown *et al.*, 1991; Monfort *et al.*, 1993; Willard and Randel, 2002).

In either case it appears that the rapid testicular proliferation associated with rut serves mainly to increase androgenesis (see Brown *et al.*, 1991; Reyes *et al.*, 1997), prompting rut behavior and the development or activation of various structures in its support. The role androgens play in the social aggression of rutting males has received the most attention (Jainudeen *et al.*, 1972; Lincoln *et al.*, 1972; Yagil and Etzion, 1980; Mossing and Damber, 1981; Bouisson, 1983; Poole *et al.*, 1984; Pelletier *et al.*, 2003; Mooring *et al.*, 2004), but these hormones have also been linked to cutaneous glandular secretion and scentmarking (Jainudeen *et al.*, 1972; Yagil and Etzion, 1980; Mossing and Damber, 1981; Poole *et al.*, 1984), calling

(Clutton-Brock and Albon, 1979; Yagil and Etzion, 1980; Li *et al.*, 2001) and diminished foraging (McMillin *et al.*, 1980; Newman *et al.*, 1998) and grooming (Kakuma *et al.*, 2003).

Many if not all of the phenomena displayed by the rutting coati may be under androgenic control as well. The patterns observed in coati testis size and testosterone level are similar to those reported for numerous northern temperate ungulate species (Short and Mann, 1966; Lincoln, 1971; McMillin *et al.* 1974; West and Nordan, 1976; Schams and Barth, 1982; Asher *et al.*, 1989; Asher and Peterson, 1991; Ditchkoff *et al.*, 2001; Mooring *et al.*, 2004; Martinez-Pastor *et al.*, 2005).

In the two procyonids previously studied (also northern temperate species), the raccoon and ringtail (*Bassariscus astutus*), testis size also peaked just prior to or early in the species' annual mating periods, but the processes of recrudescence and regression were more gradual and (near) maximum size was maintained for several months (Sanderson and Nalbandov, 1973; Dunn and Chapman, 1983; Poglayen-Neuwall and Shively, 1991; Davison, 1993). Both of these species also displayed a four- to five-month testicular nadir involving a marked reduction or cessation in sperm production (Sanderson and Nalbandov, 1973; Dunn and Chapman, 1983; Poglayen-Neuwall and Shively, 1991). Surprisingly, only scant and unclear endocrinologic data exist for the male raccoon. Davison (1993) reported only a broad, low peak in testosterone (the maximum serum concentration recorded was 3.69 ng/ml) roughly centered around the species' late winter mating period in the southeastern United States, and Kaneko *et al.* (2005) reported that testosterone concentrations were highest in the fall (achieving in the vicinity of 80 ng/ml) in feral animals in Japan; both studies were hampered by small, sporadically obtained samples.

## **Conclusion**

The reproductive pattern displayed by the male coati at Tikal is unusual in two regards:

First, the male coati's rut is more akin to that of many ungulate species than to the pattern of any other carnivore species examined to date. The highly social nature and strong reproductive seasonality of female coatis foster intense competition among males. Male coatis have

correspondingly evolved a variety of physical and behavioral adaptations to increase their competitive ability, as well as rather narrow temporal limits on the display of these adaptations to limit their associated costs. Physiologically, circannual changes in androgen levels are strongly implicated in controlling the appearance and disappearance of these adaptations.

Second, just as female coatis are exceptional among tropical mammals in their reproductive seasonality (Chapter 2), male coatis are exceptional in the synchrony of their rut. Rut is a more or less annual phenomenon for individuals of affected species wherever they reside, but the degree of synchrony within a population tends to vary greatly with latitude. At high latitudes all the males in a population typically rut at the same time, whereas inter-male synchrony weakens and in some cases even disappears at low latitudes (Goss, 1983; Bronson, 1985; Branam and Marchinton, 1987; Loudon and Curlewis, 1988); as with the coati, male patterns generally reflect female patterns in this regard. It should be noted, however, that lamentably few free-ranging tropical mammals have thus far been studied.

How male coatis achieve such tight synchrony in rut is at present unknown. Photoperiodic entrainment of an endogenous circannual rhythm in hypothalamic-pituitary-gonadal activity has been demonstrated in several rutting species (Snyder *et al.*, 1983; Lincoln *et al.*, 1984; Asher and Peterson, 1991; Sempéré *et al.*, 1992), and seems most likely in the coati as well. However, changes in the light:dark cycle at very low latitudes have traditionally been thought to be too slight by themselves for finely timing reproductive events (Goss *et al.*, 1974; Bronson, 1989). The sociality of female coatis is believed to aid them in so utilizing such changes (Chapter 2), but the solitary habits of males in the preparatory months before rut would seem to preclude this strategy. Of course, it may be that social cues which appear as part of or are coincident with rut's onset prompt synchronization at that point. It may also be that tropical species have simply been underestimated with respect to their responsiveness to photoperiodic changes; for example, Hau *et al.* (1998) found that spotted antbirds (*Hylophylax naevioides naevioides*) from 9°N responded to as little as 17 min variation in the light:dark cycle in a

laboratory setting. As scientists have been noting for over 20 years (*e.g.*, Goss, 1983; Monfort *et al.*, 1993), this area clearly offers fertile ground for future research.

The plasticity in mating system displayed by males of some rutting species, apparently including the coati, also invites further scientific inquiry. Much attention has been devoted to the ecological factors that influence choice of system (*e.g.*, Langbein and Thirgood, 1989; Gosling, 1991; Isvaran, 2005), but information is lacking on the underlying physiological mechanisms. Wingfield (1984) found that experimentally increasing testosterone levels in males of two sparrow species shifted their behavior from monogamy to polygyny; might a similar hormonal mechanism explain the differences between males in lekking and non-lekking populations of fallow deer (Langbein and Thirgood, 1989), or between territorial and non-territorial males in a sika deer (*Cervus nippon*) population (Miura, 1984)? The males' flexibility can also extend beyond choice of mating system to how long or even whether to participate in rut at all. Post-pubertal but socially immature male African elephants shorten or refrain from entering musth in the presence of mature males (Poole, 1987; 1989; Slotow *et al.*, 2000), for example, and adult male red deer (*Cervus elaphus*) at any level of maturity suddenly cease rutting after sustaining a disabling injury (Clutton-Brock *et al.*, 1982). The endocrinology of such shifts in behavior remains unclear.

## CHAPTER 5 SUMMARY

This investigation focuses on a most unusual and instructive aspect of white-nosed coati reproductive biology: the remarkably tight temporal clustering of reproductive events displayed by this tropical species. It provides support for the idea that the species' reproductive seasonality results from selection to wean young at the time of year when food availability is most consistently high, and reveals that the species' extreme birth synchrony may simply be a result of the mechanism by which reproductive seasonality is achieved rather than an adaptation in and of itself. It also reveals that male coatis have adapted to the tight clustering of receptive females by evolving a rut, a pattern commonly seen in ungulate species but unlike that of any other carnivore species yet examined. These discoveries highlight the need for information on reproductive patterns in additional long-lived tropical mammal species as well as a deeper understanding of the physiological mechanisms involved in the timing of reproduction in such species.

Data from Tikal National Park, Guatemala, confirm the highly seasonal nature of white-nosed coati reproduction and provide much greater detail on the reproductive pattern than has previously been available. The pattern documented there fits well with previous observations from other sites. Coatis mate during approximately two weeks early in the dry season. Females become solitary to nest and give birth late in the dry season. They bring the young down from the nests at approximately five weeks of age early in the wet season. Females with young join together in small groups rather quickly, but it takes a few weeks for bands to become fully reaggregated. The young begin foraging immediately after emergence but are not completely weaned until approximately midway through the wet season.

If a female's regular annual reproductive attempt is unsuccessful, the animal may undergo a second reproductive cycle in which mating apparently occurs at approximately the time when the regular cohort of young is brought down from the nests. The proportion of females in a population that goes through a second cycle undoubtedly depends upon resource availability and nestling mortality. When resources are scarce, females may not be able to maintain adequate body condition to successfully complete a second reproductive cycle. High levels of predation on nestling coatis create selective pressure on females to make repeated reproductive attempts, within limits imposed by the species' reproductive seasonality.

The timing of coati reproduction appears to have evolved to allow the young to begin foraging at the start of an extended period of peak food availability. Both leaf litter invertebrates and fruit tend to be abundant during the first half of the wet season in Tikal, as in many other neotropical sites. However, interannual variation in rainfall patterns can dramatically alter fruiting phenology, and many tropical tree species do not seem to follow annual fruiting cycles even in seasonal environments. The timing of peaks in insect abundance is more consistent, although the amplitude depends on rainfall levels. Thus, coatis likely depend primarily on a seasonal abundance of invertebrates to get the young through the weaning phase. Comparable data are not available for other neotropical insectivores/omnivores, but a similar relationship between weaning and peak food availability has been observed for large-bodied neotropical primate species (DiBitetti and Janson, 2000).

In addition to being highly seasonal, coati reproduction is extremely synchronous. Their mating and birth periods are an order of magnitude shorter than those of most tropical mammals with seasonal reproduction. Adaptive explanations for such tight synchrony are not supported by data from Tikal. For example, births are more synchronized than reaggregation, even when the formation of small groups is permissively considered reaggregation, indicating that facilitation of communal care is not the driving force behind the synchrony. Births are also more synchronized within bands than between neighboring bands, indicating that predator swamping is not an

adequate explanation for coati reproductive synchrony and suggesting that social interactions may be important in facilitating the synchrony. The most likely explanation is that the coati's tight birth synchrony is simply a byproduct of the animals' use of social cues to help them achieve seasonally timed reproduction. That is, while the females in a band that are most sensitive to environmental cues may rely on those cues to time reproduction, their associates instead likely rely on some form of social interaction for the same purpose. Although the use of social cues to time reproductive events has been experimentally demonstrated in rodents (see Chapter 3) and suspected in other carnivore species (Rood, 1975), it has not been demonstrated in the wild.

The tight, consistent seasonality of sexual receptivity in female coatis, coupled with the large size of coati bands in Tikal, creates intense male intrasexual competition for mating opportunities. Accordingly, males undergo their own form of pronounced reproductive seasonality. Androgen levels rise with the approach of the mating period, peaking at or before its onset and then declining precipitously back to baseline over the course of that brief period. In mirror-image, testis size spikes just prior to the mating period before declining more gradually. During and/or for a short time before the mating period, males exhibit increased intrasexual agonism (including considerable physical combat), reduced foraging and courtship displays unique to that time of the year. As a result, their body condition drops dramatically and they frequently suffer severe wounds from fighting. The brevity of the male coati's period of enhanced competitive/reproductive capability, which lasts about one month in total, presumably evolved to minimize such costs. It is appropriate to refer to this phenomenon as a rut, as the male coati undergoes all of the changes exhibited by species more commonly associated with that term. Rut was previously unknown among the Carnivora.

Although basic information indicating coati reproductive seasonality had been previously reported from Barro Colorado Island, Panama, some major aspects of coati reproduction in Tikal, such as replacement litter production by females and rut by males, had not been observed during three intensive long-term studies of coatis on BCI (Kaufmann, 1962; Russell, 1979; Gompper,

1994). This illustrates the risks involved in extrapolating to an entire species from observations of a single population. Moreover, ecological pressures affecting the BCI coati population may differ dramatically from those at more natural sites, as BCI is a 15 km<sup>2</sup> island that is lacking large predators (Glanz, 1982; Robinson, 1999).

Such ecological differences can and apparently do have repercussions for reproductive biology. For example, coati band sizes are an order of magnitude larger in Tikal than on BCI due to differences in predation pressure and/or food availability (Booth-Binczik, 2001), and as a result receptive females are even more clustered in space and time in Tikal than they presumably are on BCI, setting the stage for extremely intense competition among Tikal's males. The situation on BCI, with only a few adult females in each band (Kaufmann, 1962; Russell, 1979; Gompper, 1997), creates a more even distribution of mating opportunities for males.

Among mammals in general, the spatial distribution and social organization of females reflect the distribution of food resources, whereas the spatial distribution and mating strategies of males reflect the distribution of females (Clutton-Brock and Harvey, 1978). This study suggests that the timing of reproduction follows similar rules; in the coati, the female pattern is based on food availability, whereas the male pattern is based on the availability of receptive females.

Such generalities notwithstanding, the combination of the coati's ecological niche and social structure appears to be unique to this species and perhaps also its South American congener, *Nasua nasua*. Most other procyonids are much less well studied, but they are neither diurnal nor nearly as social as the coati. Among carnivores as a whole, the group-living, diurnal, insectivorous herpestids such as meerkats (*Suricata suricatta*) and banded mongooses (*Mungos mungo*) (Rood, 1986) seem to have the most in common with coatis, although the forest-dwelling, frugivorous aspects of the coati's lifestyle are more primate-like. The coati's social structure of group-living females and chiefly solitary males, on the other hand, is most similar to those of African elephants (*Loxodonta africana*) and sperm whales (*Physeter catodon*) (discussed in Booth-Binczik, 2001), species with few ecological similarities to the coati. This combination of

social and ecological factors has resulted in reproductive adaptations that are unusual among tropical mammals and unique among carnivores.

This study has clarified many points with regard to coati reproduction, but a number of questions remain unanswered:

Perhaps most notably, hormonal cycles underlying the female pattern remain undocumented. Indeed, this points to a surprisingly large gap in our current understanding of the Procyonidae, particularly given that several species are common in various parts of North America and one species, the raccoon, is widespread and abundant throughout most of the United States. So far as can be determined, aside from this study no endocrinological information is currently available for any procyonid species except the raccoon; Davison (1993) reported a few progesterone values for females, and Davison (1993) and Kaneko *et al.* (2005) provided only slightly more testosterone data for males.

With respect to the male pattern, it is unknown whether male ejaculate quality exhibits seasonal changes. The data obtained in this study suggest that males produce sperm throughout the year, but sperm production may be lower at some times of year than at others. Seasonal fluctuations in spermatogenesis have been documented in many species, and although males of many temperate species display an annual period of complete aspermatogenesis, males of tropical species are more likely to retain some reproductive capability throughout the year (discussed in Chapter 4).

The nature of the proximate cue(s) upon which the coati relies for its remarkable reproductive pattern awaits elucidation as well. It seems most likely that olfactory cues shared among associates augment photoperiodic changes, but tactile and auditory signals may play a role in addition to or instead of olfaction. As discussed in Chapter 3, all such social cues - and in some cases combinations thereof - have been found to aid various mammals in timing their reproduction. The bulk of the work in this area has focused on rodents, however, and not only procyonids but carnivores in general remain essentially unstudied.

Also as mentioned in Chapter 3, the degree of overlap among the estrous periods of individual females within a coati band has not been assessed. There is some evidence that overlapping periods of receptivity lead to female coatis having difficulty gaining access to preferred mates (Booth-Binczik, 2001). Statistically asynchronous estrous periods within a tightly seasonal mating period have been described for ring-tailed lemurs (Pereira, 1991), presumably as an adaptation to avoid such competition.

Finally, another subject warranting further study is the species' potential for delayed/deferred reproduction and the cause(s) of its expression. Most females on BCI first reproduce in their second year, but at times up to 80% apparently wait until their third or even fourth year (Kaufmann 1962, Russell 1979, 1982). Because this finding is based solely upon observations of females engaged in nesting behavior or later accompanied by young, when delays occur it is unknown whether puberty itself is deferred or whether the females cycle but are unsuccessful in being fertilized and/or completing pregnancy. Russell (1982) believed that the animals' "decision" to forego reproduction was nutritionally-based, and pointed out that such a strategy would be most appropriate for animals with the majority of their reproductive opportunities still ahead of them. Prolonged shortages in fruit (Foster 1982a) and/or leaf litter arthropods (Levings and Windsor 1982) are not uncommon on BCI, and on rare occasions are severe enough to cause widespread animal starvation (Foster 1982a). The present study found that year-to-year variance in coati food availability occurs in Tikal as well, but perhaps not to the extent necessary to delay maturation or prompt deferral of reproduction in a mature animal. Additional studies on BCI or elsewhere may therefore be required to examine the relationship between female body condition and reproductive delay/deferral. Should such a relationship exist, as seems likely, it will be another example of reproductive timing in female coatis being dependent on food availability.

APPENDIX  
RAW TESTIS VALUES

Raw testis size indices for white-nosed coatis in Tikal National Park, Guatemala. Volumes ( $\times 10^3$  mm<sup>3</sup>) calculated as  $V = L \times W_1 \times W_2 \times \pi/6$  using measurements unadjusted for surrounding fat layer, then averaged for left and right testis.

Male #	Date	Testis Vol.	Male #	Date	Testis Vol.
Non-Rut: 29 February/1 March - 22 January					
01	22-Jun-94	2.22	32	05-Mar-95	3.19
01	07-Sep-94	3.63	32	13-Apr-95	3.79
01	21-Jan-95	5.06	32	18-Jan-96	6.57
01	11-Mar-95	3.10	32	30-Sep-96	3.78
01	07-Jun-95	3.56	34	11-Sep-96	4.33
03	23-Jul-94	2.63	34	11-Oct-96	4.76
03	01-Apr-95	2.11	40	29-Mar-95	3.60
03	31-Aug-95	2.57	40	18-May-95	3.59
03	22-Jan-96	3.67	40	13-Jun-95	3.36
03	13-Aug-96	1.50	43	05-Mar-95	2.37
03	14-Oct-96	3.30	43	02-Apr-95	2.67
09	27-Aug-94	2.74	43	07-May-95	2.53
15	23-Oct-94	2.62	43	20-Jun-95	2.94
15	10-Mar-95	3.54	43	10-Oct-96	4.02
18	17-Jan-95	1.91	45	14-Mar-95	3.18
20	27-Mar-95	3.15	50	15-Apr-95	3.79
20	12-Jan-96	4.30	50	18-Jun-95	3.64
28	17-Mar-95	3.29	51	26-Apr-95	3.50
28	17-Apr-95	3.47	53	17-May-95	3.75
28	30-May-95	4.08	71	24-Aug-96	3.16
28	09-Jan-96	6.11	91	10-Aug-96	3.14
28	05-Oct-96	4.27	99	09-Jan-96	4.02
29	14-Apr-95	3.35			
Rut, Pre-Mating: 23 January - 12 February					
01	12-Feb-95	5.29	22	27-Jan-95	5.44
03	30-Jan-95	3.98	25	28-Jan-95	2.49
20	25-Jan-95	4.04	28	31-Jan-95	4.29

(continued)

## Raw testis size indices for white-nosed coatis in Tikal National Park, Guatemala (continued).

Male #	Date	Testis Vol.	Male #	Date	Testis Vol.
Rut, Pre-Mating: 23 January - 12 February (continued)					
29	05-Feb-95	6.50	87	27-Jan-96	5.47
32	07-Feb-95	5.58	88	30-Jan-96	5.05
32	02-Feb-96	5.65	89	03-Feb-96	5.31
34	27-Jan-96	5.51	90	04-Feb-96	6.6
43	26-Jan-96	5.73	91	08-Feb-96	5.32
Rut, Mating: 13 February - 28 February					
03	23-Feb-95	2.62	34	14-Feb-95	4.35
20	22-Feb-95	3.16	40	26-Feb-95	3.55
28	22-Feb-95	3.48	51	18-Feb-96	5.05

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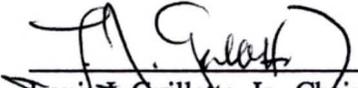
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## BIOGRAPHICAL SKETCH

Gerald Allen Binczik was born on 9 December 1960 in St. Cloud, Minnesota. He attended Willard and Ascension Elementary Schools in Minneapolis and Nelson Elementary, Central Junior High and Columbia Heights High Schools in Columbia Heights, Minnesota, graduating from the latter in 1978. He attended Northland College in Ashland, Wisconsin, and Arizona State University in Tempe, Arizona, receiving a Bachelor of Science degree in zoology from the latter in August 1984. In June 1993 he obtained a Master of Science degree in wildlife conservation from the University of Minnesota in St. Paul, Minnesota; the title of his thesis was *Reproductive Biology of Asian Small-Clawed Otters*.

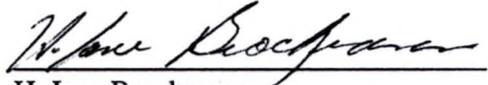
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Distinguished Professor of Zoology

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Joel H. Brendemuhl  
Professor of Animal Sciences

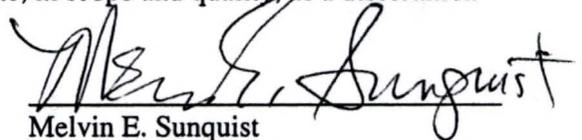
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H. Jane Brockmann  
Professor of Zoology

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Colin A. Chapman  
Professor of Zoology

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Melvin E. Sunquist  
Professor of Wildlife Ecology  
and Conservation

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and 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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Dean, Graduate School

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