

The social organization of the kinkajou *Potos flavus* (Procyonidae)

Roland W. Kays^{1*} and John L. Gittleman^{1,2}

¹ Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996-0810, U.S.A.

² Department of Biology, Gilmer Hall, University of Virginia, Charlottesville, VA 22903, U.S.A.

(Accepted 30 March 2000)

Abstract

The social organization of the kinkajou *Potos flavus* is described from 380 h of observations on habituated, free-ranging animals. Individuals were most often alone while feeding at night, yet they regularly interacted in stable social groups. Four social groups were observed, each consisting of a single adult female, two adult males, one sub-adult and one juvenile. At least one breeding female was solitary and did not reside within a group. Social groups were consolidated primarily at denning sites and large fruiting trees by group feeding, allogrooming and scent marking. However, kinkajous were most often observed solitarily, as social feeding only occurred in 19.6 of total feeding bouts (mainly among males) and individuals rarely travelled together. Although the composition of social groups was polyandrous, males also copulated with non-group females which suggests a promiscuous mating system. Female-biased dispersal and patterns of male association seem to be patrilineal and based on resource defence. The evolution of social organization in the kinkajou is discussed in relation to predation risk, resource availability, and convergence with primates of similar fission–fusion socioecology.

Key words: behaviour, carnivores, kinkajou, *Potos flavus*, primate evolution, social organization

INTRODUCTION

Mammalian species are generally classified as either gregarious or solitary. Group-living species have attracted considerable attention because of their conspicuous sociality, and the details of many taxa are well known (e.g. primates: Smuts *et al.*, 1987; Lee, 1999). However, most mammals are not gregarious (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 & Kruuk, 1996). Even though this is the predominant form of social organization, little is known about the details of solitary mammalian societies (Sandell, 1989).

New research tools and methodological advances, such as improved and long-lasting radio-collars (Gehrt & Fritzell, 1998*a,b*), night vision and remote cameras (Kruuk, 1989), and hypervariable molecular genetic markers (Gompper & 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 social interactions among individuals within solitary structures (see Creel & Macdonald, 1995; Bearder, 1999). For example, based on monitoring 74 radio-collared individuals, Gehrt & Fritzell (1998*a,b*) described a social organization within raccoons *Procyon lotor* that includes three to four adult males occasionally overlapping in home range and regularly associating while resting and foraging. Other studies report unexpectedly frequent male associations in various mammal species previously thought to be exclusively solitary (Caro, 1994; Waser *et al.*, 1994; Sterling & Richard, 1995). As the complex social life of more solitary species is described, a continuum between completely solitary and classically group-living is predicted. Understanding why these species are gregarious in some situations and solitary in others has great potential to elucidate why less flexible species have evolved permanent group life.

Here, we describe behavioural attributes within the social structure of the kinkajou *Potos flavus*, a species of the order Carnivora (Procyonidae) previously thought to be a classic solitary carnivore. Due to its arboreal, nocturnal and fruit-eating nature, the kinkajou shows characteristics that have given rise to diverse forms of sociality in mammals (Eisenberg, 1981) and, indeed,

*All correspondence to: Roland W. Kays, New York State Museum, CEC 3140, Albany, NY 12230, U.S.A. E-mail: rkays@mail.nysed.gov

may reveal convergence with social organizations in primates of similar ecologies. 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 behaviour, mating patterns, and dispersal. Observed patterns of behaviour 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 the lowland forest of Parque Nacional Soberanía in the Republic of Panama (22 100 ha; 9°9'N, 79°44'W). Work was centred on the trail network of the 104-ha Limbo research plot (Robinson, Brawn & Robinson, 2000). Elevation within the plot varied from 35 to 80 m above mean sea level, and vegetation was classified as tropical moist forest. Annual rainfall was *c.* 2600 mm with 90% falling during the late April to mid December wet season (Dietrich, Windsor & Dunne, 1982). The Limbo plot consisted of a mix of forest types and was dominated by secondary growth (*c.* 60–120 years old), but also included remnant patches of tall forest (*c.* 400 years old; Karr, 1971; Foster & Brokaw, 1982). The trees along Pipeline Road, a single-lane gravel road used to access the study area, have grown tall enough to close the canopy above the road through most of the study area.

Despite regular poaching, the animal community of Limbo plot was largely intact, including top predators such as jaguar *Panthera onca* and puma *Felis concolor* (O. Moore & 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 *c.* 12 individuals/km² (R. W. Kays, pers. obs.).

The times of sunset and sunrise were measured with a light sensor (photoresistor, Conrad Electronic, Munich, calibrated for lux measurements) with a lower sensitivity threshold of about 0.2 lx mounted in the understory onto a horizontal liana stem at a height of about 1.5 m. Data were stored onsite on a Hobo logger (Onset Inc. Pocasset).

Trapping and observation

Twenty-five kinkajous were caught in 192 total captures using 50 Tomahawk live traps (32 × 32 × 102 cm). Traps were baited for 1292 trap nights with banana and hung

in trees 4–25 m above the ground using a hoistable trap design (Kays, 1999a). Newly captured animals were immobilized with a solution of 80% ketamine hydrochloride and 20% zylazine hydrochloride (0.3 cm³), and standard physical measurements were made. Ten kinkajous were fitted with radio-collars that were marked with a unique pattern of coloured 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 (including 156 h of 4 females, 169 h of 4 adult males and 54 h of 2 sub-adult males), either from when individuals left their sleeping den at dusk until midnight or from midnight until individuals entered their sleeping den at dawn. Focal animals were observed from the ground with 10 × 40 binoculars and were illuminated with a 6-V headlamp. 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 not to shine lights continuously or directly 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 behaviour. Generally, kinkajous could be seen directly while they were feeding or resting in a tree. As individuals moved through the trees, however, they could be seen only intermittently and therefore telemetry was used to follow travelling animals. In addition to direct observation, 74 (2.4% of total) nocturnal animal locations were fixed with the triangulation of telemetric bearings.

The behaviour of a focal animal was continuously recorded as feeding, resting, travelling, social or unknown. Feeding was defined as eating or actively searching a fruiting tree for food. Travelling was defined as moving between trees. An animal was classified as resting if it stopped travelling for > 1 min while not eating or being social. Social behaviour included activities that brought 2 or more animals < 1 m from each other for ≥ 1 min. Certain silent behaviours, such as grooming, resting in contact, or scent marking, were often difficult to detect when kinkajous were hidden behind vegetation. Some of these behaviours were probably missed and recorded as rest or unknown, and may be under-represented in the results.

An allogrooming bout was defined by 1 animal grooming another by licking and biting at the fur, and ended when the animals separated for > 1 min. Fights between kinkajous were designated 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)

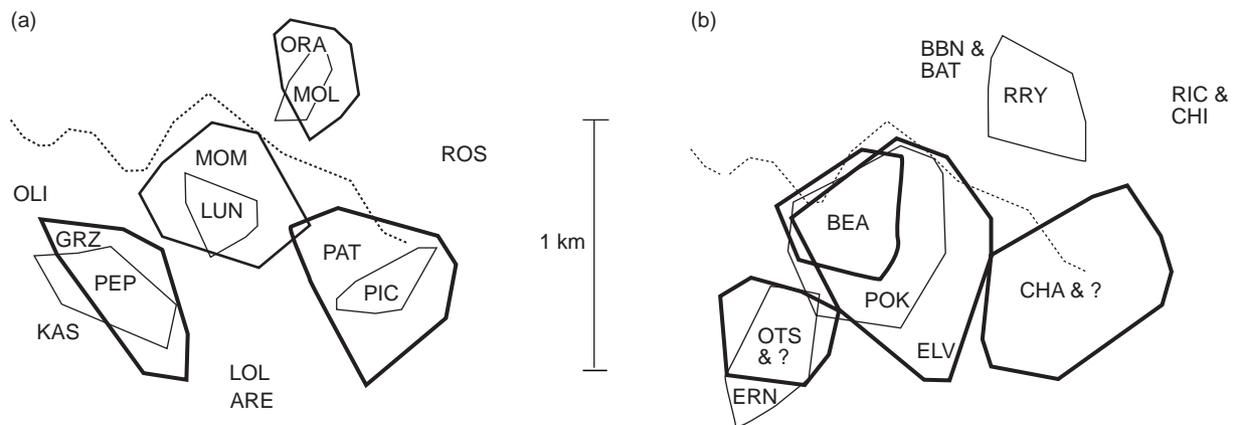


Fig. 1. Home-range boundaries (95% MCP) and general areas used for kinkajous in the Limbo plot: (a) adult females (thick lines) and their juveniles (thin lines); (b) adult males (thick lines) and sub-adult males (thin lines). Three-letter codes represent individual kinkajous (see text). Individuals outside 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 dashed line through the plot is Pipeline Road.

of the plant, and a categorical estimation of the number of fruits or flowers on the ground under the plant (< 10, < 50, < 100, < 500, < 1000, > 1000). 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 included using 95% of the data points lying closest to the arithmetic mean centre 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 & 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 non-parametric χ^2 tests.

RESULTS

Social groups and home ranges

Although kinkajous spent most of their active time alone, individuals regularly associated with others. The precise portion of time spent with another individual was difficult to assess because simultaneously moni-

toring more than one kinkajou throughout the night was not feasible. However, a general picture of the nature of their grouping behaviour can be obtained from the results on group denning, group feeding, and travelling between fruiting trees in groups (below).

Patterns of individual association were consistent in four designated groups and, throughout the study, in one intensively monitored centre group. Each group consisted of one adult female, two adult males, a sub-adult and a juvenile (Table 1). Home ranges overlapped extensively among individuals within a group but rarely or never between groups (Table 1, Fig. 1). The size of 95% MCP home ranges did not differ significantly by sex, or between adults and sub-adults (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, sub-adults = 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 & Gittleman, 1995). Although the number of fixes for juveniles were few, observed ranges were smaller than the range of adults and sub-adults, and centred in their mother's home range (Fig. 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. 2, Table 2). The core feeding areas of the two adult males of the centre group overlapped < 1 ha, whereas the female and sub-adult 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 (mean dbh inside core area = 40.5 cm, mean outside core area = 75.0, $P = 0.009$ Mann-Whitney rank sum test; no significant effect of individual $P = 0.82$, Kruskal-Wallis one-way analysis of variance on ranks).

Table 1. Group composition, weights and minimum convex polygon (MCP) home-range sizes for kinkajou *Potos flavus* on the Limbo plot. Three letter codes represent individual kinkajou (see text and Fig. 1). Overlaps are calculated with 95% MCP except for juveniles and RRY. Fixes are the number of locations used to construct the MCP. The female MAG entered centre group from east group after MOM disappeared; overlaps with both females are given for individuals in centre group with overlaps with MOM displayed above overlaps with MAG. Weight fluctuations over time were consistent for all kinkajou; this table specifies high and/or low season weight

	Weight (kg)	Home range MCP ha (fixes)		Per cent of range overlapped by:			
		100%	95%	Male 1	Male 2	Female	Sub-adult
Centre group							
Male1 ELV	Low: 3.0; high: 3.7	71.3 (539)	49.7 (107)	–	30.4	MOM 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 ^a	Low: 2.3; high: 3.6	30.3 (26)	25.7 (21)	100	42.0	– 74.5	59.9
Female MAG ^b	Low: 2.2	39.7 (326)	21.4 (88)	97.5	47.3	– 89.6	84.1
Sub-adult male POK	Low: 2.2; high: 3.0	57.5 (424)	35.0 (208)	63.6	44.7	81.5 51.4	–
Juvenile female LUN ^c	Low: 1.2; high: 1.7	6.4 (37)	–	100	38.8	100 87.2	100
East group							
Male1 CHA	Low: 2.8	54.9 (96)	40.3 (28)	–	–	61.2	–
Male2 ? ^d		–	–	–	–	–	–
Female PAT	Low: 2.4	39.4 (259)	29.4 (57)	84.0	–	–	–
Sub-adult female MAG ^b	Low: 2.2	–	–	–	–	–	–
Juvenile male PIC	Low: 1.7	5.5 (23)	–	100	–	100	–
North group							
Male1 BBN	Low: 3.2	–	–	–	–	–	–
Male2 BAT	High: 3.3	–	–	–	–	–	–
Female ORA	Low: 3.0; high: 3.1	21.0 (138)	11.3 (30)	–	–	–	51.5
Sub-adult male RRY	Low: 2.3; high: 2.8	14.2 (21)	–	–	–	40.9	–
Juvenile female MOL	Low: 1.7; high: 2.2	3.8 (24)	–	–	–	85.2	46.1
West group							
Male1 OTS	Low: 2.7; high: 3.7	24.5 (247)	16.2 (59)	–	–	–	73.9
Male2 ? ^d		–	–	–	–	–	–
Female KAS	High: 3.5	–	–	–	–	–	–
Sub-adult male ERN	Low: 2.5	26.6 (102)	14.3 (33)	65.0	–	–	–
Juvenile sex? ^d		–	–	–	–	–	–
Mosquito group ^e							
Male1 DIS	Low: 3.2	53 (210)	–	–	8.5 (4.9)	–	16.4 (9.5)
Male2 K4	Low: 3.2	–	–	–	–	–	–
Female K3	Low: 2.4	8.2 (188)	4.9 (69)	–	–	–	100
Sub-adult male K2	Low: 2.6	20.7 (168)	9.5 (75)	–	–	50.0	–
Juvenile female LOT	Low: 0.9	–	–	–	–	–	–
Between groups							
Female GRZ	Low: 2.4; high: 3.1	28.2 (237)	20.2 (59)	–	–	–	–
Juvenile PEP	Low: 1.1; high: 1.6	12.5 (61)	–	18.8	–	–	–

^a Disappeared 18 March 1996.

^b Dispersed to center group May 1996.

^c Disappeared 8 June 1996.

^d Seen, not caught.

^e Mosquito group was observed in 1993 and reported in Kays & Gittleman (1995).

Table 2. Size and overlaps of core feeding areas for kinkajous in centre group. The core feeding area is a 50% minimum convex polygon (MCP) for locations where animals fed in fruit trees. Fixes are the number of locations used to construct the MCP. Only locations obtained after the immigration of MAG into centre group are used

ID	50% MCP, ha (fixes)	Per cent 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	–

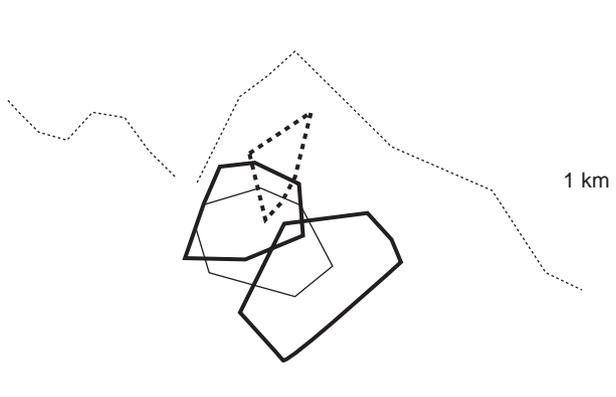


Fig. 2. Core feeding areas for the members of centre group after MAG’s immigration. The polygons were calculated by using 50% of the locations where each individual was observed feeding on a fruit tree. Thick dark polygons, adult males BEA (above) and ELV (below); dashed polygon, adult female, MAG; thin polygon, sub-adult male, POK. The irregular dashed line through the plot is Pipeline Road.

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 sub-adult males, respectively, from the west group and 15.5% or less by the males of the centre group. Her home range did not overlap with the adult female from the centre group, 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; Kays, Gittleman, & Wayne, 2000) 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 1); 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.

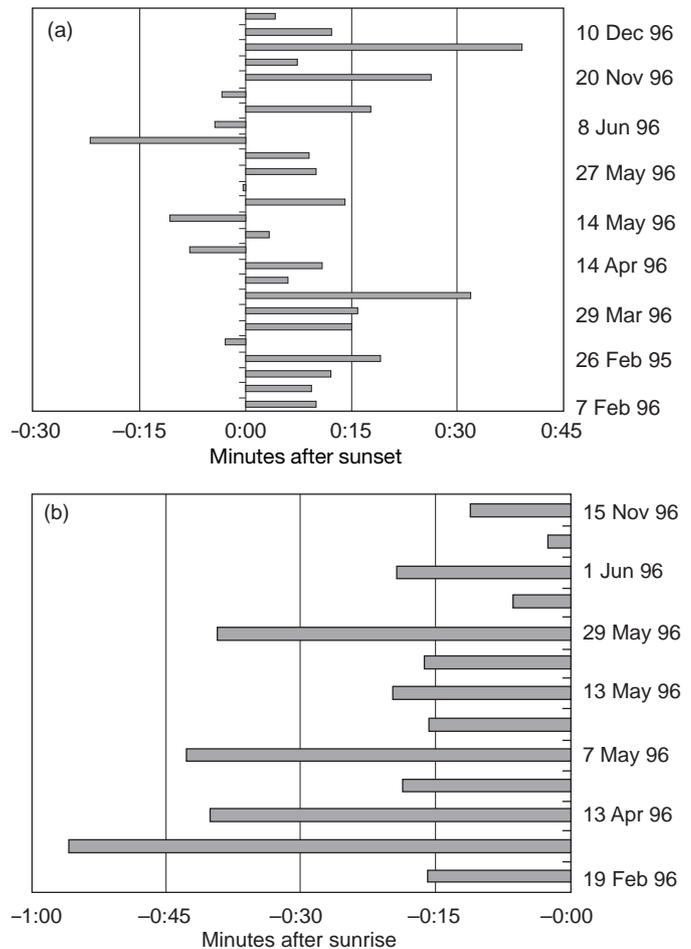


Fig. 3. The time of day that individual kinkajous: (a) exited day dens in relation to dusk; (b) entered day dens in relation to dawn.

Day dens

All kinkajous slept in dens during the day. We identified 75 den sites on 156 different occasions; 43 of these sites were directly 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. We 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 sub-adult 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

Table 3. 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 two individuals. Residuals and significance values are from non-parametric χ^2 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	-0.2	6	1.8	1	-2.1
Male-female	21	-3.1	15	-1.4	8	-4.2
Male-sub-adult	17	0	10	-1.3	14	5.6
Male-juvenile	6	-6.4	3	-5.6	2	-4.4
Female-sub-adult	11	2.8	3	-2.3	3	-0.9
Female-juvenile	11	5.1	11	7.1	9	6.1
Sub-adult-juvenile	4	1.7	3	1.7	1	0.0
χ^2 test result	$P=0.105$		$P=0.002$		$P=0.001$	
	d.f. = 6		d.f. = 6		d.f. = 6	
	$\chi^2 = 10.5$		$\chi^2 = 20.5$		$\chi^2 = 22.6$	

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 3).

Kinkajous are exclusively nocturnal, as indicated by exit and entrance times to dens (Fig. 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 & Ramos, 1972).

Although members of the centre group used at least 44 different dens, these were primarily located near the centre of their range (Fig. 4). The most used den for the centre 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 & Gittleman, 1995).

Group feeding

More than one kinkajou fed together in the crown of a fruiting tree in 30 of 153 (19.6%) observed feeding bouts. Average feeding group size was 1.24 (or 1.20 not including juveniles). Overall, males and females fed in groups of similar size (average group size: males 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 (average group size: males 1.26, females 1.09, t -test 2.17, d.f. = 171, $P=0.03$). Kinkajou groups were larger in larger feeding trees ($r=0.29$, $P<0.05$). Groups of

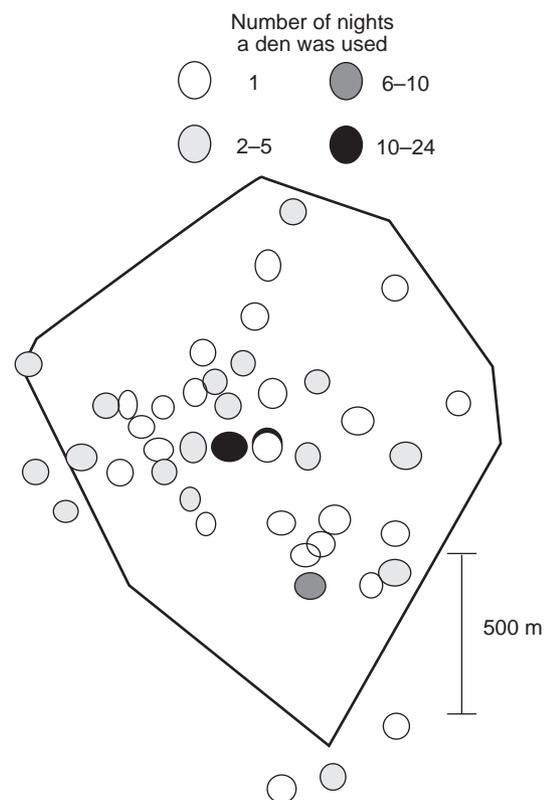


Fig. 4. Location and intensity of use of day dens by centre group. The polygon represents the 95% MCP for centre group.

kinkajous fed in 24 (35.3%) of the 68 feeding bouts in large trees (> 50 cm dbh). The three fruit species with the largest average feeding group sizes are *Ficus insipida* ($n=25$ feeding bouts), *Chrysophyllum cainito* ($n=7$), and *Hyeronima laxiflora* ($n=5$) with 1.36, 1.44 and 1.60 kinkajous per feeding bout, respectively.

Male kinkajous occasionally fed outside their normal (95% MCP) home range with unknown female kinkajous; these females were not associated with a designated social group. No kinkajous known to be associated with different social groups fed together in the same tree. Group feedings were not random for social group structure. Male-juvenile combinations

were observed much less than expected while female–juvenile combinations were much more common than expected (Table 3). Female–sub-adult, male–female and male–sub-adult combinations were all observed slightly less than expected, while male–male and sub-adult–juvenile combinations were slightly more common than expected. Even though kinkajous occasionally fed together, individuals almost never travelled in groups. Two individuals travelled together between feeding bouts in only four of the 145 consecutive bouts observed; three of these groups were mother–offspring pairs and the fourth was an adult and sub-adult 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), with the longest bout lasting 28 min between an adult male and a sub-adult male. Allogrooming was most frequent at large (> 50 cm dbh) fruiting trees ($n = 19$ grooming bouts), but also occurred in smaller fruiting trees ($n = 4$) and near day dens just after dusk ($n = 9$).

Most allogrooming was between members of the same social group and never between individuals known to be from different groups; however, centre 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–sub-adult and female–juvenile combinations were observed significantly more than expected, whereas male–female, male–male, and male–juvenile combinations were observed significantly less than expected (Table 3).

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 behaviour was observed on four occasions between a juvenile and an adult or sub-adult. Play bouts were 18, 9, 6 and 6 min long and took place in fruiting trees ($n = 2$), non-fruiting trees ($n = 1$) or next to a day den ($n = 1$). 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 on at least one occasion.

Vocalizations and scent marking

Kinkajous regularly elicit brief vocalizations (< 30 s) in social situations, especially upon first meeting another group member. The hiss and screams described in

captive animals by Poglayan-Neuwall (1962) were heard in aggressive situations. The most frequently given call was the two-part snort–weedle ('puff and bark' in Poglayan-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 with, presumably, many different functions. The snort–weedle call was given in bouts of 4 min or longer (maximum of 15 min) on 20 different occasions in nights with no observed copulations. Both adult and sub-adult 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 min on nine different occasions and CHA on five occasions. Eighty-five per cent of calls were given from non-fruiting trees and 15% from small fruiting trees. These extended vocalizations were always given by solitary kinkajous. On four occasions the vocalization bout was followed within 15 min by a meeting with other group members: three between PAT and her juvenile (PIC) and sub-adult (MAG), and one between CHA and an unknown kinkajou.

Scent marking was difficult to observe. However, nine scent marking bouts of 3 min or more were observed in adult females and adult and sub-adult males. These events involved marking a branch with the paired mandibular scent glands, the throat gland, and the abdominal gland (Poglayan-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 function 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 sub-adult 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 social groups, independent of copulations. All interactions were between the two adult males of a group, involving brief fights and aggressive vocalizations lasting 3 min or less, and did not result in detectable injury. Afterwards, one animal would remain at the fight location, presumably the winner, and the other would leave. These fights seemed 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 7 min and 10 min

by an unknown kinkajou. Both of these chases ended when GRZ jumped *c.* 8 m to the ground and climbed up another tree. On the second night, GRZ was near the border of her home range with centre group where she climbed *c.* 25 m from centre 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 behaviour

Twelve copulations were observed on four different nights; on 5 and 6 June 1996, involving the two centre 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 6 months earlier. In each copulation, the males followed an oestrous female, zigzagging over 2–5 ha in the first 4 or 5 h of the night. At between 22:09 and 23:47 the animals stopped copulating and then dispersed in different locations, presumably to feed. Each night had two to four copulations lasting from 4 to 150 min each for a total of 88–210 min of copulation.

Despite these consistent patterns, the June and November copulations were different in several ways. On 5 and 6 June, the dominant ELV was the only male to copulate with the unknown female; the subordinate 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 4 m from the copulating couple while vocalizing and inching closer. If he approached within 1 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 sub-adult male from centre group (POK) was within 25 m of most of the copulations on both nights. POK seemed excited by the activity and occasionally vocalized while rapidly climbing around the branches near the couple. However, as this sub-adult was no threat to the couple, POK was able to sniff at and rest <1 m from them with no aggression from ELV.

In contrast, during copulations in November with MAG there was no aggression between the two adult males, both males copulated, and the sub-adult did not respond to the copulations. However, the female (MAG) reacted 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 *c.* 10 m 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 seem to resist copulation with BEA as aggressively as she did with ELV.

Breeding seasonality

The size of juveniles and the lactation state of females suggest that three kinkajous were born on the Limbo plot just before the beginning of the study in August/September 1995, and two in August/September 1996. Given the 115 day gestation period for kinkajous in captivity (Poglayen-Neuwall, 1962), these five fertilizations probably occurred in May or June. One juvenile, MOL, was 0.8 kg larger than other pups in November 1995. Given neonatal weight gain similar to individuals in captivity (Poglayen-Neuwall, 1962), MOL must have been born 2 to 5 months earlier than the other juveniles, between May and July. However, MOL lost weight in the low fruit season and weighed the same as other juveniles by March.

Given this pattern of births, and the copulations observed in June and late November, kinkajous on the Limbo plot seem 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 > 1 year.

Parental care

Females were the primary provider of parental care including nursing, grooming, carrying young juveniles, and travelling slowly between feeding trees with older juveniles. Males did not provide any direct care, but did interact affiliatively with the juveniles on occasion (Tables 3 & 4). Detailed information on care to juveniles <3 months old was scant, but one mother (PAT) 'parked' her pup near or in a den while feeding on fruiting trees during the night on two occasions; she was not observed to return to the young pup during the 6 h observation period, but did carry it to a new den and nurse it upon returning at dawn. Females were never observed carrying juveniles to feeding trees. As pups grew they fed less with their mother, but regularly denned together with her or other group members.

Dispersal

One dispersal event was observed. Because the individual was radio-collared, detailed information on dispersal was documented for *c.* 1 month. Dispersal of the sub-adult female to the centre group occurred after the disappearance of MOM, the adult female of the centre group. Despite 157 trap nights and 39 half-nights of observation in her home range, MOM was never trapped or located after 18 March 1996. Before this, she had been captured 14 times, or once every 17.8 trap nights, and was frequently observed interacting with other group members at night. Therefore, it seems that she disappeared soon after this last capture.

At the time of MOM's disappearance, MAG was a sub-adult female that had been trapped and observed

Table 4. Details of the dispersal of a sub-adult female kinkajou (MAG) in 1996

Date	Observations
18 March	Adult female in centre group (MOM) last seen. MAG is a sub-adult female in neighbouring range
22–25 April	MAG was trapped three times, progressively closer to centre 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 morning, then quickly travelled further south-east to her old range and denned with her mother (PAT)
14 May	MAG had a quick quiet interaction with male from centre 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 & 22 May	MAG had excited 30 min interaction with sub-adult male from centre group (POK) near centre of MOM's old range including scent marking by POK and vocalizations by MAG
31 May	MAG foraged in the south-east portion of MOM's old range in early morning, met briefly and quietly with ELV; she travelled 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 & 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 centre group males 26 and 27 November

interacting with east group. From 22–25 April 1996, MAG was captured three times, each time progressively closer to the centre of MOM's old range (Table 4). On 25 April MAG was fitted with a radio-collar during which we 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; Kays *et al.*, 2000). In May, MAG non-aggressively interacted with an adult (ELV) and sub-adult male (POK) from centre group in MOM's old range. On 11 June MAG denned with ELV for the first time and was apparently fully integrated into the social group. MAG copulated with both centre group males on 26 and 27 November 1996. Because MOM disappeared *c.* 1 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 centre group. MOM's pup (LUN) was trapped and observed interacting with all three males from centre 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 sub-adult 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 with an injury to her hindquarters (T. Robinson, pers. comm.). No obvious dispersal behaviour was observed by the three sub-adult males (ERN, POK, and RRY).

DISCUSSION

'Solitary' is often just a default term given to a species that has been little studied. Leyhausen (1965) recognized

this: '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 some of these 'solitary' species, suggesting a continuum of sociality between strictly solitary and highly gregarious species (Caro, 1994; Waser *et al.*, 1994; Sterling & Richard, 1995). Clearly, being a predominantly solitary species does not preclude the evolution of complex social behaviours and even group living (Charles-Dominique, 1977; Bearder, 1999).

In this study, kinkajous were primarily solitary yet exhibited a social group life. Individuals regularly interacted in social groups of one female and two males. Groups were consolidated at day dens and large fruiting trees, while individuals fed singly at small trees and almost never travelled together between feeding trees. Group members overlapped extensively in home ranges but exclusively avoided areas used by other groups, suggesting 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 seemed to be female biased.

In the following, we discuss conditions associated with the solitary and grouping nature of kinkajou social organization and the different strategies of males and females within this society. We conclude by discussing the territorial and patrilineal nature of social groups and speculate about potential geographic variation in social structure.

Why be solitary?

Solitary individuals are usually more vulnerable to predation and, consequently, group living in mammals is often viewed as an adaptation to reduce predation risk (Pulliam & Caraco, 1984; Isbell, 1994). Groups confer protection from predators by active group defence, increased vigilance, and the dilution effect. Nocturn-

ality, arboreality and large body size are other adaptations that may reduce predation risk (Isbell, 1994; Hill & Dunbar, 1998). 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. By using the middle and upper canopy (Charles-Dominique *et al.*, 1981; R. W. Kays, pers. obs.), kinkajous avoid predation by large terrestrial felids. No nocturnal arboreal hunters, such as forest owls (e.g. *Pulsatrix perspicillata*) or tree climbing felids (e.g. *Leopardus wiedii*), are large enough to regularly attack an adult kinkajou. In mammals a slow reproductive rate is consistent with a low predation rate (Eisenberg, 1981). Kinkajous have a litter size of one and an interbirth interval of 1–2 years. Clearly, a population with such a low reproductive rate cannot 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 & Dunbar, 1998). Finally, the behaviour of kinkajous was not strongly affected by moonlight. This suggests that they do not perceive a high predation risk since nocturnal prey often alter their behaviour to avoid moonlight, thereby minimizing predation risk (Clarke, 1983; Daly *et al.*, 1992; Kays, 1999b).

In general, kinkajous are not highly vulnerable to predation and consistent group-living is of little benefit in this regard. In the study area, individuals typically fed alone. 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 (Symington, 1988; Wrangham, Gittleman & Chapman, 1993; Chapman, Wrangham & Chapman, 1995). 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?

Although the benefits of kinkajou social life are not immediately obvious, potential costs to sociality seem low. 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 source for kinkajous (ripe fruit) is distributed in depletive clusters that are patchy in temporal and spatial distribution (Chapman *et al.*, 1995; see also Kays, 1999c). Although such resource distribution may increase scramble competition, the costs of individuals sharing a home range may not be increased if dominant individuals can defend large areas to accommodate spatial and seasonal variation in food availability. The resource dispersion hypothesis (Carr & Macdonald, 1986; Bacon, Ball & Blackwell, 1991a,b) suggests that if

the main food of a species 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 access to fruiting trees during all seasons of the year. Thus, territory size is set not by food richness but by the spatial and temporal variability of the resource. An additional subordinate male may share a territory without negatively affecting the food availability of the breeding pair, even in the season of lowest overall food abundance.

Second, 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 where feeding competition is less important (Utami *et al.*, 1997), individuals do not travel together between feeding bouts, and other social interactions are most frequent at large feeding 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 are often related (Kays *et al.*, 2000), further decreasing the inclusive fitness costs of grouping. For kinkajous, the cost of living in a 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. 1), seems 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 (especially for males), 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 sharing a feeding area could be offset by some benefits of co-operative behaviours. Grouping at day dens may provide protection from any potential threat from diurnal predators. Allogrooming occurs between group members, and may be more common inside dens; consistent with this observation is that individuals had few ticks or other large ectoparasites (R. W. Kays, pers. obs.). We suspect the most important advantages of kinkajou group life are social factors, especially related to male territoriality. Because females lead less social lives they probably receive fewer social benefits from group life.

The sociality of females

Given the high costs of reproduction, it is widely accepted that the spatial distribution of females is

closely tied to the availability of resources (e.g. Bradbury & Vehrencamp, 1977; Emlen & Oring, 1977; Wrangham, 1980; Clutton-Brock, 1989). 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. Kinkajous follow these rules, as females respond more to fluctuations in local and seasonal food abundance than males (Kays, 1999b). Therefore, it is not surprising that female kinkajous have exclusive home ranges from other females, as this minimizes competition for fruiting trees. All adult females strictly avoided each other, and generally avoided feeding with the males of their group as well (Fig. 1, Table 3), further decreasing feeding competition. Females of other highly frugivorous species with flexible grouping patterns, such as spider monkeys *Ateles* sp. and chimpanzees *Pan paniscus*, also avoid contact with each other, presumably to minimize feeding competition or avoid infanticide (Symington, 1988; Chapman, 1990; Chapman *et al.*, 1995). Given the high energetic costs of reproduction and parental care, female kinkajous may be more sensitive to the potential costs feeding competition and therefore live solitarily more 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 seemed to be between centre 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 centre 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, Anderson & Macdonald, 1997).

Year-round association between males and females in primates has been attributed to infanticide avoidance because males of the same group offer protection to juveniles from unfamiliar males (van Schaik, 1996; van Schaik & Kappeler, 1997). However, we suspect this is not the case for kinkajous. Although females regularly associate with male members of their group throughout the year, most of their time is spent alone. Furthermore, some females (e.g. GRZ) raised a juvenile outside of a social group. Maternal behaviour does not suggest that infanticide is a risk since young juveniles are 'parked' while the mother feeds. Older juveniles spend more time feeding with their mother, but still travel and feed independently for much of the night. No aggression was observed between males and juveniles. Moreover, both adult and sub-adult males from the centre group were observed in affiliative interactions with the group juvenile, even after her mother disappeared. Finally, non-group males probably have little opportunity to harm juveniles because of the strict territoriality observed.

The sociality of males

If female mammals live in groups, males often form coalitions to reside with multiple females (Clutton-Brock, 1989). If females are asocial and live in non-overlapping territories, males may not be able to monopolize more than one female. Thus, adult males should not associate, but form a bond with a single female or range widely to overlap with as many females as possible (e.g. nocturnal Prosimians; Charles-Dominique, 1977; Bearder, 1987). 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 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 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 *Herpestes sanguineus* females have small non-overlapping territories. Stable coalitions of up to four males form and defend a large territory overlapping two or more female ranges (Rood, 1989; Waser *et al.*, 1994). Thus, it seems 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 seem 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 & Fritzell, 1998a).

In kinkajous, male coalitions were dominated by one individual (e.g. CHA and ELV in Fig. 1; K1 in Kays & Gittleman, 1995) that used an area large enough to overlap completely with one female and have occasional access to non-group females. Although the home-range size of females was not found to be statistically smaller than males, females ranges 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 behaviour of centre 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 via co-operative territorial 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 typical social unit consists of two adult males and one adult female, kinkajous may be considered socially polyandrous. However, because group males also mate with neighbouring females that are not members of any social groups, kinkajous are probably best viewed as having a promiscuous mating system.

Kinkajou territories

We suggest that kinkajou males form coalitions to mark and defend exclusive territories large enough to completely encompass the food resources used by 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 source for kinkajous, and may be crucial to females during low food abundance (Kays, 1999c).

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 designate territorial boundaries; in mammals, specialized scent glands often function for marking and defence of resource-based territories (Gosling, 1986). Although we 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 & Gittleman, 1995). Strict territorial boundaries, specialized scent marking, and aggression at large feeding trees along territorial boundaries all support the notion that male kinkajous defend resources, thereby giving them access to females using these resources. Males were observed to fight over access to females in oestrus, but these fights were only between group members, and no outside males were near these reproductive females.

Territorial defence of resources by males is also consistent with our limited dispersal data. Greenwood (1980) suggested that female biased dispersal is the rule in species with mating systems based on resource defence (i.e. most birds) and male dispersal for systems based on mate defence (i.e. most mammals). Field observations indicated that the two sub-adult female kinkajous on the Limbo plot dispersed in their second or third year, whereas none of the three sub-adult male kinkajous dispersed. Female biased dispersal in the study population is also supported by genetic data

(Kays *et al.*, 2000). Thus, territorial and dispersal data suggest that kinkajous are unusual among mammals in having a social system based on resource defence.

Kinkajou territories seem to be patrilineal; males remain in their natal group to inherit the home range or bud off to form a new neighbouring group alone or with a relative. We do not have sufficient data to show the inheritance or group formation but do have suggestive observations. 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 and son (Kays *et al.*, 2000). 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 (Tables 4 & 5).

Patrilineal groups with female dispersal are unknown in the Carnivora, but are known in spider monkeys and chimpanzees (Pusey & Packer, 1987; Waser, 1996). Interestingly, like kinkajous, these primates also have low predation risk and a diet of ripe tropical fruit (Wrangham, 1986; Nishida & Hiraiwa-Hasegawa, 1987; Robinson & Janson, 1987; Chapman, 1990), suggesting that these shared traits may have led to parallel patterns of social evolution.

Social flexibility

We have characterized kinkajou social organization as 'solitary group-life'. Social groups are comprised of two males and one female, and seem patrilineally based. Sociality within groups is flexible, similar to fission–fusion systems of *Ateles*, *Pan* and orang-utans *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 & Macdonald, 1995; van Schaik, 1999). We predict that kinkajou social organization may also be flexible over their large geographic range from Mexico to Brazil. Populations with smaller body sizes and/or in habitats with high levels of 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's home range; male coalitions may be larger or more co-operative 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.

Acknowledgements

Thanks to Instituto Nacional de Recursos Naturales Renovables (INRENARE) for allowing me to work in their beautiful National Park and to the Smithsonian Tropical Research Institute for funding and other support in Panama. Generous support was also provided by a pre-doctoral fellowship from the National Science Foundation, the Science Alliance and Department of Ecology and Evolutionary Biology at the University of Tennessee, the National Geographic Society, the American Museum of Natural History, Eagle Creek and The Sharper Image. Thanks to R. Azipure, C. Carasco, C. Foster, J. Kays, N. Kays, C. Krieger, L. Slatton, N. Smythe, D. Staden, and J. Young for help in the field. D. Robinson and T. Robinson expertly created the trail network at the Limbo research area and allowed me to work there. M. Wikelski and E. Hau provided the light meter data for the Limbo plot. M. Dean, J. Kays, S. Echternacht, G. McCracken, and R. Wrangham gave helpful comments on the manuscript.

References

- Bacon, P. J., Ball, F. & Blackwell, P. (1991a). Analysis of a model of group territoriality based on the resource dispersion hypothesis. *J. Theor. Biol.* **148**: 433–444.
- Bacon, P. J., Ball, F. & Blackwell, P. (1991b). A model for territory and group formation in a heterogeneous habitat. *J. Theor. Biol.* **148**: 445–468.
- Bearder, S. K. (1987). Lorises, bushbabies, and tarsiers: diverse societies in solitary foragers. In *Primate societies*: 11–24. Smuts, B. B., Cheney, D. D., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds). Chicago: University of Chicago Press.
- Bearder, S. K. (1999). Physical and social diversity among nocturnal primates: a new view based on long term research. *Primates* **40**: 267–282.
- Bradbury, J. W. & Vehrencamp, S. L. (1977). Social organisation and foraging in emballonurid bats. *Behav. Ecol. Sociobiol.* **2**: 1–17.
- Caro, T. M. (1994). *Cheetahs of the Serengeti plains: group living in an asocial species*. Chicago: University of Chicago Press.
- Carr, G. M. & Macdonald, D. W. (1986). The sociality of solitary forager: a model based on resource dispersion. *Anim. Behav.* **34**: 1540–1579.
- Chapman, C. A. (1990). Association patterns of spider monkeys: the influence of ecology and sex on social organization. *Behav. Ecol. Sociobiol.* **26**: 409–414.
- Chapman, C. A., Wrangham, R. W. & Chapman, L. J. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav. Ecol. Sociobiol.* **36**: 59–70.
- Charles-Dominique, P. (1977). *Ecology and behaviour of nocturnal primates: prosimians of Equatorial West Africa*. New York: Columbia University Press.
- Charles-Dominique, P., Atramentowicz, M., Charles-Dominique, M., Gérard, H., Hladik, A., Hladik, C. M. & Prévost, M. F. (1981). Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: inter-relations plantes-animaux. *Terre Vie* **35**: 341–435.
- Clarke, J. A. (1983). Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.* **13**: 205–209.
- Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proc. R. Soc. Lond. B Biol. Sci.* **236**: 339–372.
- Creel, S. & Macdonald, D. W. (1995). Sociality, group size, and reproductive suppression among carnivores. *Adv. Study Behav.* **24**: 203–257.
- Daly, M., Behrends, P. R., Wilson, M. I. & Jacobs, L. F. (1992). Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim. Behav.* **44**: 1–9.
- Dietrich, W. E., Windsor, D. M. & Dunne, T. (1982). Geology, climate, and hydrology of Barro Colorado Island. In *The ecology of a tropical forest: seasonal rhythms and long-term changes*: 21–46, Leigh, E. G., Rand, A. S. & Windsor, D. M. (Eds). Washington, DC: Smithsonian Institution Press.
- Doncaster, C. P. & Macdonald, D. W. (1997). Activity patterns and interactions of red foxes (*Vulpes vulpes*) in Oxford city. *J. Zool. (Lond.)* **241**: 73–87.
- Eisenberg, J. F. (1981). *The mammalian radiations*. Chicago: Chicago University Press.
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215–223.
- Forman, L. (1985). *Genetic variation in two procyonids: phylogenetic, ecological and social correlates*. Unpubl. PhD thesis, New York University.
- Foster, R. B. & Brokaw, N. V. L. (1982). Structure and history of the vegetation of Barro Colorado Island. In *The ecology of a tropical forest: seasonal rhythms and long-term changes*: 67–81, Leigh, E. G., Rand, A. S. & Windsor, D. M. (Eds). Washington, DC: Smithsonian Institution Press.
- Gehrt, S. D. & Fritzell, E. K. (1998a). Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. *Anim. Behav.* **55**: 1211–1227.
- Gehrt, S. D. & Fritzell, E. K. (1998b). Sexual differences in home ranges of raccoons. *J. Mammal.* **78**: 921–931.
- Gittleman, J. L. (1989). Carnivore group living: comparative trends. In *Carnivore behavior, ecology, and evolution* **1**: 183–207. Gittleman, J. L. (Ed.). Ithaca: Cornell University Press.
- Gompper, M. E. & Wayne, R. K. (1996). Genetic relatedness among individuals within carnivore societies. In *Carnivore behavior, ecology, and evolution* **2**: 429–453. Gittleman, J. L. (Ed.). Ithaca: Cornell University Press.
- Gosling, L. M. (1986). Economic consequences of scent marking in mammalian territoriality. In *Chemical signals in vertebrates* **4**: 385–395. Duvall, D., Muller-Schwarze, D. & Silverstein, R. M. (Eds). New York: Plenum Press.
- Greenwood, P. J. (1980). Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* **28**: 1140–1162.
- Hill, R. A. & Dunbar, R. I. M. (1998). An evaluation of the roles of predation rate and predation risk on selective pressures on primate grouping behavior. *Behaviour* **135**: 411–430.
- Isbell, L. A. (1994). Predation on primates: ecological patterns and evolutionary consequences. *Evol. Anthropol.* **3**: 61–71.
- Jarman, P. J. & Kruuk, H. (1996). Phylogeny and social organisation in mammals. In *Comparison of marsupial and placental behavior*: 80–101. Croft, D. B. & Ganslober, U. (Eds). Furth: Filander Verlag.
- Julien-Laferrrière, D. (1993). Radio-tracking observations on ranging and foraging patterns by kinkajous (*Potos flavus*) in French Guiana. *J. Trop. Ecol.* **9**: 19–32.
- Karr, J. R. (1971). Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.* **41**: 207–233.
- Kavanau, J. L. & Ramos, J. (1972). Twilights and onset and cessation of carnivore activity. *J. Wildl. Manage.* **36**: 653–657.
- Kays, R. W. (1999a). A hoistable arboreal mammal trap. *Wildl. Soc. Bull.* **27**: 298–300.
- Kays, R. W. (1999b). *The solitary group life of a frugivorous carnivore: ecology, behavior and genetics of kinkajous (Potos flavus)*. PhD dissertation, University of Tennessee.

- Kays, R. W. (1999c). Food preferences of kinkajous (*Potos flavus*): a frugivorous carnivore. *J. Mammal.* **80**: 589–599.
- Kays, R. W. & Gittleman, J. L. (1995). Home-range size and social behavior of kinkajous (*Potos flavus*) in the Republic of Panamá. *Biotropica* **27**: 530–534.
- Kays, R. W., Gittleman, J. L. & Wayne, R. K. (2000). Micro-satellite analysis of kinkajou social organization. *Mol. Ecol.* **9**: 743–751.
- Kruuk, H. (1989). *The social badger*. Oxford: Oxford University Press.
- Lee, P. C. (1999) *Comparative primate socioecology*. Cambridge: Cambridge University Press.
- Leyhausen, P. (1965). The communal social organisation of solitary mammals. *Symp. zool. Soc. Lond.* No. 14: 249–263.
- Lott, D. F. (1991). *Intraspecific variation in the social systems of wild vertebrates*. Cambridge: Cambridge University Press.
- Moher, C. O. (1947). Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37**: 223–249.
- Nishida, T. & Hiraiwa-Hasegawa, M. (1987). Chimpanzees and bonobos: cooperative relationships among males. In *Primate societies*: 165–178. Smuts, B. B., Cheney, D. D., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds) Chicago: University of Chicago Press.
- Poglayen-Neuwall, I. (1962). Beiträge zu einem ethogram des Wickelbären (*Potos flavus* Schreber) *Z. Säugetierkd.* **27**: 1–44.
- Poglayen-Neuwall, I. (1966). On the marking behavior of the kinkajou (*Potos flavus* Schreber). *Zoologica* **51**: 137–141.
- Pulliam, H. R. & Caraco, T. (1984). Living in groups: is there an optimal group size? In *Behavioural ecology: an evolutionary approach*: 122–147. 2nd edn. Krebs, J. R. & Davies, N. B. (Eds). Sunderland: Sinauer Press.
- Pusey, A. E. & Packer C. (1987). Dispersal and philopatry. In *Primate societies*: 250–266. Smuts, B. B., Cheney, D. D., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds). Chicago: University of Chicago Press.
- Robinson, J. G. & Janson, C. H. (1987). Capuchins, squirrel monkeys, and atelines: socioecological convergence with Old World primates. In *Primate societies*: 69–82. Smuts, B. B., Cheney, D. D., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds). Chicago: University of Chicago Press.
- Robinson, W. D., Brawn, J. D. & Robinson, S. K. (2000). Structure of a forest bird community in Panama: effects of spatial scale and biogeographic history. *Ecol. Monogr.* **70**: 209–235.
- Rood, J. P. (1989). Male associations in a solitary mongoose. *Anim. Behav.* **38**: 725–728.
- Sandell, M. (1989). The mating tactics and spacing patterns of solitary carnivores. In *Carnivore behavior, ecology, and evolution* **1**: 164–182. Gittleman, J. L. (Ed.). Ithaca: Cornell University Press.
- Smuts, B. B., Cheney, D. D., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (1987). *Primate societies*. Chicago: University of Chicago Press.
- Sterling, E. J. & Richard, A. F. (1995). Social organization in the aye-aye (*Daubentonia madagascariensis*) and the perceived distinctness of nocturnal primates. In *Creatures of the dark: the nocturnal prosimians*: 439–451. Alterman, L., Izard, M. K. & Doyle, G. A. (Eds). New York: Plenum Press.
- Stewart, P. D., Anderson, C. & Macdonald, D. W. (1997). A mechanism for passive range exclusion: evidence from the European badger (*Meles meles*). *J. Theor. Biol.* **184**: 279–289.
- Symington, M. M. (1988). Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour* **105**: 117–134.
- Todd, I. A. (1995). *WILDTRAK II: the integrated approach to home range analysis*. Oxford: Oxford University.
- Utami, S. S., Wich, S. A., Sterck, E. H. M. & van Hooff J. A. R. A. M. (1997). Food competition between wild orangutans in large fig trees. *Int. J. Primatol.* **18**: 909–926.
- van Schaik, C. P. (1996). Social evolution in primates: the role of ecological factors and male behavior. In *Evolution of social behavior patterns in primates and man*: 9–31. Runciman, W. G. & Maynard Smith, J. (Eds) Oxford: Oxford University Press.
- van Schaik, C. P. (1999). The socioecology of fission–fusion sociality in orangutans. *Primates*. **40**: 69–86.
- van Schaik, C. P. & Kappeler, P. M. (1997). Infanticide risk and the evolution of male–female association in primates. *Proc. R. Soc. Lond. B Biol. Sci.* **264**: 1687–1694.
- Waser, P. M. (1996). Patterns and consequences of dispersal in gregarious carnivores. In *Carnivore behavior, ecology, and evolution* **2**: 267–295. Gittleman, J. L. (Ed.). Ithaca: Cornell University Press.
- Waser, P. M., Keane, B., Creel, S. R., Elliott, L. F. & Minchella, D. J. (1994). Possible male coalitions in a solitary mongoose. *Anim. Behav.* **47**: 284–294.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour* **75**: 262–297.
- Wrangham, R. W. (1986). Ecology and social relationships in two species of chimpanzee. In *Ecological aspects of social evolution: birds and mammals*: 352–378. Rubenstein, D. I. & Wrangham, R. W. (Eds). Princeton: Princeton University Press.
- Wrangham, R. W., Gittleman, J. L. & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav. Ecol. Sociobiol.* **32**: 199–209.