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Microsatellite analysis of kinkajou social organization

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Abstract

Kinkajou social groups generally consist of one adult female, two males, one subadult and one juvenile. Based on analysis of variation in 11 microsatellite loci, we assess the degree of kinship within and between four social groups totaling 25 kinkajous. We use exclusion and likelihood analyses to assign parents for seven of the eight offspring sampled, five with ≥ 95% certainty, and two with ≥ 80% certainty. Five of six identified sires of group offspring came from the same social group as the mother and pup. Adult males and females within a group were unrelated and subadults and juveniles were offspring of the group adults, suggesting a family structure. All five identified paternities within a social group were by the dominant male of the group. However, this copulation asymmetry does not necessarily reflect cooperation due to kinship ties between the two adult males within a group as one of two adult male pairs sampled was unrelated. Neighbouring male kinkajous were more closely related to each other than neighbouring female kinkajous, suggesting that females disperse more often or farther than males.

Keywords: Carnivora, dispersal, paternity, patrilineal, *Potos*, relatedness

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Introduction

Although most mammal species are considered solitary (Eisenberg 1981) the social organization of gregarious species has attracted more scientific attention (Sandell 1989; Packer *et al.* 1991; Girman *et al.* 1997; De Ruiter & Geffen 1998; Gompper *et al.* 1998; Surridge *et al.* 1999). However, solitary species have been studied with modern field and genetic techniques and some have in fact been found to be social and to 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 & Fritzell 1998a,b) and slender mongooses (*Herpestes sanguineus*, Rood 1989; Waser *et al.* 1994) found males associating in stable and non-agressive groups of three to four individuals. Genetic fingerprinting of slender mongooses showed that no single group male monopolized access to females and that group members can be related or unrelated (Waser *et al.* 1994). Thus, a continuum of sociality may exist between exclusively solitary and social species. Molecular genetic techniques are powerful tools to describe this continuum because they provide essential details about relatedness, parentage, and dispersal patterns.

The kinkajou (*Potos flavus*) is a medium sized (2.0–3.5 kg), nocturnal, arboreal, mammal related to raccoons and coatis. They are mostly frugivorous, and are a common species in Neotropical forests (Kays 1999a,b). Previously, kinkajous were thought to be solitary and asocial (Poglayen-Neuwall 1962, 1976; Ford & Hoffmann 1988). Recent observations on 25 habituated, free ranging, kinkajous in central Panama confirmed their mostly solitary nature, but revealed surprising sociality (Kays & Gittleman 1995; Kays 1999b). Although kinkajous travelled and fed in small trees alone, they regularly congregated in groups of two to five while feeding in large fruit trees and slept together in day dens. This behaviour is similar to the fission-fusion social systems of some primates (Wrangham 1986; Chapman 1990; Van Schaik 1999). Membership of kinkajou social groups consistently included two adult males, one adult female, one subadult, and one juvenile, suggesting they may be family groups (Fig. 1). Some females raised offspring outside of this group structure (e.g. GRZ in Fig. 1), and had ranges that overlapped slightly with those of neighbouring group

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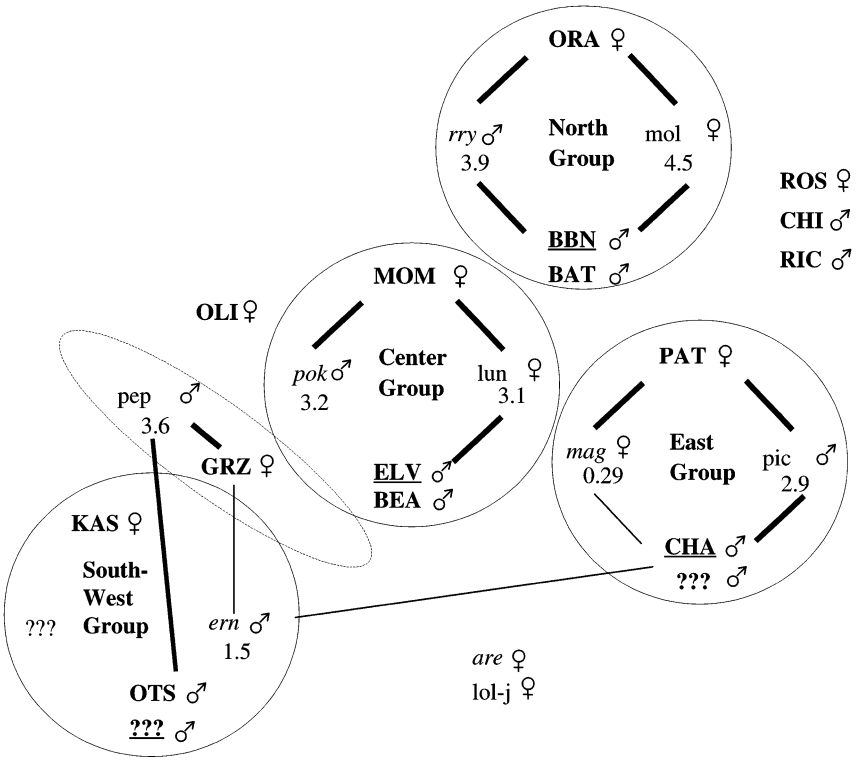

Fig. 1 Schematic of social group structure and genetic parentage for kinkajous in the Limbo plot. Three letter codes are marked kinkajous. Capitals refer to adults, lowercase refers to subadults (italics) or juveniles. Question marks indicate individuals that were observed but never captured. Circles represent approximate group home range boundaries and are not to scale. The dashed circle represents the home range of a female and her pup that bordered two groups, but they did not associate with a social group. Individuals outside of circles were not radio-collared and could not be assigned to a group or home range. Underlined males were dominant in their group. Thick lines show parentage at 95% confidence level and thin lines show parentage at 80% confidence levels. Numbers below offspring labels are LOD scores.

males. The coalition of two males is likely cooperate to mark and defend a territory that is large enough to completely overlap with one group female, and partially overlap with neighbouring nongroup females (Kays & Gittleman, in press).

One explanation for this family group structure is that both adult males share reproduction with the group female and that subadults are young from previous years. This hypothesis predicts that juveniles and subadults will share a common mother but may have different fathers within the groups. In previous studies of reproductive sharing in carnivores, male coalitions between related individuals mated asymmetrically, whereas unrelated males shared females equivalently (Packer *et al*. 1991; Caro 1994). Subordinate males accrue indirect fitness benefits if they are related to the dominant reproductive male, and therefore have less incentive to reproduce themselves. Coalitions of unrelated males must share females more equally to receive fitness benefits from group living. Preliminary behaviour data on reproductive sharing in pairs of kinkajous suggests a single male is dominant and obtains most copulations (Kays & Gittleman, in press). This observation predicts that the dominant male will obtain the majority of fertilizations and that the subordinate male may remain within the group because he receives indirect fitness benefits through relatedness to the dominant male or though future inheritance of the group territory.

In this report we test these genetic predictions through analysis of paternity and relatedness in 25 kinkajous that define four social groups in Parque National Soberanía in the Republic of Panamá. This population was the subject of a previous telemetry study (Kays 1999b), hence behavioural observations can be compared directly with patterns of genetic kinship. Our results confirm expectations based on observations of behaviour and dispersal between kinkajou social groups.

Materials and Methods

Study site and animals

Field research was conducted in lowland forest of Parque National Soberanía in the Republic of Panamá (22100 ha; 9°9′ 35′ N, 79°44′ 36′ W). Work was centred around the trail network of the 104 ha Limbo research plot (Robinson *et al*., in press). Elevation within the plot varies from 35 to 80 m above sea level and 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/km^2 (R. W. Kays, unpublished data).

Twenty-five kinkajous were captured 192 times with 50 large ($32 \times 32 \times 102$ cm) Tomahawk live traps (Kays 1999c). Previous telemetry observation established that

these kinkajous lived in four social groups (Fig. 1, Kays & Gittleman, in press). Individuals were classified as juveniles (< 1 years), subadults (1–2 years), or adults (> 2 years) by body mass and tooth wear. The composition of each social group consistently included two adult males, one adult female, one subadult, and one juvenile. Not all individuals lived in a social group (e.g. GRZ). Captured animals were immobilized with 0.3 cc of a solution of 80% Ketamine hydrochloride and 20% Zylazine hydrochloride. A 3-ml blood sample was drawn from the femoral vein, and a small (< 1 cm^2) clip of tissue was taken from the ear of each animal to mark them permanently. 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.

Microsatellite techniques

Microsatellite primers were developed with DNA extracted from kinkajou blood samples by proteinase K digestion followed by DNA isolation with phenol/chloroform/isoamyl alcohol (Sambrook *et al*. 1989). Fragments in the size range of approximately 350–700 bp were isolated from the gel and adapted with oligonucleotides that simultaneously provided a *Hin*dIII restriction site and a template for PCR amplification. The mixture of adapted fragments was subjected to a magnetic bead capture procedure developed at Genetic Identification Services (Chatsworth, California) designed to enrich fragments containing microsatellite motifs. The captured fragments were ligated into the *Hin*dIII cloning site of plasmid pUC19, and the ligation products electroporated into *Escherichia coli* DH5′. Recombinant plasmid-containing cells were identified by standard blue–white selection and white colonies were subcloned. Sequencing chemistry was performed using dye-labelled chain terminators, and the fragments were separated on an ABI Model 373 automated sequencer. Thirty clones were sequenced. We designed PCR primer pairs for 13 microsatellite sequences using DESIGNER PCR, version 1.03 (Research Genetics, Huntsville, AL), of which 11 gave useful results (Table 1). Seventeen of the sequenced clones were not used because one was a repeat, four had small microsatellites, five had no microsatellites, and seven had microsatellites positioned too close to the beginning or end of the repeat sequence to design primers.

The 11 microsatellite loci that gave useful results were used to characterize a population of 25 kinkajous living within a 2-km^2 area as well as individuals of 12 other members of the Carnivora, including nine procyonids, two mustelids, and one ursid (Table 2). Microsatellite alleles were amplified from genomic DNA by PCR in which one primer was end-labelled with a 32 gamma-ATP (Amersham) in a T4 polynucleotide kinase reaction (Sambrook *et al*. 1989). PCR was carried out in a 25-mL reaction volume using 20 pmol of each primer, 50 ng of target DNA, 2 mM $MgCl_2$, and 0.8 U of Taq DNA polymerase (Promega). Twenty-eight cycles were run with the following reaction conditions: 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. Three μL of each product was mixed with 2 μL of formamide loading dye, heated to 94 °C for 5 min, and then loaded onto a 6% sequencing gel containing 50% (w/v) urea. A M13 control region was run adjacent to the samples to provide an absolute size marker for the microsatellite alleles. Gels were dried onto Whattman paper and autoradiographed overnight.

Statistical analyses

We used the Queller & Goodnight (1989) index of relatedness (R) calculated by the computer program RELATEDNESS 5.0 (Goodnight 1998) to estimate kinship of Limbo plot kinkajous. Relatedness values can vary from –1 to 1, and in populations at Hardy–Weinberg equilibrium the values for parent–offspring or full sibling relationships should approach 0.5. The standard deviation of relatedness values were estimated by jackknifing over all loci (Queller & 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. This procedure was repeated until all loci were sampled. The difference between consecutive samplings was expressed as a function of the total number of loci drawn. 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.

The mean relatedness of male and female kinkajous was evaluated with a two-sample randomization test (De Ruiter & Geffen 1998; Surridge *et al*. 1999), using the program RT 2.0 (Manly 1991). In this test, the observed mean difference was compared with the means of 5000 random samplings of the same set of relatedness values.

The probability of paternity exclusion for the population was calculated following Chakraborty *et al*. (1988) and Chakravarti & Li (1983). However, these calculations assume close relatives are not putative parents more frequently than expected at random, an assumption that may not be valid for our study population. To account for this we followed Double *et al*. (1997) and also calculated the probability of excluding a first-order relative. For this calculation we used a lower relatedness value (0.39) than the theoretical first-order relationship (0.5) because this

Table 1 Sequences for 11 microsatellite loci, their observed (H_O) and expected (H_E) heterozygosity, and the number of alleles in a population of 25 kinkajous. *P*-values indicate the significance of deviations from Hardy–Weinberg equilibrium (probability test, Raymond & Rousset 1995)

Locus	Primer sequences 5′–3′	Core repeats	Annealing temp °C	Allele size range (bp)	No. of alleles	Frequencies	H_O	H_E	*P*-value
Pfl1	F-CATGCCAGAGTTTGAGTGACAGAAG								
	R-CATTGTGGCTTCCCGTTCTTG	$(GA)_{10}$	55	179–187	4	0.72, 0.20, 0.06, 0.02	0.48	0.45	*n*.s.
Pfl2	F-TTCTTAGACGGTGACTCTGCTCCC								
	R-AACGAAGGCATAGCCACATCCG	$(AC)_{16}$	53	202–206	3	0.68, 0.22, 0.10	0.52	0.49	*n*.s.
Pfl3	F-AGGTTTGGTGAGCATCCAC								
	R-TGGACGCATACACATAAGTG	$(TG^*)_{20}$	53	156–158	2	0.80, 0.20	0.32	0.33	*n*.s.
Pfl4	F-AGGGAATGTTGCTTCTAATCC								
	R-GCAGCCAAACAAACTAAAGTCC	$(CA)_{12},(AT)_5$	51	173–185	5	0.70, 0.13, 0.09,	0.57	0.50	*n*.s.
Pfl5	F-CAGAAGAGAAATCTGATCCTGGCAG					0.06, 0.02			
	R-CCTTGTGGGAAAGACTGTCAAAGG	$(GA^*)_{13}$	55	183–195	2	0.86, 0.14	0.20	0.25	*n*.s.
Pfl6	F-TCCACTTTGCAGGACTGCTG								
	R-CCACCCTGACCAAGAGAAATGAG	$(TG^*)_{17},(TA)_4$	54	149–153	3	0.65, 0.29, 0.06	0.46	0.50	*n*.s.
Pfl7	F-TTTGGCTCAGGTCAGGATC								
	R-GAATTGAACTGGGTAAGATCAC	$(CT)_3,(CT)_{15}$	52	186–200	5	0.76, 0.11, 0.07,	0.48	0.41	*n*.s.
Pfl8	F-GCATCCAGGGGAGCCTAG					0.04, 0.02			
	R-CATGCACATGAGTGCGAGGC	$(CT^*)_{15}$	56	185–195	3	0.68, 0.28, 0.04	0.32	0.47	< 0.05
Pfl9	F-GCCTTCATTTAGTTGAGGTCAG								
	R-GCATTCTGTCAGTGGCTTTCAC	$(GT^*)_{22}$	52	223–239	7	0.32, 0.18, 0.16, 0.10,	0.96	0.83	*n*.s.
Pfl10	F-CCACAATGCTCAGATGAACAAGG					0.10, 0.08, 0.06			
	R-ATCTCACAGCTTACAGCGAGGGAG	$(CA)_4,(TC)_{15},(CT)_7,(CT^*)_7$	53	234–236	2	0.64, 0.36	0.62	0.47	*n*.s.
Pfl11	F-CATGCAAATAACACGCAC								
	R-CTGAACAAGGTAGGAAAGTCACTC	$(CA)_3,(CA^*)_{37}$	55	182–186	2	0.96, 0.04	0.08	0.078	*n*.s.

*Imperfect repeats. *ns*, not significant.

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Table 2 The number of alleles scored for 11 microsatellite loci in 13 carnivore species. Numbers in parentheses indicate sample size if different than column two. Absence of microsatellite amplification is indicated by 'x'. Samples not surveyed for a loci are indicated with '—'. Species with more than two bands and low sample sizes could not be accurately scored and are indicated with '*'. Weak bands are indicated with 'w'

Species	Sample size and origin	Pfl1	Pfl2	Pfl3	Pfl4	Pfl5	Pfl6	Pfl7	Pfl8	Pfl9	Pfl10	Pfl11
Procyonidae												
Ailurus fulgens	3 zoo	1	1	1	x	2	x	x	1 w	1	x	x
Bassariscus astutus	1 Nevada, 1 New Mexico	1	1 (1)	x	3 w	1	1	x	1	3	x	1
Bassariscus sumichrasti	1 Mexico	1	1	2	*	1	1	2	x	2	x	2
Bassaricyon gabbii	5 Panama	1 w	4	1 w	2 w	2	2	2	x	3	x	4
Nasua narica	4 Panama, 7 zoo, 1 Arizona	1	5	6	4	1	1	1	2	6	1	2 w
Nasua nasua	1 Bolivia	1	2	2	1	1	1	1	2	2	x	x
Nasuella olivacea	1 Colombia	1	1	2	x	1	1	1	x	2	x	x
Procyon cancrivorus	1 Bolivia, 1 Uruguay	1	1 (1)	x	1	1	1	x	x	3	x	2
Procyon lotor	5 Tennessee	1	1	1	9	1	1	1	1 w	7	x	5
Potos flavus	25 Panama	5	3	2	5 w	3	5	5	3	7	2	2
Other Carnivores												
Martes americana	2 Wyoming	2	—	*	2	1	1	1	1 w	*	x	*
Spilogale putorius	1 California	*	—	*	x	1	2 w	1	x	1	x	1
Ursus americana	1 Montana	*	—	*	x	1	1 w	x	x	x	x	x

was the relatedness value observed between first order relatives in the study population (see below).

In addition to deducing parentage through exclusion, we used the likelihood method (Thompson 1976; Meagher 1986) as implemented in the program CERVUS 1.0 (Marshall *et al*. 1998). Paternity for each adult male/offspring combination was estimated from the ratio of the likelihood that the mother and putative father were the parents relative to that of a randomly chosen individual from the population. Likelihood ratios for each male at each locus and the LOD score, defined as the natural logarithm of the product of ratios across all loci were calculated (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 (ΔLOD) was used to quantify the certainty of each assignment with CERVUS 1.0 (Marshall *et al*. 1998). CERVUS predicts critical ΔLOD 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: (i) total number of candidate males (10); (ii) proportion of candidate males sampled (0.80); (iii) proportion of missing genotypes (0.03); (iv) rate of typing errors (0.005); and (v) confidence levels (80% and 95%). We assessed the LOD scores for all adult/subadult combinations to determine if the most likely parents were within the social group.

Genotype frequencies were tested against expected Hardy–Weinberg equilibrium values with a probability test as implemented in the program GENEPOP 3.1 (Raymond & Rousset 1995). GENEPOP 3.1 also was used to test for genotypic disequilibrium between each pair of loci using a Fisher exact test.

Results

Exclusion and likelihood analyses allowed both parents to be assigned for seven of the eight offspring sampled (Fig. 1). 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. The paternity exclusion probability across all loci was 0.96 for randomly chosen males and 0.82 for first-order relatives. The ΔLOD with 80% and 95% levels of certainty was 0.01 and 1.82 if one parent was known, and 0.72 and 2.26 if no parents were known, respectively. Paternity was assigned to five offspring with ≥ 95% certainty, and to two offspring with ≥ 80% certainty (Fig. 1). The sire of subadult offspring *pok* remains unknown, although his mother was confirmed with ≥ 95% certainty.

Five of six identified paternities of group offspring came from the same social group as the mother and pup (three juveniles and two subadults, Fig. 1). Subadult *ern* from the south-west group was in a social group that did not include his genetic mother or father. GRZ, an adult female that did not associate with a group, was *ern's* probable genetic mother and CHA, his probable genetic father, was the dominant male of the East group. The adult male, OTS, with whom *ern* shared a group territory was excluded as his sire by one allele. The LOD certainty values for both parents of *ern* was at the 80% level and, therefore, these relationships should be viewed with

caution. The adult female from the centre group, MOM, was confirmed to be the mother of *pok* with ≥ 95% certainty. However, a father for *pok* could not be identified and was unlikely sampled as all candidate males were excluded by at least one locus. *Pok* was conceived before our field study began and his genetic father may have disappeared before trapping began. The juvenile, pep, was raised outside of the typical group structure. Log likelihood analyses confirm with ≥ 95% certainty that pep was being raised by his genetic mother, GRZ. His sire was an adult male (OTS) from the neighbouring South-west group, an individual with whom pep occasionally associated (Kays & Gittleman, in press).

Due to the fact that kinkajous have no more than one offspring per year, it is difficult to evaluate the extent to which dominant males monopolize fertilizations. However, the genetic analysis of subadults that may be offspring of previous years adds support for reproductive dominance by a single male. All five group offspring were sired by the dominant male of each group (Fig. 1). In East and North groups, both the juvenile and subadult were sired by the dominant male. The dominant male of Center group, ELV, was the sire of the juvenile, but not the subadult (*po*k) of his group. However, as mentioned above, *pok* was conceived before our field study began, when group membership and dominance relationships may have been different.

Relatedness

Average heterozygosity across the 11 loci was 0.46 and ranged from 0.08 to 0.96 (Table 1). In the kinkajou population the average number of alleles per locus was 3.45 and ranged from 2 to 7. The number of loci that amplified in the other carnivore taxa generally decreased with increasing genetic distance (Table 2) (Wayne *et al*. 1989). All loci were in genotypic disequilibrium and all but one did not deviate significantly from Hardy–Weinberg equilibrium ($P < 0.05$, Fisher's exact test and Probability test, respectively). One locus, Pfl8, marginally deviated from Hardy–Weinberg equilibrium ($P = 0.013$) and was found to be heterozygote deficient ($P = 0.0057$, probability test, Raymond & Rousset 1995). Rarefaction analysis showed that relatedness estimates changed by less than one per cent after seven loci were sampled (Girman *et al*. 1997). Therefore, the inclusion of more than the 11 loci used in this study would not have significantly changed the relatedness estimates.

To assess the accuracy of Queller–Goodnight *R*-values in estimating relatedness between individuals of unknown relationship, we calculated average *R*-values for pairs of known relationship (Fig. 2). Pairs with a predicted relatedness of 0.50 (father-offspring, mother-offspring, or full siblings) were identified based on the parentage

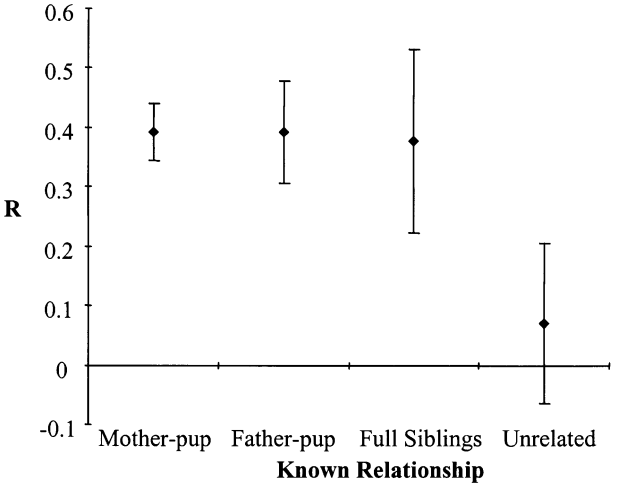

Fig. 2 Relatedness values for known relationships among kinkajous of the Limbo plot.

analyses. Seven father-offspring pairs had an average Queller–Goodnight relatedness of 0.39 ± 0.09, eight mother-offspring pairs averaged 0.39 ± 0.05, and two full sibling pairs averaged 0.38 ± 0.16. These relatedness estimates are consistently 0.11–0.12 lower than the predicted value. This underestimate probably reflects an over-representation of close relatives in our study population. Although this sampling bias causes the relatedness estimates to be lower than predicted, it should not negate their use for deducing relatedness when comparing individuals from the same population (see De Ruiter & Geffen 1998).

Pairwise relatedness values were used to evaluate the relationships between classes of individuals within groups. Five of the six within group adult male–adult female pairs were unrelated (−0.55, −0.31, −0.26, −0.11, −0.03, 0.47; mean = −0.13 ± 0.15). Relatedness between OTS and KAS, an adult male–adult female pair from the South group was 0.47. However the significance of this result should be interpreted with caution, because KAS was not captured until the end of the study, was not radio-collared, and may not have been the resident adult female of South-west group. Two within group adult male–male pairs were sampled. A pair from North group had a low value of relatedness of −0.06, whereas the Centre group pair had a relatedness value of 0.49. Therefore, within a group same sexed adults were not consistently related.

Finally, adult male kinkajous on the Limbo plot were more closely related to each other than adult female kinkajous. The average value of relatedness between males of 0.118 ± 0.25 was significantly greater than the value of −0.02 ± 0.31 between females ($P < 0.05$, two-sample randomization test, Manly 1991). This suggests that females disperse more often or farther than males.

Discussion

Social groups as families

Kinkajou social groups contained two adult males and one adult female. Both males were observed to copulate with the group female (Kays & Gittleman, in press), and therefore we expected that they would be unrelated to her. With one exception, genetic data support this expectation as average relatedness of five adult male and female within group pairs was -0.13 ± 0.15. Behavioural observations showed that juveniles and subadults maintained strong social bonds with group adults (e.g. denning, eating, playing and grooming together; Kays 1999b). Sociality and cooperation is common between subadults and juveniles siblings in some carnivore social groups (e.g. Moehlman 1986). Furthermore, we 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 (Kays 1999b). These expectations were supported by the genetic data because parents of group offspring were living in the same social group (Fig. 1).

Five out of eight offspring had both parents within their natal group. 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 we thoroughly sampled the kinkajou groups in the area, we suspect that his sire had left the study area after conception. For subadult *ern*, the 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* may have moved out of his natal range to associate with a neighbouring adult male in a social group.

GRZ also was observed caring for the juvenile, pep, which was confirmed to be her offspring in the parentage analyses. On three occasions the juvenile interacted (denned, ate, groomed, and played) with the adult male, OTS, from the neighbouring South-west group (Kays 1999b). 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 and an early social bond between male kinkajous.

Male coalitions

Although the two adult males of a kinkajou social group generally had neutral or affiliative interactions, they occasionally fought, revealing clear dominance relationships (Kays & Gittleman, in press). One male consistently dominated these fights, and with one exception, was the partner in the 12 observed copulations. The genetic data show that dominant males were responsible for all fertilizations within North and East groups, and perhaps Center group (Fig. 1). The dominant male of Center group, ELV, was the sire of the group juvenile, but not the group subadult (*pok*). No sire could be identified for *pok*, suggesting that the true father had disappeared from the study site before our field work began. The paternity of the subadult *ern* is complicated because he was apparently born outside of a social group to the nongroup female GRZ (Fig. 1). The dominant male of East group, CHA, was the most likely sire of *ern* (80% probability). Although the sample sizes are small, this suggests that reproduction is not shared evenly between the two males in a kinkajou social group. Other male carnivore coalitions appear to have more equitable sharing of mating opportunities (Caro 1994), and fertilizations (Packer *et al*. 1991; Waser *et al*. 1994). Sharing of mating opportunities by a dominant individual encourages the subordinate to remain in the group. Subordinate male kinkajous may associate with a dominant male for a chance at rare mating opportunities with the group female, and the possibility of achieving dominant status in the future.

Of the two male coalitions that were sampled, one showed high relatedness, and the other low. Male coalitions in other carnivore species tend to be close relatives, but also can include nonrelatives (Packer *et al*. 1991; Caro 1994). 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 form groups. Our results suggest that kinship alone may not explain asymmetry in mating of carnivore male coalitions (e.g. Packer *et al*. 1991; Caro 1994).

Dispersal

None of the three subadult males dispersed during the study. One of the two subadult females, East group's *mag*, dispersed to a neighbouring group to become the reproductive female. The second subadult female, *are*, may also have dispersed as she was observed 400 m away from her normal range soon after the end of our field study (T. Robinson, personal communication). This very limited field data suggesting a female dispersal bias is supported by the genetic data. Female kinkajous were less related to female neighbours than were male kinkajous to male neighbours. Therefore, females must be moving farther or more often from their natal group. Female-biased dispersal is unusual in mammal systems, and is not known from other carnivore species (Greenwood 1980; Fuller *et al*. 1992; McNutt 1996; Waser 1996). Thus, kinkajous appear to be unusual among mammals in having female biased dispersal, which may

be based on resource defense rather than mate defense (Greenwood 1980; Kays 1999b). Female biased dispersal also supports the hypothesis that kinkajous groups are patrilineal (Kays 1999b), with young males inheriting the natal territory and females dispersing to a new social group.

Two other mammals with female biased dispersal are also very similar to kinkajous ecologically. Spider monkeys (*Ateles* sp.) and chimpanzees (*Pan* sp.) both live in large communities in which females separate into small feeding groups and males associate in larger coalitions (Pusey & Packer 1987; Robinson & Janson 1987; Symington 1987). Although these primate social communities are much larger and more social than kinkajou groups, their fission-fusion grouping pattern, male-male sociality, female biased dispersal, and patrilineal groups are similar to behaviours we observed in kinkajous. Important ecological traits shared between kinkajous, chimpanzees, and spider monkeys include low predation risk, flexible foraging group size, and a diet consisting primarily of ripe tropical fruit (Symington 1987; Chapman 1990; Chapman *et al*. 1995; Kays 1999a,b). This convergence suggests that some aspect of extreme frugivory and low predation risk in tropical forests may promote the evolution of fission-fusion grouping, female biased dispersal, and male philopatry.

In summary, kinkajous spend most of their foraging time alone, but observational and genetic methods have uncovered surprising sociality (Kays 1999b). Most animals live in groups with related individuals, including both parents and one sibling. Within a group, pairs of adult males appear to cooperate and may be related or unrelated. Dispersal appears to be female biased, suggesting that males may inherit their natal territory while females may migrate into new social groups.

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