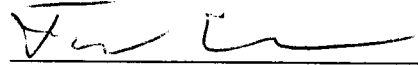


To the Graduate Council:

I am submitting herewith a dissertation written by Roland Wesley Kays entitled " The Solitary Group Life Of A Frugivorous Carnivore: Ecology, Behavior And Genetics Of Kinkajous (*Potos flavus*). " I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.



John L. Gittleman, Major Professor

We have read this dissertation
and recommend its acceptance:



Accepted for the Council:



Associate Vice Chancellor and
Dean of The Graduate School

**THE SOLITARY GROUP LIFE OF A FRUGIVOROUS CARNIVORE:
ECOLOGY, BEHAVIOR AND GENETICS OF KINKAJOUS (POTOS FLAVUS)**

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Roland Wesley Kays
August 1999

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ABSTRACT

The kinkajou (*Potos flavus*) is a neotropical, nocturnal, arboreal and frugivorous member of the Procyonidae. Although they are common throughout much of their range, they have rarely been studied and very little is known about their ecology, behavior, or genetics. General natural history and morphological data suggests that the lifestyle of the kinkajou has converged in many ways with primates. This dissertation presents the results of field and laboratory research on a population of 25 free-ranging kinkajous in central Panama.

The diet of the kinkajou is described from analysis of feces and observations of habituated individuals. Ripe fruit was the primary food comprising 90.6% of feeding bouts and present in 99% of feces. Leaves and flowers made up <10% of the diet. No animal prey was eaten. Seventy-eight species of fruit from 29 families were detected. Moraceae was the main plant family in the diet and *Ficus* was the most used plant genus. Kinkajous preferentially fed in large fruit patches. Selection indices were calculated for 37 fruit species. Compared with other large mammalian frugivores in central Panama the diet of kinkajous is most similar to the spider monkey (*Ateles geoffroyi*).

The behavior of kinkajous is described from 380 hr of observations on habituated, free-ranging animals. Social groups (n = 5) were consistent in membership and included a single adult female, two adult males, a subadult and a juvenile. Some females did not live in this group structure. The social groups were consolidated primarily at denning sites and large fruiting trees via allogrooming, scent marking and vocalizations. However, kinkajous were more often solitary as they fed together in 19.6% of their feeding bouts and almost never traveled between feeding bouts in groups. Female biased

dispersal and patterns of male association suggest that kinkajou groups are patrilineal and based on resource defense. The evolution of this social organization is discussed in respect to predation risk, resource availability, and convergence with primates of similar ecology. This study, along with others, now supports the idea that mammals with social organizations based on solitary living can reveal surprising flexibility, sociality, and complexity.

Relatedness and paternity of the study population was estimated with data from 11 microsatellite loci. Heterozygosity of the population at these loci was 0.43. With a combination of exclusion and likelihood analyses both parents for seven of the eight offspring sampled were assigned, five with $\geq 95\%$ certainty, and to two with $\geq 80\%$ certainty. Five of six identified sires of group offspring came from the same social group as the mother and pup. Furthermore, males and females within a group were unrelated, illustrating the family nature of groups. Males pairs within a group could be related or unrelated. All five identified sires were dominant males suggesting that one male can dominate breeding within a group. Neighboring male kinkajous were more closely related to each other than neighboring female kinkajous, suggesting that females disperse more often and/or further than males. These genetic results provide new detail about the paternity and relatedness of kinkajou social groups which strengthen explanations about the dispersal and patrilineal nature of kinkajou social organization made with limited field data.

Food and predation are critical factors influencing the evolution of mammalian social organization. However, the relative importance of each remains equivocal and few studies have simultaneously measured these factors. In this dissertation the nocturnal

activity and grouping patterns of kinkajous are analyzed for adaptations to changing food availability (from bimonthly fruit census) and predation risk (from moonlight). Traveling was the most frequent activity, followed by eating, resting and socializing. The average distance traveled per night was 2210 m. Females traveled significantly more (m and min) than males, whereas males were marginally more social. The daily activity pattern showed constant levels of activity throughout the middle of the night, with increased traveling at dusk and dawn. Variation in activity patterns reflected seasonal changes in fruit abundance. Females responded to changes in food availability by traveling more (m and min) and eating less as fruit increased, and feeding in larger trees and feeding groups as patches became farther apart. Overall, adjustments by males to seasonal fruit changes were not significant. However, outside the breeding season, males did respond significantly to increased fruit abundance by eating less and resting more. Both sexes reduce predation risk by resting more when the moon is bright, whereas males also travel less in bright moonlight. Changing fruit abundance had a more significant effect on activity budgets than did moonlight, suggesting that food abundance is more important than predation risk. This helps to explain the mostly solitary nature of kinkajous: individuals are not forced to form groups to reduce predation risk but change their subgroup size in response to varying levels of resource availability. Sex differences in response to feeding competition also correspond with different social and ranging patterns observed in male and female kinkajous.

A comparison of the biology of kinkajous, spider monkeys (*Ateles* sp.), and chimpanzees (*Pan troglodytes*) shows that all three have evolved similar social solutions to the reduced predation, frugivory niche, but have reached it from different evolutionary

origins. *Ateles* and *Pan* maintain their ancestral social nature, but have evolved smaller and flexible foraging groups that permit them to minimize feeding competition.

Kinkajous maintain their mainly solitary ancestral nature, but have evolved a sociality permitted by their variable and patchy fruit diet. The patrilineal nature of all three social groups suggests that female dispersal and male sociality may also be favored by a diet of ripe fruit, perhaps related to resource defense by males.

PREFACE

This dissertation is comprised of four main chapters flanked by an introduction and summary. The first is a brief review of the knowledge of kinkajou natural history prior to my research. Chapters 2-5 include empirical results on the diet, social behavior, genetics and activity of kinkajous. Each chapter is written as an independent paper with an introduction, methods, results, and discussion section. Therefore, there is some repetition in the material presented, especially in methods sections. Chapters 2-5 will be published separately. Chapter 2, on the diet of kinkajous, was published in the May 1999 issue of the *Journal of Mammalogy*. Chapter 3 has been submitted to the *Journal of Zoology*. I plan to submit Chapter 4 to *Molecular Ecology*, and Chapter 5 to *Behavioral Ecology*. The final chapter summarizes the ecology, behavior and natural history of kinkajous via comparison with two ecologically similar but phylogenetically distant primates, spider monkeys and chimpanzees.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION TO THE KINKAJOU.....	1
Overview.....	1
The Procyonidae.....	1
The kinkajou.....	1
II. FOOD PREFERENCES OF A FRUGIVOROUS CARNIVORE	4
Introduction.....	4
Materials and methods.....	5
Results.....	9
Discussion.....	12
III. THE SOCIAL ORGANIZATION OF KINKAJOU SOLITARY GROUP LIFE.....	17
Introduction.....	17
Materials and methods.....	18
Results.....	22
Discussion.....	32
IV. THE GENETICS OF SOLITARY GROUP LIFE: A MICROSATELLITE ANALYSIS OF KINKAJOU SOCIAL ORGANIZATION.....	42
Introduction.....	42
Methods.....	46
Results.....	50
Discussion.....	53
V. BEHAVIORAL RESPONSES OF KINKAJOUS TO FLUCTUATING FOOD RESOURCES AND PREDATION RISK	59
Introduction.....	59
Materials and Methods.....	62
Results.....	66
Discussion.....	69
VI. SUMMARY OF THE CONVERGENCE BETWEEN KINKAJOUS, SPIDER MONKEYS, AND CHIMPANZEES.....	76
Introduction.....	76
Similarities and differences.....	77
Evolution of social organization.....	81
LITERATURE CITED.....	85
APENDIX – TABLES AND FIGURES.....	110
VITA.....	167

LIST OF TABLES

TABLE	PAGE
II-1. Characters of fruits eaten by kinkajous on the Limbo Plot as revealed by observation of 202 feeding bouts, analysis of 194 feces, and bimonthly fruit censuses.....	113
II-2. Primary fruits in the diet of kinkajous on the Limbo plot.....	120
II-3. Dietary importance and overlap of figs, moraceous fruits, and all fruit species eaten by kinkajous and large frugivorous mammals from central Panama.....	121
III-1. Hours and half-nights of observation and number of radio-collared kinkajous....	122
III-2. Group composition, weights, and minimum convex polygon (MCP) home range sizes for kinkajous on the Limbo plot.....	123
III-3. Size and overlaps of core feeding areas for member of Center Group.....	126
III-4. Composition of 59 kinkajou group dennings and 39 group feeding bouts, and 38 grooming bouts on nights without copulations.....	127
III-5. Summary of play behavior observed by kinkajous.....	128
III-6. Details of the dispersal of a subadult female kinkajou (MAG) in 1996.....	129
IV-1. Characteristics of 11 microsatellites in kinkajous.....	130
IV-2. Pairwise relatedness values between 25 kinkajous from the Limbo plot.....	132
V-1. Travel distances, activity budgets and feeding behaviors for kinkajous.....	134
V-2. Correlations between kinkajou activity and the number of eatable fruit patches available in a ½ month period.....	135
V-3. Correlations of kinkajou feeding behavior with a) the number of eatable fruit patches available in a ½ month period, and, b) the average distance between feeding patches.	136

V-4. Relationships between kinkajou group feeding and patch size.....	137
V-5. Results of a model built to describe kinkajou behavior based on moonlight and available fruit.....	138
V-6. Summary of differences in the behavior of male and female kinkajous.....	139
VI-1. Summary of similarities and differences between kinkajous, spider monkeys, and chimpanzees.....	140

LIST OF FIGURES

FIGURE	PAGE
I-1. Phylogenetic tree of the extant Procyonidae based on morphological characters...	143
I-2. Photo of a male kinkajou (ELV) from the Limbo plot.....	144
II-1. Availability of fruits and average distance between feeding patches on the Limbo plot in 1996.....	145
II-2. Availability and use of four fruit types for kinkajous.	146
II-3. A) High and B) low selection indices (S_i) for fruits eaten by kinkajous.....	147
III-1. Home range boundaries (95% MCP) and general areas used for kinkajous in the Limbo plot.	148
III-2. Core feeding areas for the members of center group after MAG's immigration...	149
III-3. Times that kinkajous left and entered day dens in relation to dusk and dawn.....	150
III-4. Location and intensity of use of day dens by center group.....	151
III-5. A) Average group size and B) frequency of grouping for kinkajous feeding in 11 species of fruiting trees.....	152
IV-1. Schematic of social group structure for kinkajous in the Limbo plot.....	154
IV-2. Mean difference between consecutive relatedness estimates using one to eleven kinkajou microsatellite loci.	155
IV- 3. Schematic of genetic parentage within the social groups of kinkajous on the Limbo plot.	156
IV-4. Relatedness values for known relationships among kinkajous of Limbo plot.....	157
IV-5. Relatedness values for neighboring male dyads compared to neighboring female dyads.	158

V-1. Nightly activity patterns for kinkajous averaged from 380 hrs of focal animal observation.	159
V-2. Monthly activity budgets and fruit availability for female and male kinkajous on the Limbo plot.	160
V-3. Regression lines indicating the relationships between number of eatable fruit patches available and the min/hr spent traveling, eating and resting for A) all female data, B) all male data, and C) male data excluding the peak breeding season.....	162
V-4. Correlation of predicted minutes A) resting and B) traveling per hour and the percent of the moon illuminated per night, after taking the effect of fruit abundance into account.	165

CHAPTER I

INTRODUCTION TO THE KINKAJOU

OVERVIEW

In this section I review background material which preceded my research on the behavior, ecology, and genetics of kinkajou social structure. I begin with a brief summary of the ecology and social organizations of the Procyonidae. Then, I present information currently known about the ecology, behavior, and genetics of the kinkajou.

THE PROCYONIDAE

The carnivore family Procyonidae is an entirely New World taxon consisting of nine species in six genera: *Potos*, *Bassaricyon*, *Bassariscus*, *Procyon*, *Nasua* and *Nasuella* (Fig. I-1)¹. All members of this family eat some fruit, are capable climbers, and range, at least partially, into tropical or subtropical areas. With respect to social structure, procyonids range from the classical solitary systems (e.g. *Procyon*, *Bassariscus*) (Lotze and Anderson 1979; Poglayen-Neuwall and Toweill 1988), with intrasexual but little intersexual range overlap, to the female bonded societies of the coatis (*Nasua*) (Kaufmann 1962; Gompper 1995).

THE KINKAJOU

The kinkajou (*Potos flavus*) is an unusual member of the order Carnivora. Despite their terrestrial, meat-eating ancestry, kinkajous are mainly frugivorous and completely arboreal, more like many primate species than phylogenetically related carnivores (Clutton-Brock and Harvey 1977; Smuts et al. 1987). The affinity between the kinkajou and the Primates does not end with their ecologies, as there also are morphological

similarities (Kortlucke 1973). Like many primates, the kinkajou is a medium-sized mammal with a short, rounded face, forward facing eyes, and a long prehensile tail (Fig. I-2). The appearance of kinkajous is so similar to primates that many native peoples refer to them as "monkeys of the night" (Emmons 1990). This mistaken identity reached an extreme when the kinkajou was described to the scientific community as a primate (*Lemur flavus*) (Schreber 1774). Its presently recognized generic name, *Potos*, was given because of similarity to an African primate, the potto (*Perodicticus potto*) (Kortlucke 1973).

The kinkajou lives in tropical forests of the Americas, from southern Mexico south to the Matto Grosso of Brazil. It is common throughout most of its range, and is able to live in most types of primary and disturbed tropical forests (Ford and Hoffman 1988). Densities of kinkajous in eight different study sites throughout Central and South America ranged from 3.7 - 74 individuals/km² (Wright et al. 1994).

Kinkajous have not been extensively studied in the field. Even the diet is known mostly from anecdotal reports or studies with very small sample sizes (Redford et al. 1989, Ford and Hoffman 1988). Preliminary research has shown that kinkajou behavior may be more similar to social primates than to solitary carnivores, but the details of their social organizations are far from conclusive. Some censuses of kinkajou populations have found individuals to be mostly solitary, only occasionally congregating into small groups (Walker and Cant 1977; Julien-Laferrière 1989). However, two recent studies (Forman 1985, Kays and Gittleman 1995), which actually marked and followed individuals or groups of kinkajous through the forest, found them to be more social than

¹ All tables and figures are in Appendix.

previously assumed. These studies observed cooperative behaviors characteristic of the social primates including: allogrooming, communal denning, extensive intra- and intersexual home range overlap, and group foraging. These behaviors involved interactions not only between adult males and females but also between adult males.

One study has investigated the genetic variability of kinkajous with an analysis of allozyme genetic markers (Forman 1985). In examining 32 allozyme loci, Forman found levels of genetic variability ($H = .1313$, $p = .39$) which are the highest reported for any carnivore (Gompper and Wayne 1996). Ecological and behavioral data from this study are scant, but one social group was studied. This group foraged together nightly, and consisted of an adult female, an adult male, an immature female, and an immature male. Genetic data showed that the immature female was the daughter of the adult female, but the adult male was not the sire of either juveniles, and the immature male was not the offspring of either adult. These observations further demonstrate the potential complexity of the social organization exhibited by kinkajous.

CHAPTER II

FOOD PREFERENCES OF A FRUGIVOROUS CARNIVORE

INTRODUCTION

The kinkajou (*Potos flavus*) is a medium-sized procyonid common throughout most Neotropical forests (Ford and Hoffmann 1988). Despite their nocturnal and arboreal habits, numerous authors have commented on the diet of kinkajous, mainly from studies of stomach contents or chance observations (e.g., Bisbal 1986; Charles-Dominique et al. 1981; Goldman 1920). From those observations, kinkajous appear to eat primarily fruit, and supplement their diet with insects, flowers, and leaves. Some have suggested that kinkajous eat small vertebrates or bird eggs (Alvarez del Toro 1952; Husson 1978), although there is no direct evidence for this. Insects, especially ants, may be an important seasonal resource in some localities (Redford et al. 1989). No long-term study has examined quantitatively the diet of kinkajous.

Detailed description and analysis of diet are critical for understanding behavioral ecology (Chapman et al. 1995; Wrangham 1980; Zhang 1995) and conservation biology (Dietz 1997; Mittermeier and Cheney 1987). This may be especially true for a species with an unusual diet (e.g., red panda, *Ailuropoda melanoleuca* - Schaller et al. 1985). Likewise, many aspects of the biology of kinkajous have converged with primates including their diet, morphology, and social structure (Hershkovitz 1972; Kays and Gittleman 1995; Kortlucke 1973). However, because details of the natural history of kinkajous remain unknown, precise comparisons to reveal evolutionary forces behind convergence with primates are not possible.

Here I report the results of a 1 year study of the diet of kinkajous. I determine their dietary preferences by comparing relative use of the fruit of individual plant species with their relative availability and show how kinkajous fit into the large frugivore guild of central Panama by highlighting dietary similarities with other carnivore and primate taxa.

MATERIALS AND METHODS

Study site – Field research was conducted in lowland forest of Parque Nacional Soberanía in the Republic of Panama (22,100 ha; 9°9'N, 79°44'W). Work was centered around the trail network of the 104-ha Limbo research plot (Robinson 1998). Elevation within the plot varied from 35 to 80 m above mean sea level, and surrounding areas reached an elevation of 225 m. Vegetation was classified as tropical moist forest. Annual rainfall was ca. 2,600 mm with 90% falling during the wet season in late April to mid-December (Dietrich et al. 1982).

The Limbo plot was a heterogeneous mix of forests of various ages, ranging from a few years old in recent blowdowns to ca. 400 years in remnant patches of tall forest (Karr 1971). The forest within 10 - 30 m of the single-lane gravel Pipeline Road was ca. 30 years old and had grown tall enough to have closed the canopy above the road through most of the study area. South of the road, the forest was 60 - 120 years old, having been disturbed by farmers and the United States military earlier this century (Foster and Brokaw 1982).

Despite regular hunting pressure, the animal community of the Limbo plot was largely intact, including top predators such as jaguar (*Panthera onca*) and puma (*Felis concolor*) (O. Moore and T. Robinson pers. comm.). The spider monkey (*Ateles*

geoffroyi) was the only frugivorous mammal extirpated from the area. Other arboreal frugivores seen frequently on the Limbo plot included olingos (*Bassaricyon gabbii*), howler monkeys (*Alouatta palliata*), capuchins (*Cebus capucinus*), night monkeys (*Aotus trivirgatus*), and several species of opossums. Density of kinkajous around the Limbo plot is ca. 12 individuals/km² (R.Kays unpublished data).

Trapping and observation – Twenty-five kinkajous were captured 192 times with 50 Tomahawk live traps (32 by 32 by 102 cm). Traps were baited for 1,292 trap nights with banana and hung in trees 4 - 25 m above the ground using a hoistable trap design (Kays 1999). Newly-captured animals were immobilized with 0.3 cc of a solution of 80% Ketamine hydrochloride and 20% Zylazine hydrochloride, and standard physical measurements were made. Ten kinkajous were fitted with radio collars that were marked with a unique pattern of colored reflective tape. Fifteen kinkajous were fitted with a similar reflective identification collar without a radio transmitter.

Marked kinkajous habituated quickly and could be followed and observed without obvious disturbance. Radio-collared animals were followed on 74 half-nights for 380 h, either from when they left their sleeping den at dusk until midnight or from midnight until they entered their sleeping den at dawn. Focal animals were observed from the ground with binoculars and were illuminated with a 6-V head lamp. A red filter was used when an animal was in the understory and a 12-V spotlight was used when an animal was in the upper canopy. Care was taken to not shine lights continuously on the focal animal. Animals could not always be seen clearly because of understory vegetation and darkness. Therefore, sporadic visual observation, falling fruit, and sounds were used in combination to determine a focal animal's behavior. Generally, kinkajous could be seen directly while

they were feeding or resting in a tree. As they moved through the trees, however, they could be seen only intermittently, and I had to rely on telemetry to follow traveling animals.

Each time a kinkajou fed on fruit, flowers, or leaves the following were recorded: plant species, location, diameter at breast height (DBH) of the plant, and a categorical estimation of the number of fruits or flowers on the ground under the plant (<10, <50, <100, <500, <1,000, >1,000). For unknown species, samples of fruit and leaves were collected and identified.

Dietary measure – Diet was measured by behavioral observation and analysis of feces. Behavioral feeding data were collected while following focal animals. A feeding bout began when a focal animal entered a fruiting patch to feed and ended when the animal left. A fruiting patch usually consisted of a single fruiting tree or vine but occasionally included two fruiting plants if their canopies were adjacent. Kinkajous did not feed continuously in bouts longer than ca. 30 min. Therefore, measures of bout length and total feeding time were not actually measures of time ingesting food but time spent in feeding patches. Behavioral data were analyzed in terms of percentage of total feeding bouts ($n = 202$) and percentage of total feeding time ($n = 138$ h).

A total of 194 fecal samples was analyzed; two-thirds were collected from free-ranging animals and one-third came from animals in traps. Kinkajous do not use latrines but defecate while feeding and traveling in trees; their feces fall to the ground and are scattered by understory vegetation. I collected as much of each defecation as possible, but usually was some fraction of the total actually eliminated. Defecations collected from

the bottom of traps were complete feces. Banana bait in feces was excluded from analysis.

Feces were refrigerated until analyzed, usually overnight. They were weighed, dissected, and divided into component parts. Relative volume of each component was visually estimated. Fruit pulp, seeds, and flower parts were identified and included in a reference collection. Eaten fruits were analyzed in terms of percentage of total number of feces in which they occurred and percentage of total feces volume. Percentage of total feces did not sum to 100 across food species because many individual feces contained more than one species.

Monitoring of fruit – Production of fruit on the Limbo plot was monitored at the beginning and middle of each month from February 1996 to December 1996 using transect counts of fallen fruit. The transect covered most of the Limbo plot and was 0.5m wide and 11.4 km long. To minimize inclusion of dispersed fruits, only patches with more than 2 fruits were included in the census. Wind dispersed species and fruits >2 weeks old were not counted. When more than two, new, non-wind dispersed fruits were encountered, they were identified by species, location along the transect, and number of fruits within the 0.5m wide transect. Additionally, the total number of fruits laying on the ground within a patch was estimated by category (<10, <50, <100, <500, <1,000, >1,000). When the fruiting tree was easily located, its DBH also was measured. A fruit species was classified as edible if it was detected in the diet of kinkajous at least once.

Data analysis – Selectivity indices were calculated for all fruit species that were eaten by kinkajous and detected in the census of fruits. The index was a simple ratio, $S_i = f_i/a_i$ where f_i was the relative amount of the diet occupied by a fruit species and a_i was the

relative abundance of that species in the census of fruits compared with all other edible fruit species in the census (Leighton 1993). Selection indices >1.0 indicated that a species was eaten more than expected given its availability; values <1.0 indicated that the species was eaten less than expected.

RESULTS

Fecal and behavioral data showed that kinkajous were almost exclusively frugivorous: 99.0% of feces examined contained fruit while 90.6% of feeding bouts and 90.5% of total feeding time was on fruit. Flowers made up 1.6%, 6.9%, and 8.6% of the feces, feeding bouts, and feeding time, respectively. Leaves comprised only 2.6%, 2.0%, and 0.7% of feces, feeding bouts, and feeding time, respectively. Kinkajous were not recorded to feed on animal matter. Small insect fragments were found in feces twice, but the amount and type were expected from accidental ingestion with fruits or flowers.

Nearly all fruit eaten was ripe. Unripe fruit of only one species, *Astrocaryum standleyanum*, was eaten twice in November when fruit was not abundant. Individuals ingested seeds while feeding on many fruit species, but did not appear to harm them; physically damaged seeds were rare in the feces. All observed feeding was on arboreal food.

Kinkajous were observed eating 51 species of fruit, and 58 species were found in the fecal analyses; a total of 78 species of fruit from 29 plant families were eaten (Table II-1). Thirteen of those species remain unidentified. Of the 29 families, 14 were represented by only 1 species, 9 by 2 species, 5 by 3 species, and 1 by 15 species. The Moraceae, including genera *Brosimum*, *Cecropia*, *Ficus*, *Poulsenia*, and *Pourouma*, was the most represented family in the diets of kinkajous.

Seven species of flowers from four families were eaten; none were eaten frequently. Kinkajous destroyed some flowers as they ingested floral components (e.g., *Philodendron*). Female palm flowers were ingested, but the cluster of flowers was never destroyed completely (e.g., *Astrocaryum standleyanum*, *Oenocarpus panamanus*, and *Scheelea zonensis*). Flower species from which only nectar was ingested (e.g., *Ochroma pyramidale*, *Pseudobombax septenatum*, and *Tetrathylacium johansenii*) were handled more carefully by kinkajous; the same individual flower was often visited more than once per night, and white pollen could be seen on the kinkajou's facial fur. Leaves were found in seven fecal samples in six months, always in small amounts. Leaves in four samples were *Ficus*.

Fig fruits were the most important food of kinkajous (Table II-2). *Ficus insipida* was the most abundant species in all four dietary measures. Early in the study *Ficus* sp.? from feces was not identified to species, however, it is thought that these were primarily *F. insipida*. The nine most important fruits comprised 48.5 - 63.4 % of the total kinkajou diet, depending on the method used to assess diet (Table II-2).

The majority (55.5%) of fruits eaten by kinkajous were from trees, 36.5% were from climbers (i.e., lianas, vines, epiphytes, and hemiepiphytes), and 8.0% were from shrubs (Table II-1). Compared with available patches of edible fruit, kinkajous fed in larger fruit patches, as measured by DBH ($X^2 = 136$, d.f. = 6, $p < 0.001$) and number of fruits on the ground ($X^2 = 172$, d.f. = 5, $p < 0.001$).

Bi-monthly census of fruit revealed strong seasonal changes in availability of fruit (Fig. II-1). The subset of species eaten by kinkajous followed the trend shown by all fruiting species on the Limbo plot - a sharp increase in abundance from February to a

peak in May followed by a slow decrease until the low point in December. Greater density of edible fruits was correlated negatively with distance between patches of edible fruit ($r = 0.566, p = 0.0076$).

Fruits of four tree species were selected to illustrate three patterns of fruit availability and consumption by kinkajous. *Chrysophyllum cainito* (Fig. II-2a) was a rare fruit but was frequently eaten by kinkajous in February and therefore strongly preferred. *Astrocaryum standleyanum* (Fig. II-2b) was one of the most common fruiting species on the plot but was rarely eaten relative to its abundance. Fruits of *Chrysophyllum* and *Astrocaryum* occurred seasonally, as is typical of most species eaten by kinkajous, and were only available for a few months a year. Peak abundance of fruit in patches occurred 1 month after the peak of those species in the diet of kinkajous. That suggested that fruits were available to kinkajous in the trees ca. 1 month before they were detected by census of fruits on the ground. Unlike most fruit species, no seasonality was evident in the fruiting pattern of fruits of *Ficus* (Figs. II-2c and d).

Selection indices (S_i) were calculated for 37 fruits eaten by kinkajous and detected in the census of fruits. S_i for percent feces and percent volume were strongly correlated ($r = 0.917, p < 0.0001$) and the data for percent feces is presented with the S_i for percent feeding bouts and hours (Fig. II-3). The three indices gave similar values for most fruits but were contradictory for some species that were marginally selected for or against.

Comparison with other frugivores – Kinkajous ate a higher percentage of fruit than any large frugivore that has been studied in central Panama and were closest to *Ateles* in overall dietary patterns (Table II-3). I calculated the overlap of the specific fruits eaten

by kinkajous and four other large frugivores studied on the nearby Barro Colorado Island, Panama. To compensate for fruit species eaten by frugivores on Barro Colorado Island that were not available on the Limbo plot, I calculated the total number of fruit species shared from the subset of fruits detected on the Limbo plot by the census of fruits. Again, diets of kinkajous and *Ateles* were most similar. *Alouatta* also shared a high percentage of fruits eaten with kinkajous, but *Cebus* and *Nasua* shared <50% of the total fruit species and <60% of the species detected in the Limbo census of fruits. Like kinkajous, both *Ateles* and *Alouatta* fed on a large number of figs and other Moraceae.

DISCUSSION

Kinkajou ecology – Kinkajous on the Limbo plot were almost exclusively frugivorous. The proportion of their diet made up by fruit was higher than other carnivores (Charles-Dominique 1978; Joshi et al. 1995; Lovari et al. 1994) and primates (Defler and Defler 1996; Hladik and Hladik 1969; Leighton 1993; Peres 1994), and may be the highest of any non-volant mammal. However, not all populations of kinkajous are as frugivorous as the one in the present study (Estrada and Coates-Estrada 1985; Redford et al. 1989).

Because of their diet and feeding behavior kinkajous may be important to the reproduction of many neotropical plants. Kinkajous ingest, but do not damage seeds from most of the 78 fruit species eaten. Thus they appear to disperse seeds for many plant species. Kinkajous also may be acting as pollinators for those flower species from which they drink the nectar but do not damage flowers.

The palm *Scheelea zonensis* was used often based on behavioral observations but was not detected in fecal analysis (Table II-2). This may be related to the unusual way kinkajous fed on their large, hard fruits; they chewed on single fruits for ca. 30 min

before dropping the large seed under the tree. Such extended mastication may allow kinkajous to ingest juice and oils from the fruit that would not be detected in feces.

Kinkajous preferentially fed in large fruiting patches. This also has been observed in other large-bodied primate frugivores (Leighton 1993; Strier 1989) and permits individuals to feed longer in one patch, visit fewer feeding patches, and travel less (Zhang 1995). Of the fruits that were eaten, the majority were from trees, but 36.5% were from climbing vegetation. This illustrates the importance of a ground-based census of fruits to study potentially available fruit when the diet of a frugivore is unknown. Climbing plants are difficult to census using a tree-based census of fruits (e.g., tree transects or fruit trails - Chapman and Wrangham 1994); thus, if a tree-based census of fruits had been the only census method used, more than one-third of the species eaten by kinkajous would have been missed.

All fleshy fruits, and the subset of species eaten by kinkajous on the Limbo plot in 1996, showed seasonal changes in abundance similar to that reported for Barro Colorado Island (Croat 1978; Milton 1980; Foster 1982). The 1-month time lag between when fruits were available to arboreal kinkajous and when they were observed with the ground-based census also was reported by Zhang and Wang (1995) in their comparison of census methods for fruit.

Fruit preferences of kinkajous – The selection indices (S_i) illustrate the relative amount a fruit was eaten compared with its relative availability. A high S_i for feeding bouts, feeding time, and feces indicated that kinkajous visited a fruiting species more often than expected, spent more time in a species than expected, or ingested a fruit species more frequently than expected, respectively. These values may conflict with each other if, for

example, kinkajous visited many trees of a certain species but did not spend much time in any one tree because it was small and had little fruit per tree.

Of the most important fruits in the kinkajou's diet (Table II-2), only *Astrocaryum* was eaten substantially less than expected (Fig. II-3). *Coccoloba paramensis* was eaten slightly less and *Scheelea* slightly more than expected. The other five species were selected for by kinkajous. Kinkajous selected all but one fig species. *Ficus columbrinii* was not selected; this species differs from the other figs eaten in that it is small, red, and considered to be a bird-dispersed fruit (Kalko et al. 1996). The other eight species of figs selected by kinkajous are large, green, and dispersed by large mammals or bats.

In addition to 13 unidentified fruits, 27 species were eaten by kinkajous but were so rare they were not detected in the census of fruits. Clearly, these species also are selected for but can not be directly compared with selection indices. These fruits were rarely eaten; the three most frequently eaten species not detected in the census of fruits were *Abuta racemosa* (4.6 % of feces), *Passiflora nitida* (2.6 % of feces), and *Brosimum alicastrum* (2.1 % of feces).

Importance of figs –The only plant family that had more than three fruit species eaten by kinkajous was the Moraceae, which was represented by 15 species, including nine *Ficus*. Figs were the most important fruits for kinkajous, and most were selected over other fruits. *Ficus insipida*, a large free standing fig, was the single most important species of fruit eaten. The nine species of figs formed 21.8% - 44.9% of the kinkajou's diet, depending on the dietary measure.

Because of their abundance and year-round availability, figs are important for frugivores throughout the tropics (Janzen 1979). However, there is controversy over their

nutritional importance. Some authors have asserted that figs have low or baseline nutrient levels, are eaten because they are abundant, and therefore are not selected for, especially in the Old World (Conklin and Wrangham 1994; Leighton 1993; Milton 1980). However, recent comparisons of the nutrient content of figs and non-fig fruits showed that figs are an excellent source of calcium and other minerals for frugivores, especially in the New World (O'Brien et. al. 1998). Furthermore, Panamanian figs have higher levels of lipids, protein, and carbohydrates, and lower tannin levels than Ugandan figs (M. Wendeln in litt.). These higher nutrient levels help explain why kinkajous on the Limbo plot preferred figs over other fruits.

The frugivorous guild – Although no other large mammalian frugivores have been studied on the Limbo plot, diets of coatis (*Nasua narica*) and five primates (*Alouatta palliata*, *Aotus trivirgatus*, *Ateles geoffroyi*, *Cebus capucinus* and *Saguinus geoffroyi*) have been reported for Barro Colorado Island, <10 km E of the Limbo Plot.

A comparison of diets of this guild shows that kinkajous are the most frugivorous, and most similar to *Ateles* in broad dietary description (Table II-3). Furthermore, kinkajous and *Ateles* also are the most similar in overlap of specific fruits eaten, sharing 100% of fruits known to occur on the Limbo plot and eaten by *Ateles* on Barro Colorado Island. Although *Alouatta* eat many more leaves and flowers than kinkajous, most of the fruits consumed overlap between species. Number of fruit species eaten is highest in *Cebus* and lowest in *Ateles*. However, each species has been studied with different intensity, and this value may not reflect actual dietary diversity.

The diet of kinkajous is most similar to *Ateles* - a large, diurnal, arboreal primate. Preliminary results from studies of kinkajous suggest that these two species also have

similar social organizations, with individuals from a group or community usually foraging alone or in small groups and stronger social bonds between adult males than females (Kays and Gittleman 1995; Robinson and Janson 1987). The following four chapters will describe aspects of the social organization of kinkajous and conclude by comparing them with ecologically similar primates.

CHAPTER III

THE SOCIAL ORGANIZATION OF KINKAJOU SOLITARY GROUP LIFE

INTRODUCTION

Mammal species are typically described as either social or solitary. Social species have attracted more attention and the details of many social taxa are well known (e.g., Primates, Smuts et al. 1987). However, the majority of mammals are not social (Eisenberg 1981). At least 80-90% of all mammals are classified as solitary characterized by a single individual spatially and temporally living on its own exclusive of mating (Jarman and Kruuk 1996). Despite this, little is known about the details of solitary mammal societies (Sandell 1989).

New research tools and methodological advances such as improved and long-lasting radio collars (Gehrt and Fritzell 1998a; b), night vision and remote cameras (Kruuk 1989) and hypervariable molecular genetic markers (Gompper and Wayne 1996) are revealing more detailed information about solitary species. As anticipated in early studies of mammalian social organization (Leyhausen 1965), we are increasingly discovering complex interactions among individuals within solitary structures (see Creel and Macdonald, 1995); indeed, recent studies have documented surprising sociality in species previously considered solitary. For example, by monitoring 74 radio collared individuals Gehrt and Fritzell (1998a, b) found raccoons (*Procyon lotor*) to display a social organization of 3-4 adult males, occasionally overlapping in home range and regularly associating while resting and foraging. Moreover, other studies are finding that male associations are more frequent than expected in a number of other mammal species

previously thought to be exclusively solitary (cheetah, *Acinonyx jubatus*, Caro 1994; slender mongoose, *Herpestes sanguineus*, Waser et al. 1994; aye-aye, *Daubentonia madagascariensis*; Sterling and Richard 1995). As the complex social life of more solitary species is discovered, a continuum between completely solitary and classically social is predicted. Understanding why these species are social in some situations and solitary in others has great potential to elucidate why less flexible species have evolved permanent group life.

In this chapter, I describe specific behavioral attributes of the social structure in the kinkajou, *Potos flavus*, a species of the order Carnivora (Procyonidae). Due to its arboreal, nocturnal and fruit-eating nature, the kinkajou shows many characters that have given rise to other forms of sociality (Eisenberg 1981) and, indeed, may reveal convergence with social organizations in primates with similar ecology. The present study describes critical elements of the kinkajou social organization: level and form of interactions among individuals (allogrooming, play, vocalizations, scent marking, aggression, mating), home range movements, den location and usage, feeding behavior, mating patterns, and dispersal. These descriptions are placed in the context of a flexible social structure that bridges the continuum between classically solitary and social systems.

MATERIALS AND METHODS

Study site - Field research was conducted in lowland forest of Parque Nacional Soberanía in the Republic of Panama (22,100 ha; 9°9' N, 79°44'W). Work was centered around the trail network of the 104-ha Limbo research plot (Robinson 1998). Elevation within the

plot varied from 35 to 80 m above mean sea level, and surrounding areas reached an elevation of 225 m. Vegetation was classified as tropical moist forest. Annual rainfall was ca. 2,600 mm with 90% falling during the wet season in late April to mid-December (Dietrich et al. 1982).

The Limbo plot was a heterogeneous mix of forests of various ages, ranging from a few years old in recent blowdowns to ca. 400 years in remnant patches of tall forest (Karr 1971). The forest within 10 - 30 m of the single-lane gravel Pipeline Road was ca. 30 years old and had grown tall enough to have closed the canopy above the road through most of the study area. South of the road, the forest was 60 - 120 years old, having been disturbed by farmers and the United States military earlier this century (Foster and Brokaw 1982).

Despite regular poaching pressure, the animal community of the Limbo plot was largely intact, including top predators such as jaguar (*Panthera onca*) and puma (*Felis concolor*) (O. Moore and T. Robinson pers. comm.). The spider monkey (*Ateles geoffroyi*) was the only frugivorous mammal extirpated from the area. Other arboreal frugivores seen frequently on the Limbo plot included olingos (*Bassaricyon gabbii*), howler monkeys (*Alouatta palliata*), capuchin monkeys (*Cebus capucinus*), night monkeys (*Aotus trivirgatus*), and several species of opossums. Density of kinkajous around the Limbo plot was ca. 12 individuals/km² (R.Kays unpublished data).

Trapping and observation - Twenty-five kinkajous were captured 192 times with 50 Tomahawk live traps (32 by 32 by 102 cm). Traps were baited for 1,292 trap nights with banana and hung in trees 4 - 25 m above the ground using a hoistable trap design (Kays 1999). Newly-captured animals were immobilized with 0.3 cc of a solution of 80%

Ketamine hydrochloride and 20% Zylazine hydrochloride, and standard physical measurements were made. Ten kinkajous were fitted with radio collars that were marked with a unique pattern of colored reflective tape. Fifteen kinkajous were fitted with a similar reflective identification collar without a radio transmitter.

Marked kinkajous habituated quickly and could be followed and observed without obvious disturbance. Radio-collared animals were followed on 74 half-nights for 380 h (Table III-1), either from when they left their sleeping den at dusk until midnight or from midnight until they entered their sleeping den at dawn. Focal animals were observed from the ground with 10x40 binoculars and were illuminated with a 6-V head lamp. A red filter was used when an animal was in the understory and a 12-V spotlight was used when an animal was in the upper canopy. Care was taken to not shine lights continuously on the focal animal. Animals could not always be seen clearly because of understory vegetation and darkness. Therefore, sporadic visual observation, falling fruit, and sounds were used in combination to determine a focal animal's behavior. Generally, kinkajous could be seen directly while they were feeding or resting in a tree. As they moved through the trees, however, they could be seen only intermittently, and I had to rely on telemetry to follow traveling animals. In addition to direct observation, 74 (2.4% of total) nocturnal animal locations were fixed with the triangulation of telemetric bearings.

The behavior of a focal animal was categorically recorded each minute as feeding, resting, traveling, social or unknown. Feeding was defined as eating or actively searching a fruiting tree for food. Traveling was defined as moving between trees. An animal was classified as resting if it stopped traveling for >1 min while not eating or being social. Social behavior included activities that brought 2 or more animals <1m

from each other for ≥ 1 min. Certain silent behaviors, such as grooming, resting in contact, or scent marking, were often difficult to detect when kinkajous were hidden behind vegetation. Some of these behaviors were probably missed and recorded as rest or unknown, and may be underrepresented in the results.

An allogrooming bout was defined by 1 animal grooming another by licking and biting at the fur, and ending when the animals separated for >1 min. Fights between kinkajous were made obvious by loud screams, aggressive chases, and combative physical contact. Any instance of 2 or more kinkajous simultaneously feeding from the same fruit patch was considered group feeding. A fruiting patch usually consisted of a single fruiting tree or vine but occasionally included 2 fruiting plants if their canopies were adjacent. Each time a kinkajou fed on fruit, flowers, or leaves the following were recorded: plant species, location, diameter at breast height (DBH) of the plant, and a categorical estimation of the number of fruits or flowers on the ground under the plant (<10 , <50 , <100 , <500 , $<1,000$, $>1,000$). For unknown species, samples of fruit and leaves were collected and identified.

Data analysis - Home range size was calculated with the minimum convex polygon (MCP) method (Moher 1947) using the WILDTRAK computer program, Version 2 (Todd 1995). To exclude outlying points from a MCP and prevent a few extreme and atypical points from contributing a large additional area, a 95% MCP was used. This was done by using 95% of the data points lying closest to the arithmetic mean center of the range. Likewise, core feeding ranges were determined by calculating a 50% MCP, using only locations of feeding kinkajous collected by direct observation. When calculating the 95% and 50% MCP home ranges an independence interval of 70 min was used to avoid

temporal autocorrelation of consecutive locations. This is approximately the amount of time it would take a kinkajou to cross a home range (Doncaster and MacDonald 1997). Overlaps were calculated with both 100% and 95% polygons whenever possible. Observed patterns of grooming, group feeding, and group denning were compared using nonparametric chi-squared tests.

RESULTS

Social groups and home ranges - Although kinkajous spent most of their active time alone, individuals regularly associated with others. Patterns of association were consistent in five designated groups and, throughout the study, in one intensively monitored Center Group. Groups consisted of one adult female, two adult males, a subadult and a juvenile (Table III-2). Home ranges overlapped extensively among individuals within a group but rarely or never between groups (Table III-2 and Fig. III-1). The size of 95% MCP home ranges did not differ significantly by sex, or between adults and subadults (males = 29.0 ± 4.7 ha, females = 22.6 ± 5.13 ha, t-test d.f. = 9, $p = 0.38$; adults = 26.4 ± 4.0 ha, subadults = 24.7 ± 8.5 ha, t-test d.f. 9, $p = 0.86$) and were similar to previous published estimates for kinkajous (Julien-Laferrière 1993; Kays and Gittleman 1995). Although the number of fixes for juveniles were few, observed ranges were smaller than the range of adults and subadults, and centered in their mother's home range (Fig. III-1).

While following focal animals the location and size of all trees in which feeding occurred was noted. Although group members overlapped extensively in home range movements and used similar fruiting trees throughout their range, individuals focused

their feeding in core areas that overlapped little (Fig. III-2, Table III-3). The core feeding areas of the two adult males of the Center Group overlapped less than one ha, whereas the female and subadult male overlapped more with each other and with the two adult males. Individuals tended to eat in mostly small fruit trees in their core feeding area, but fed at larger trees in other areas within their total home range.

Not all individuals could be assigned to a group. The female GRZ was followed on eight half-nights and was never observed to associate closely with any male. She never denned with another adult kinkajou and groomed with an adult only once. Her home range was overlapped 43.9% and 30.1% by the adult and subadult males, respectively, from the West Group and 15.5% or less by the males of the Center Group. Her home range did not overlap with either of the two adult females from the Center Group (MOM and MAG), nor was she observed using the area where the female from the West Group (KAS, not radio-collared) was captured and observed. GRZ's juvenile, PEP, generally used the same area, but was also observed feeding with a male from the West Group (OTS, his genetic father, chapter 4) in the area where KAS was trapped and observed. In the Limbo plot, six other non-radio collared individuals could not be assigned to social groups (Table III-2); three (CHI, RIC and ROS) were captured near one another and may have associated in a group. No other males were captured near the female OLI, and she may have been living between social groups, similar to GRZ.

Day dens - All kinkajous slept in dens during the day. I identified 75 den sites on 156 different occasions; 43 of these den sites were observed, while the location of the others were designated from triangulation of radio-collared animals. Most observed dens were in tree holes (83.7%), the remainder were in the fronds of *Scheelea zonensis* palm trees.

Kinkajous usually denned in groups, but were also observed singly. I observed individuals exiting or entering day dens on 66 occasions. Individuals generally left the den within a few minutes of each other in the evening, but would enter at different times in the morning. Therefore, den exits are a more reliable indicator of group denning patterns: individuals were observed leaving a den independent of another individual in 30.2% of the 43 exits observed and in groups of 2, 3, 4, and 5 in 39.6%, 18.6%, 9.3% and 2.3% of the exits, respectively. Excluding juveniles, kinkajous denned with at least one other adult or subadult on at least 55.8% of the den exit observations. These estimates should be considered minimum values because non-radio-collared animals exiting a day den more than a few minutes after the focal animal would not have been detected. Kinkajous were never observed denning with animals from other social groups. Within-group dennings were not distributed significantly different than expected if at random, although male-juvenile combinations were rare (Table III-4).

Kinkajous are exclusively nocturnal as revealed by their exit and entrance times to their dens (Fig. III-3). Individuals were never observed to enter a den after sunrise, and only seven of the 43 exit times were before dusk; the most extreme of these (20 min before dusk) was an adult male that left a tree hole den early on the second consecutive night of copulations. Such strict nocturnality was also observed in captive kinkajous (Kavanau and Ramos 1972).

Although members of the Center Group used at least 44 different dens, they primarily used dens near the center of their range (Fig. III-4). The most utilized den for Center Group was occupied by both the resident female (MOM) at the beginning of the study and the immigrant female (MAG) that moved into the area after MOM's

disappearance. In total, the centrally located tree hole was used on at least 24 different nights and 66.7% of the exits were by groups of more than one kinkajou. This general pattern of den use was also observed in the other social groups, as well as in other studies (Julien-Laferrière 1993; Kays and Gittleman 1995).

Group feeding - More than one kinkajou fed together in the crown of a fruiting tree in 30 (19.6%) observed feeding bouts. Average feeding group size was 1.24 (or, not including juveniles, 1.20). Overall, males and females fed in similar groups (males avg. group size 1.27, females 1.19, t-test 1.05, *d.f.* 183, $P = 0.30$). However, most group feedings by females were with juveniles. Considering only feedings involving more than one adult, males fed in groups more often than females (males avg. group size 1.26, females 1.09, t-test 2.17, *d.f.* = 171, $P = 0.03$). Kinkajous were more likely to feed together in large trees, and kinkajou groups were larger in larger trees (Fig. III-5). Groups of kinkajous fed in 21.2% of the feeding bouts in large trees (>75cm DBH). The three fruit species with the largest average feeding group sizes are *Ficus insipida*, *Chrysophyllum cainito*, and *Hyeronima laxiflora* with 1.36, 1.44, and 1.60 kinkajous per feeding bout, respectively.

Male kinkajous occasionally fed outside of their normal (95 % MCP) home range with unknown female kinkajous. However, these females were not known to be associated with a social group (e.g., see discussion of GRZ). No kinkajous known to be associated with different social groups fed together in the same tree. Group feedings were not random with respect to social group structure. Male-juvenile combinations were observed much less than expected while female-juvenile combinations were much more common than expected (Table III-4). Female-subadult, male-female and male-

subadult combinations were all observed slightly less than expected, while male-male and subadult-juvenile combinations were slightly more common than expected. Even though kinkajous occasionally fed together, individuals almost never traveled in groups. Two individuals traveled together between feeding bouts in only 4 of the 145 consecutive bouts observed; three of these groups were mother-offspring pairs, the fourth was an adult and subadult male.

Allogrooming and play - Individuals were allogroomed on 38 occasions for a total of 254 min, excluding four nights when copulations were observed; the mean length of allogrooming was 6.44 min (SD 5.44), the longest a 28 min bout between an adult male and a subadult male. Allogrooming was most frequent at large fruiting trees, but also occurred in other fruiting and non-fruiting trees, and near day dens just after dusk.

Most allogrooming was between members of the same social group and never between individuals known to be from different groups; however, Center Group males groomed with females of unknown group association south of their normal (95% MCP) home range on three different occasions. Allogroomings were not distributed randomly: male-subadult and female-juvenile combinations were observed more than expected, whereas male-female, male-male, and male-juvenile combinations were observed significantly less than expected (Table III-4).

Although some allogrooming was unidirectional, both animals received grooming in most (60.5%) bouts. This was accomplished either by the two animals grooming each other simultaneously, or by one animal reciprocating immediately after the first stopped. Typically, allogrooming involved one animal lying on top of another individual and

grooming the ears, head, and back of the neck, though animals also groomed face-to-face and face-to-tail.

Play behavior was observed on four occasions between a juvenile and an adult or subadult (Table III-5). The adult female PAT ignored the juvenile and did not reciprocate with play, but the males clearly did participate in the play, and initiated it in at least one occasion.

Vocalizations and scent marking - Kinkajous regularly elicit brief vocalizations (<30 sec) in social situations, especially upon first meeting another group member. The hiss and screams described in captive animals by Poglayen-Neuwall (1962) were heard in aggressive situations. The most frequently given call was the two-part snort-weedle ("puff and bark" in Poglayen-Neuwall 1962): one quick snort sound, followed by a variable number of weedle vocalizations. This call was often given for a few seconds in many different social and solitary situations in which its precise function was difficult to discern.

The snort-weedle call was given in bouts of four minutes or longer on 20 different occasions in nights with no observed copulations. Both adult and subadult males and females gave these extended vocalizations, but individual variability was observed in their frequency. For example, BEA and ELV never called extensively (exclusive of nights with copulations) whereas PAT vocalized in bouts of 4-15 minutes on 9 different occasions and CHA on 5 occasions. Eighty-five percent of calls were given from non-fruiting trees and 15% from small fruiting trees. These extended vocalizations were always given by solitary kinkajous. In four occasions the vocalization bout was followed

within 15 minutes by a meeting with other group members: three between PAT and her juvenile (PIC) and subadult (MAG), and once between CHA and an unknown kinkajou.

Scent marking was difficult to observe because it could be done unnoticed while the animal moved along a branch. However, nine scent marking bouts of three minutes or more were observed by adult females and adult and subadult males. These events involved marking a branch with the paired mandibular scent glands, the throat gland, and the abdominal gland (Poglayen-Neuwall 1966). In at least five of these bouts the animal also wrapped its tail around a branch for support and rolled around with its back on the branch. This could have been to mark the branch with a scent from the animals back, or to anoint the animals back with scent that had just been deposited on the branch from the other scent glands. Two of these extended marking bouts were by a subadult male (POK) upon meeting a female (MAG) that had recently dispersed into his social group; two others were near the edge of the animal's home range.

Aggression - Aggression was observed on six occasions within kinkajou social groups, independent of copulations. All interactions between the two adult males of a group, involved brief fights and aggressive vocalizations lasting 3 minutes or less, and did not result in detectable injury. Afterwards, one animal would remain at the fight location, presumably because he won the contest, and the other would leave. These fights appeared to reflect a dominance relationship because the same individual consistently won every contest. BEA always retreated from ELV, and OTS always retreated from the unmarked adult male of his group.

Aggression between individuals of different groups was only observed on two nights, both involving GRZ, an adult female not closely associated with a group of males.

The first night GRZ was twice aggressively chased at the northern edge of her home range for seven and 10 min by an unknown kinkajou. Both of these chases ended when GRZ jumped approximately 8m to the ground and climbed up another tree. On the second night, GRZ was near the border of her home range with Center Group where she climbed approximately 25m from Center Group's adult female (MAG). GRZ moved to the end of a branch and shook it vigorously in the direction of MAG. Both kinkajous left the area without further interaction.

Mating behavior - Copulations were observed on 4 different nights; on 5 and 6 June, 1996, involving the two Center Group males (BEA and ELV) and an unknown female kinkajou from the west, and on 26 and 27 November involving BEA, ELV, and the female (MAG) that had joined their group about six months earlier. In each copulation, the males followed an estrous female, zigzagging over two to five ha in the first four or five hours of the night. At between 22:09 and 23:47 the animals stopped copulating and then dispersed in different locations. Each night had two to four copulations lasting from four to 150 minutes each for a total of 88-210 minutes of copulation.

Despite these consistent patterns, the June and November copulations were different in a number of ways. On 5 and 6 June ELV was the only male to copulate with the unknown female; BEA followed closely, vocalized with snort-weedles for 145 and 110 min/night, respectively, and fought with ELV six and eight times per night, respectively. BEA rested about four m from the copulating couple while vocalizing and inching closer. If he approached within one m ELV would aggressively yell and snap in his direction sending him back down the branch. If BEA persisted, a fight would ensue and consequently disrupt the copulation. In June, the subadult male from Center Group

(POK) was within 25m of most of the copulations on both nights. POK appeared excited by the activity and occasionally vocalized while rapidly climbing around the branches near the couple. However, as this subadult was no threat to the couple, he was able to sniff at and rest less than one m from them with no aggression from ELV.

In contrast, during the copulations in November with MAG there was no aggression between the two adult males, both males copulated, and the subadult did not appear interested in the copulations. However, the female (MAG) protested with aggressive screams and lunges 22 and 17 times when ELV attempted to copulate with her on 26 and 27 November, respectively. Despite this, ELV copulated with MAG six times for 114 min in the two nights. While ELV pursued and copulated with MAG, BEA followed silently from ca 10m and never disrupted the couple. On 27 November, ELV stopped following MAG at 21:14 and 19 min later BEA and MAG copulated for 68 min. MAG did not appear to resist BEA's copulation as aggressively as she did with ELV.

Breeding seasonality - From the size of juveniles and the lactation state of females, it appears that three kinkajous were born on the Limbo plot in August/September of 1995, and two in August/September of 1996. Given the 115 d gestation period for kinkajous in captivity (Poglayen-Neuwall 1962), most successful mating likely occurs in May or June. One juvenile, MOL, was 0.8 kg larger than other pups in November of 1995. Given neonatal weight gain similar to individuals in captivity (Poglayen-Neuwall 1962), MOL must have been born two to five months earlier than the other juveniles, from May to July. However, MOL lost weight in the low fruit season and weighed the same as other juveniles by March. From these observations, Limbo plot kinkajous appear to conceive at any time of the year but have a peak breeding season in May and June. Furthermore,

some, but not all females had pups in both 1995 and 1996, indicating that the interbirth interval for female kinkajous may sometimes be greater than one year.

Dispersal – One dispersal event was observed. Because the individual was radio-collared and I was able to collect detailed information over the course of this ca. one month long dispersal. Dispersal of the subadult female to the Center Group occurred after the disappearance of MOM, the adult female of the Center Group. Despite 157 trap nights and 39 half-nights of observation in her home range, MOM was never trapped or seen after 18 March, 1996. Before this, she had been captured 14 times, or once ever 17.8 trap nights, and was seen frequently interacting with other group members. Therefore, it appears that she disappeared soon after this last capture.

At the time of MOM's disappearance, MAG was a subadult female that had been trapped and observed interacting with East Group. From 22-25 April, 1996 MAG was captured three times, each time progressively closer to the center of MOM's old range (Table III-6). On 25 April MAG was fitted with a radio collar during which I noted four puncture wounds: two on the tail, one on the arm and one on the head. From 3 May until 31 May MAG was observed feeding in MOM's old range, but occasionally returned to her previous range where she reunited and denned with her mother (PAT, chapter 4). In May MAG non-aggressively interacted with an adult (ELV) and subadult male (POK) from Center Group in MOM's old range. On 11 June MAG denned with ELV for the first time and was apparently fully integrated into the group. MAG copulated with both Center Group males on 26 and 27 November, 1996. Because MOM disappeared approximately one month before MAG began to disperse, and MAG interacted non-aggressively with both the males of her new group and the female of her old group,

MAG's scars were probably the results of fights with other females for access to Center Group. MOM's pup (LUN) was trapped and observed interacting with all three males from Center Group on nine different nights after MOM's disappearance. However, she was never seen or trapped again after 8 June. MAG and LUN were never seen together.

No other dispersal was observed in such detail. However, one observation suggests that another subadult female marked on the Limbo plot also dispersed. On 4 June, 1997, ARE was observed 400 m away from her previous range at 07:00 hrs with an injury to her hindquarters (T. Robinson pers. com.). No obvious dispersal behavior was observed by the three subadult males monitored on the Limbo plot (ERN, POK, and RRY).

DISCUSSION

Individuals of most mammal species forage alone. The social behavior of such solitary species has been difficult to study because social interactions are rare and cryptic. However, "solitary" is often just a default term given to a species that has been little studied. Leyhausen (1965) recognized this: "For the main reason why so many mammals are said to be solitary seems to be that they can only be shot one at a time". Using more accurate and less intrusive methodologies, researchers have recently uncovered surprising sociality in these "solitary" species, suggesting a continuum between the completely solitary and classically social species (Caro 1994; Sterling and Richard 1995; Waser et al. 1994). Clearly, being solitary does not preclude the evolution of complex social behaviors and even group living.

Kinkajous on the Limbo plot were primarily solitary yet exhibited a social group life. They regularly interacted in social groups of one female and two males. These groups were consolidated at day dens and large fruiting trees, while individuals fed singly at small trees and almost never traveled in groups between feeding trees. Group members overlapped extensively in home range but were very strict about avoiding areas used by other groups, suggesting precise territorial boundaries. Not all females were members of social groups, with some living in areas between groups. Males were the more social sex, while dispersal appeared to be female biased.

The following sections discuss what conditions are associated with the solitary and grouping nature of kinkajou social organization and the different strategies of males and females within this society. I conclude by discussing the territorial and patrilineal nature of their groups and speculate about potential geographic variation in social structure.

Why be solitary? - Group living is an adaptation many mammal species have evolved to reduce predation risk and/ or increase foraging efficiency. Groups offer individuals protection from predators by active group defense, increased vigilance, and the dilution effect (Pulliam and Caraco 1984). Nocturnality, arboreality and large body size are other adaptations that may reduce predation risk (Hill and Dunbar 1998; Isbell 1994).

Kinkajous combine these latter three characteristics to virtually eliminate regular predation by all possible predators in neotropical forests. Strict nocturnality protects kinkajous from large diurnal raptors, and no forest owls or arboreal felids are large enough to regularly attack an adult kinkajou. By spending most of their time in the middle and upper canopy (Charles-Dominique et al. 1981; Kays unpublished data)

kinkajous avoid regular predation by large terrestrial felids. An indirect indicator of low predation rate is slow reproductive rate. Kinkajous have a litter size of one, and females probably have an interbirth interval of one to two years. Clearly, a population with such a low reproductive rate can not sustain a high predation rate. Support for this generalization comes from a comparative study of primates that found reproductive rate to be the best predictor of predation rate (Hill and Dunbar 1998).

Therefore, kinkajous are not very vulnerable to predation and consistent group-living is of little benefit in this regard. In the study area, individuals typically fed solitarily. The advantage of solitary foraging over group foraging is that it reduces competition for food. Specifically, as feeding group size increases an individual group member has to travel further and feed in more food patches than if it were foraging alone (Chapman et al. 1995; Symington 1988a; Wrangham et al. 1993). However, kinkajous regularly associated in small groups that overlapped extensively in home range, occasionally fed together in large fruiting trees, denned together on most days and allogroomed.

Why group? – Numerous aspects of kinkajou behavior and ecology reduce the cost of living in a group. This is most relevant for males because they are more social than females and do not have the added energetic costs of reproduction. First, the main food for kinkajous (ripe fruit) is distributed in depletive clusters that are patchy in their temporal and spatial distribution (Chapman et al. 1995; chapter 2). This pattern of food availability can remove, or lower, feeding costs of group living relative to solitary life. The Resource Dispersion Hypothesis (RDH) (Bacon et al. 1991a; b; Carr and Macdonald 1986) suggests that if a species' main food is renewable and patchily distributed in space

and time, the territory size needed for a breeding pair may also contain the resources to support other individuals at no added cost. Specifically, a breeding pair of kinkajous must defend a territory large enough to have trees in fruit during all seasons of the year. Additional subordinate animals may share this territory without negatively affecting the feeding security of the breeding pair, even in the season of lowest overall food abundance.

Secondly, kinkajous primarily feed alone, limiting most social interactions to specific situations where grouping will not increase feeding competition. Group feeding is restricted to very large fruiting trees, individuals do not travel together between feeding bouts, and other social interactions are most frequent at large trees or day dens. Furthermore, kinkajous lower their chances of encountering a small fruiting tree that another group member has recently depleted by usually eating in exclusive core feeding areas and advertising their location with vocalizations.

The patchy distribution of food, combined with flexible feeding groups, minimizes the costs of within group feeding competition. Additionally, group members can be related (chapter 4), further decreasing the inclusive fitness costs of grouping. The cost of living in a kinkajou group may simply be less than the effort it would take to drive away group members. This is especially true in an area saturated with kinkajous, which, based on the tightly spaced territorial boundaries (Fig. III-1), appears to be the case for the Limbo plot. Judging from the injuries found on dispersing individuals, leaving home can be dangerous. The low ecological costs of group living, combined with the high costs of dispersing in a saturated habitat, are critical factors influencing kinkajou group life.

But are there any advantages, if only ephemeral, to group living in kinkajous? The low costs of forming groups could permit cooperative behaviors with very small advantages to evolve. Grouping at day dens could provide protection from diurnal predators. Allogrooming was observed between group members, and may be more common inside dens. Individuals appear to benefit from this grooming since most had no ticks or other large ectoparasites (R. Kays, unpublished data). I suspect the most important advantage of kinkajou group life are social factors, especially related to male territoriality (see below). Because females lead less social lives they probably receive fewer social benefits from group life.

The sociality of females - Because the cost of reproduction is high, it is widely accepted that the spatial distribution of females is closely tied to availability of resources (e.g., Bradbury and Vehrencamp 1977; Clutton-Brock 1989; Emlen and Oring 1977; Wrangham 1980). Males, on the other hand, are less constrained by reproductive costs in most mammals and tend to be more affected by the distribution of females than resources. This also appears to be the case for kinkajous, where females respond more to fluctuations in the local food abundance than males (chapter 5). Therefore, it is not surprising that female kinkajous do not overlap in their home range with other females, as this would increase competition for food trees.

All adult females strictly avoided each other, and generally avoided feeding with the males of their group as well (Fig. III-1, Table III-4), further minimizing feeding competition. Females of other highly frugivorous species with flexible group size, such as spider monkeys (*Ateles* sp.) and chimpanzees (*Pan paniscus*), also avoid contact with each other, presumable to minimize feeding competition or avoid infanticide (Chapman

1990; Chapman et al. 1995; Symington 1988a). Because females face high energetic costs during reproduction, female kinkajous may be more sensitive to feeding competition and live more solitary lives than males.

The social patterns and home ranges of four of the radio-collared females (MOM, MAG, PAT, ORA) were closely associated with a social group, but one (GRZ) was not. GRZ occupied a home range that appeared to be between Center Group and West Group and did not closely associate with any males. Other non radio-collared females on the Limbo plot may also have been living like this (e.g., OLI). Because group members usually sleep in day dens near the center of their group range, kinkajous tend to concentrate their feeding in the middle of their range and feed less along the border. Thus fruiting trees along the borders of two social groups are less likely to be fed in by group members in a given night, which may allow non-group females to successfully live and raise litters in this rarely used area (see Stewart et al. 1997).

The sociality of males – Typically, if female mammals live in groups males may tolerate each other to live with these females. If females are asocial and live in non-overlapping territories males should not be able to monopolize more than one. In this case adult males should not associate but either form a bond with a single female or range widely to overlap with as many females as possible (Clutton-Brock 1989). Kinkajou males, however, did not follow this model. Although females did not live together, males associated in pairs. Because females have small home ranges, pairs of males in coalition may be able to defend an area large enough to completely overlap with one female and partially overlap the area used by non-group females (e.g., GRZ).

Male coalitions form for similar reasons in other carnivores. Female cheetahs (*Acinonyx jubatus*) live alone in very large overlapping home ranges, but depend on a few areas that have the combination of sufficient cover and adequate concentrations of gazelles. Males form small coalitions to defend these smaller preferred areas that females must visit to obtain resources (Caro 1994). Near rocky outcroppings in areas used by humans, slender mongoose females (*Herpestes sanguineus*) have small nonoverlapping territories. Stable coalitions of up to four males form and appear to defend a large territory overlapping two or more female ranges (Rood 1989; Waser et al. 1994). In this instance, it appears that the small size of female territories (at least in some habitats) allows them to be monopolized by groups of males. Female raccoons (*Procyon lotor*) in Texas forage alone, but appear to be defensible by male coalitions because of both their smaller home range size, and their dependence on a limited number of water sources (Gehrt and Fritzell 1998a)

Kinkajou male coalitions were dominated by one individual (e.g. CHA and ELV in Fig. III-1, K1 in Kays and Gittleman 1995) that uses an area large enough to overlap completely with one female and give occasional access to non-group females. Although the home range size of females was not found to be statistically smaller than males, they were never as large as those of the dominant adult males. Subordinate males used smaller areas providing them less access to non-group females. This difference was also reflected in the mating behavior of Center Group males. The dominant male copulated with the group female and a non-group female, whereas the subordinate male only copulated with the group female, and was driven away from the non-group female by the dominant male.

Thus, male and female kinkajous differ both ecologically and socially. Females are strongly tied to food resources and avoid contact with other individuals to minimize feeding competition. Males are associated with the distribution of females, and form coalitions to maximize the number of females with which they can overlap, presumably with cooperative territory scent marking. In this way, males monopolize one group female and also associate with non-group females. Dominant males range widely in their territories and receive most copulations. Subordinate males have less contact with non-group females, but do occasionally copulate with the group female, and form bonds with younger males. Dominant males may not drive subordinate males out of their territory because feeding competition is less important to males, they may be close relatives, and they may help mark and defend the territory.

Because their normal social unit consists of two adult males and one adult females, kinkajous may be considered socially polyandrous. However, because group males also mate with neighboring females that are not members of any social groups, kinkajous are probably best viewed as having a promiscuous mating system.

Kinkajou territories - I suggest that kinkajou males form coalitions to mark and defend exclusive territories large enough to completely encompass the home range of one female, who becomes a group member, and also give access to other females that are not members of other groups (e.g., GRZ). Males may strategically defend areas likely to include large fruiting trees (e.g., *Ficus* sp.), which are a preferred food sources for kinkajous, and may be crucial to females in the period of low food abundance.

The high overlap between group males and the lack of overlap between males of different groups supports the idea of territoriality. Kinkajous have four unique scent

glands (Poglayen-Neuwall 1966) which are probably used to mark these exact territorial boundaries. Although I did not observe any aggression between males of different groups, it has been reported in other studies, primarily in large fruiting trees at territory boundaries (Julien-Laferrière 1993; Kays and Gittleman 1995).

Male territoriality is consistent with the dispersal data. Greenwood's (1980) dispersal theory suggests that female biased dispersal is the rule in species with mating systems based on resource defense (i.e., most birds) and male dispersal for systems based on mate defense (i.e., most mammals). Field observations indicated that the two subadult female kinkajous on the Limbo plot dispersed in their 2nd or 3rd year, whereas none of the three subadult male kinkajous dispersed. Female biased dispersal in the study population is also supported by genetic data (chapter 4). Thus, territorial and dispersal data suggest that kinkajous are unusual among mammals in having a social system based on resource defense.

Kinkajou territories appear to be patrilineal; males remain in their natal group to inherit the home range or bud off to form a new neighboring group alone or with a relative. I do not have the long-term data to show the inheritance or group formation but do have short-term data that support this assertion. First, dispersal is female biased so that males are more likely to remain with their natal group. Second, at least one of the male associations on the Limbo plot was between two highly related males that were probably brothers or father-son (chapter 4). Third, male kinkajous from the same group had affiliative relationships. Adults were tolerant of each other and associations between adults and younger males were always affiliative (Table III-4, III-5).

Patrilineal groups with female dispersal are very rare in the Carnivora (Frame and Frame 1976, Frame et al. 1979, Waser 1996), but are known from two primate groups: spider monkeys and chimpanzees. Interestingly, like kinkajous, these primates also have low predation risk and a diet of ripe tropical fruit, suggesting that these shared traits may have led to similar social evolution.

Social flexibility - I have described kinkajou social organization as a solitary group-life. Social groups have two males and one female, and appear patrilineally based. The sociality within groups is flexible, similar to the fission-fusion systems of *Ateles*, *Pan*, and Orangutans (*Pongo pygmaeus*) (Wrangham 1986; Chapman 1990 ;Van Schaik 1999). Individuals usually sleep together and feed alone but also congregate in feeding groups of up to five individuals, depending on fruit abundance and patch size. Many social species that feed solitarily show considerable flexibility in social organization depending on habitat structure and food availability (Gittleman 1989; Lott 1991, Creel and Macdonald 1995, Van Schaik 1999).

I predict that kinkajou social organization may also be flexible over their large geographic range. Populations with smaller body sizes or in habitats with increased predation may be more gregarious to minimize predation risk (e.g., Forman 1985). If females reside in smaller non-overlapping home ranges in forests that are more productive, or less seasonal, males may be able to defend an area fully including more than one female home range; male coalitions may be larger or more cooperative to accomplish this. Forests that are less productive (e.g., reduction in fruit availability) or more seasonal should require larger female home ranges. If a single female's range reaches an upper size limit that a single male can cover, male coalitions would not help

give access to additional females and kinkajous may revert to a monogamous social system.

CHAPTER IV

THE GENETICS OF SOLITARY GROUP LIFE:

A MICROSATELLITE ANALYSIS OF KINKAJOU SOCIAL ORGANIZATION.

INTRODUCTION

The social organization of a species has been traditionally described solely from behavioral observations in the field. Interactions between individuals could be described from the short or medium-term observations on habituated individuals, but pedigree relationships could only be inferred from longitudinal studies of mating and immigration. The revolution of genetic techniques now allows immediate estimates of relatedness between individuals and more certain identification of parentage. This has provided new details about the social life of animals, confirming conclusions from field observations in some cases while challenging them in others. The reassessment of established hypotheses through the use genetic data and ensuing reanalysis has advanced the understanding of many social organizations and their evolutionary origins.

These modern genetic tools have primarily been used with social species. Predictions from field data on grouping patterns, dominance hierarchies, and copulations have been tested with new detail and accuracy. Many established hypotheses based on field data have survived the reanalyzes. For example, as predicted, males from within the pride were the only genetic fathers of cubs in African lions (*Panthera leo*, Packer et al. 1991), and behaviorally dominant male baboons (*Papio cynocephalus*) mated more often and sired more offspring than did submissive males (Altmann et al. 1996). Dispersal patterns, notoriously difficult to quantify with field data, have also been confirmed with

genetic data (e.g., wolves, *Canis lupus*, Lehman et al. 1992; coati *Nasua narica*, Gompper et al. 1998).

The details of the social life of nongregarious species remain poorly known. These species have traditionally been difficult to study because of their solitary and often secretive nature. As some of these presumed solitary species are analyzed with modern field and genetic techniques, they are found, in fact, to be social and associate in stable groups. For example, although individuals belonging to both species spend most of their time alone, intensive field work with raccoons (*Procyon lotor*, Gehrt and Fritzell 1998a, b) and slender mongooses (*Herpestes sanguineus*, Rood 1989; Waser et al. 1994) found males associating in stable and non-aggressive groups of three to four individuals. Genetic fingerprinting of the mongooses showed that no single group male monopolized access to females and that group members can be related or unrelated.

The continuum of social organization that lies between completely solitary and completely social will be better understood as intensive telemetry and observation are applied to other elusive mammal species presently classified as solitary. In addition to field work, genetic analyses will be crucial to fill in details about relatedness, parentage, and dispersal patterns important in understanding why a species has evolved to be solitary, gregarious, or a combination of both.

Here I describe the results of a microsatellite analysis of kinkajou (*Potos flavus*) social structure. The kinkajou is a medium sized (2.5-3.5 kg), nocturnal, arboreal, frugivore related to raccoons and coatis. When this study began, kinkajous were thought to be solitary and asocial (Ford and Hoffmann 1988; Poglayen-Neuwall 1962; 1976). Using tree-traps, telemetry, and observation, data was collect on 25 habituated, free-

ranging, kinkajous in central Panama. These field data confirmed their mostly solitary nature, but surprisingly, also documented a consistent and unusual group structure and social life (chapter 3). Kinkajous traveled and fed in small trees alone, but regularly congregated in groups of two to five while feeding in large fruit trees and sleeping in day dens, similar to the fission-fusion social systems of some primates (Wrangham 1986; Chapman et al. 1995; Van Schaik 1999). Membership of these groups was consistently included two adult males, one adult female, one subadult, and one juvenile. The membership and relative location of these groups is shown in Figure IV-1. Some females did not associate in this group structure (e.g. GRZ in Fig. IV-1). Territories were apparently well established as there was virtually no spatial overlap between groups. Furthermore, kinkajous from different social groups were never observed to directly interact.

Social group members, however, regularly interacted by grooming each other (38 bouts observed), sleeping together in the same tree hole ($\geq 59.8\%$ of dennings), or feeding together in the same large fruiting tree (group feeding in 35% of large feeding trees). These affiliative interactions were most frequent involving males with subadult males, and females with juveniles. The female provided all of the parental care for the juvenile of a group, including carrying it between den sites, and traveling slowly with it between feeding trees as it matured. The adult males and subadults did not directly care for juveniles, but did regularly sleep and feed with the pups, and occasionally had playful interactions with them. The two adult males in a group denned and fed together occasionally, but rarely groomed each other. Short (average <1 min) fights were observed on six occasions between the two adult males of a group. More extended fights between

males were observed on nights when females were in estrous. One male consistently dominated the other in all of these fights, holding his ground while the other fled down a branch. The dominate male received all but one of the 11 copulations observed with two females on four nights. Although fights and copulations were not observed for all pairs of group males, likely dominance could still be assigned based on ranging patterns and physical condition (Fig. IV-1).

Although I do not have the long term data to document the inheritance of group territories, a number of lines of evidence suggest that kinkajou groups may be patrilineal. The strict female-female asociality and range exclusion combined with the male-male sociality of kinkajou group life all support the possibility of a patrilineal society (chapter 3). Given the social group structure observed in the field, I have produced the following hypotheses about the relatedness and paternity within groups and the nature of male coalitions.

Genetic hypotheses - Kinkajou social groups appear to be based on a family structure. Therefore I expect both the mother and father for each pup to be from within the group. Furthermore, the subadults socialized with both the male and female of the group, and appeared to still be in their natal group; therefore genetic data should confirm that both parents for each subadult are also from the same group. Since both males in a social group were attempting to breed with the female of their group, the males should be unrelated to the adult female of the group.

In most cases male coalitions in carnivores are between related individuals (e.g., Caro 1994, Packer et al. 1991). This should also be the case in patrilineal groups. Therefore, I predict that the relatedness of within-group male dyads will be high

indicating a father-son or brother-brother relationship. One of the two males in a group dominated the other in fights and obtained all but the final copulations observed.

Therefore, I predict that the dominate male will obtain all of the fertilizations in a group and be the sire of both the juvenile and the subadult of each group.

METHODS

Study site and animals - Field research was conducted in lowland forest of Parque Nacional Soberanía in the Republic of Panamá (22100 ha; 9° 9' 35" N, 79° 44' 36" W). Work was centered around the trail network of the 104 ha Limbo research plot (Robinson 1998). Elevation within the plot varies from 35 to 80 m above sea level, while the surrounding areas reach 225 m. The vegetation is classified as tropical moist forest. Annual rainfall is approximately 2600 mm with 90% falling during the late April to mid-December wet season (Dietrich et al., 1982). Density of kinkajous around the Limbo plot was approximately 12/km² (Kays, unpublished data).

Twenty-five kinkajous were captured 192 times with 50 large (32x32x102cm) Tomahawk live traps. Traps were baited for 1,292 trap nights with banana and hung in trees 4-25 m above the ground using a hoistable trap design (Kays 1999). Newly-captured animals were immobilized with 0.3 cc of a solution of 80% Ketamine hydrochloride and 20% Zylazine hydrochloride, and standard physical measurements were taken. Three cc of blood was drawn from the femoral vein, and a small (<1 cm²) clip of tissue was taken from each animal's ear to mark them permanently. Ten kinkajous were fitted with radio collars that were marked with a unique pattern of colored reflective tape. Fifteen kinkajous were fitted with a similar reflective identification collar without a radio transmitter.

Marked kinkajous habituated quickly and could be followed and observed without obvious disturbance. Radio-collared animals were followed for 74 half-nights, either from when they left their sleeping den at dusk until midnight or from midnight until they entered their sleeping den at dawn, for a total of 380 h. Focal animals were observed from the ground with binoculars and were illuminated with a 6v head lamp. A red filter was used when an animal was in the understory and a 12v spotlight was used when an animal was in the upper canopy. Care was taken to not shine lights continuously on the focal animal. Animals could not always be seen clearly because of understory vegetation and darkness. Therefore, sporadic visual observation, falling fruit and sounds were used in combination to determine a focal animal's behavior. Generally, kinkajous could be directly seen while they were feeding or resting in a tree. As they moved through the trees, however, they could only be seen intermittently and I had to rely on telemetry to follow traveling animals.

Microsatellite techniques - DNA was extracted from blood samples with a proteinase K digestion followed by DNA isolation with phenol/chloroform/isoamyl alcohol (PCI) (Sambrook et al. 1989). Using 11 tandem repeat microsatellite loci designed specifically for kinkajous (Kays et al. in prep; Table IV-1), microsatellite alleles were detected from genomic DNA by end-labeling one primer with a standard 32g-ATP (Amersham) and T4 polynucleotide kinase reaction (Sambrook et al. 1989) and performing 28 cycles of polymerize chain reaction amplification in a 25-ml reaction volume using 20 pmol of each primer, 50 ng of target DNA, 2 mM MgCl₂, and 0.8 U of Taq DNA polymerase (Promega). Reaction conditions were denaturation at 94°C for 45 s, annealing at 51°C to 56°C for 45 s, and extension at 72°C for 60 s. I mixed 3 µl of each product with 2 µl of

formamide loading dye, heated it to 94°C for 5 min, and loaded it onto a 6% sequencing gel containing 50% (w/v) urea. An M13 control region was run adjacent to the samples to provide an absolute size marker for the microsatellite alleles. Completed gels were dried on Whattman paper and autoradiographed overnight.

Statistical analyses- I calculated the Queller and Goodnight (1989) index of relatedness (R) with the computer program RELATEDNESS 5.0 (Goodnight 1998) to estimate kinship of all pairs of Limbo plot kinkajous. Values can vary from -1 to 1, and in populations at Hardy-Wienberg equilibrium the values for parent-offspring or full sibling relationships should approach 0.5. However, R values for pairs of individuals are expected to vary due to stochasticity. The standard deviation of relatedness values were estimated by jack-knifing over all loci (Queller and Goodnight 1989).

The number of loci needed to provide consistent estimates of relatedness was assessed by rarefaction analysis. A locus was selected at random, the relatedness was calculated, another locus was selected without replacement, and the relatedness was recalculated based on both loci. The number of loci was increased by addition without replacement until all eleven loci were selected. The difference between consecutive samplings was expressed as a function of the total number of loci drawn (Fig. IV-2). This procedure was repeated 1000 times and mean difference values were calculated (see Altmann et al. 1996). The number of loci needed was then evaluated by observing at which point the curve approached a plateau.

To assign paternity to juvenile kinkajous I used the likelihood approach pioneered by Thompson (1976) and Meagher (1986), recently refined and computerized into the program CERVUS 1.0 by Marshall et al. (1998). Paternity for each male pup

combination was estimated from the ratio of the likelihood that the mother and alleged father are the parents of the pup relative to the likelihood that the mother is the parent and the father is randomly chosen from the population. Likelihood ratios were calculated for each male at each locus, and the natural logarithm of the product across all loci was taken, termed the LOD score (Meagher 1986). The male with the highest LOD score was considered to be the most likely sire of that pup, and the magnitude of the difference between his LOD score and that of the next-most-likely sire (Δ LOD) was used to quantify the certainty of each assignment with CERVUS 1.0 (Marshall et al. 1998). CERVUS predicts critical Δ LOD scores to assign paternity at a given level of statistical confidence based on simulations with genotype data from the study population. The following input parameters were used: total number of candidate males (10), proportion of candidate males sampled (0.80), proportion of missing genotypes (0.03), rate of typing errors (0.005), and confidence levels (80 and 95%).

To assign parentage to subadult kinkajous I first used CERVUS 1.0 to confirm that the subadult was still living in the social group with its mother or father by testing against critical Δ LOD scores estimated for situations when neither parent is known. Within group parentage at this level was confirmed in three cases (POK, RRY, and MAG) but not for one (ERN). ERN's most likely mother (80% confidence level) was a female (GRZ) unattached to any social group and living in an area next to ERN's group. Once a parent was thus assigned, candidate second parents were evaluated with critical Δ LOD scores estimated for situations when one parent is known.

Linkage and Hardy-Wienberg equilibrium of microsatellite loci were tested with chi-square and G -test, respectively, using the program GENEPOP 3.1 (Raymond and Rousset 1995).

RESULTS

Parentage - With a combination of exclusion and likelihood analyses both parents were assigned for seven of the eight offspring sampled (Fig IV-3). At least one allele excluded all but one male as a potential sire in four cases, and all but two males in three cases. The average number of alleles excluding a male was 2.2 ± 1.3 (for 64 male-offspring combinations). For the log likelihood approach to determining paternity the critical Δ LOD values for assigning certainty in this population were found. For one parent known the values were 0.01 and 1.82, for two parents known Δ LOD was 0.72 and 2.26, with 80% and 95% levels of certainty, respectively. Using these values, paternity was assigned to five offspring with $\geq 95\%$ certainty, and to two offspring with $\geq 80\%$ certainty. The sire of one subadult offspring (POK) remains unknown, although his mother was confirmed with $\geq 95\%$ certainty.

These basic paternity results were evaluated in terms of the group membership of each parent-offspring pair. Five of six identified sires of group offspring came from the same social group as the mother and pup. One offspring, the subadult ERN, was in a social group that did not include his genetic mother or sire. ERN's genetic mother (GRZ) was living outside of any group structure, to the north of ERN, and his genetic father (CHA) was the dominant male of a social group to the east. The adult male with whom ERN shared a group territory (OTS) was excluded as his sire by 1 allele. The LOD certainty values for both parents of ERN were lower than most (80%) and therefore these

relationships should be viewed with caution. Although the adult female from the subadult POK's group was confirmed to be his mother with $\geq 95\%$ certainty, his father could not be identified and was likely not sampled. POK was conceived before my field study began and his genetic father may have disappeared before trapping began. One juvenile (PEP) was raised outside of the typical group structure. Log likelihood analyses confirm with $\geq 95\%$ certainty that PEP was being raised by his genetic mother. His sire was an adult male (OTS) from a neighboring group, an individual with whom PEP occasionally associated.

Because kinkajous have no more than one offspring per year, it is difficult to evaluate the extent to which dominant males monopolize fertilizations. However, by testing both juveniles and subadults from each social group the data suggest that one male can dominate breeding. None of the six group offspring were sired by a subordinate male in a group; all five identified sires were dominant males. Furthermore, in East and North Group, both the juvenile and subadult were sired by the same, dominant male of their group. The dominant male of Center Group (ELV) was the sire of the juvenile, but not the subadult (POK) of his group. However, POK was conceived before my field study began, when group membership and dominance relationships may have been different.

Relatedness - Standard tests showed that the methods selected were appropriate, and that the Limbo population meets necessary genetic assumptions. The rarefaction analysis of relatedness estimates calculated with microsatellite loci changed little after six or seven loci (Fig. IV-2). Therefore, the inclusion of more than the 11 loci used in this study would not have significantly changed the relatedness estimates. The study population

was in Hardy-Wienberg equilibrium for all loci (at the $p=0.005$ level) and no loci were found to be linked (at the $p=0.005$ level).

To assess the accuracy of Queller-Goodnight R values in estimating relatedness between individuals of unknown familiar relationships I compared average R values for dyads of known relationships (Fig. IV-3). Pairs with a predicted relatedness of 0.50 (father-offspring, mother-offspring, or full siblings) were identified based on the parentage analyses. Seven father-offspring dyads averaged a Queller-Goodnight relatedness of 0.39 ± 0.09 , eight mother-offspring dyads averaged 0.39 ± 0.05 , and two full sibling dyads averaged 0.38 ± 0.16 . These relatedness estimates are consistently 0.11-0.12 lower than predicted values for known relationships. This was probably due to the sample of 25 neighboring kinkajous including too few unrelated individuals, thereby causing an underestimate of Queller-Goodnight relatedness values (see De Ruiter and Geffen 1998). Although this sampling bias causes the relatedness estimates to be lower than predicted, it does not affect their accuracy when comparing individuals from within this population.

Pairwise relatedness values were used to evaluate the relationships between classes of individuals within groups (Table IV-2). Five of the six adult male-adult female dyads were unrelated, averaging $R = -0.13 \pm 0.15$. One dyad from South Group, between OTS and KAS, was related at $R = 0.47$. However this pair should be evaluated with caution, because KAS was not captured until the very end of the study, was not radio-collared, and may not have been the resident adult female of South Group. Two within group adult male-male dyads were sampled. The pair from North Group had a low value of relatedness ($R = -0.06$), while the Center Group pair was highly related ($R = 0.49$).

Therefore, within a group, the adults of the two sexes were unrelated, but the two males of a group could be related or unrelated.

To assess the genetic neighborhood of adult kinkajous I calculated the relatedness between a group member and non-group members of the same sex on the Limbo plot. If one sex disperses further or more often than the other, it should be living among unrelated individuals as an adult. Neighboring male kinkajous were more closely related to each other than neighboring female kinkajous (Fig. IV-4) (males $R = 0.151 \pm 0.085$, females $R = -0.161 \pm 0.084$, 1 tailed T-test, d.f. = 34, $p < 0.001$). This suggests that females disperse more often and/or further than males.

DISCUSSION

Analyses of microsatellite genetic data confirmed the family nature of kinkajou groups, with both most likely parents coming from within the group, and unrelated breeding pairs. Although only two male coalitions were fully sampled, they had very different relatedness values, showing that they can be related or unrelated. Dominant males were the only sires of group offspring. Patterns of relatedness between neighbors suggested a female biased dispersal in kinkajous, confirming field observations and supporting a patrilineal view of kinkajou groups.

Social Groups as families – The groups contained two adult males and one adult female. Both males copulated with the group female, and therefore I expected that both males were unrelated to the female, and form a breeding unit. Genetic data support this hypothesis: average relatedness of adult males and females within a group was -0.13.

Because of the sociality between both juveniles and subadults towards the adults of their social group I expected that all of these young animals were still living in their

natal groups with both genetic parents. Furthermore, I did not expect to find extra-group paternity for any of the juveniles because adults from different groups were never observed to interact or cross territorial boundaries (chapter 3). These expectations were supported by the genetic data: both the mother and sire of all three group juveniles were living in the same social group (Fig. IV-3).

The paternity results of subadults must be evaluated with caution because they were conceived approximately 18 months before my field study began. Two of the four group subadults (MAG and RRY) were in a social group with both genetic parents. A third (POK) was in a social group with his mother, but his sire could not be identified. Because I thoroughly sampled the kinkajou groups in the area, I suspect that his sire had disappeared from the area since conception. The situation of the subadult ERN is more complicated, since both most likely parents were not members of his current group. Unlike most females, his mother (GRZ) did not associate with a group but lived between the territories of two social groups, and was never observed to den or groom with male kinkajous. ERN apparently moved out of his natal range to associate with a neighboring adult male in a social group.

GRZ was also observed caring for a juvenile which was confirmed to be her offspring in the parentage analyses. On three occasions the juvenile interacted (denuded, ate, groomed, and played) with an adult male from a neighboring group (OTS, chapter 3.) who proved to be his most likely sire. This association of father and son, despite the fact that the mother was not observed to associate with the male, suggests some form of kin recognition. This father-son association is another line of evidence showing early social bonds between male kinkajous and supporting the possibility of patrilineal groups.

Male coalitions - Although the two adult males of a kinkajou group generally had neutral or affiliative interactions, they occasionally fought, revealing clear dominance relationships (chapter 3). One male consistently dominated these fights, and received most copulations. However, the subordinate male was observed to copulate once, for 68 minutes. The subordinate achieved this only after the dominate male quit his pursuit of the receptive female, presumably to feed. Despite this single copulation by a subordinate, the genetic data show that the dominant males received all fertilizations, and are able to dominate breeding over time in a social group. All of the identified genetic sires of group offspring were dominate males (Fig IV-3). Although the sample sizes are small, this suggests that reproduction is not be shared evenly between the two males in a kinkajou social group. Behavioral data support this result, a subordinate male was observed to copulate only once. Other male carnivore coalitions appear to have more equitable sharing of mating opportunities (cheetah, *Acinonyx jubatus*, Caro 1994), and fertilizations (slender mongoose, *Herpestes sanguineus*, Waser et al. 1994; African lion, *Panthera leo*, Packer et al. 1991). Sharing of mating opportunities by a dominant individual encourages the subordinate to remain in the group. Subordinate male kinkajous may associate with a dominate male with the hopes of a chance at mating with the group female, and the possibility of achieving dominant status in the future.

Unfortunately, the second male of some groups was not trapped and could not be included in the genetic analyses. The two male coalitions that were fully sampled gave mixed results; one pair showed high relatedness, and the other low (Table IV-2, Fig. IV-4). Male coalitions in other carnivore species tend to be close relatives, but also can include nonrelatives (Caro 1994; Packer et al. 1991). Because kinkajous have a litter size

of one and breed no more than once a year, it may be difficult for some males to find related males with which to group. I do not have sufficient behavioral observations on the unrelated male pairs to test ideas about the effect of genetic relationship on the social relationship of male coalitions. However, given that kinkajou male coalitions can be related or unrelated, it is possible to make specific predictions about the behavior of male coalitions (Caro 1994, Packer et al. 1991). Because inclusive fitness offsets costs of sharing reproduction, larger groups of male kinkajous should include only highly related individuals. Copulations should be shared more equitably in groups of unrelated males than related males, in order to retain the help of an unrelated individuals. Finally, because social bonds tend to be stronger among relatives, grooming should be more frequent between related individuals.

Dispersal – If kinkajous are patrilineal, young females should be the primary dispersers from their natal group. I trapped and marked three male and two female subadult kinkajous on the Limbo plot. None of the three subadult males dispersed during the study. One of the subadult females dispersed to a vacancy in a neighboring group. She presumably fought other females to obtain this new group position because she had a number of fresh bite scars (chapter 3). The second female (ARE) was not radio-collared, but apparently did not disperse during the study because she was trapped in the same area throughout. However, after the end of the field-work, ARE was observed injured and 400m (ca. the width of one kinkajou territory) away from her nearest capture (T. Robinson pers. com.). This unusual observation suggests that ARE may have been dispersing. The genetic data supported these limited field observations, suggesting that kinkajou dispersal is female biased. Female kinkajous were less related to their female

neighbors than male kinkajous were to their male neighbors (Fig. IV-5), therefore females must be moving further and more often from their natal group.

This dispersal pattern, along with the coalition of highly related males and male-male sociality, support the suggestion that kinkajous live in patrilineal societies (chapter 3). This pattern is unlike most mammal species, including other carnivore groups with solitary foragers and male coalitions (Caro 1994; Waser et al. 1994). Typically, male mammals defend groups of females and are the primary dispersers (Greenwood 1980). Males from mammal societies with female-biased dispersal generally defend resources rather than females. The data on kinkajou territoriality also supports Greenwood's hypothesis. Groups of male kinkajous defended territories, but there is no evidence that they specifically defend females from other male groups. Female-biased dispersal is unusual in mammal systems, and is only known from one other carnivore species (African wild dog, *Lycaon pictus*, Frame and Frame 1976; Frame et al. 1979). Thus, kinkajous appear to be unusual among mammals in having female biased dispersal, which is probably based on resource defense.

Interestingly, two other mammal groups with patrilineal groups and female biased dispersal are also very similar to kinkajous ecologically. Spider monkeys (*Ateles* sp.) and chimpanzees (*Pan* sp.) both live in large communities wherein females separate into small feeding groups and males associate in larger coalitions (Symington 1987; Pusey and Packer 1987; Robinson and Janson 1987). In these primates, females disperse into neighboring communities as they reach adulthood, while most males remain with their natal groups for their whole lives. Although these primate social communities are much larger than kinkajou groups, the behavioral patterns of male-male sociality, female biased

dispersal, and patrilineal groups are similar. Important ecological traits shared between kinkajous, chimpanzees, and spider monkeys including low predation risk, flexible foraging group size, and a diet consisting primarily of ripe tropical fruit (chapter 6). This convergence suggests that some aspect of a extreme frugivory and low predation risk in tropical forests may promote the evolution of female biased dispersal and male philopatry.

In conclusion, kinkajou social organization is difficult to observe in the wild because of their solitary, nocturnal and arboreal nature. The use of hypervariable microsatellite genetic loci provided new detail about the family nature of kinkajou groups, documented the relatedness and paternity from male coalitions, and confirmed an unusual sex biased dispersal.

CHAPTER V

BEHAVIORAL RESPONSES OF KINKAJOUS TO FLUCTUATING FOOD RESOURCES AND PREDATION RISK

INTRODUCTION

Food and predation are critical factors influencing the evolution of mammalian social organization (e.g., Clutton-Brock 1989; Eisenberg 1981; Wilson 1975). However, the relative importance of each for most groups remains largely equivocal (Janson and Goldsmith 1995; Terborgh and Janson 1986, Van Schaik 1999). For example, group living in anthropoid primates may have evolved to protect individuals from predators (Isbell 1994) or to maximize access to fruit trees (Wrangham 1980). Conversely, solitary life in many prosimian primates may have evolved to hide from predators or to maximize capture of insect prey (Bearder 1987, Charles-Dominique 1977).

If some aspect of procuring food is the limiting factor for a species, fluctuations in food abundance and distribution should result in changes in the behavior of an individual. For frugivores, behavioral adaptations to fluctuating fruit resources have been evaluated both in terms of grouping patterns and activity budgets. For example, chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles* sp.) formed significantly smaller subgroups in the low fruit season (Chapman et al. 1995; Symington 1988a). Additionally, when fruit was scarce, spider monkeys spent less time traveling and foraged in longer feeding bouts (Roosmalen 1980).

While food abundance can generally be estimated from vegetational surveys, predation is more difficult to measure. Predation events are generally rare, quick, and often are nocturnal, when observers are less likely to be present (Isbell 1994). It is

widely believed that predation risk, and not predation rate, is the more important variable to consider when evaluating the social organization of a particular species (e.g., Hill and Dunbar 1998). Predation risk represents the likelihood of attack by a predator, and is the basis on which antipredator strategies are implemented. Measuring predation risk in group living mammals is relatively new, and has been accomplished primarily by modeling the riskiness of different habitat features. In two independent studies (Cowlinshaw 1997; Dunbar 1996), baboon groups (*Papio* sp.) adjusted their behavior by implementing antipredator strategies in habitats that had higher predation risk because of differences in the number of safe refuges, potential ambush sites, and predator density. For nocturnal species, moonlight affects predation risk because some predators are more effective hunters when the moon is bright (Clarke 1983). Potential prey species react to this increased risk with antipredator behaviors such as decreased activity and more localized movement when the moon is bright (Clarke 1983; Daly et al. 1992). Conversely, the lack of a reaction to moonlight in a nocturnal species has been interpreted as evidence for a very low perceived predation risk (Gannon and Willig 1997).

Although food and predation are acknowledged as important for influencing mammalian social organization, few studies have *simultaneously* evaluated these factors (Cowlinshaw 1997). Here, I analyze kinkajou (*Potos flavus*) nocturnal activity and grouping patterns for adaptations to changing food availability (from bimonthly fruit census) and predation risk (from moonlight) in central Panama. These analyses highlight the relative effects of feeding and predation risk on kinkajous, thus allowing an examination of the factors influencing their unusual social organization.

The kinkajou (*Potos flavus*) is a nocturnal, frugivorous, arboreal mammal of Neotropical forests with flexible grouping patterns similar to the fission-fusion systems of some primates (Wrangham 1986; Chapman 1990; Van Schaik 1999). Although kinkajous feed solitarily in most small fruiting trees, they regularly associate with up to four group members at large feeding trees and day dens (chapter 3). Home range overlap was extensive among members of the same social group, but home ranges of different groups did not overlap. In central Panama, ripe fruit comprised 90-99% of kinkajou diet, and the abundance of ripe fruit varies seasonally (chapter 2; Fig. II-1). Based on this basic natural history, the following predictions can be made about the importance of predation risk and food abundance to kinkajous.

Feeding competition predictions - Because tropical fruit grows in seasonally rare and depletable patches, I believe it is a limiting factor and that intraspecific feeding competition is important for kinkajous. They should vary their activity budget and flexible social structure according to how much fruit is available. Specifically, 1) as more fruit becomes available individuals should feed on higher quality fruits, and therefore spend less time feeding. Because feeding competition costs related to grouping are lower when fruit is abundant, 2) individuals should be more social in the times of year when there is more food available, and 3) should be more social in larger fruiting trees. Because of the patchy nature of fruit trees, their distribution (average distance between patches) may have an effect independent of patch density. As food patches are further apart, travel costs between patches will increase. I predict that individuals will minimize travel when fruit is widely dispersed by 4) feeding at larger fruit patches, so that they can feed in fewer patches and travel less. Because they are using larger trees, they will also

5) feed in groups more often. Additionally, because female mammals bear the costs of pregnancy, lactation, and parental care, they are tightly tied to their resources. Therefore, I predict that 6) female kinkajous will respond more to fluctuating food resources than males. However, because kinkajous breed seasonally, 7) males may show behavioral responses to fluctuating food outside of the breeding season.

Predation risk predictions - Because kinkajous are arboreal, relatively large, and nocturnal they apparently have few possible predators and a very low predation risk (chapter 3). Therefore, they should not increase their feeding competition with costly behavioral responses to changes in predation risk. Specifically, 8) kinkajous should not travel less, rest more or eat less with increased moonlight. 9) If there is a response to increased predation risk, it should be stronger in males because feeding competition is less important for them.

MATERIALS AND METHODS

Study site - Field research was conducted in lowland forest of Parque National Soberanía in the Republic of Panama (22,100 ha; 9°9' N, 79°44'W). Work was centered around the trail network of the 104-ha Limbo research plot (Robinson 1998). Elevation within the plot varied from 35 to 80 m above mean sea level, and surrounding areas reached an elevation of 225 m. Vegetation was classified as tropical moist forest. Annual rainfall was ca. 2,600 mm with 90% falling during the wet season in late April to mid-December (Dietrich et al. 1982).

The Limbo plot was a heterogeneous mix of forests of various ages, ranging from a few years old in recent blowdowns to ca. 400 years in remnant patches of tall forest (Karr 1971). The forest within 10-30 m of the single-lane gravel Pipeline Road was ca.

30 years old and had grown tall enough to have closed the canopy above the road through most of the study area. South of the road, the forest was 60-120 years old, having been disturbed by farmers and the United States military earlier this century (Foster and Brokaw 1982).

Despite regular poaching pressure, the animal community of the Limbo plot was largely intact, including top predators such as jaguar (*Panthera onca*) and puma (*Felis concolor*) (O. Moore and T. Robinson; pers. comm.). Two large avian predators, *Morphnus guianensis* and *Harpia harpyja*, have not been recorded in the area of Limbo Plot since the mid 1980's (D. Robinson personal communication), but still occur in other parts of Parque Nacional Soberanía. The spider monkey (*Ateles geoffroyi*) was the only frugivorous mammal extirpated from the area. Other arboreal frugivores seen frequently on the Limbo plot included olingos (*Bassaricyon gabbii*), howler monkeys (*Alouatta palliata*), capuchin monkeys (*Cebus capucinus*), night monkeys (*Aotus trivirgatus*), and several species of opossums. Density of kinkajous around the Limbo plot was ca. 12 individuals/km² (R.Kays unpublished data).

Trapping and observation – Twenty-five kinkajous were captured 192 times with 50 Tomahawk live traps (32 by 32 by 102 cm). Traps were baited for 1,292 trap nights with banana and hung in trees 4-25 m above the ground using a hoistable trap design (Kays 1999). Newly-captured animals were immobilized with 0.3 cc of a solution of 80% Ketamine hydrochloride and 20% Zylazine hydrochloride, and standard physical measurements were made. Ten kinkajous were fitted with radio collars that were marked with a unique pattern of colored reflective tape. Fifteen kinkajous were fitted with a similar reflective identification collar without a radio transmitter.

Marked kinkajous habituated quickly and could be followed and observed without obvious disturbance. Radio-collared animals were followed on 74 half-nights for 380 h, either from when they left their sleeping den at dusk until midnight or from midnight until they entered their sleeping den at dawn. Focal animals were observed from the ground with 10x40 binoculars and were illuminated with a 6-V head lamp. A red filter was used when an animal was in the understory and a 12-V spotlight was used when an animal was in the upper canopy. Care was taken to not shine lights continuously on the focal animal. Animals could not always be seen clearly because of understory vegetation and darkness. Therefore, sporadic visual observation, falling fruit, and sounds were used in combination to determine a focal animal's behavior. Generally, kinkajous could be seen directly while they were feeding or resting in a tree. As they moved through the trees, however, they could be seen only intermittently, and I had to rely on telemetry to follow traveling animals.

The behavior of a focal animal was categorically recorded each minute as feeding, resting, traveling, social or unknown. Feeding was defined as eating or actively searching a fruiting tree for food. Traveling was defined as moving between trees. An animal was classified as resting if it stopped for >1 min while not eating or socializing. Resting in a day den at dusk or dawn was not included in measures of resting time. Social behavior included activities involving 2 or more animals <1 m from each other for ≥ 1 min. Certain silent behaviors such as grooming, resting in contact or scent marking were often difficult to detect when kinkajous were hidden behind vegetation. Some of these behaviors were mostly likely missed and recorded as rest or unknown, and may be underrepresented in the results. Any instance of 2 or more kinkajous simultaneously

feeding from the same fruit patch was considered to be group feeding. A fruiting patch usually consisted of a single fruiting tree or vine but occasionally included 2 fruiting plants if their canopies were adjacent. Each time a kinkajou fed on fruit, flowers, or leaves the following were recorded: plant species, location, diameter at breast height (DBH) of the plant, and a categorical estimation of the number of fruits or flowers on the ground under the plant (<10, <50, <100, <500, <1,000, >1,000). For unknown species, samples of fruit and leaves were collected and identified.

Data analysis – The distances traveled were calculated as the minimum distance moved during each ½-night with WILDTRAK (Todd 1995). This was a simple addition of all the straight-line distances between consecutive fixes from the beginning to the end of a ½ night of observation.

Correlation analyses between variation in fruit abundance and behavior were completed with the JMP statistical program (SAS institute 1995). Behavioral data comprised: averages of the m traveled/½ night; min traveled/hr; min eating/hr; min resting/hr; min social/hr; fruit patches used/hr; % group feeding/night; and patch size/night. Fruit data included: fruit patches available/½ month and the average distance between fruit patches/½ month. All data were tested for normality at the $p = 0.05$ level with the Shapiro-Wilk W test. Standard transformations were used to normalize non-normal data, if possible. Associations between normal data sets were measured with pairwise Pearson product-moment correlations. Correlations involving non-normal data were measured with the Spearman Rho nonparametric measure of association.

To assess the effect of moonlight on the activity of kinkajous I compared behavioral changes with the percent of the moon illuminated, which was calculated in

hourly intervals by the Astronomical Applications Department of the U. S. Naval Observatory, Washington, DC (<http://aa.usno.navy.mil/AA/>). Behavioral data included: the percent of each hour a focal animal was observed to travel, eat, rest or other. The data were recorded in minutes of activity per hour, and the response variable was the percent of time each hour for each activity during the observation period; these data are compositional in the sense that the percents from the four categories must add up to 100. To stabilize the variance of the response the arcsine transformation was applied to the proportions (Zar 1996). The variables tested were gender, the percent of the moon illuminated and the amount of edible fruit patches available. Because the data were continuously recorded, the hour-to-hour observations each night were not independent as reflected by autocorrelations of 0.276, 0.363, and 0.331 between successive hours for traveling, eating and resting, respectively.

The SAS procedure MIXED was used to build a statistical model that explains variation in kinkajou activity patterns based the sex of the focal animal, the percent of the moon illuminated, and the amount of edible fruit available, accounting for the autocorrelation of the errors for each model (Littell et al. 1996). PROC MIXED was used to test for significant effects and interactions of these explanatory variables on the three response variables.

RESULTS:

Environmental fluctuations - Bi-monthly census of fruit revealed strong seasonal changes in availability and distribution of fruit eaten by kinkajous (Fig. II-1). There was a sharp increase in abundance from February to a peak in May followed by a slow decrease until the low point in December. Greater density of edible fruits was negatively correlated

with distance between patches of edible fruit ($r = 0.566$, $p = 0.0076$). The fraction of the moon illuminated at night varied on a regular cycle and 56.7, 13.5, and 29.8% of the behavioral data were collected when the moon was $<1/3$, $>1/3$ but $<2/3$, and $>2/3$ illuminated, respectively. Thus substantial variation was observed in the amount of edible fruit and moonlight.

Activity budget - The general activity budget of kinkajous can be summarized by the average min/hr spent traveling, eating, resting and socializing. Traveling was the most frequent activity (24.1 ± 10 min/hr) followed by eating (20.9 ± 11), resting (9.9 ± 7.1) and socializing (1.4 ± 2.5) (Table V-1). The activity budget of males and females differed significantly only in the min/hr traveling. Males spent more time in social activities, but this was only marginally significant. Feeding group size was larger for males. Females traveled further per hr and per $\frac{1}{2}$ night than males. The distance traveled was not different between the AM and PM hours (t-test, d.f. = 62, $p = 0.126$), therefore the average distance traveled per night can be estimated at twice the $\frac{1}{2}$ night average, or 2210 m. Overall, females traveled significantly more than males while males were marginally more social.

The daily activity pattern showed relatively constant levels of activity throughout the middle of the night, with increased traveling at dusk and dawn (Fig. V-1). The increased travel at dusk and dawn typically included individuals climbing to and from a day den and the first or last feeding tree. The peak in social activity from 19:00 – 23:00 is largely due to extended copulations observed at this time on 4 different nights (chapter 3). Social activities, such as allogrooming, were also observed around the day dens at

dusk and dawn. Limbo plot kinkajous did not show a consistent rest period midway through their activity.

Do kinkajous respond to fruit seasonality? – Variation in the average activity patterns of kinkajous reflected seasonal changes in fruit abundance (Fig. V-2). As food patches increased in abundance individuals traveled more (m and min) and ate less. However, when analyzed by sex, the relationship between traveling and fruit availability was only significant for females (Table V-2, Fig. V-3). Considering all male data, there was no relationship between time eating and fruit abundance for male kinkajous, however, this relationship was significant when the 3 data points around the peak breeding season were excluded (Table V-2, Fig. V-3). Additionally, outside of the breeding season, males rested more as fruit increased. No activity measures were significantly correlated with fluctuations in the distribution (average distance between patches) of fruit.

In addition to activity budgets, other behavioral measures were correlated with fruit abundance. As fruit increased kinkajous fed in more fruit patches/hr; this relationship was marginally significant for females, significant for males, and not significant for males outside of the breeding season (Table V-3). Female kinkajous fed in groups more often and fed in larger trees when fruit patches were further apart (Table V-3).

Do kinkajous respond to individual patch size? - Patch size was positively correlated with the percent feeding bouts with more than one kinkajou (Table V-4). Furthermore, larger feeding patches hosted larger groups of kinkajous. The DBH measure of patch size used did not differ between sexes, but the males fed in trees with significantly more fruits on

the ground than females ($647 \pm 413 > 417 \pm 356$, Wilcoxon/Kruskal-Wallis, d.f. = 1, $p = 0.024$).

Do kinkajous avoid moonlight? – After accounting for the effect of fruit, the model described significant relationships between moonlight and the activity of kinkajous (Table V-5, Fig. V-4). The amount of rest per hour increased with increasing moonlight, but the slope was shallow and significance level was not particularly strong ($p = 0.075$). In the analysis of travel time no main effect for either gender or moon was found, but there was a significant interaction between the two variables. Because the direction of the moon effect was opposite for the two sexes, the main effect was lost. For females, the percent of minutes spent traveling each hour was shown to increase with increasing moonlight, but significance was weak ($p = 0.22$). For males, the opposite effect was seen. Males traveled less when the moon was bright, and the significance was quite strong (0.016). There was no relationship between moonlight and minutes eating.

Fruit vs. moon - Modeled correlations of activity with fruit abundance using this hourly data confirmed the results from pairwise correlations reported above: kinkajous generally traveled more and ate less with increasing food (Table V-5). Because predation risk and food abundance were measured in different units, their coefficients from this analysis could not be directly compared. However, the p -values for the relationships between fruit and activity were two orders of magnitude more significant, suggesting that fruit was the more important.

DISCUSSION

Flexibility in behavior permits a species to adapt to a dynamic environment. Insight into the daily and seasonal priorities for a species can be gained by characterizing

the specific environmental variables that influence behavior and comparing their effects. These priorities can be extended when considering the evolution of a species, since variables that are important daily or seasonally are likely the same factors that have been important in the broader behavioral evolution of a species. Feeding competition for fruiting trees and risk of death from predators are two of the most critical factors in the life of arboreal frugivores and their social evolution (Terborgh and Janson 1986; Wrangham 1987; Dunbar 1996).

The behavior of kinkajous was correlated with fruit abundance in a number of ways. Combined, these correlations suggest that individuals modify their behavior and social strategies to minimize feeding competition. Sexual differences in correlations show that changes in food abundance are more important to females than males. Finally, correlations of behavior with moonlight confirmed predictions that food competition was more important to kinkajous than predation risk, although males were more sensitive to predation risk than expected.

General activity budget - Comparisons of the overall activity budget of kinkajous with other species suggests that diet and activity period may be major influences. Compared to other species, the time kinkajous spent eating (34.6%) was roughly similar to other frugivorous primates, less than insectivorous primates, and more than folivorous primates (e.g., Boinski 1987; Milton 1980; Rose 1994; Symington 1988a). The proportion of time kinkajous spent traveling (40.2%) was higher than most diurnal primates (IBID), but similar to that found for two individual kinkajous in French Guiana (Julien-Laferrière 1993) as well as other nocturnal, arboreal primates (Ancrenaz et al 1994; Andriamasimanana 1994; Garcia and Braza 1987). Thus, eating time is probably related

to diet, while travel time may be related to activity period, with nocturnal species traveling more often (and probably slower).

Reactions to fluctuating fruit abundance – A number of behavioral measures were correlated with fruit abundance and distribution, suggesting that fruit is a limiting resource for kinkajous. Individuals spent less time eating when fruit was more abundant (Table V-2, Fig V-3), as predicted. This suggests that they are able to forage on higher quality foods when fruit is abundant and therefore spend less time foraging (Altmann and Muruthi 1988; Eley et al. 1989). As foraging time decreases, males and females respond differently by increasing their resting or travel time, respectively. This difference may be related to the different energetic priorities of males and females (see below).

Kinkajous also matched predictions (Chapman et al. 1995) by responding to fluctuating fruit by being more social (min/hr and % group feeding) when fruit was more abundant, and therefore when feeding competition was less important (Table V-2).

Unlike most primate frugivores, kinkajous travel between feeding patches individually (chapter 3) which gives them flexibility to respond to the size of individual fruit patches and not just the overall fruit abundance. A group of frugivores would deplete a small fruiting tree quickly and therefore have to travel further to obtain enough food. By traveling independently, kinkajous are able to modify their group size to feed in groups only at large trees where fruits are bountiful and feeding competition is less important (Table V-4). This flexibility is less likely in social primates which may be able to adjust their subgroup size to seasonal fruit abundance, but travel between fruiting trees together, therefore revealing weak relationships between patch size and subgroup size (Stevenson et al 1998).

Variations in predation risk – I used moonlight as a surrogate for predation risk, and expected that kinkajous would not modify their behavior when predation risk was high because they have so few potential predators (chapter 3). However, after removing the effects of fruit abundance, the model revealed significant correlations (Table V-5, Fig. V-4). Both males and females rested more when the moon was bright. This is consistent with a anti-predatory hypothesis whereby kinkajous should be less conspicuous when predators are better able to hunt (Hill and Dunbar 1998). However, the slope for this relationship was shallow and significance was weak.

More interesting was the relationship between travel time and moonlight (Table V-5, Fig. V-4). Overall, there was no significant relationship. However, this was because males and females responded in opposite ways. Males traveled less as the moon brightened while females traveled marginally more. Arboreal travel can be a noisy and conspicuous activity that could attract the attention of a predator. The reduction of travel by males is probably an adaptation to reduce overall predation risk when bright moonlight makes their environment more dangerous. Females do not reduce their travel time, rather, they marginally increase it. Moonlight could make nocturnal arboreal travel more efficient, which may explain the positive slope of the female relationship. Female kinkajous are not larger or better protected than males and therefore have the same intrinsic predation risk. Their ignorance of increased predation risk when traveling highlights differences in the priorities of male and female kinkajous (see below).

Male and female differences - Responses of males and females to changes in food abundance and predation risk reflect the different priorities for each sex (Table VI-6). Because female kinkajous bear all of the costs of reproduction (i.e., pregnancy, lactation,

parental care) they have additional energetic and nutritional needs compared with males. To meet these needs females travel more than males. Unlike males, females travel more when fruit is more abundant, probably in search of high quality or specialized fruits that will help them meet the nutritional (e.g., calcium, O'Brien et al. 1998), as well as energetic demands of reproduction.

Males are not under such energetic and nutritional stress and they appear more focused on the distribution of females and minimizing predation risk. Rather than traveling more when fruit is more abundant, males spent more time resting, feeding in groups and socializing, at least outside of the peak breeding season. These relationships were not significant when data from the breeding season is included, which suggests that males have other priorities at this time, chiefly, the location of females and competition with other males.

No measures of male behavior were correlated with the distribution of fruit. However, females fed in larger trees and in groups more often when fruit was widely dispersed. When the distance between fruiting trees increases, so do the costs of traveling between them. By feeding in larger trees at this time females may minimize travel costs by feeding in fewer trees, although travel time and distance was not correlated with fruit dispersion. Because the travel costs of finding another fruiting patch are higher when food is dispersed females may have to accept the higher costs of feeding competition from groups.

Males traveled significantly less when the moon was bright, while females traveled marginally more. By traveling less, males remained less conspicuous and minimized predation risk. Females did not avoid this peak in predation risk but traveled

more when the moon was bright. Since females are more nutritionally stressed than males they may have to take advantage of easier arboreal locomotion in bright moonlight to find more high quality fruit.

Food Competition vs. Predation Risk – Contrary to expectations, I did find risk-reducing correlations between kinkajou behavior and moonlight, especially for males. This suggests that they do face predation risk and have adapted behavioral strategies to minimize it. However, when compared to the behavioral responses that minimize feeding competition, those to minimize predation risk were weak, with p-values differing by two orders of magnitude (Table V-5). This suggests that feeding competition is more important to kinkajous than predation risk, and has played a more significant role in their social evolution. Their mostly solitary nature supports this assertion; individuals were not forced to form groups to reduce predation risk, but changed their sub-group size in response to varying levels of feeding competition. The sexual differences in a number of behavioral responses indicate that feeding competition is more important to females than males (Table V-6). These results also fit well with their recently described social organization (chapter 3); females lived in exclusive home ranges while males formed coalitions that grouped completely with one female and ranged widely enough to overlap with other non-group females.

Models of primate sociality consider group size to largely be the result of the maximizing effects of predation risk and the minimizing effects of feeding competition (Terborgh and Janson 1986; Wrangham 1987; Dunbar 1996). The ecology of kinkajous is very similar to many primate species, and my analysis of their social organization suggests that predation risks and feeding competition have had similar effects on their

social evolution. Kinkajous feed in small groups and, as predicted by the primate model, have low predation risk but are more sensitive to feeding competition. This is a taxonomically independent confirmation of the roles of predation risk and feeding competition in the evolution sociality in carnivores, primates, and frugivorous mammals in general.

CHAPTER VI
SUMMARY OF THE CONVERGENCE BETWEEN KINKAJOUS, SPIDER
MONKEYS, AND CHIMPANZEES

INTRODUCTION

Evolution is descent with modification or change through time. The results of evolutionary change often are correlations between phenotypes and environmental demands. For example, swimming animals tend to be streamlined and fliers have light bones. Such correlations illustrate adaptive fits between animals and their environments. Especially strong tests of adaptation are found when these correlations occur independently several times in different taxonomic groups of organisms that are subject to similar environmental demands. This phenomenon, convergence, is again evident in streamlined bodies of both aquatic fishes and mammals or light weight bones of flying birds and bats.

Studies of convergent evolution are common in anatomy and physiology. Recently, patterns of convergence have proven important in studying the evolution of social organization in mammals, especially in the carnivores and primates. For example, in carnivores and primates the availability and distribution of food influences species differences in population group size and home range size (Wrangham et al. 1993). This pattern involves general measures of diet and social structure. More rigorous tests of convergence use precise measures of single-species variation. For example, group stability was tied to seasonal fluctuations in fruit availability in a comparison of two ecologically similar primates: gibbons have stable groups and feed on food with stable

levels of availability while spider monkey groups are dynamic in size to take advantage of their fluctuating food supply (Robbins et al. 1991).

As with tests of convergence in general, comparisons between species are stronger if they extend across independently evolved taxa. That is, the above study showing dietary correlates of group size in gibbons and spider monkeys would be more definitive and broadly applicable if they had used a non-primate in their test. The kinkajou offers this unique opportunity because it is a carnivore that has evolved into a primate-like lifestyle. Here I briefly compare important natural and life history traits for kinkajous and two ecologically similar primates: spider monkeys (*Ateles* sp.) and chimpanzees (*Pan troglodytes*), highlighting common lifestyle traits that could have led to convergence in social organization.

SIMILARITIES AND DIFFERENCES

Ateles and *Pan* are well studied taxa. This study of kinkajous, the first long-term study of marked animals, was planned to collect data similar to that available for these primates so that reasonable comparisons of their ecology and social organizations could be made. A summary of these comparisons, with citations for the primate data, is given in Table VI-1.

General – Kinkajous are in the mammalian order Carnivora, and most likely evolved from a solitary and terrestrial meat eater (Eisenberg 1981; Decker and Wozencraft 1991). Spider monkeys and chimpanzees are both classified as Primates, but are in different families and only distantly related. However, nearly all primates are social and therefore both *Ateles* and *Pan* most certainly evolved from social and gregarious ancestors (Wrangham 1987). All three taxa live in tropical forests, with the chimpanzee being

restricted to central Africa, and the kinkajou and six species of spider monkeys ranging widely in tropical America. *Ateles* and kinkajous are exclusively arboreal, while *Pan* feeds both on the ground and in the trees.

Because of their large size (41-49 kg), chimpanzees have very few predators and face a low predation risk. Spider monkeys are smaller (6-8 kg), but have low predation risk because they avoid large terrestrial predators with their arboreal lifestyle. Kinkajous are the smallest of the three (~3kg), but maintain a similar low predation risk because they are not only arboreal but also are nocturnal (chapters 3 and 5). Another indicator of low predation risk is a low reproductive rate (Hill and Dunbar 1998), since a population with a low reproductive rate cannot sustain a high predation rate. All three taxa have a low reproductive rate (small litter size and long interbirth interval) yet maintain relatively high densities in their habitat, further suggesting a very low predation risk.

. Males appear to be slightly larger in all three groups (kinkajous 1.05, *Ateles* 1.03, *Pan* 1.2), most significantly in chimpanzees. Sex ratios in chimpanzees and spider monkeys are biased towards females. No such bias was found in kinkajous caught in the Limbo Plot (12 males:13 females). Sexual biases were found in the dispersal patterns of all three taxa, with females being the predominant disperser.

Thus, kinkajous are similar to *Ateles* and *Pan* in having low predation risk, a slow reproductive rate, slight sexual dimorphism, and female biased dispersal. Perhaps the most significant difference in kinkajous and these primates is that they evolved from a solitary carnivore, whereas *Ateles* and *Pan* evolved from social primates. Other differences include a smaller body size and an even sex ratio in kinkajous.

Ecology - Kinkajous of the Limbo plot proved to be one of the most frugivorous mammals yet studied, with ripe fruit making up 90-99% of their diet. Although *Ateles* and *Pan* eat slightly less fruit (~70-80%), they are also amongst the most frugivorous mammals. The specific make up of fruit in each taxa's diet is also similar; all three taxa focus on ripe fleshy fruit, especially figs and fruit from other large fruiting trees. Furthermore, a population of *Ateles* that was studied near the Limbo plot shared with kinkajous 100% of the fruit species recorded in their diet and known from the Limbo fruit census (Table II-2).

The distribution of food is widely thought to be one of the most important determinants of ranging and social behavior in mammals, especially for females (Bradbury and Verencamp 1977; Clutton-Brock 1989; Wrangham 1980). Ripe fruit probably has the same general distribution pattern across the tropics: depletable patches that are clumped in both space and time. However, at a finer scale, habitats provide differences in the exact distribution and abundance of fruiting trees. These have been quantified (e.g., patches/ha, food stability and coefficient of dispersion) in primate studies and found to explain fine differences in grouping patterns (Chapman et al. 1995). Like *Ateles* and *Pan*, male kinkajous outside of the breeding season grouped more when fruit was abundant (Table V-3). Furthermore, larger groups of kinkajous fed in larger trees (Table V-4, Fig III-5). This feeding patch-group size connection was also found in *Ateles*, although the relationship was weak (Stevenson et al. 1998).

Although broadly similar, kinkajous have slightly smaller home ranges *Ateles* or *Pan*, this is probably related to their smaller body size. Home range overlap between groups is minimal for all three groups, and probably least in kinkajous; their smaller

home range size may permit more exact boundaries. Travel distances are surprisingly similar, given their different home range and body sizes.

Activity budgets are broadly similar for kinkajous and *Ateles*. Feeding time is the most similar, as expected given such similar diets. Kinkajous travel more often and rest less, which may be the result of less efficient arboreal travel at night. Because of the darkness, kinkajous probably travel slower, and need more time to cover similar distances.

Thus, kinkajous, *Ateles*, and *Pan* are similar in their high frugivory, non-overlapping group ranges, and activity budgets. Ranging patterns of the three taxa are broadly similar, and differences are probably related to differences in body size.

Social Organization – Kinkajous, *Ateles* and *Pan* have similar fission-fusion social organizations in that all three live within a group and associate in smaller, flexible subgroups. The most striking difference is that the kinkajou social group consists of no more than 5 animals, while that of the two primates usually contains ca. 30 individuals, and may contain up to 100. The average size of subgroups is also different, with kinkajous usually foraging alone or in small groups, and not traveling in groups between fruiting trees, while *Ateles* and *Pan* usually feed and travel in subgroups of four or five.

Although the two primate taxa group more often and are more social the underlying patterns of sociality are similar to those found in kinkajous. Females are the less social sex and are more likely to feed alone or in small groups. Males are more social and may form alliances. Adult male kinkajous in the same group may not show the very strong sociality and coalitions found in *Ateles* and *Pan*, but they do regularly sleep and feed together, share copulations and probably cooperate to mark their group

territory. These behaviors were never observed between females. Furthermore, adult and subadult male kinkajous had close social relationships (e.g., the most frequent grooming combination (Table III-4)). Observations of adult and juvenile males playing together suggest that relationships between adult and young male kinkajous may start at early age (Table III-5).

Social relationships between males in these three taxa may be related to the pattern of group inheritance. Unlike most mammal species (Greenwood 1980), kinkajous, *Ateles*, and *Pan* all have female biased dispersal and patrilineal groups. This suggests that males should defend resources instead of mates (Greenwood 1980). Resource defense is consistent with data on kinkajous [e.g., non-overlapping territories, fights at large feeding trees at home range boundaries (Kays and Gittleman 1995)], but has not been suggested for *Ateles* or *Pan*.

The social organizations of kinkajous, *Ateles*, and *Pan* are based on small subgroups feeding together in the context of a larger social group or community. Kinkajous are much different in the size of their groups and subgroups and overall levels of sociality, but similar in their flexible subgroup size and patterns of male-male coalitions and female asociality. Furthermore, all three taxa stand out as being among the very few mammal social systems with female dispersal and patrilineal groups.

EVOLUTION OF SOCIAL ORGANIZATION

The social organization of a species is generally considered to be the result of adaptations to present environmental (mainly feeding and predation) and social conditions, constrained by phylogenetic limits of behavioral and morphological adaptation (Clutton-Brock 1989, Eisenberg 1981). Teasing apart the adaptive and

phylogenetic affects has been a long struggle in evolutionary biology (Gould and Lewontin 1979; Clutton-Brock & Harvey 1979). These efforts have been quite successful in broad comparisons of many phylogenetically independent taxa (Brooks & McLennan 1991; Harvey & Pagel 1991).

This study of kinkajous has provided an excellent opportunity for the study of convergence between a carnivore and the Primates. Because of the separate evolutionary paths of the two groups, phylogenetic constraints should be similar only at the broadest mammalian level. Therefore, similarities in social organizations of kinkajous and primates are most likely the result of convergent adaptation to similar ecological or social conditions.

The low predation risk of these three taxa reduces the predator-related benefits they could obtain from gregarious living (Isbell 1994). This gives them the flexibility to feed in small subgroups or alone; predators are not driving them into groups. Feeding alone or in small groups is beneficial when the food source is patchy and depletable, as is for kinkajous, *Ateles*, and *Pan*. Larger groups would deplete fruit trees quicker, and force individuals to travel further to obtain enough food. However, fruit sometimes occurs in very large fruiting trees in which feeding competition is less important, and the patchy nature of fruit may reduce the cost of sharing a territory with other individuals (i.e., RDH: Bacon et al. 1991a, b; Carr and Macdonald 1986). Thus, the feeding costs of living in groups is variable, and may not always be important. This is more likely to be the case for males which do not bear the energetic costs of reproduction and therefore are less concerned with the distribution of fruit. The reproductive success of males is more reliant on the distribution of females, and they may accept the energetic costs of higher

sociality to forge the social bonds with other males necessary for territory maintenance (kinkajous, *Ateles*, and *Pan*) or female acquisition (*Pan*).

Thus, the similar flexible subgroup sizes of kinkajous, *Ateles*, and *Pan* can be explained by feeding competition and the variable nature of ripe fruit. The common sexual differences in sociality may be due to energetic differences between males and females. The biggest difference between kinkajous and these primates remains the overall level of sociality and grouping. If kinkajous eat the same foods and have similarly low predation risk, why do they have such small groups? I believe the answer to this is tied to the differences in phylogenetic background. Kinkajous have evolved from a solitary ancestor, and have adapted a mostly solitary solution to living in the low predation, frugivorous niche. *Ateles* and *Pan*, on the other hand, have evolved from a gregarious ancestor. Their behavioral adaptations to feeding on ripe fruit have led them to a less gregarious lifestyle than most primates, but they remain social animals. The environmental conditions facing the ancestors of *Ateles* and *Pan* has always included a strong social component, which can reinforce benefits of gregarious living (Wrangham 1980). In an evolutionary sense, sociality has only more recently been important for kinkajous.

Kinkajous, *Ateles*, and *Pan* have evolved a similar social solution to the low-predation, frugivorous niche, but they have reached it from different starting points. *Ateles* and *Pan* maintain their ancestral social nature, but have evolved smaller and flexible foraging groups that permit them to minimize feeding competition. Kinkajous maintain their mainly solitary ancestral nature, but have evolved a sociality permitted by the variable and patchy fruit diet. The patrilineal nature of all three social groups

suggests that female dispersal and male sociality may also be favored by a diet of ripe fruit, perhaps related to a male strategy of resource defense.

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APPENDIX
TABLES AND FIGURES

CONTENTS – APPENDIX

Table II-1. Characters of fruits eaten by kinkajous on the Limbo Plot as revealed by observation of 202 feeding bouts, analysis of 194 feces, and bimonthly fruit censuses.....	113
Table II-2. Primary fruits in the diet of kinkajous on the Limbo plot.....	120
Table II-3. Dietary importance and overlap of figs, moraceous fruits, and all fruit species eaten by kinkajous and large frugivorous mammals from central Panama.....	121
Table III-1. Hours and half-nights of focal observation and number of radio-collared kinkajous.	122
Table III-2. Group composition, weights, and minimum convex polygon (MCP) home range sizes for kinkajous on the Limbo plot.	123
Table III-3. Size and overlaps of core feeding areas for member of Center Group.....	126
Table III-4. Composition of 59 kinkajou group dennings and 39 group feeding bouts, and 38 grooming bouts on nights without copulations.....	127
Table III-5. Summary of play behavior observed by kinkajous.....	128
Table III-6. Details of the dispersal of a subadult female kinkajou (MAG) in 1996.	129
Table IV-1. Characteristics of 11 microsatellites in kinkajous.	130
Table IV-2. Pairwise relatedness values between 25 individual kinkajous from the Limbo plot.....	132
Table V-1. Travel distances, activity budgets and feeding behaviors for kinkajous. ..	134
Table V-2. Correlations between kinkajou activity and the number of eatable fruit patches available in a ½ month period.....	135
Table V-3. Correlations of kinkajou feeding behavior with a) the number of eatable fruit patches available in a ½ month period, and, b) the average distance between feeding patches.	136
Table V-4. Relationships between kinkajou group feeding and patch size.....	137
Table V-5. Results of a model built to describe kinkajou behavior based on moonlight and available fruit.	138
Table V-6. Summary of differences in the behavior of male and female kinkajous.	139
Table VI-1. Summary of similarities and differences between kinkajous, spider monkeys, and chimpanzees.	140
Fig. I-1. Phylogenetic tree of the extant Procyonidae based on morphological characters.....	143
Fig. I-2. Photo of a male kinkajou (ELV) from the Limbo plot.....	144
Fig. II-1. Availability of fruits and average distance between feeding patches on the Limbo plot in 1996.....	145
Fig. II-2. Availability and use of four fruit types for kinkajous.....	146
Fig. II-3. A) High and B) low selection indices (S_i) for fruits eaten by kinkajous.....	147
Fig. III-1. Home range boundaries (95% MCP) and general areas used for kinkajous in the Limbo plot.....	148
Fig. III-2. Core feeding areas for the members of center group after MAG's immigration.....	149
Fig. III-3. Times that kinkajous left and entered dens in relation to dusk and dawn....	150

CONTENTS – APPENDIX (continued)

Fig. III-4. Location and intensity of use of day dens by center group.....	151
Fig. III-5. A) Average group size and B) frequency of grouping for kinkajous feeding in 11 species of fruiting trees.....	152
Fig. IV-1. Schematic of social group structure for kinkajous in the Limbo plot.....	154
Fig. IV-2. Mean difference between consecutive relatedness estimates using one to eleven kinkajou microsatellite loci.....	155
Fig. IV-3. Schematic of genetic parentage within the social groups of kinkajous on the Limbo plot.....	156
Fig. IV-4. Relatedness values for known relationships among kinkajous.....	157
Fig. IV-5. Relatedness values for neighboring male dyads compared to neighboring female dyads.....	158
Fig. V-1. Nightly activity patterns for kinkajous averaged from 380 hrs of focal animal observation.....	159
Fig. V-2. Monthly activity budgets and fruit availability for female and male kinkajous on the Limbo plot.....	160
Fig. V-3. Regression lines indicating the relationships between number of eatable fruit patches available and the min/hr spent traveling, eating and resting for A) all female data, B) all male data, and C) male data excluding the peak breeding season.....	161
Fig. V-4. Correlation of predicted minutes A) resting and B) traveling per hour and the percent of the moon illuminated per night, after taking the effect of fruit abundance into account.....	165

Table II-1. Fruits and associated foraging behavior of kinkajous on the Limbo Plot as revealed by observation of 202 feeding bouts, analysis of 194 feces, and bimonthly fruit censuses.

Plant family	Fruit species	Vegetation type	Observation		Fecal analysis		Relative abundance % of edible patches	Selection Index (%used/%available)		Mean DBH (cm)
			% feeding bouts	% feeding time	% feces	% volume		Bouts	Hrs	Scats
Anacardiaceae	Spondias mombin	tree	1.49	1.83	2.58	1.07	16.28	0.09	0.11	0.16
Annonaceae	Annona spraguei	midstory	2.97	0.70	0.52	0.39	0.84	3.56	0.84	0.62
Araceae	Monstera dilacerata	epiphyte	N/A	N/A	0.52	0.31	N/A	N/A	N/A	N/A
Araceae	Monstera dubia	epiphyte	0.50	0.10	0.52	0.01	N/A	N/A	N/A	N/A
Araceae	Philodendron sp.		1.98	0.23	N/A	N/A	N/A	N/A	N/A	N/A
Bombacaceae	Quararibea asterolepis	tree	0.99	1.89	1.55	1.21	0.42	2.37	4.52	3.70
Boraginaceae	Cordia lasiocalyx	understory	N/A	N/A	0.52	0.01	N/A	N/A	N/A	N/A
Boraginaceae	Cordia panamensis	shrub	3.47	4.08	9.79	7.63	0.63	5.53	6.51	15.64
Burseraceae	Protium panamense	tree	0.50	0.25	N/A	N/A	2.51	0.20	0.10	N/A
Burseraceae	Tetragastris panamensis	tree	0.50	0.11	N/A	N/A	0.63	0.79	0.17	N/A
										16.00

Table II-1 (continued)

Cochlosperma ee	Cochlosperma vitifolium	tree	N/A	N/A	0.52	0.01	N/A	N/A	N/A	N/A	N/A
Cucurbitaceae	Cayaponia granatensis	vine	0.50	0.05	1.55	0.27	0.42	1.19	0.12	3.70	90.00
Cucurbitaceae	Gurania makoyana	vine	N/A	N/A	0.52	0.41	N/A	N/A	N/A	N/A	N/A
Dilleniaceae	Doloiocarpus olivaceus	liana	0.50	0.41	0.52	0.01	6.05	0.08	0.07	0.09	N/A
Ebenaceae	Diospyros artanthifolia	understory	0.99	0.63	2.58	0.68	0.42	2.37	1.50	6.17	15.00
Euphorbiaceae	Hyeronima laxiflora	tree	2.48	1.43	1.03	0.08	0.21	11.86	6.86	4.94	57.00
Flacourtiaceae	Lindackeria laurina	understory	N/A	N/A	2.06	1.00	2.71	N/A	N/A	0.76	N/A
Flacourtiaceae	Zuelania guidonia	tree	0.50	0.12	N/A	N/A	0.63	0.79	0.19	N/A	23.00
Guttiferae	Clusia odorata	hemi- epiphyte	N/A	N/A	1.03	0.78	1.04	N/A	N/A	0.99	N/A
Guttiferae	Tovomitopsis nicaraguensis	understory	N/A	N/A	0.52	0.24	0.63	N/A	N/A	0.82	N/A
Guttiferae	Vismia billbergiana	shrub	N/A	N/A	2.06	0.82	N/A	N/A	N/A	N/A	N/A

Table II-1 (continued)

Loranthaceae	Phthirusa pyrifolia	hemi- epiphyte	N/A	N/A	1.55	1.55	N/A	N/A	N/A	N/A	N/A
Loranthaceae	Struthanthus orbicularis	hemi- epiphyte	1.49	1.67	N/A	N/A	N/A	N/A	N/A	N/A	48.00
Marcgraviaceae	Marcgravia nepenthoides	hemi- epiphyte	0.50	1.66	N/A	N/A	N/A	N/A	N/A	N/A	20.00
Melastomataceae	Miconia elata	understory	N/A	N/A	0.52	0.17	N/A	N/A	N/A	N/A	N/A
Melastomataceae	Miconia impetularis	shrub	N/A	N/A	0.52	0.01	N/A	N/A	N/A	N/A	N/A
Melastomataceae	Miconia sp.		0.50	0.13	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Menispermaceae	Abuta racemosa	liana	0.50	2.02	4.64	3.75	N/A	N/A	N/A	N/A	N/A
Mimosoideae	Inga sp	tree	5.94	5.26	13.40	9.17	5.64	1.05	0.93	2.38	39.33
Moraceae	Brosimum alicastrum	tree	2.97	3.92	2.06	1.85	N/A	N/A	N/A	N/A	99.17
Moraceae	Cecropia insignis	tree	1.49	0.59	4.12	2.53	0.21	7.11	2.82	19.75	111.00
Moraceae	Cecropia obtusifolia	midstory	1.49	0.79	1.55	0.87	N/A	N/A	N/A	N/A	118.33
Moraceae	Cecropia sp		0.50	0.29	N/A	N/A	0.42	1.19	0.69	N/A	118.33
Moraceae	Ficus colubrinii	hemi- epiphyte	0.50	0.42	0.52	0.09	0.63	0.79	0.67	0.82	N/A
Moraceae	Ficus dugandii	hemi- epiphyte	N/A	N/A	0.52	0.52	0.21	N/A	N/A	2.47	N/A

Moraceae	Ficus insipida	tree	10.89	24.2 ⁹	18.04	16.25	4.18	2.61	5.82	4.32	69.47
Moraceae	Ficus nymphifolia	midstory	0.50	0.10	1.03	0.86	N/A	N/A	N/A	N/A	N/A
Moraceae	Ficus obtusifolia	hemi-epiphyte	0.50	0.39	N/A	N/A	0.21	2.37	1.84	N/A	N/A
Moraceae	Ficus paraensis	hemi-epiphyte	4.46	1.00	7.22	4.26	1.67	2.67	0.60	4.32	N/A
Moraceae	Ficus popenoei	hemi-epiphyte	0.99	0.53	N/A	N/A	N/A	N/A	N/A	N/A	27.50
Moraceae	Ficus sp?		0.99	0.76	15.46	8.12	N/A	N/A	N/A	N/A	N/A
Moraceae	Ficus trigonata	hemi-epiphyte	0.99	0.16	N/A	N/A	0.21	4.74	0.75	N/A	54.00
Moraceae	Ficus yoponensis	tree	1.98	2.00	2.06	1.96	0.84	2.37	2.39	2.47	66.33
Moraceae	Poulsenia armata	tree	0.50	0.19	1.03	0.69	2.51	0.20	0.08	0.41	N/A
Moraceae	Pourouma guianensis	midstory	N/A	N/A	3.09	1.17	3.13	N/A	N/A	0.99	N/A
Myristicaceae	Virola bozo	midstory	0.50	0.10	N/A	N/A	1.25	0.40	0.08	N/A	83.00
Myristicaceae	Virola surinamensis	tree	0.50	0.08	N/A	N/A	5.01	0.10	0.02	N/A	52.00
Myrtaceae	Eugenia oerstedeana	understory	0.50	0.45	2.06	1.38	N/A	N/A	N/A	N/A	15.00

Table II-1 (continued)

Palmae	Astrocaryum standleyanum	understory	7.43	6.71	10.82	5.07	23.80	0.31	0.28	0.45	115.82
Palmae	Scheelea zonensis	tree	6.93	9.11	N/A	N/A	6.89	1.01	1.32	N/A	36.88
Palmae	Socratea durissima	understory	3.96	0.61	N/A	N/A	2.30	1.72	0.27	N/A	19.31
Papilionoideae	Dipteryx panamensis	tree	0.99	2.79	1.03	0.52	2.09	0.47	1.34	0.49	14.00
Passifloraceae	Passiflora nitida	vine	0.50	0.08	2.58	0.80	N/A	N/A	N/A	N/A	N/A
Polygonaceae	Coccoloba parimensis	liana	2.48	4.63	4.12	3.46	2.51	0.11	1.85	1.65	39.00
Rubiaceae	Chomelia psilocarpa	liana	N/A	N/A	0.52	0.10	N/A	N/A	N/A	N/A	N/A
Rubiaceae	Guettarda foliacea	understory	0.50	0.05	N/A	N/A	0.63	0.79	0.08	N/A	17.00
Rubiaceae	Randia armata	understory	0.50	0.14	1.55	0.87	N/A	N/A	N/A	N/A	N/A
Sapindaceae	Chrysophyllum cainito	tree	4.46	3.61	6.19	4.56	0.42	0.50	8.65	14.81	80.51
Sapindaceae	Cupania rufescens	understory	1.49	1.02	N/A	N/A	0.42	3.56	2.45	N/A	13.67

Table II-1 (continued)

Sapindaceae	Paullinia rugosa	liana	N/A	N/A	0.52	0.10	N/A	N/A	N/A	N/A	N/A
Solanaceae	Cyphomandra hartwegii	shrub	N/A	N/A	1.55	0.02	N/A	N/A	N/A	N/A	N/A
Solanaceae	Solanum hayesii	shrub	N/A	N/A	0.52	0.17	N/A	N/A	N/A	N/A	N/A
Solanaceae	Solanum lancifolium	vine	1.49	0.55	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Sterculiaceae	Theobroma cacao	understory	N/A	N/A	1.03	0.07	N/A	N/A	N/A	N/A	N/A
	Unk. species a		1.49	2.54	6.19	4.41	N/A	N/A	N/A	N/A	N/A
	Unk. species b		N/A	N/A	0.52	0.31	N/A	N/A	N/A	N/A	N/A
	Unk. species c		N/A	N/A	0.52	0.25	N/A	N/A	N/A	N/A	N/A
	Unk. species d		N/A	N/A	0.52	0.01	N/A	N/A	N/A	N/A	N/A
	Unk. species e		0.50	0.24	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	Unk. species f		0.50	0.54	N/A	N/A	N/A	N/A	N/A	N/A	N/A
	Unk. species g		N/A	N/A	0.52	0.01	N/A	N/A	N/A	N/A	N/A
	Unk. species h		N/A	N/A	1.03	1.03	N/A	N/A	N/A	N/A	N/A
	Unk. species i		N/A	N/A	1.55	0.84	N/A	N/A	N/A	N/A	N/A
	Unk. species j		N/A	N/A	7.22	2.64	N/A	N/A	N/A	N/A	N/A

Table II-1 (continued)

Unk. species k	N/A	N/A	2.58	1.48	N/A	N/A	N/A	N/A	N/A
Unk. species l	N/A	N/A	0.52	0.52	N/A	N/A	N/A	N/A	N/A
Unk. species m	0.99	0.28	0.52	0.01	1.25	0.79	0.22	0.41	33.00

Table I I-2. The most important fruits in the diet of kinkajous, estimated from the five most frequently eaten fruit species based on different measured of feeding.

Family	Species	Vegetation type	Feeding bouts	Feeding time	Feces	Fecal volume
Boraginaceae	<i>Cordia panamensis</i>	Shrub	3.5	4.1	9.8	7.6
Mimosoideae	<i>Inga</i>	Tree	6.0	5.3	13.4	9.2
Moraceae	<i>Ficus insipida</i>	Tree	10.9	24.3	18.0	16.3
Moraceae	<i>Ficus sp.?</i>		1.0	0.8	15.5	8.1
Moraceae	<i>Ficus paraensis</i>	Hemiepiphyte	4.5	1.00	7.2	4.3
Palmae	<i>Astrocaryum standleyanum</i>	Understory	7.4	6.7	10.8	5.1
Palmae	<i>Scheelea zonensis</i>	Tree	6.9	9.1	0	0
Polygonaceae	<i>Coccoloba parimensis</i>	Liana	2.5	4.6	4.1	3.5
Sapindaceae	<i>Chrysophyllum cainito</i>	Tree	5.9	7.5	6.2	4.6
Total			48.6	63.4	N/A	58.7
All figs			21.8	29.6	44.9	32.06
All Moraceae			28.7	35.4	56.7	39.16

Table II-3. Comparison of the dietary importance and overlap of figs, moraceous fruits, and all fruit species eaten by kinkajous and other large frugivorous mammals from central Panama. Censused fruits are those detected at least once with the fruit census on the Limbo plot.

Species	Method	Fruit	Flowers and leaves	Prey	Figs only % (n)	All Moraceae % (n)	Total sp. eaten sp. (n)	Total sp. shared with <i>Potos</i> % (n)	Censused fruit sp. eaten (n)	Censused sp. shared with <i>Potos</i> (n) %	Reference
<i>Potos</i>	% time % occurrence in feces	90.5 99	8.9 5.2	0 0	14.1 (9)	23.4 (15)	64		40		This study
<i>Nasua</i>	% time % time % occurrence in feces	26.8 55.4 72.1	0 0 0	73.2 44.6 41.9	6.5 (3)	15.2 (7)	46	20	26	15	Russell, 1982; Gompper, 1994
<i>Alouatta</i>	% time Observations & stomach contents	42.1 60	57.8 40	<1 <1	20.0 (9)	35.5 (16)	45	20	22	18	Milton, 1980; Hladik and Hladik, 1969
<i>Ateles</i>	Observations & stomach contents	80	20	<1	8.3 (2)	29.2 (7)	24	15	13	13	Hladik and Hladik, 1969; Milton, 1993
<i>Cebus</i>	Observations & stomach contents	65	15	20	3.8 (3)	9.1 (7)	77	22	33	18	Hladik and Hladik, 1969
<i>Aotus</i>	Observations & stomach contents	65	30	5							Hladik and Hladik, 1969
<i>Saguinus</i>	Observations & stomach contents	60	10	30							Hladik and Hladik, 1969

Table III-1. Hours and half-nights of focal observation and number of radio-collared kinkajous.

	Observation Time	Half-nights of observation
Females (n=4)	156:06	30
Males: all (n=6)	224:00	44
adult (n=4)	169:41	32
subadult (n=2)	54:19	12
Total (n=10)	380:06	74

Table III-2. Group composition, weights, and minimum convex polygon (MCP) home range sizes for kinkajous on the Limbo plot. Overlaps are calculated with 95% MCP except for juveniles and RRY. The female MAG entered center group from east group after MOM disappeared; overlaps with both females are given for individuals in center group with overlaps with MOM are displayed above overlaps with MAG. Weight fluctuations over time were consistent for all kinkajous; this table specifies high and/or low season weight.

Weight kg		Home range		Percent of range overlapped by:				Notes
		100% MCP ha (fixes)	95% MCP ha (fixes)	Male 1	Male 2	Female	Sub- adult	
Center Group				MOM MAG				
Male1 ELV	low: 3.0 high: 3.7	71.3 (539)	49.7 (107)	--	30.4	51.8 41.9	63.6	
Male2 BEA	low: 3.1 high: 3.6	30.9 (419)	18.5 (96)	81.6	--	58.3 54.5	84.5	
Female MOM	low: 2.3 high: 3.6	30.3 (26)	25.7 (21)	100	42.0	-- 74.5	59.9	disappeared 18 March 1996 entered group May 1996
Female MAG	low: 2.2	39.7 (326)	21.4 (88)	97.5	47.3	89.6 --	84.1	
Subad male POK	low: 2.2 high: 3.0	57.5 (424)	35.0 (208)	63.6	44.7	81.5 51.4	--	
Juv. female LUN	low: 1.2 high: 1.7	6.4 (37)	--	100	38.8	100 87.2	100	

Table III-2 (continued)

East Group								
Male1	low: 2.8	54.9	40.3	--	--	61.2		
CHA		(96)	(28)					
Male2		--	--	--	--	--	--	seen, not caught
?								
Female	low: 2.4	39.4	29.4	84.0	--	--		
PAT		(259)	(57)					
Subad	low: 2.2	--	--	--	--	--	--	dispersed to center group May 1996
female								
MAG								
Juv.	low: 1.7	5.5	--	100	--	100	--	
male		(23)						
PIC								
North Group								
Male1	low: 3.2	--	--	--	--	--	--	
BBN								
Male2	high: 3.3	--	--	--	--	--	--	
BAT								
Female	low: 3.0	21.0	11.3	--	--	--	51.5	
ORA	high: 3.1	(138)	(30)					
Subad	low: 2.3	14.2	--	--	--	40.9	--	
male	high: 2.8	(21)						
RRY								
Juv.	low: 1.7	3.8	--	--	--	85.2	46.1	
female	high: 2.2	(24)						
MOL								
West Group								
Male1	low: 2.7	24.5	16.2	--	--	--	73.9	
OTS	high: 3.7	(247)	(59)					
Male2		--	--	--	--	--	--	seen, not captured
?								
Female	high: 3.5	--	--	--	--	--	--	
KAS								
Subad	low: 2.5	26.6	14.3	65.0	--	--	--	
male		(102)	(33)					
ERN								

Table III-2 (continued)

Juv. sex?		--	--	--	--	--	--	seen, not captured
Mosq. group (a)								
Male1 DIS	low: 3.2 high:	53 (210)	--	--	8.5 (4.9)	--	16.4 (9.5)	
Male2 K4	low: 3.2 high:	--	--	--	--	--	--	
Female K3	low: 2.4 high:	8.2 (188)	4.9 (69)	--	--	--	100	
Subad male K2	low: 2.6 high:	20.7 (168)	9.5 (75)	--	--	50.0	--	
Juv. female LOT	low: 0.9 high:	--	--	--	--	--	--	
Btwn. Groups								
Female GRZ	low: 2.4 high: 3.1	28.2 (237)	20.2 (59)	--	--	--	--	
Juv. PEP	low: 1.1 high: 1.6	12.5 (61)	--	18.8	--	--	--	
Group Status Unk.								
Male CHI	high: 3.5	--	--	--	--	--	--	
Male RIC	low: 3.0 high: 3.4	--	--	--	--	--	--	
Female OLI	high: 3.3	--	--	--	--	--	--	
Female ROS	low: 2.6 high: 2.9	--	--	--	--	--	--	
Subad female ARE	low: 2.3 high: 2.5	--	--	--	--	--	--	
Subad female LOL	low: 2.4	--	--	--	--	--	--	

a. Mosquito group was observed in 1993 and reported in Kays and Gittleman (1995).

Table III-3. Size and overlaps of core feeding areas for member of center group. The core feeding area is a 50% minimum convex polygon (MCP) for locations where animals fed in fruit trees. Only locations obtained after the immigration of MAG into center group are used.

ID	50% MCP, ha (fixes)	Percent of area overlapped by			
		ELV	BEA	POK	MAG
ELV	10.0 (26)	--	3.1	17.4	0
BEA	6.4 (19)	4.8	--	63.9	14.2
POK	6.1 (17)	28.4	66.8	--	5.2
MAG	16.2 (30)	0	41.4	14.6	--

Table III-4. Composition of 59 kinkajou group dennings, 39 group feeding bouts, and 38 grooming bouts on nights without copulations. Numbers do not add up to 59 or 39 because some groups had more than 2 individuals. Residuals and significance values are from nonparametric chi-squared tests using expected values calculated from kinkajou group structure and focal animal sample size.

Combination	Observed denning (days)	Residual	Observed feeding (bouts)	Residual	Observed grooming (bouts)	Residual
male - male	6	-2	6	1.8	1	-2.1
male - female	21	-3.1	15	-1.4	8	-4.2
male - subadult	17	0	10	-1.3	14	5.6
male - juvenile	6	-6.4	3	-5.6	2	-4.4
female - subadult	11	2.8	3	-2.3	3	-0.9
female - juvenile	11	5.1	11	7.1	9	6.1
subadult - juvenile	4	1.7	3	1.7	1	0.0
Chi-squared test result	p = 0.105 df = 6 X ² = 10.5		p = 0.002 df = 6 X ² = 20.5		p = 0.001 df = 6 X ² = 22.6	

Table III-5. Summary of play behavior observed by Limbo kinkajous.

Juvenile	Playmate	Date	Time	Length (min)	Tree	Description
PIC	PAT (female)	4/10/96	20:02	18	fruiting <u>Inga</u> sp.	PIC rolled around on top of PAT, grabbed at her head, hung by his tail and put his feet in her face. PAT did not retaliate with play, but did groom him.
PEP	OTS (male)	5/9/96	2:40	6	fruiting <u>Ficus insipida</u>	OTS started the play by grabbing at PEP's head as he walked by. They both grabbed each others heads and wrestled around, then both hung by their tails and swatted at each other's heads. Then OTS ran down the branch and PEP chased him out of sight where they apparently continued to play as a tree branch broke and fell to the ground.
LUN	POK (subadult male)	5/13/96	2:12	6	non-fruiting tree	LUN grabbed at POK's tail and they wrestled around and groomed each other.
PEP	OTS (male)	9/6/96	5:21	9	next to day den	PEP chased OTS around the branches of two adjacent trees.

Table III-6. Details of the dispersal of a subadult female kinkajou (MAG) in 1996.

Date	Observations
18 March	Adult female in center group (MOM) last seen. MAG is a subadult female in neighboring range.
22-25 April	MAG was trapped 3 times, progressively closer to center of MOM's old range, and given a radio collar. Four bite wounds were observed on tail, arm and head.
3 May	MAG fed in south east portion of MOM's old range in the early AM, then quickly traveled further south east to her old range and denned with her mother (PAT).
14 May	MAG had a quick quiet interaction with male from center group (ELV) while foraging in MOM's old range.
19 May	MAG denned in MOM's old range, foraged in north east portion in the early evening.
20 and 22 May	MAG had excited 30 min interactions with subadult male from center group (POK) near center of MOM's old range including scent marking by POK and vocalizations by MAG.
31 May	MAG foraged in the SE portion of MOM's old range in early AM, met briefly and quietly with ELV. She traveled back to old range and met up with PAT. Denned alone in old range. This was the last time she was observed in her old range.
3 and 7 June	MAG denned alone in new range.
11 June	MAG denned with ELV and foraged alone in new range.
12 June - end of study	MAG is only observed in new range. MAG's range overlaps 74.5% of MOM's old range. MAG copulates with both center group males 26 and 27 November.

Table IV-1 Characteristics of 11 kinkajou microsatellites. Imperfect repeats are indicated by '*'. H_o denotes observed heterozygosity.

Locus	Primer sequences 5'-3'	Core repeats	Annealing temp °C	Allele size range (bp)	No. of alleles	Frequencies	H _o
kink 13	F- CATGCCAGAGTTTGAGTGACAGAAG R- CATGTGGCTTCCCGTTCTTG	(GA) ₁₀	55	179-187	4	.72, .20, .06, .02	48.0
kink 18	F- TTCTTAGACGGTGACTCTGCTCCC R- AACGAAGGCATAGCCACATCCG	(AC) ₁₆	53	202-206	3	.68, .22, .10	52.0
kink 19	F- AGGTTTGGTGAGCATCCAC R- TGGACGCATACACATAAGTG	(TG*) ₂₀	53	156-158	2	.80, .20	32.0
kink 21	F- AGGGAATGTGCTTCTAATCC R- GCAGCCAAACAACTAAAGTCC	(CA) ₁₂ , (AT) ₅	51	173-185	5	.70, .13, .09, .06, .02	56.5
kink 24	F- CAGAAAGAGAAATCTGATCCTGGCAG R- CCTTGTGGGAAAGACTGTCAAAGG	(GA*) ₁₃	55	183-195	2	.86, .14	20.0
kink 55	F- TCCACTTTGCAGGACTGCTG R- CCACCCCTGACCAAGAGAAATGAG	(TG*) ₁₇ , (TA) ₄	54	149-153	3	.65, .29, .06	45.8
kink 65	F- TTTGGCTCAGGTCAGGATC R- GAATTGAACTGGGTAAGATCAC	(CT) ₃ , (CT) ₁₅	52	186-200	5	.76, .11, .07, .04, .02	47.8
kink 69	F- GCATCCAGGGGAGCCCTAG R- CATGCACATGAGTGCAGGC	(CT*) ₁₅	56	185-195	3	.68, .28, .04	32.0
kink 72	F- GCCTTCATTTAGTTGAGGTCAG R- GCATTCTGTCAGTGGCTTTCAC	(GT*) ₂₂	52	223-239	7	.32, .18, .16, .10, .10, .08, .06	96.0

Table IV-1 (continued)

kink 108	F- CCACAATGCTCAGATGAACAAGG R- ATCTCACAGCTTACAGCGAGGGAG	(CA) ₄ , (TC) ₁₅ (CT) ₇ , (CT*) ₇	53	234-236	2	.64, .36	61.9
kink 117	F- CATGCAAAATAACACGCAC R- CTGAACAAGGTAGGAAAAGTCACTC	(CA) ₃ , (CA*) ₃₇	55	182-186	2	.96, .04	8.0

Table IV-2 Pairwise relatedness values between 25 individual kinkajous from limbo plot.

	ARE	BAT	BBN	BEA	CHA	CHI	ELV	ERN	GRZ	KAS	LOL	LUN	MAG	MOL
ARE	*													
BAT	0.045	*												
BBN	-0.09	-0.13	*											
BEA	-0.3	-0.31	-0.13	*										
CHA	-0.4	-0.08	-0.11	0.058	*									
CHI	-0.17	-0.09	-0.26	-0.44	-0.54	*								
ELV	-0.03	-0.17	-0.09	0.477	0.089	-0.07	*							
ERN	-0.33	-0.05	-0.47	0.303	0.432	-0.45	0.328	*						
GRZ	-0.25	0.119	-0.43	-0.5	0.192	-0.69	-0.28	0.18	*					
KAS	-0.04	-0.08	-0.28	0.057	0.205	-0.09	0.484	0.079	-0.13	*				
LOL	0.425	-0.18	-0.25	0.015	-0.41	-0.28	0.046	-0.26	-0.39	-0.19	*			
LUN	-0.18	0.243	0.198	0.044	0.194	0.009	0.344	0.305	-0.15	0.056	-0.32	*		
MAG	-0.28	-0.08	-0.27	-0.08	-0.07	-0.31	0.089	-0.28	-0.29	0.339	-0.08	-0.36	*	
MOL	-0.2	-0.33	0.569	-0.52	-0.37	0.287	-0.22	-0.53	-0.79	-0.37	-0.54	0.253	-0.62	*
MOM	-0.53	0.19	-0.25	-0.35	0.123	0.058	-0.3	-0	-0.46	-0.48	-0.53	0.409	-0.63	0.059
OLI	-0.39	-0.07	-0.25	-0.2	0.217	-0.41	0.23	0.318	0.208	0.214	-0.51	-0.06	-0.18	-0.34
ORA	-0.34	-0.35	-0.18	-0.28	-0.12	0.553	0.183	0.04	-0.55	0.023	-0.24	0.296	-0.26	0.232
OTS	0.335	0.017	-0.1	-0.42	0.258	-0.37	-0.27	0.05	0.263	0.259	-0.18	0.031	-0.17	-0.21
PAT	-0.74	-0.82	-0.32	-0.63	-0.61	-0.34	-0.58	-0.83	-0.47	-0.37	-0.53	-0.99	0.213	-0.39
PEP	-0.38	-0.29	-0.12	-0.22	0.526	-0.62	-0.18	0.162	0.581	0.285	-0.5	-0.22	-0.08	-0.46
PIC	-0.68	-0.13	-0.5	-0.41	0.25	-0.25	-0.37	-0.21	-0.05	0.122	-0.67	-0.41	0.253	-0.54
POK	-0.61	-0.36	-0.02	-0	0.154	-0.5	0.032	-0.1	-0.76	-0.14	-0.49	-0	-0.28	-0.04
RIC	0.239	0.556	0.018	-0.08	0.255	-0.09	0.054	0.242	0.134	-0.07	-0.08	0.572	-0.29	-0.11
ROS	0.024	0.456	0.247	0.116	0.348	0.264	0.359	0.226	0.11	0.237	-0.1	0.562	0.13	0.078
RRY	-0.19	-0.31	0.575	0.01	-0.1	-0.01	0.041	-0.52	-0.62	0.147	-0.11	-0.12	0.151	0.322

Table IV-2 (continued)

	MOM	OLI	ORA	OTS	PAT	PEP	PIC	POK	RIC	ROS	RRY
MOM											
OLI	-0.29 *										
ORA	0.085	-0.11 *									
OTS	-0.26	0.158	-0.1 *								
PAT	-0.86	-0.47	-0.42	-0.43 *							
PEP	-0.44	0.293	-0.25	0.512	-0.02 *						
PIC	-0.23	0.005	-0.32	0.077	0.15	0.322 *					
POK	0.23	-0.12	-0.19	-0.48	-0.43	-0.27	-0.2 *				
RIC	0.433	-0.06	-0.11	0.195	-0.89	-0.18	-0.12	-0 *			
ROS	0.181	0.134	0.21	0.086	-0.73	-0	-0.04	-0.03	0.546 *		
RRY	-0.47	-0.22	0.113	-0.31	-0.15	-0.11	-0.16	0.105	-0.42	0.176 *	

Table V-1. Travel distances, activity budgets and feeding behaviors for kinkajous. P-values are for differences between males and females from t-tests (regular text) or Wilcoxon / Kruskal-Wallis tests (*italicized text*).

	All	Females	Males	df	p value
<u>Travel distance</u>					
Travel, m/ ½night	1104±492	1263.3±90	987±77	64	0.013
Travel, m/hr	208.8±88.9	239.0±16	183.8±15	62	0.014
<u>Activity budget</u> min/hr (%)					
Travel	24.1±10 (40.2)	27.7±9.7 (46.2)	21.2±9.7 (35.3)	<i>1</i>	<i>0.0054</i>
Eating	20.9±11 (34.8)	19.1±10 (31.8)	22.2±12 (37.0)	<i>1</i>	<i>0.20</i>
Resting	9.9±7.1 (16.5)	8.5±6.6 (14.2)	11.1±7.3 (18.5)	<i>1</i>	<i>0.12</i>
Social	1.4±2.5 (1.7)	0.8±1.6 (1.3)	1.9±3.0 (3.2)	<i>1</i>	<i>0.057</i>
Unknown	3.7±4.4 (6.2)	3.9±5.0 (6.5)	3.6±3.8 (6.0)	<i>1</i>	<i>0.74</i>
<u>Ave. feeding group</u> <u>size</u>					
all	1.24±0.53	1.19±0.43	1.27±0.60	183	0.30
adults only	1.20±0.51	1.09±0.34	1.26±0.60	171	0.03
<u>Ave. feeding patch</u> <u>size</u>					
cm DBH/ night	58.8±29	53.6±25	62.9±32	<i>1</i>	<i>0.28</i>
n fruits under patch/ night	542±402	417±356	647±413	<i>1</i>	<i>0.024</i>

Table V-2 Correlations between kinkajou activity and the number of eatable fruit patches available in a ½ month period. Data for males is also analyzed after excluding data collected around the peak breeding season (4/20-5/16). Results in normal font are pairwise Pearson product-moment correlations, italicized results are Spearman Rho correlations.

	All r (p-value)	Females r (p-value)	all times r (p-value)	Males outside of breeding season r (p-value)
Travel, m/half-night	0.51 (0.025)	0.655 (0.009)	0.082 (0.78)	0.16 (0.64)
Travel, min/hr	0.68 (0.001)	0.73 (0.002)	0.46 (0.10)	0.35 (0.28)
Eating, min/hr	<i>-0.59</i> (0.008)	<i>-0.53</i> (0.043)	<i>-0.48</i> (0.083)	<i>-0.70</i> (0.017)
Resting, min/hr	-0.10 (0.68)	-0.21 (0.46)	0.099 (0.74)	0.69 (0.019)
Social, min/hr	<i>0.74</i> (0.0003)	<i>0.051</i> (0.86)	<i>0.38</i> (0.19)	<i>0.63</i> (0.04)

Table V-3. Correlations of kinkajou feeding behavior with a) the number of eatable fruit patches available in a ½ month period, and, b) the average distance between feeding patches. Data for males is also analyzed after excluding data collected around the peak breeding season (4/20-5/16). Results in normal font are pairwise Pearson product-moment correlations, italicized results are Spearman Rho correlations.

	All r (p-value)	Females r (p-value)	all times, r (p-value)	Males outside of breeding season r (p-value)
A				
Fruit patches per hour	0.58 (0.01)	0.45 (0.09)	0.62 (0.017)	0.16 (0.65)
Feeding group size	<i>-0.16</i> (0.03)	<i>0.47</i> (0.076)	0.25 (0.40)	<i>0.61</i> (0.044)
Mean patch size, cm DBH	-0.056 (0.82)	0.22 (0.43)	0.11 (0.71)	0.48 (0.13)
Mean patch size, n fruits under tree	-0.014 (0.954)	0.25 (0.37)	0.063 (0.82)	0.35 (0.30)
B				
Fruit patches per hour	-0.09 (0.70)	-0.31 (0.0047)	-0.04 (0.69)	-0.06 (0.57)
Feeding group size	<i>0.14</i> (0.067)	<i>0.21</i> (0.054)	0.06 (0.53)	-0.14 (0.18)
Mean patch size, cm DBH	0.38 (0.11)	0.64 (0.01)	0.031 (0.91)	-0.14 (0.69)
Mean patch size, n fruits under tree	0.11 (0.67)	0.41 (0.13)	0.44 (0.12)	0.37 (0.26)

Table V-4. relationships between kinkajou group feeding and patch size.

	^a Correlation between feeding group size feeding patch size	^b Patches fed in by kinkajous of three group sizes. mean±S.D., (n)			
		1	2	3+ ^c	p-value
Fruit patch size (DBH cm)	$r = 0.24$ ($p = 0.0003$)	53±40 (120)	67±37 (26)	110±33 (6)	0.0007
(n fruits under tree)	$r = 0.20$ ($p = 0.0025$)	496 ±545 (145)	668 ±594 (28)	1187.5 ±458 (8)	0.0015

a) Spearman Rho correlations

b) One way Anova

c) There was one feeding group of 4 animals

Table V-5. Significant results of a model built to describe kinkajou behavior based on moonlight and available fruit.

	Regression coefficient	Std. Err.	t-stat	p-value
Traveling min/hr				
Intercept	27.9	3.44	8.1	0.0001
Moon * Sex Females	5.36	4.31	1.2	0.215
Moon * Sex Males	-10.92	4.51	-2.4	0.016
Fruit	0.47	0.126	3.7	0.0002
Eating min/hr				
Intercept	43.9	3.85	11.4	0.0001
Fruit	-0.45	0.142	-3.2	0.0015
Resting min/hr				
Intercept	17.11	1.52	11.2	0.0001
Moon	4.99	2.79	1.8	0.075

Table V-6. Summary of differences behavior of male and female kinkajous.

Topic	Behavioral Differences
General	
Travel, minutes and meters	Females travel more often and further.
Social minutes	Males are marginally more social.
Feeding group size	Males feed with adults & subadults more than females
Size of feeding patch	Males feed at larger fruit patches.
Fruit	
Travel time and increasing fruit	Females travel more often and further. Males show no relationship.
Resting time and increasing fruit	Males rest more often outside of the breeding season. Females show no relationship.
Social time and increasing fruit	Males are social more often outside of the breeding season. Females show no relationship.
Feeding patches /h and increasing fruit	Males eat at more feeding patches. Females show no relationship.
Group feeding and increasing fruit	Males feed in groups more often outside of the breeding season. Females show no relationship.
Group feeding and increasingly dispersed fruit	Females feed in groups more often. Males show no relationship.
Feeding patch size and increasingly dispersed fruit	Females feed in larger trees. Males show no relationship.
Predation risk	
Travel time and increasing moonlight	Males travel significantly less. Females travel marginally more.

Table VI-1. Summary of similarities and differences between kinkajous, spider monkeys and chimpanzees.

	Kinkajous	Ateles sp.	Pan troglodytes
General			
Taxonomy	Mammalia – Carnivora – Procyonidae	Mammalia – Primates – Cebidae	Mammalia – Primates – Pongidae
Range	Tropical American Forests	Tropical American Forests	Tropical African Forests
Substrate use	Completely arboreal	Completely arboreal	Arboreal and terrestrial
Activity	nocturnal	diurnal	diurnal
Strata used most	middle canopy	upper & middle canopy ⁴	ground and middle canopy?
Weight M:F (kg)	3.15:3.0	7.9:7.7 ¹²	49:41 ⁸
Sexual Dimorphism	1.05	1.03	1.2
Predation risk	low	low	low
Population Density (/km²)	~10	<28 ² , 7.3 ⁴	
Biomass (kg/km²)	~24	90 ⁷	96 ⁷
Dispersal bias	female	female	female ⁸
Sex Ratio	~1:1	female biased, >1:2	1:1-3.5 ⁸
Reproductive			
Litter Size	1	1?	1
Interbirth interval (years)	1-2	2-4	4-8 ⁸
Gestation length (days)	~115	210 ³ ~230 ⁵	228 ⁸
Lactation period (months)	2-4	18	
Age at maturity	m 1.5 f 2.5	7-8 ³ 4.5-5.5 ¹²	10 ¹⁵
Parental care	female only	female only	female only

Table VI-1 (continued)

Diet(% time)			
Fruit	90.6	71 ² , 77.4 ⁴	68 ¹³ , 58 ¹³ , 80 ⁷
Leaves	0.7	7.9 ⁴ , 13 ²	28 ¹³ , 20 ¹³ , 20 = (12 herbs + 8 leaves) ⁷
Flowers	8.6	6.4 ⁴ , 14 ²	0
Insects	0	0.2 ⁴ , 2 ²	4 ¹³
Figs	29.6	31 ² ,	89% of feces ⁷
Fruit feeding bout length (min)	41	14 ²	88.5 ⁷
Patch Size used (cm DBH)	58.8	43.1 ²	75.1 ⁷
# fruit species eaten	78	171 ⁴	
Overall food abundance (patches/ha/mo.)	0.728 (0.035-1.56)	25.7 ⁷	3.3 ⁷
Food stability (range & CV)	2-89 total patches CV = 61%	0.6-24.6 patches/ha ² CV = 85.6 ² CV patch/ha = 54% ⁷	CV patch/ha = 164% ⁷
Ranging			
Distance / day (m)	m - 1974 f - 2526	1977 ⁹ 500-1600 ¹²	2000-6400 ¹³
Individual Home Range (ha)	26.4	53 ² f- 37. M-98 ¹⁰	?
Community Range	40-50	250 ²	1490 ²
Overlap between groups	0	10-15% ⁹	?
Activity			
% travel	m - 35 f - 45	26 ⁹	?
% eat	34	29 ⁹	?
% rest	16.5	45 ⁹	?
% social	m - 3.2 f - 1.3	?	?

Table VI-1 (continued)

Grouping			
Community size	4 – 5	~30	20-105 ⁸
Ave Feeding sub-group size	~1.1	3-5, 4.9 ²	5.07 ⁷
Subgroup size determinants	size of fruit patch and seasonal fruit abundance	seasonal fruit abundance ⁷ ₉	seasonal fruit abundance ⁷
% solitary feeding	91.1	4.6 ⁷ (subgroups) 20 ¹⁰ (subgroups)	8.2 ⁷ (subgroups)
Core feeding areas?	y	y	?
Group Inheritance	Patrilineal	Patrilineal	Patrilineal
Sociality			
Male-male association	moderate	strong	very strong ⁸
female-female association	none	weak	very weak ⁸
Male-female association	moderate	moderate	weak ⁸
Male-subadult association	strong		
Grooming	male-subadult most, male-male least		male-male most, female-female least ¹⁵

1) If possible, data from the Central American *Ateles paniscus* is given.

2) Chapman & Wrangham 1993

3) derived from Harvey et al. 1987

4) Van Roosmalen 1980

5) Eisenberg 1973

6) Eisenberg 1976

7) Chapman et al. 1995

8) Nishida & Hiraiwa-Hasegawa 1987

9) Symington 1988a, b

10) Fedigan and Baxter 1984

11) Ahumada 1989

12) Robinson & Janson 1987

13) Wrangham 1977



Figure I-2. Photo of a male kinkajou (ELV) from the Limbo plot.

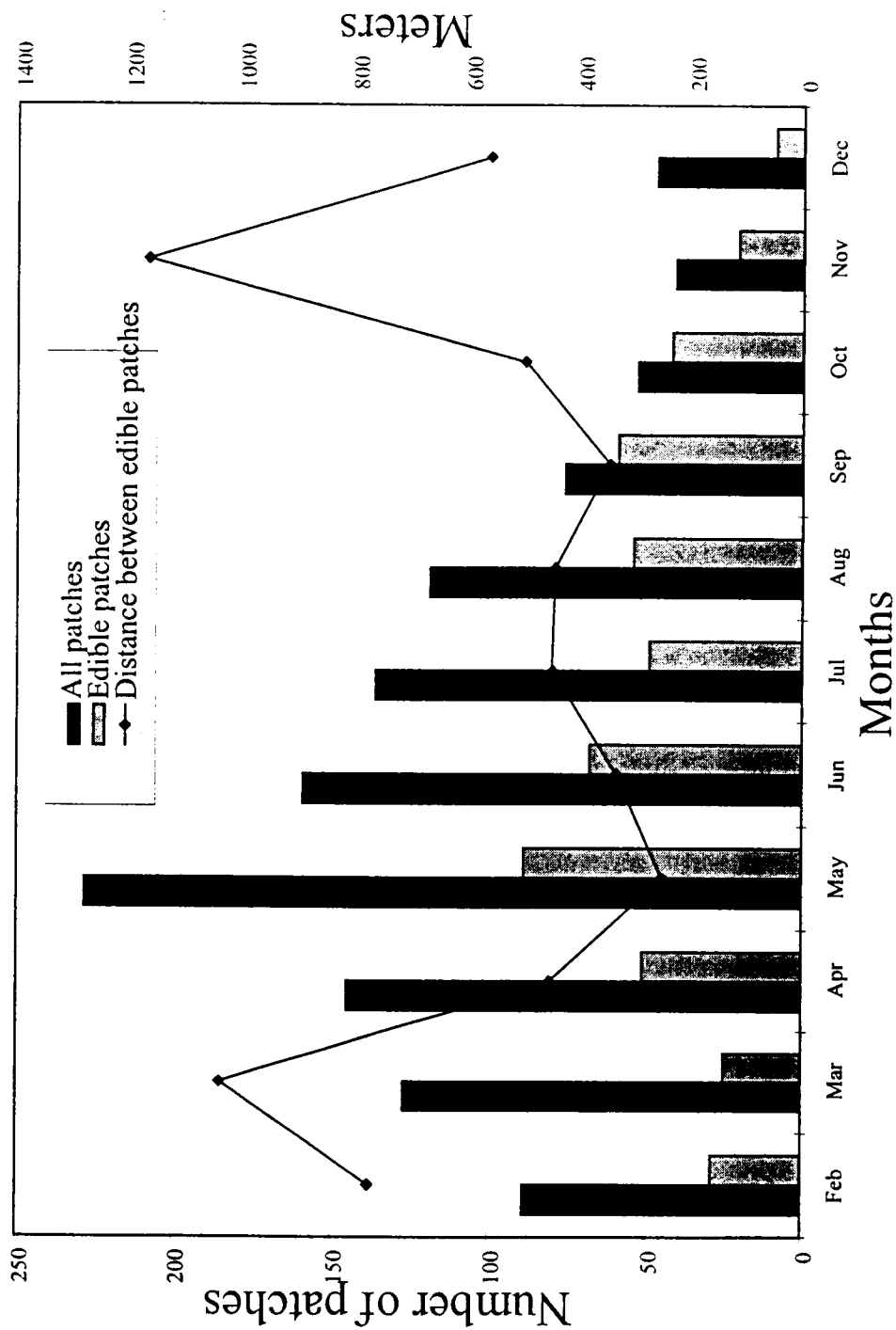


Figure II-1. Availability of fruits and average distance between feeding patches on the Limbo plot in 1996 revealed by the number of non-wind dispersed fruit patches encountered on bi-monthly counts of fallen fruit on 11.4-km transects. Edible species are those that kinkajous ate during the study. Fruits actually were available to arboreal kinkajous ca. 1 month before they were detected in the census.

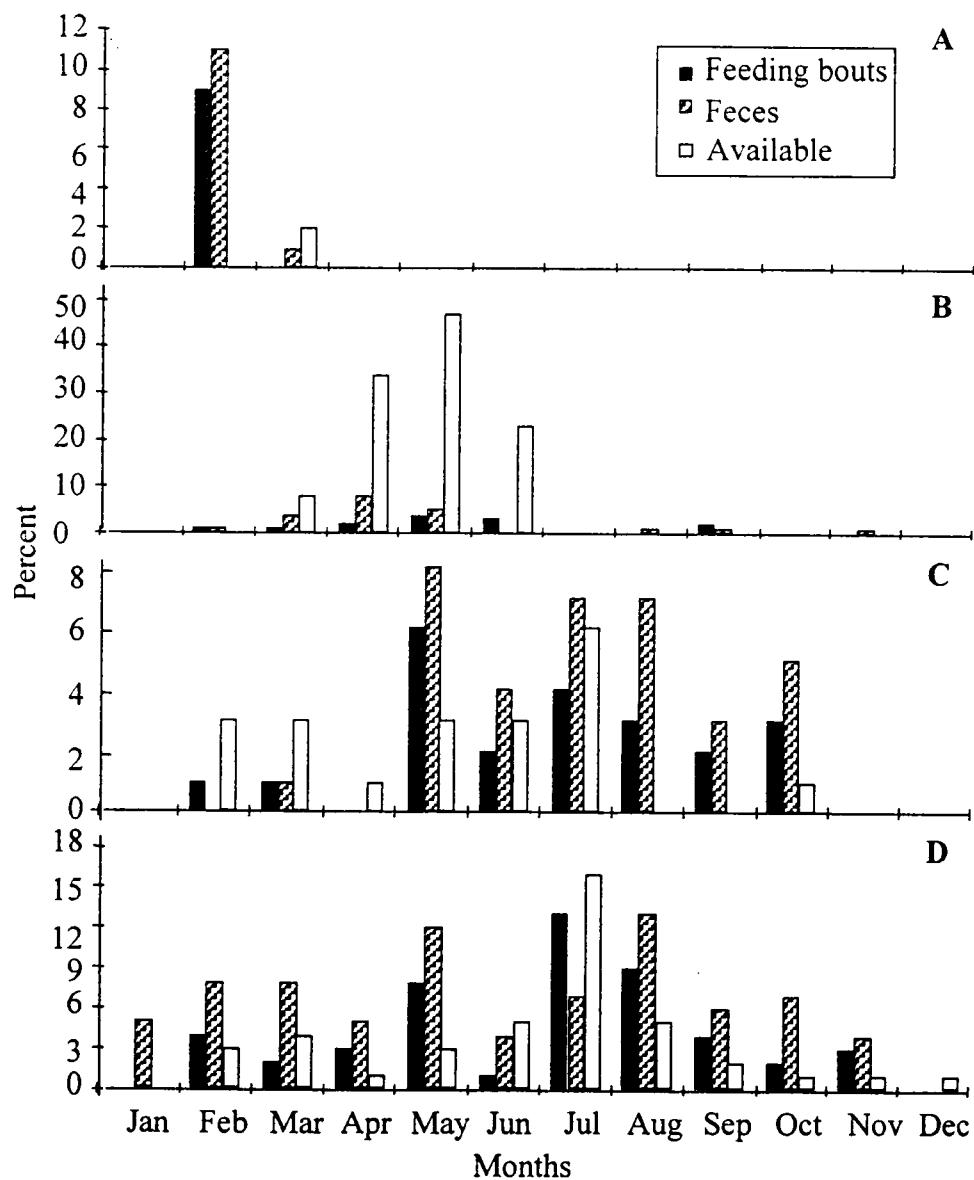


Figure II-2. Availability and use of four fruit types for kinkajous. A) *Chrysophyllum cainito*, B) *Astrocaryum standleyanum*, C) *Ficus insipida*, and D) all *Ficus*. Intensity of use by kinkajous is shown by the number of feeding bouts and feces involving each fruit; availability is shown by the number of fruit patches encountered in the census of fruits.

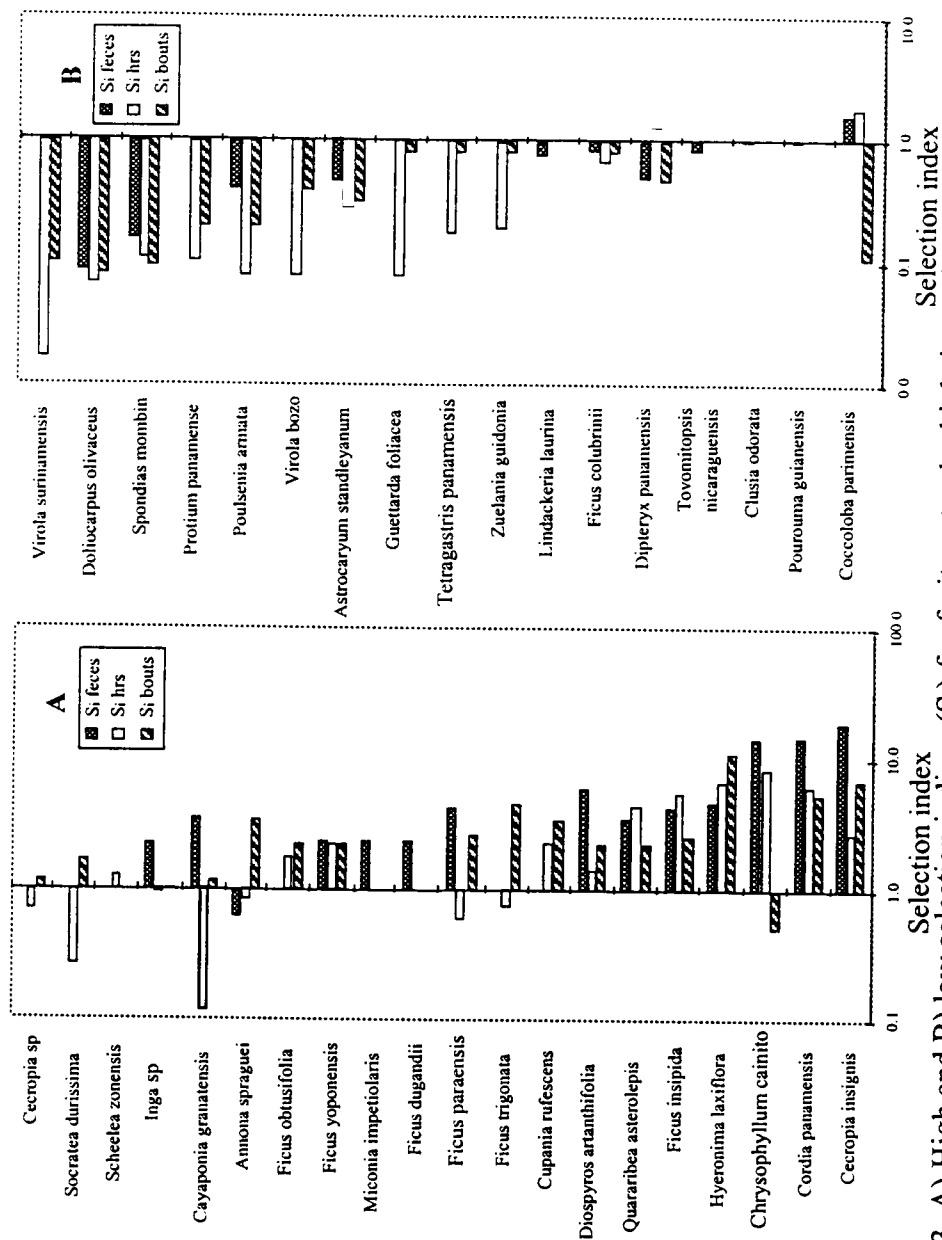


Figure II-3. A) High and B) low selection indices (S_i) for fruits eaten by kinkajous. (>1 = selected for, <1 = selected against). High S_i -values for feeding bouts indicated that kinkajous visited a fruiting species more often than expected; high S_i -values for hours feeding (h) indicated that they spent more time in a fruit species more frequently than expected; high S_i -values for feces indicated that they ingested a fruit species more frequently than expected.

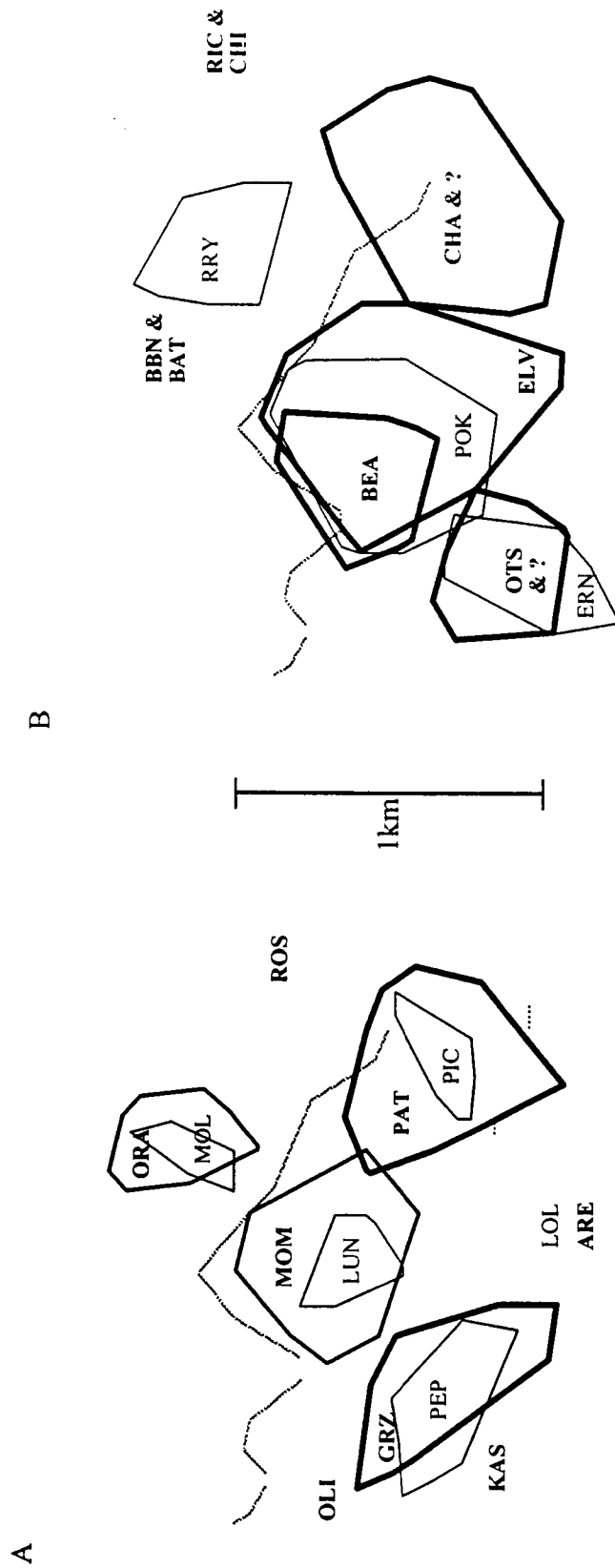


Figure III-1. Home range boundaries (95% MCP) and general areas used for kinkajous in the Limbo plot. A) adult females (thick lines) and their juveniles (thin lines); B) adult males (thick lines) and subadult males (thin lines). Three letter codes represent individual kinkajous (see text). Individuals outside of polygons did not have enough fixes to estimate an accurate home range boundary and their placement indicates the general area where they were trapped and observed. The irregular gray line through the plot is Pipeline road and the vertical line represents 1km.

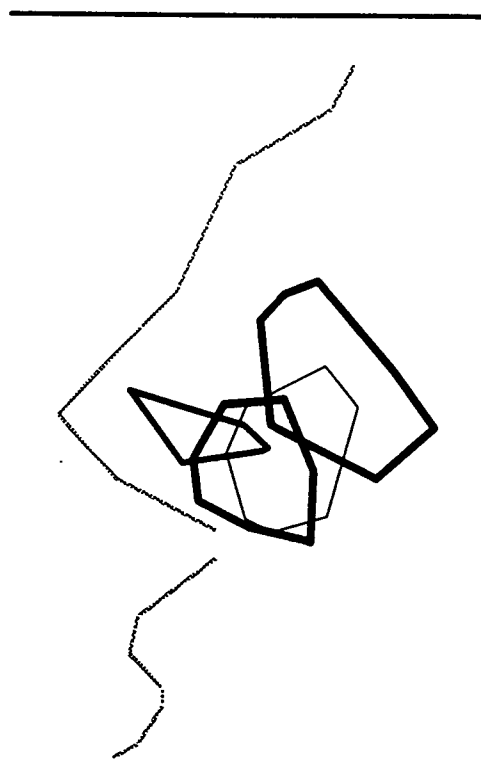


Figure III-2. Core feeding areas for the members of center group after MAG's immigration. The polygons were calculated by using 50% of the locations where each individual was observed feeding on a fruit tree. The two thick dark polygons represent the adult males BEA (above) and ELV (below); the thick gray polygon is for the adult female, MAG, and the thin polygon is for the subadult male, POK. The irregular gray line through the plot is Pipeline road and the vertical line to the right of the polygons represents 1 km.

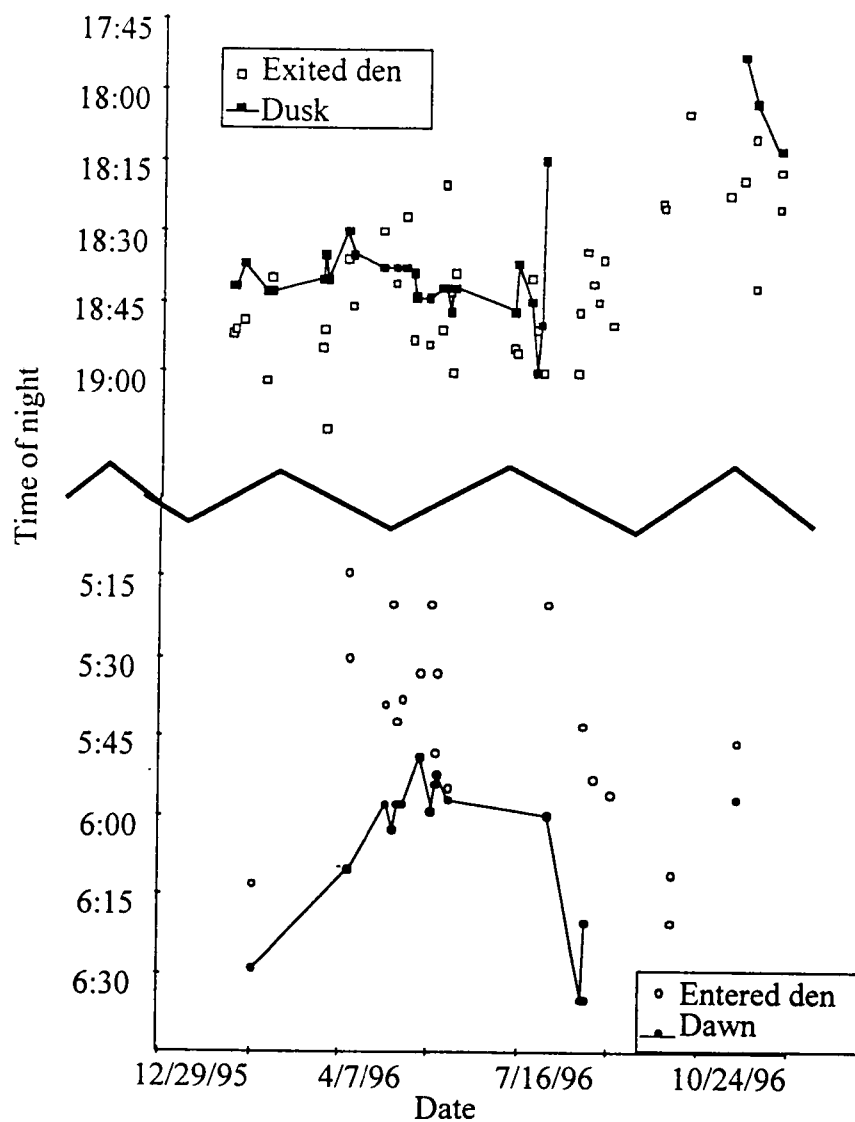


Figure III-3. Times that individual kinkajous entered and exited day dens in relation to dusk and dawn.

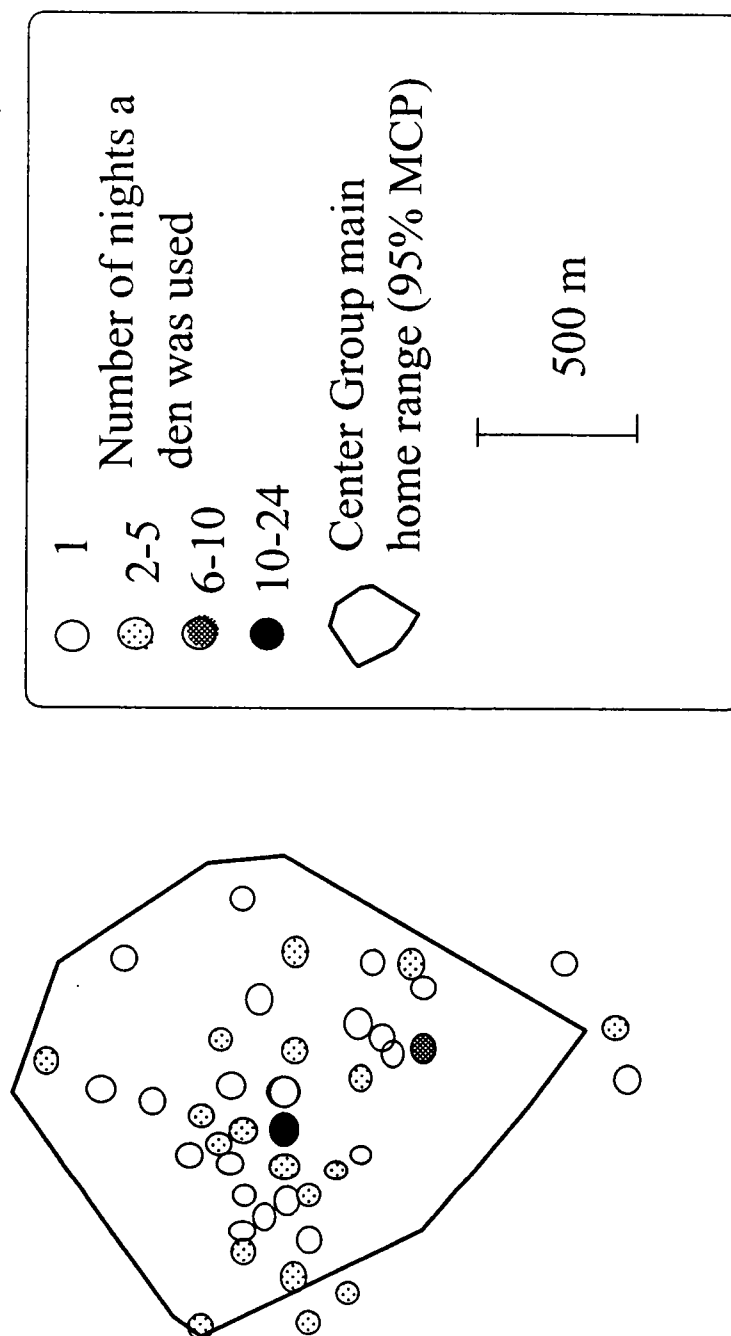


Figure III-4. Location and intensity of use of day dens by Center Group.

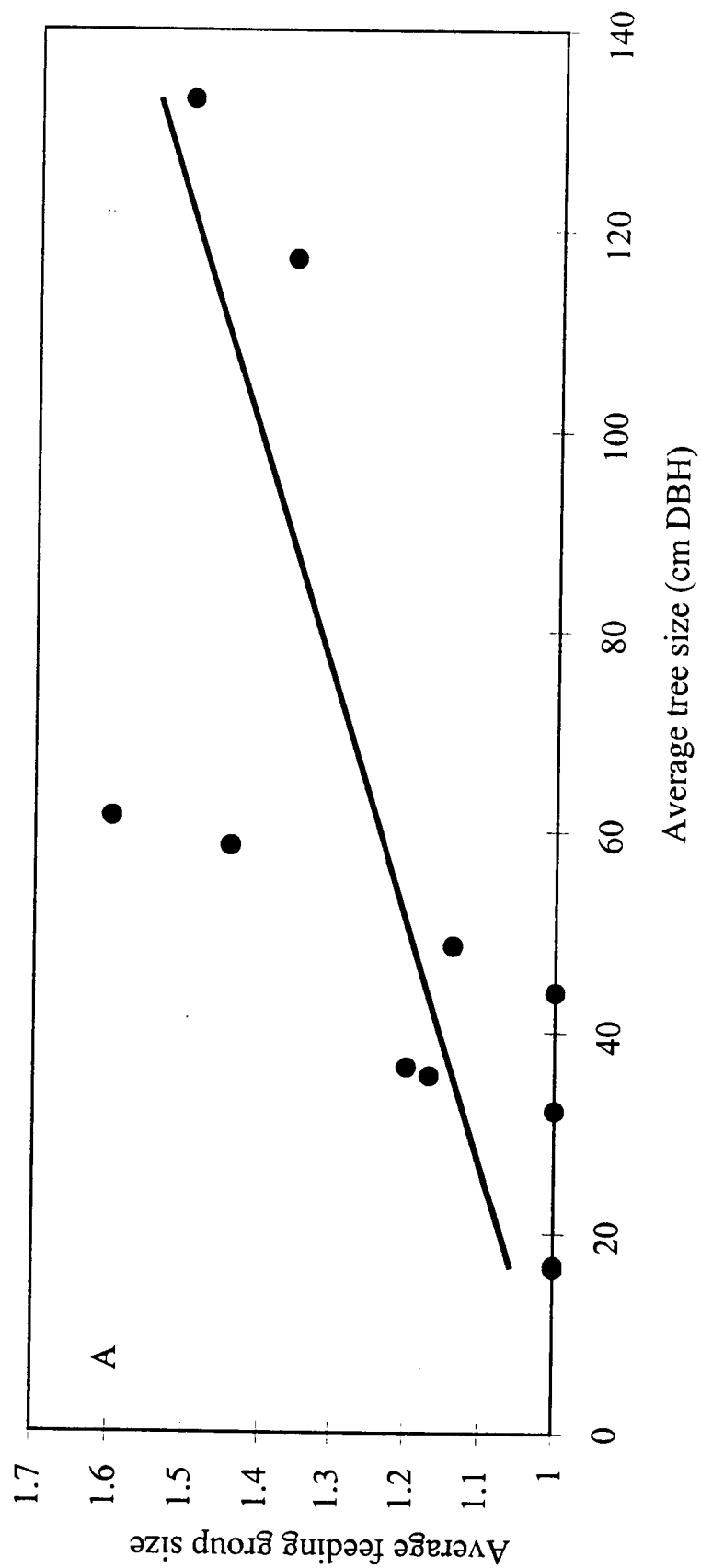


Figure III-5. A) Average group size ($r = 0.83$, $p = 0.0016$) and B) frequency of grouping ($r = 0.837$, $p = 0.0013$) for kinkajous feeding in 11 species of fruiting trees.

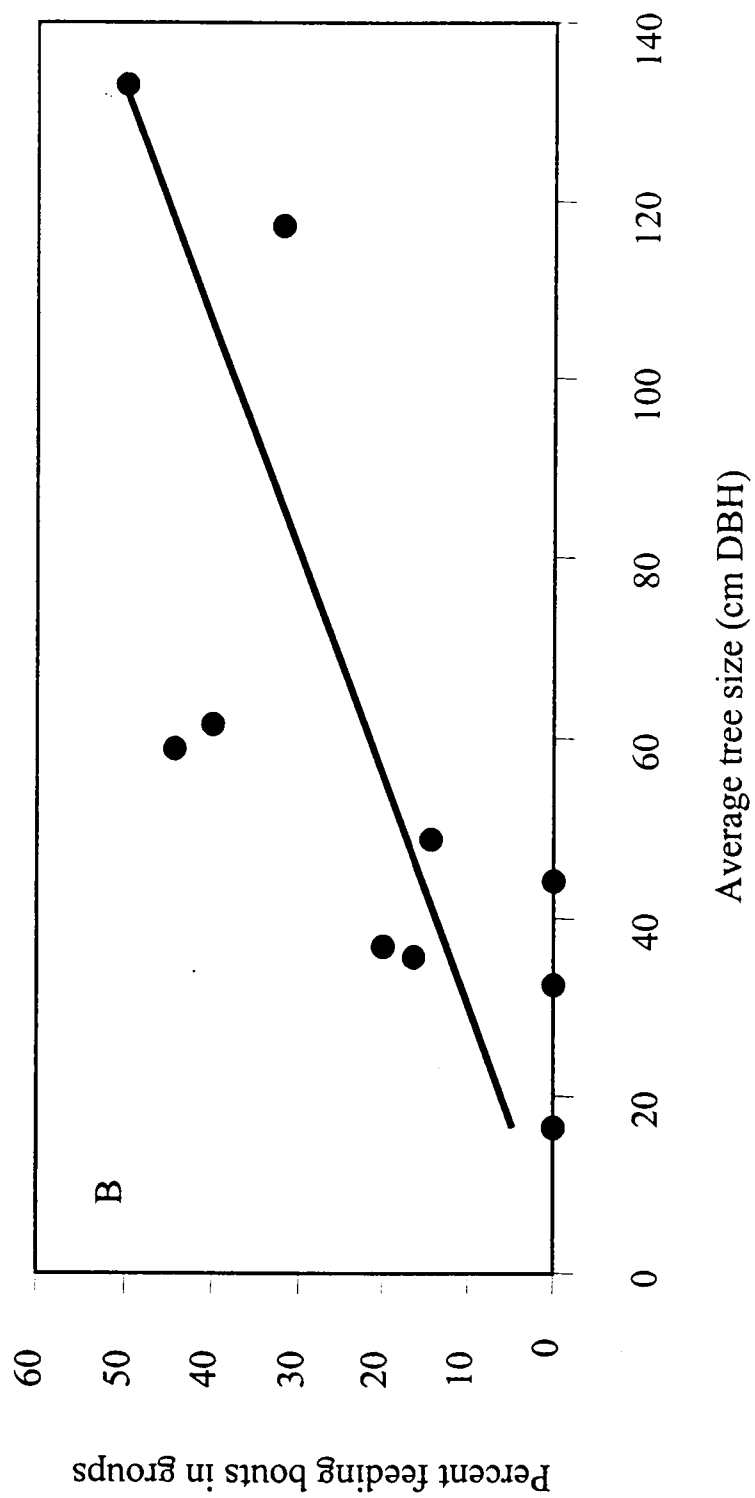


Figure III-5 (continued)

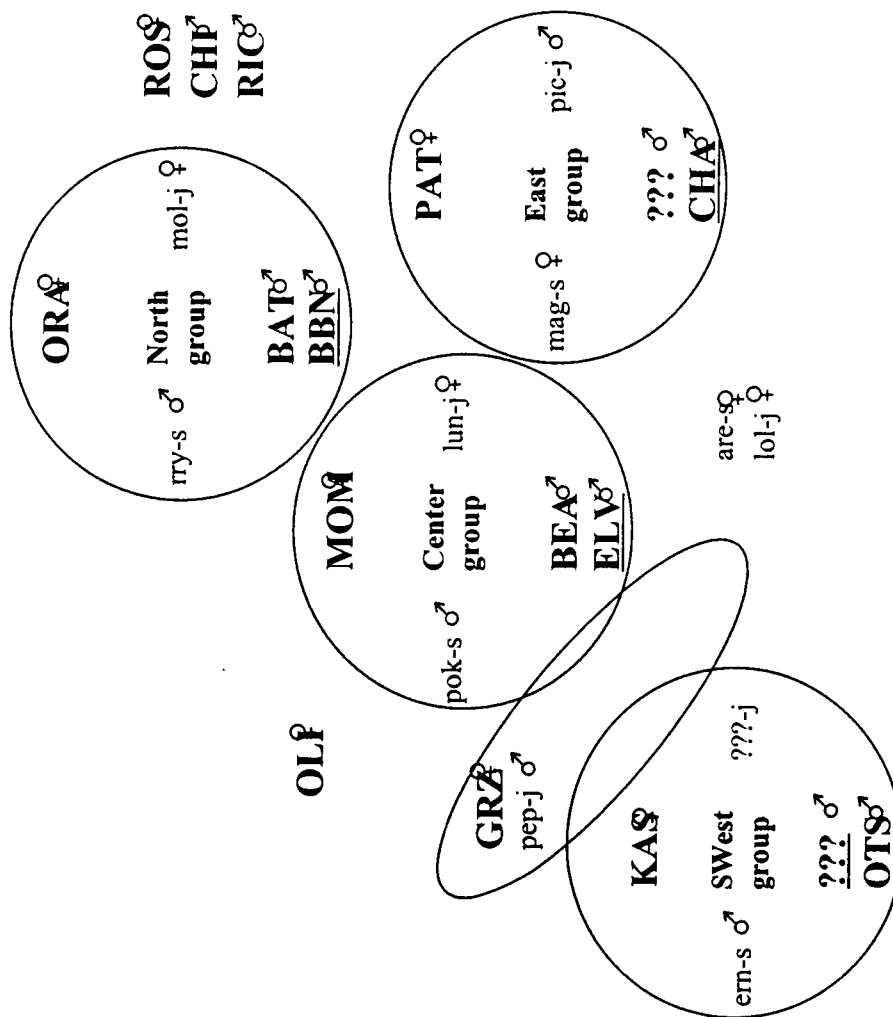


Figure IV-1. Schematic of social group structure for kinkajous in the Limbo plot. Three letter codes are marked kinkajous. Capitals refer to adults, lowercase refers to subadults (-s) or juveniles (-j). Question marks indicate individuals that were observed but never captured. Circles represent approximate group home ranges when known. Underlined males were dominant in their group. GRZ did not associate closely with a social group.

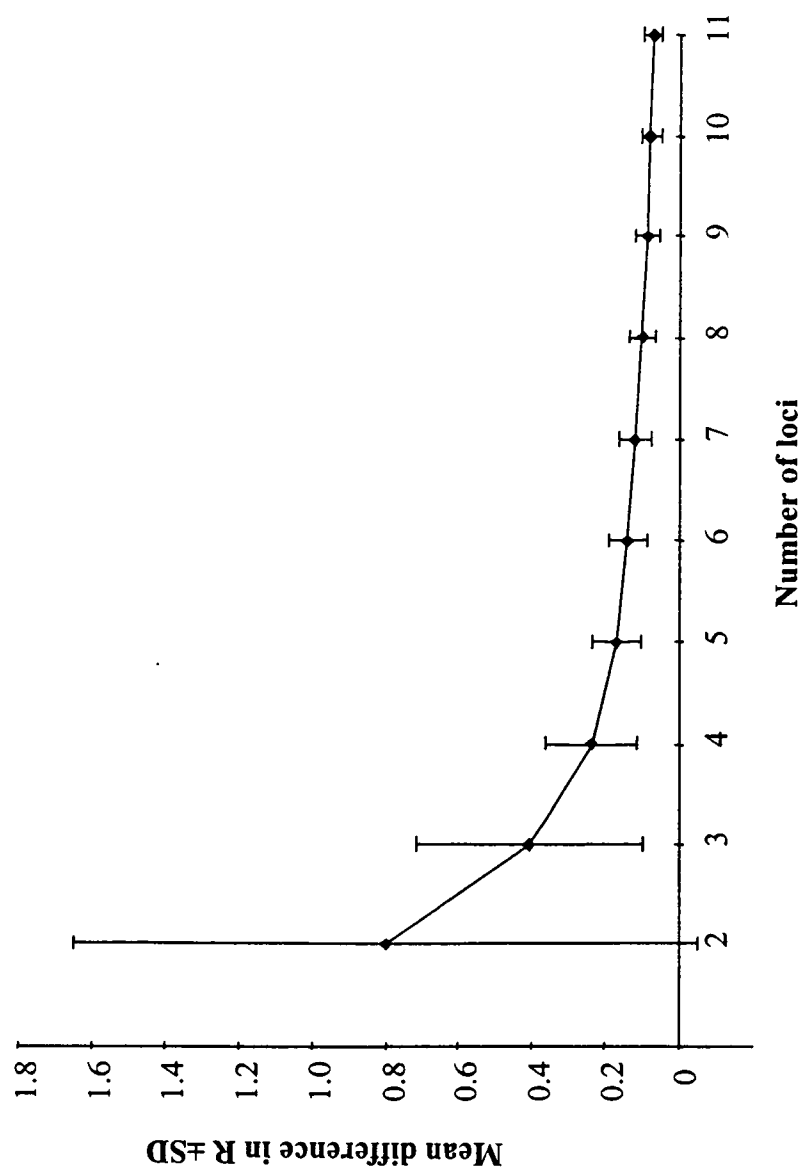


Figure IV-2. Mean difference between consecutive relatedness estimates (R) using one to eleven microsatellite loci.

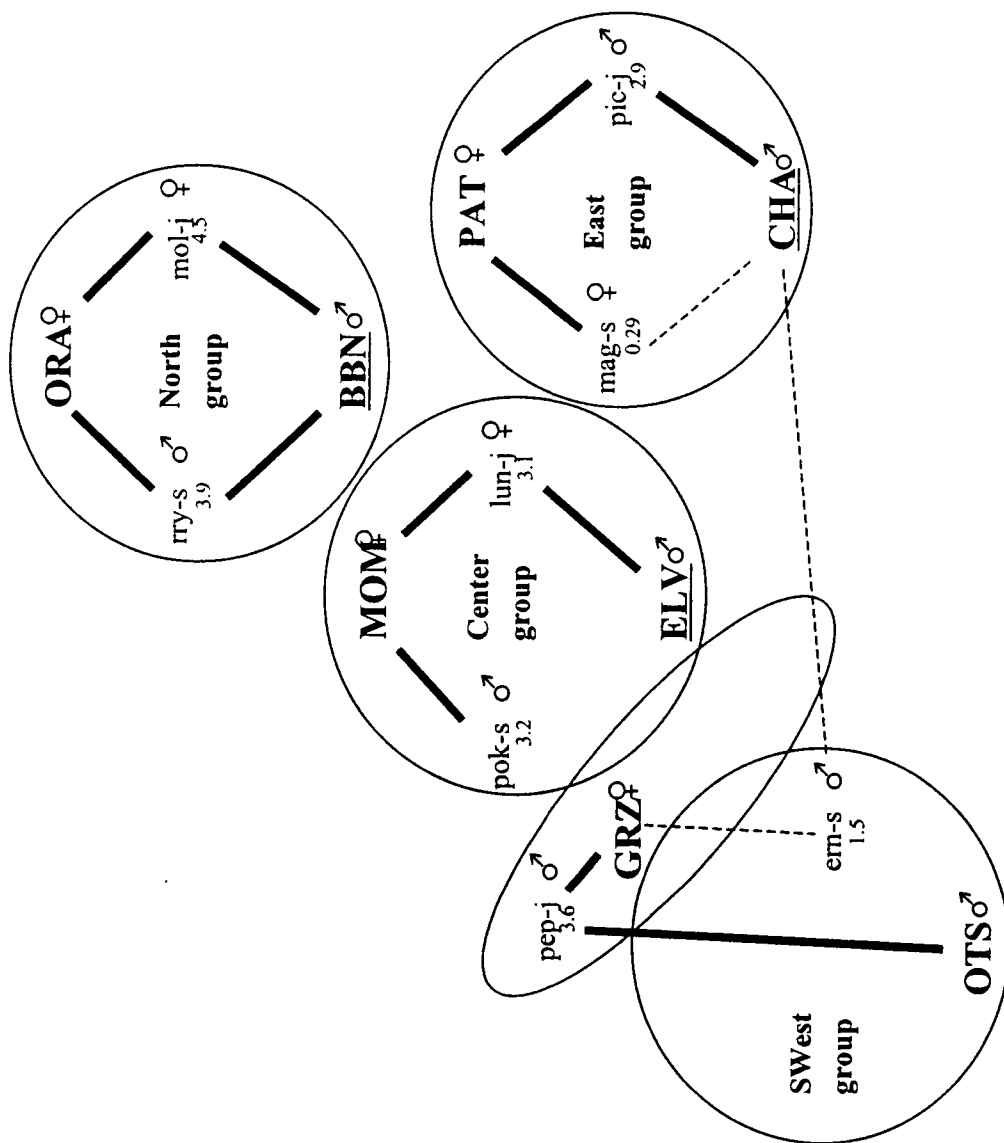


Figure IV - 3. Schematic of genetic parentage within social groups of kinkajous on the Limbo plot. Thick lines show parentage at 95% confidence level and dashed lines show parentage at 80% confidence levels. Numbers are LOD scores. Other symbols as Fig. IV-1.

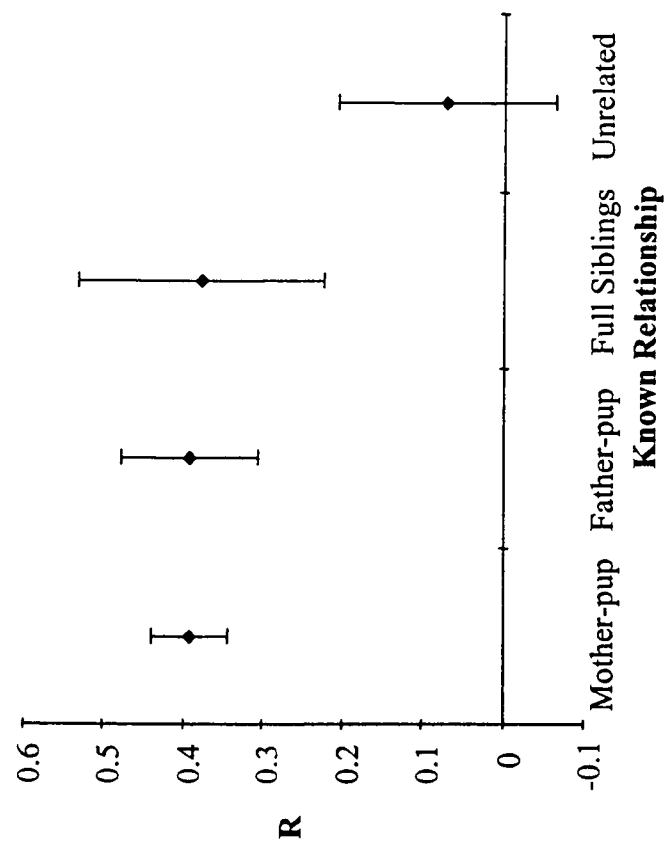


Figure IV-4. Relatedness values for known relationships among kinkajous of the Limbo plot.

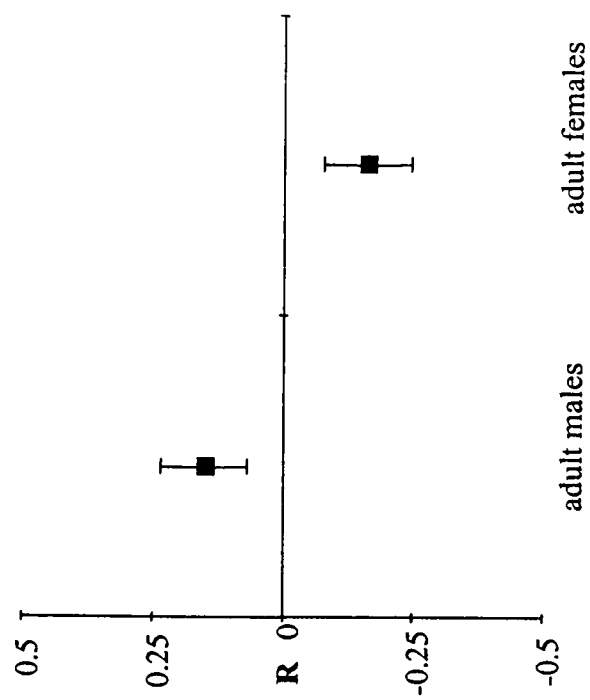


Figure IV-5. Relatedness values for neighboring male dyads compared to neighboring female dyads.

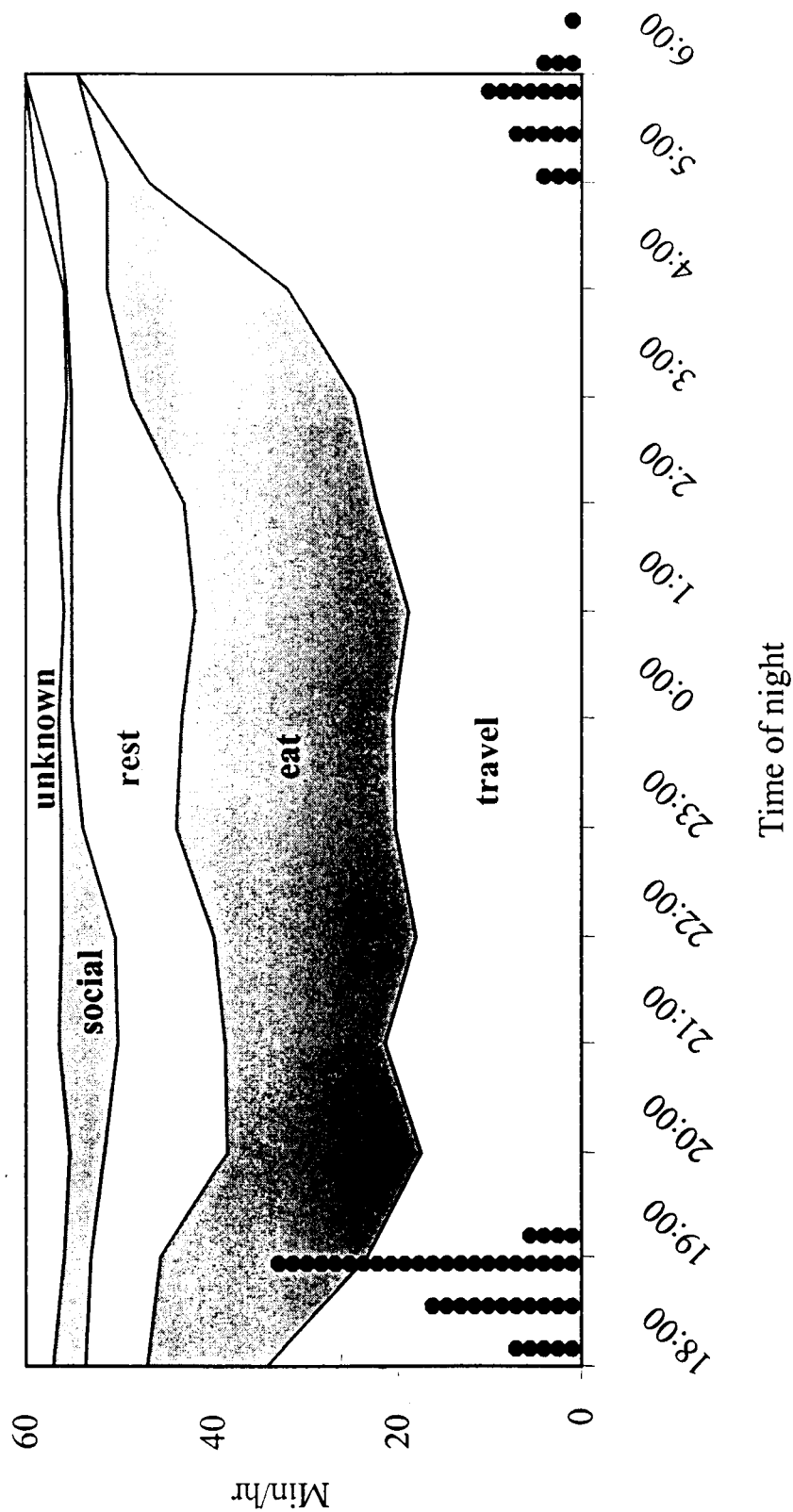


Figure V-1. Nightly activity patterns for kinkajous averaged from 380 hrs of focal animal observation. Columns of small dark hexagons at dusk and dawn indicate the recorded exits and entrances from and to day dens; each hexagon represents one exit/entrance of a focal animal. Hourly activities are not calculated for 6:00 because kinkajous were rarely active then.

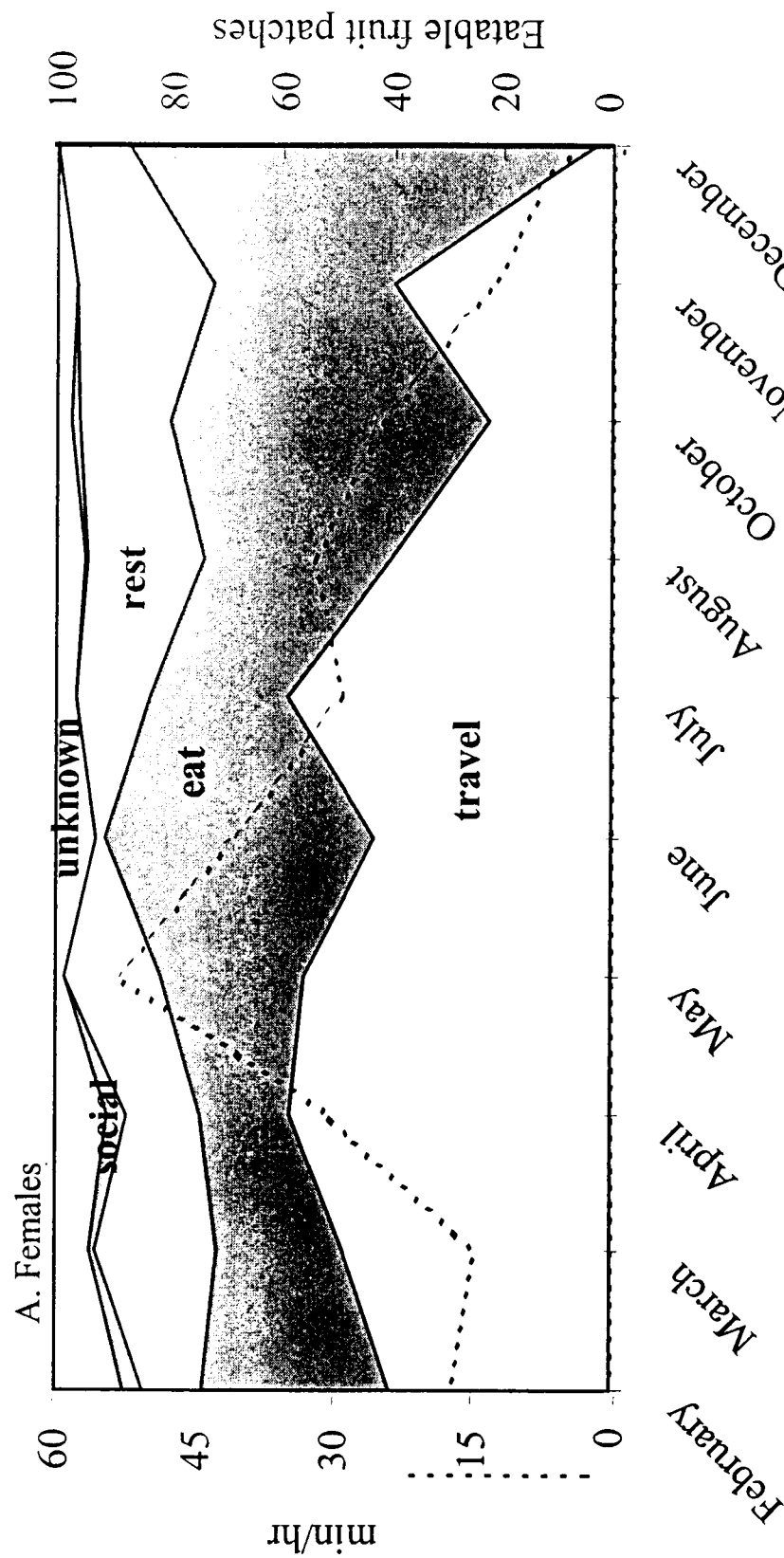


Figure V-2. Monthly activity budgets and fruit availability for A) female and B) male kinkajous on the Limbo plot. The dashed line represents the number of eatable fruit patches available. The filled box on the x axis of the males graph represents the main breeding season.

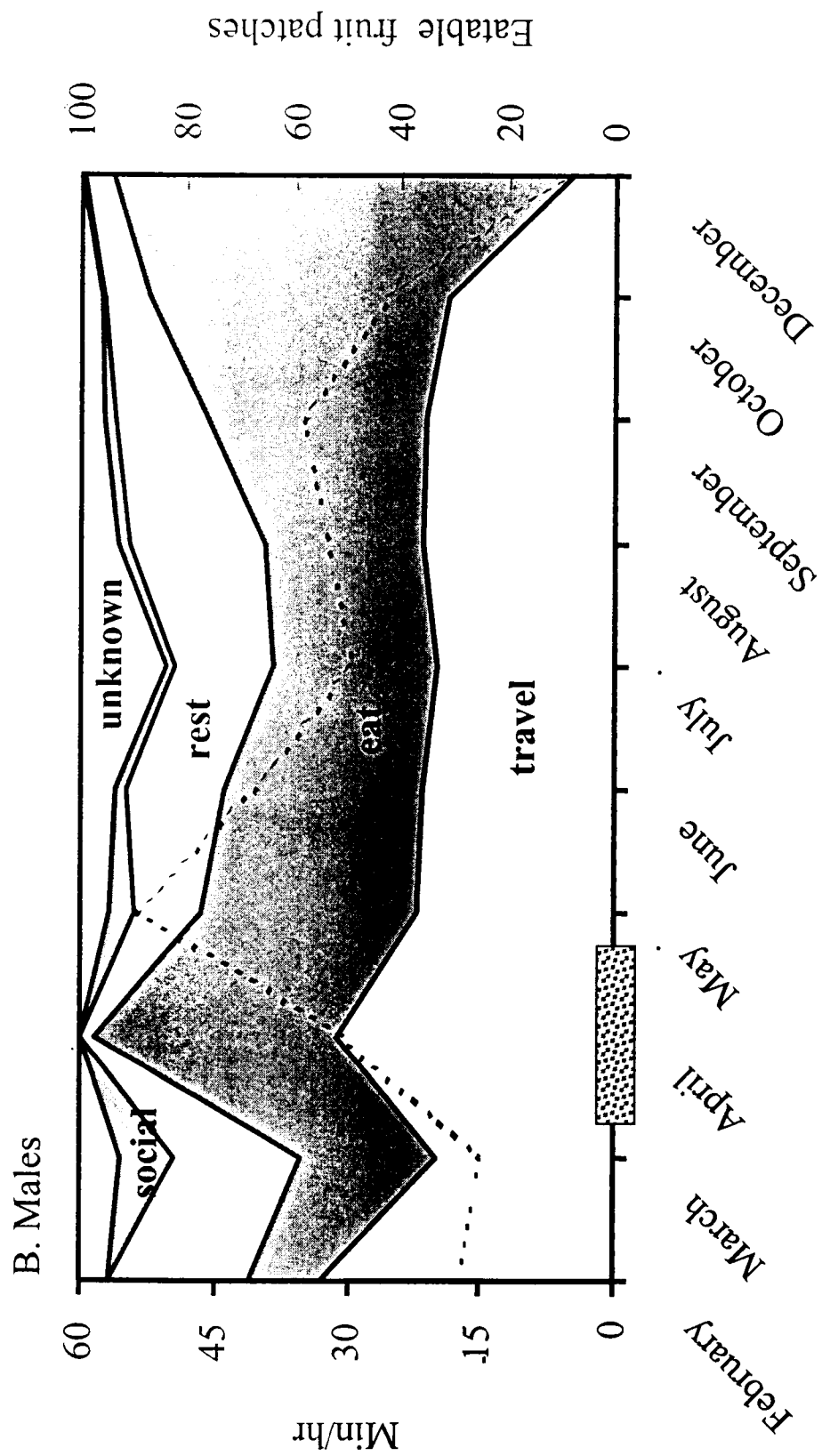


Figure V-2 (Continued)

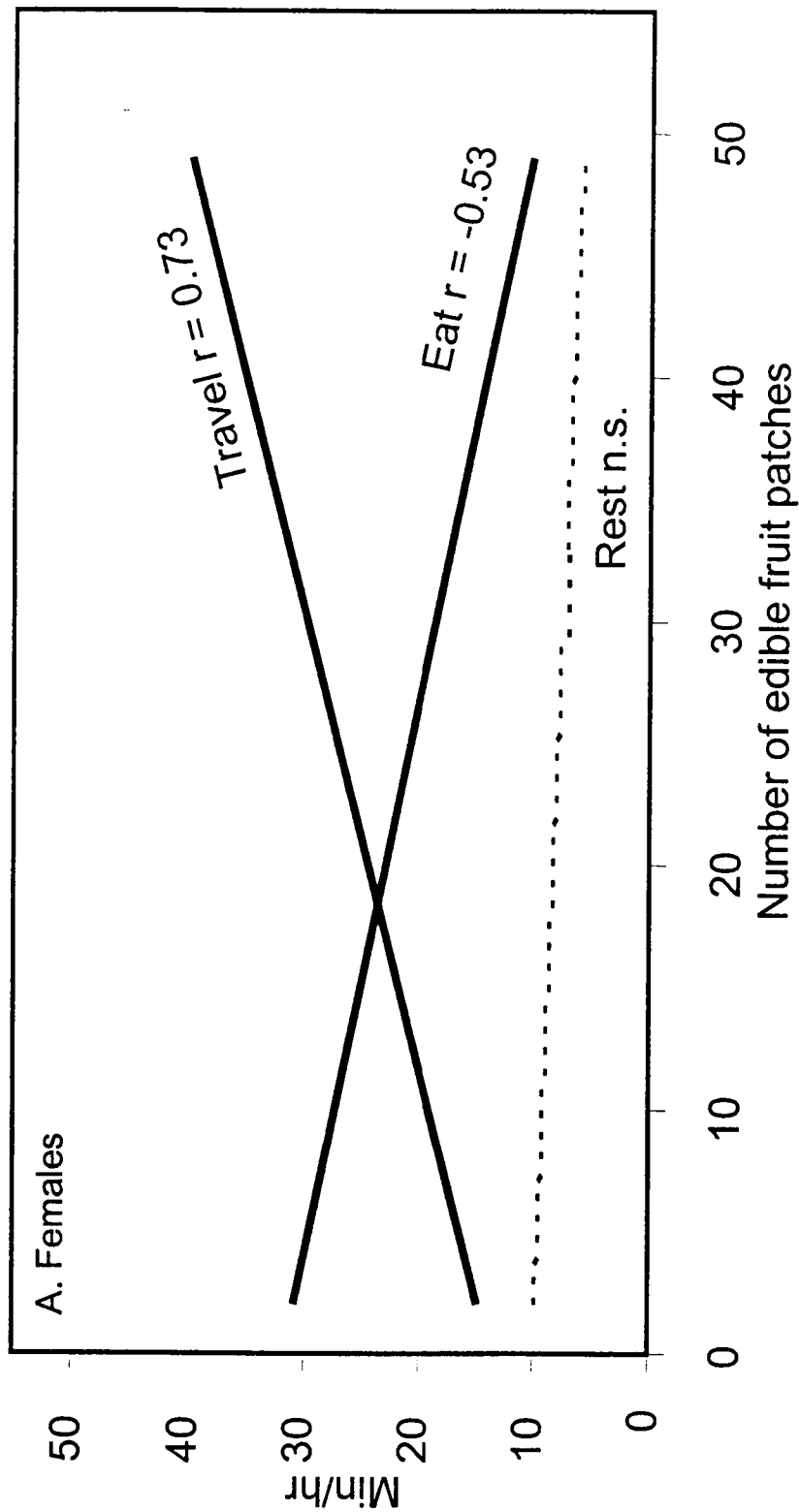


Figure V-3. Regression lines indicating the relationships between number of eatable fruit patches available and the min/hr spent traveling, eating and resting. Regressions were calculated for A) all female data, B) all male data, and C) male data excluding the peak breeding season. Solid lines represent relationships significant at the $p < 0.05$ level, dashed lines represent relationships with p values ≥ 0.1 .

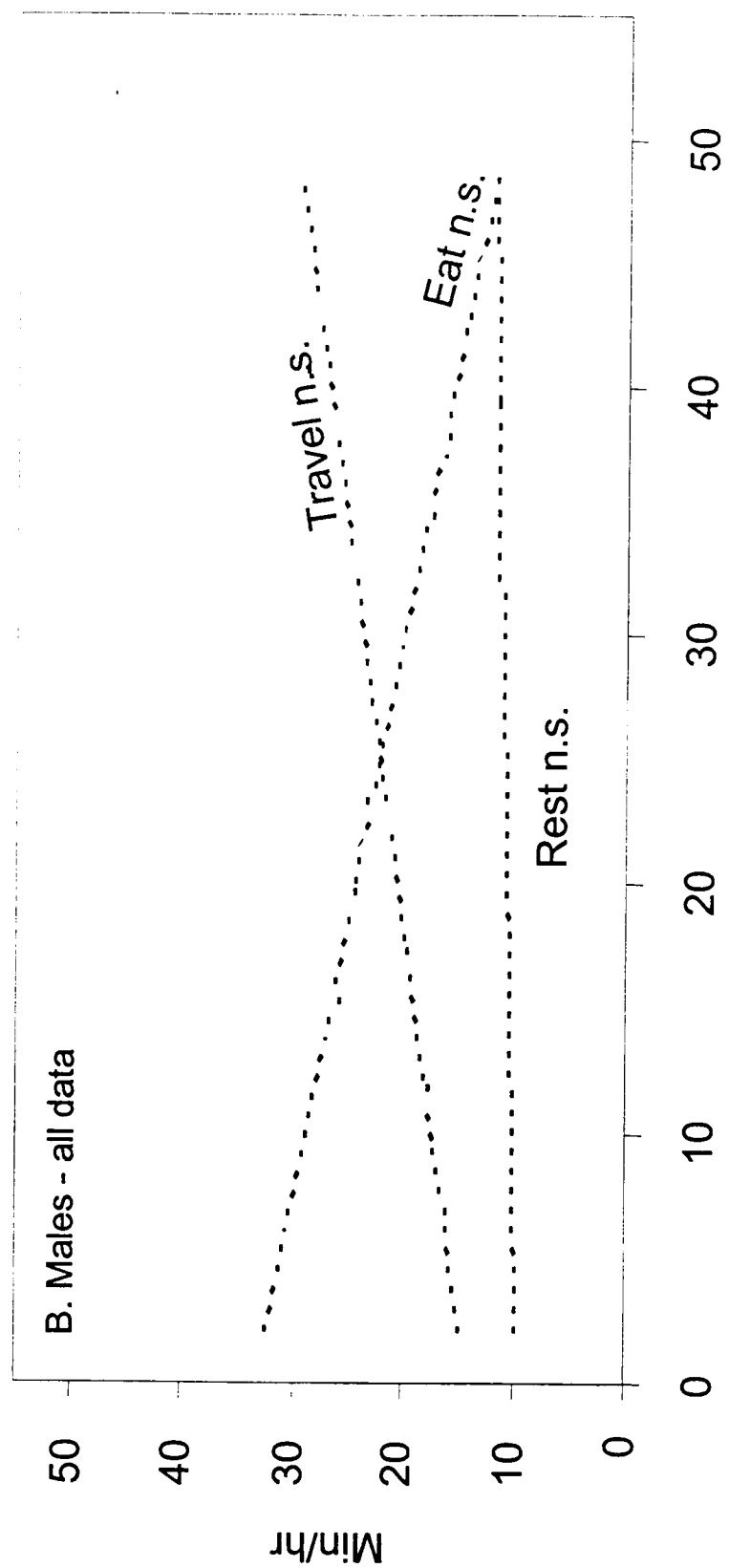


Figure V-3 (continued)

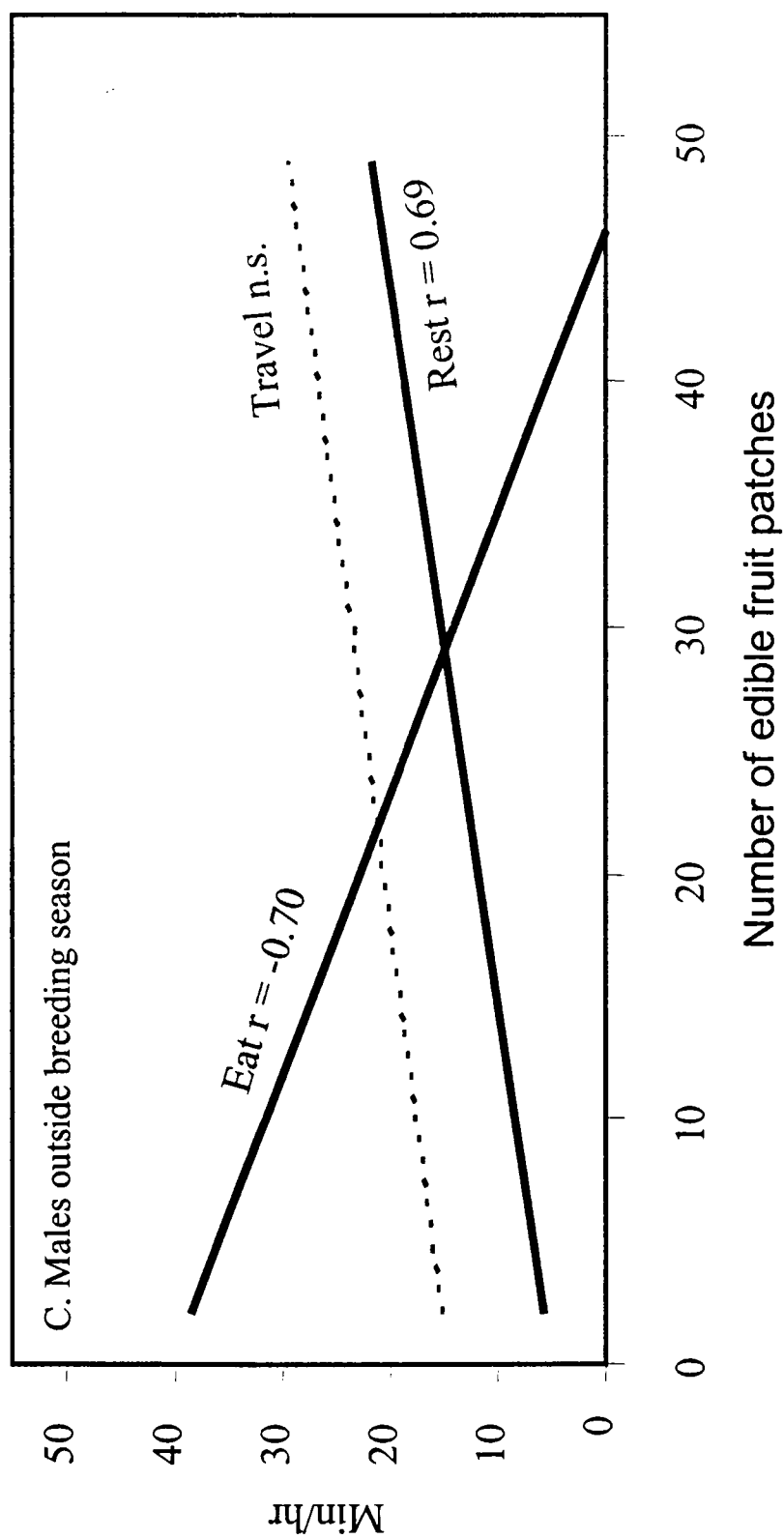


Figure V-3 (continued)

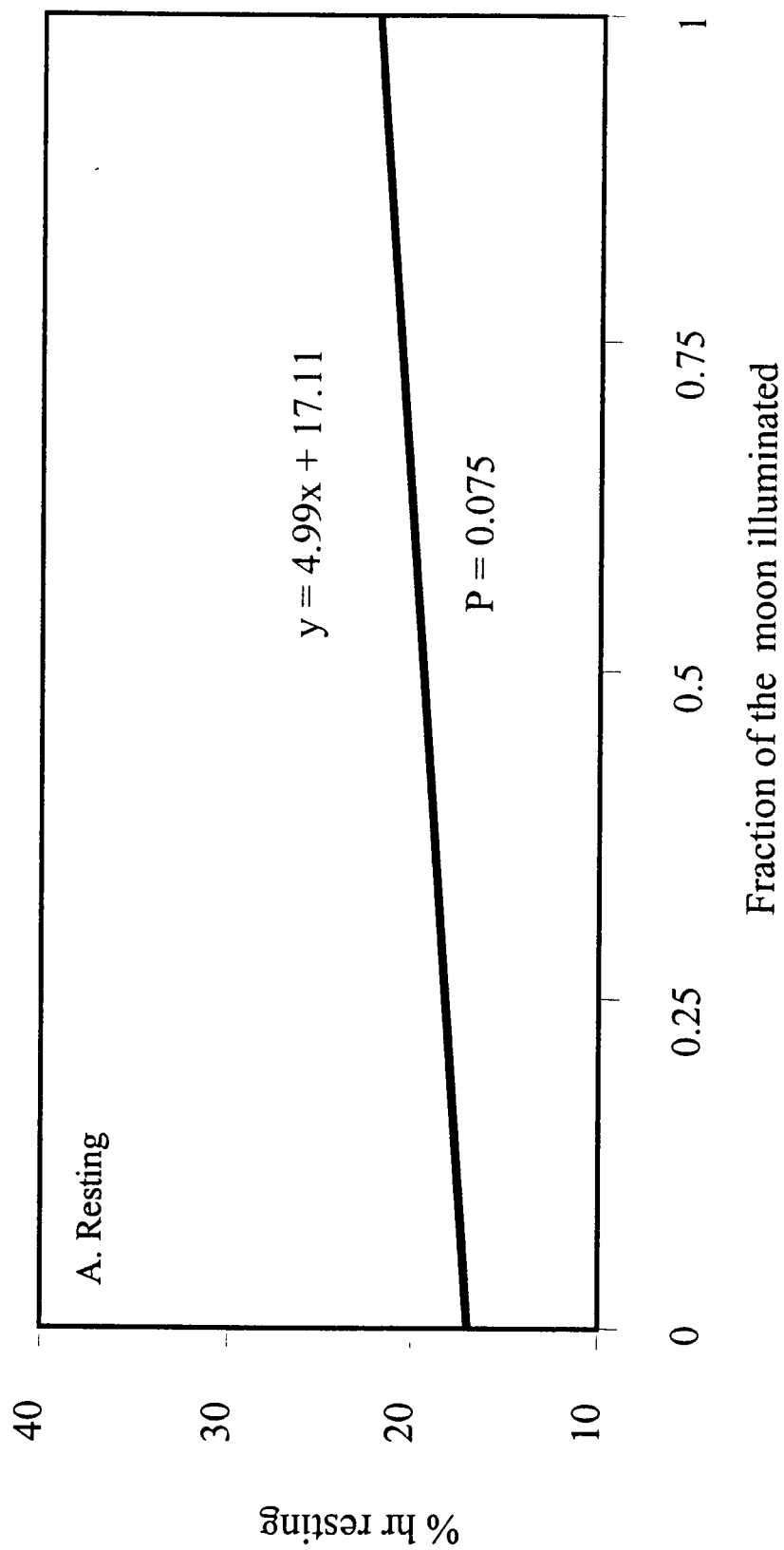


Figure V-4. Correlation of predicted minutes per hour A) resting and B) traveling and the percent of the moon illuminated per night, after taking the effect of fruit abundance into account.

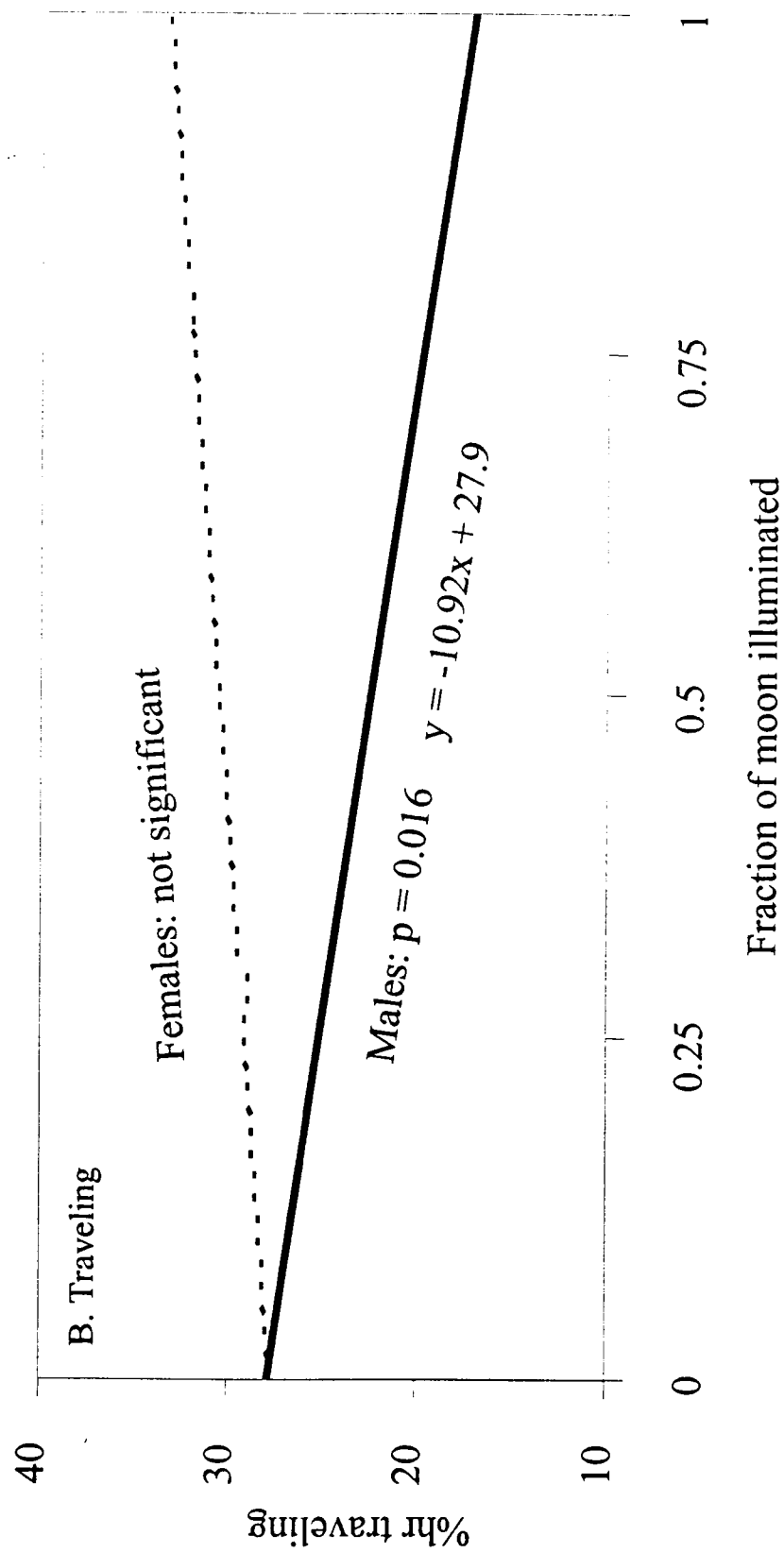


Figure V-4 (continued)

VITA

Roland Wesley Kays was born in Sacramento, California. He graduated from West Bloomfield High School, West Bloomfield Michigan in 1989. The following fall he began his college training at Cornell University, in Ithaca, NY. After four years of class work and independent research under Dr. Deedra McClearn, Roland graduated in the spring of 1993 with a B.S. in Biology (with honors) and a specialization in ecology and systematics. In the summer of 1993 he held an internship with the American Museum of Natural History that entailed work with Dr. Robert Voss at the museum in New York City, as well as mammal survey work in Paracou, French Guiana. That fall he began his research with kinkajous with a preliminary study at the Smithsonian Tropical Research Institute, Panama. He enrolled at the University of Tennessee in January, 1994, to begin his graduate training. Over the next 5.5 years this included coursework, 16 months of field work in Panama, ~ 4 months of laboratory work in the Laboratory of Dr. Robert Wayne at the University of California, Los Angeles, and analyses and writing in Knoxville. His graduate career concluded with the awarding of a doctoral degree in Ecology and Evolutionary Biology in the summer of 1999.

Roland is presently a post-doctoral associate at The Field Museum, Chicago, IL, studying variation in the social organization of maned and maneless lions in Tsavo, Kenya.