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Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*

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Abstract. The white-nosed coati, *Nasua narica*, lives in large social groups, called bands, and displays a variety of complex cooperative behaviours. These behavioural patterns, such as coalition support, may influence the ability of an individual to gain access to limited resources and have attracted theoretical attention because they may be maintained by reciprocal altruism. To better understand the mechanisms influencing cooperation, coalition dynamics and time individuals spend away from the band, the relationship between kinship and specific social behaviours was assessed. The genetic relationships of individuals from six coati bands were estimated by measuring the similarity of multilocus DNA fingerprints. Results showed that coati bands primarily consist of highly related individuals. The variance in relatedness was high, however, and four bands contained some individuals that were unrelated to other band members. Males who monopolized access to band females during the breeding season did not sire most offspring. Unrelated individuals spent more time away from the group than did band members with close relatives in the band. Moreover, unrelated individuals received more aggression from band members and received less coalition support than did individuals with close relatives in the band.

A central focus of behavioural ecology is understanding the underlying causes for cooperative interactions between individuals, which is problematic because of at least two interacting factors. First, although genetic relatedness is well accepted to be important for explaining broad patterns of individual interactions in social groups, a variety of kinship ties may exist in social groups and lead to variability in the quality and quantity of specific behaviour patterns. Second, the benefits and costs for individuals living in social groups frequently change, both in the short and long term, so average measures of benefits and costs may not explain the interactions of particular individuals in groups.

In this study, we examined the genetic relationships of individuals from six white-nosed coati, *Nasua narica* (Procyonidae), social groups (‘bands’) and related these findings to observed patterns of interactions between individuals. The social structure of the coati is unique within the order Carnivora and consists of group-living females and solitary males (Kaufmann 1962; Gittleman 1989; Gompper 1995). The female-bonded groups may contain over 30 adult females and their immature offspring. All adult males remain solitary except during a brief (approximately 2-week) synchronous breeding season when they may temporarily join a band. Coatis are the only truly social procyonid, and bands display a variety of cooperative behaviours not found in the solitary raccoons, ringtails, olingos and kinkajous (but see Kays & Gittleman 1995). These behaviour patterns may influence the ability of an individual to gain access to limited food sources (e.g. coalition support: Gompper 1994,

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1996) and have attracted theoretical analysis because they may be maintained by reciprocal altruism (e.g. allogrooming: Russell 1979, 1983; Wilkinson 1988). The coati has also attracted interest because individuals have complex cooperative behaviours rarely observed except in primate societies (Harcourt 1989; Zabel et al. 1992), and because bands may act as a model system to understand the evolution of female-bonded societies in primates (Wrangham 1986).

We integrated results of multilocus DNA fingerprint analyses with 5 years of behavioural observations on coati group structure. First, we calibrated the relationship between DNA fingerprint similarity and known relatedness (Wright's *r*, 1922) for individuals from zoo families and wild populations. We then used fingerprint data to classify paired individuals (dyads) of unknown relationships as unrelated, slightly related, or highly related. This approach permits assessment of the variance in relatedness among individuals within bands. Analyses of the DNA fingerprints also allowed us to assess the breeding success of adult males. We tested the hypothesis that bands consist of individuals related as parent–offspring or siblings ($r=0.5$) and that paternity of offspring born to band females can be attributed to the single male that attends the band during the mating season (Kaufmann 1962; Gompper 1994). If these hypotheses are verified, then the resulting uniform high relatedness between individuals within coati bands would suggest a limited influence of kinship on social interactions.

If unrelated individuals are found within bands, however, then social interactions may differ between individuals having many within-band kinship ties and those having few or no within-band ties. Presumably, unrelated individuals should receive fewer of the benefits of group living than related individuals (Vehrencamp 1979; Emlen 1991, 1995). Therefore, we assessed the influence of relatedness on social and asocial behaviours, specifically (1) the duration of time individuals were separated from the social group, (2) directed aggression between band members and (3) support given and received in the form of coalition formation during agonistic interactions. As with most social mammals (Wrangham 1980; Clutton-Brock 1989), time spent alone is a cost for female coatis; it renders them less able to gain access to patchily distributed food (Gompper 1994, 1996) and potentially makes them more vulnerable to predation (Burger & Gochfeld 1992). The ability to form coalitions (individuals acting in concert against an opponent(s): Nöe 1986) is central to many aspects of sociality in coatis, especially the ability of individual females to access resources while foraging with directly competing band members and to access food patches controlled by solitary adult males (Gompper 1996).

METHODS

Study Site and Subjects

Field work occurred on Barro Colorado island (BCI), Panama for 23 months between August 1989 and November 1993 (August–December 1989, June–August 1990, September 1991–July 1992, September–October 1992, July 1993, November 1993). BCI (9°9′N, 79°51′W) is a 1500-ha island in Gatun lake, an artificial body of water created in 1912 by the damming of the Chagres river to create the Panama Canal. BCI is separated from the surrounding mainland by 200–1000 m, and many mammals, including coatis, have been observed swimming in the lake, so migration between the mainland and island populations may occur. The island is covered by lowland tropical moist forest (Croat 1978; see also Leigh et al. 1982; Gentry 1990).

During this study, the population density of coatis on BCI was 48.2–55.6 individuals/km^2, mean ± SD group size was 15.3 ± 6.1 individuals, and foraging group size was 7.3 ± 2.8 individuals (Gompper 1994, in press; Wright et al. 1994). Population density is high relative to most other neotropical sites studied, but variation in group size and foraging group size are similar (Gompper 1994, 1995, in press; Wright et al. 1994).

Individuals were live-trapped, anaesthetized with ketamine hydrochloride (0.1 ml/kg) and marked with freeze brands (Rood & Nellis 1980; Russell 1981a), coloured ear tags or coloured tape around the base of the tail. Blood samples or small muscle biopsies were taken from all individuals, placed on crushed ice and stored in liquid nitrogen within 3 h. Most individuals from five bands (Table I) were captured and marked, or were recognizable from natural markings. Marked individuals included all adult females and the majority of their offspring during 1989–1991 (or 1992 for band KB). All band members were

Table I. Number of individuals per year in coati bands studied on Barro Colorado island

Band	1989	1990	1991	1992	1993
T	8 (3 af, 1 saf, 4 sa)	6 (2 af, 3 jf, 1 jm)	7 (2 af, 3 saf, 1 sam, 1 jm)	8 (3 af, 5 j)	9 (3 af, 3 sa, 3 j)
X	Unknown	18 (11 af+sa, 7 j)	18 (7 af, 3 sa, 8 j)	19 (7 af, 5 sa, 7 j)	16 (8 af, 5 sa, 3 j)
K	21 (6 af, 4 saf, 4 sam, 4 jm, 2 jf, 1 am*)	26 (7 af, 4 sam 1 saf, 13 j, 1 am*)	n/a	n/a	n/a
KPLT†	n/a	n/a	17 (4 af, 4 sa, 9 j)	17 (8 af, 4 sa, 5 j)	19 (6 af, 3 sa, 10 j)
KL†	n/a	n/a	22 (6 af, 9 sa, 6 j, 1 am*)	8 (6 af, 1 sa, 1 j)	8 (5 af, 3 j)
KB†	n/a	n/a	n/a	14 (8 af, 1 sa, 5 j)	16 (6 af, 4 sa, 6 j)
RCS	Unknown	Unknown	14 (11 af+sa, 3 j)	9 (6 af+sa, 3 j)‡	6 (3 af, 1 saf, 2 j)‡

af=Adult females (>24 months), sa=second year subadults (12–24 months), j=first year juveniles (<12 months), am=adult males (>24 months).*

*Adult males with the band outside the breeding season (Gompper & Krinsley 1992). These individuals were probably offspring of a band member.

†The K band fissioned in 1991 into KL and KPLT. Band KB formed in 1992 from individuals leaving band KL.

‡Possibly an underestimate because band was not studied intensively in 1992–1993.

habituated to the presence of an observer. Six individuals from a sixth band (band RCS), although not habituated, were sampled in 1991. A few individuals from several other bands were also sampled. Ninety-seven individuals were live-trapped, including members of nine bands and 29 solitary adult males.

To compute the DNA fingerprint similarity values of unrelated individuals, blood or tissue samples were taken from six individuals trapped at several localities on the mainland site of Gigante peninsula. Gigante peninsula is separated from BCI by a minimum of approximately 300 m, and animals were trapped 2–5 km inland. Blood samples were also obtained from two zoo families to document Mendelian inheritance of bands and to assess linkage (Bruford et al. 1992). For these zoo families, parentage was known, although the exact origin of the founders was not. The Granby Zoo family (parents and six offspring) was founded by two captive-born individuals thought to be unrelated. The Fossil Rim family (parents plus five offspring) was founded by two immature individuals, thought to be siblings, that were confiscated at a market in southern Texas. The geographical source of these individuals, although unknown, was suspected to be northern Mexico.

Genetic Analyses

Genetic fingerprinting followed standard techniques (Gilbert et al. 1990; Gompper 1994). White blood cells or minced tissue samples were digested overnight in 1 × TNE, 10% proteinase-K at 60°C. Genomic DNA was then isolated via buffered phenol, phenol–chloroform–isoamyl and chloroform–isoamyl extractions. We also used this protocol to obtain additional high-quality DNA from either ear tissue (saved after ear tagging) or from red blood cell pellets when initial DNA quantities were depleted.

Initially, to optimize the variability of fingerprint patterns, we digested DNA from known related and unrelated coatis with a panel of restriction endonucleases (*Alu* I, *Hae* III, *Hinf* I, *Msp* I, and *Hinc* II) and hybridized with two multilocus probes (33.6, 33.15; Jeffreys et al. 1985a, b). We also varied voltage and running times to optimize separation and clarity of bands. Our final protocol used the restriction endonuclease *Hae* III with 4 mM spermidine. After digestion, the sample was phenol-extracted, ethanol-precipitated and re-suspended in gel running buffer (1 × TAE). DNA fragments were separated by electrophoresis in a 20 × 22-cm 1% agarose gel with a 20-slot 1 mm wide comb for 17 h at 70 V. The DNA was transferred to a nylon membrane (Amersham Hybond N+) by capillary blotting (Southern 1975), and baked at 80°C for 2 h. Membranes were pre-hybridized for 2 h at 65°C in 0.5 M sodium phosphate (pH 7.2), 7% SDS, 1 mM EDTA and 1% BSA. Hybridization was performed in the same buffer with the addition of 1×10^6 cpm/ml ^{32}P-labelled 33.6 or 33.15 Jeffrey's probe at 65°C for 12–18 h with constant shaking. Following two 10-min low-stringency washes (2 × SSC, 0.5% SDS, room temperature) and two 30-min high-stringency washes (0.1 × SSC, 0.5% SDS, 50°C), the probed membranes were placed on X-ray film and several exposures were made for varying periods of time (1–21 days, − 70°C) to allow accurate scoring of fragments of differing intensity. Membranes were then stripped of radioactive probe in boiling 0.5% SDS and re-hybridized if necessary.

Nineteen individuals were loaded on each gel, with duplication of one sample in the first and last lanes for alignment purposes. Scoring of DNA fragment patterns was performed by eye. All fragments in the molecular weight range of 1.0–12.0 kb were scored; those showing similar molecular weight (± 1 mm) and intensity were considered identical. Only fingerprints on the same gel were compared; consequently we placed as many individuals as possible from a single band on the same gel. Similarly, for analyses of paternity, potential fathers were placed on the same gel as the putative mother and offspring pairs. For each gel, a presence or absence matrix of restriction fragments was tabulated and used to calculate pair-wise fragment sharing (similarity) values between individuals (see below).

Paternity was assigned by exclusion of putative fathers through the presence of diagnostic DNA fragments found only in the offspring (e.g. Burke & Bruford 1987). As a measure of relatedness, we used the proportion of DNA fragments shared between individuals (e.g. Wetton et al. 1987). We estimated the expected band-sharing value for siblings and parent–offspring (r=0.5) through analysis of a captive family of known genealogy and analysis of mothers and their offspring from the BCI population deduced from behavioural observations. Behavioural criteria for identifying mother–offspring pairs included (1) nursing between offspring and a putative mother during every period of nursing and exclusion of other females by the absence of nursing, or (2) the putative mother being the only lactating female in the band. We estimated the expected band-sharing value for unrelated (r=0) individuals through comparisons of individuals from the BCI and Gigante populations. Pair-wise band-sharing, or similarity (S), is defined as the number of fragments shared between two individuals divided by the total number of fragments (Gilbert et al. 1990). The mean similarity value for a band (S_g) is the average of all S values between all band members. Because of non-independence of pair-wise S values, an unbiased estimation of the standard error (SE) is calculated as $[2S_g(1-S_g)(2-S_g)\,n(4-S_g)]^{0.5}$, where n=mean number of restriction fragments per individual (Lynch 1990, 1991). A 95% confidence interval was established by multiplying the standard error by 1.96. Although calculating a confidence interval in this manner assumes S_g is normally distributed, this may not be the case if unrelated individuals join bands. Calculations were multiplied by 100 for ease of presentation. The method for calculating mean within-group relatedness devised by Reeve et al. (1992) was not used because it would require cross-gel identifications of fragments having similar mobility. Such comparisons are difficult to make with multilocus fingerprints (Lynch 1991).

Standard parametric tests cannot be applied to pair-wise similarity data because of the interdependence of similarity values (Dietz 1983). To assess significance of differences between similarity distributions, we used a permutation test appropriate for similarity data (Dietz 1983; Wayne et al. 1991; Lehman et al. 1992). Using a computer program (E. Geffen, unpublished software), two sets of S values of the same size as those being compared were randomly subsampled from the pooled distribution 100 times. Each subsampling computed the average similarity difference between the two groups and contrasted this difference with the observed difference. The frequency of difference values equal to or more than the observed value is the one-tailed probability that the difference is greater than that generated by chance alone.

Behavioural Data

When a band or a solitary individual was first observed, individuals were identified and then followed at a distance of a few metres. This allowed collection of behavioural data on known individuals. Data on agonism were collected ad libitum (Altmann 1974), with information on the aggressor(s), recipient of aggression and context of the agonistic event recorded (Gompper 1994, 1996).

Coalition formation is common during agonistic episodes between coati band members. The definition of the term 'coalition' varies between studies. For example, coalitions of lions and cheetahs refer to long-term associations of males that enable them to maintain reproductive access to females, although asymmetries in reproduction may occur among the coalition members (Packer & Pusey 1983; Caro 1994). Coati coalitions are more similar to short-term interactions observed among primates (e.g. Harcourt 1992), defined by Nöe (1986) as '. . . any event when individuals combine forces, either one comes to the aid of the other(s), or two or more individuals direct aggression on the same target at the same time' (page 384). Some researchers distinguish coalitions from alliances, which are defined as the relationship between two individuals who combine forces over an extended period (Nöe 1986; Connor et al. 1992; de Waal & Harcourt 1992). Consequently, alliances may better describe the type of coalitions found in lion and cheetah (but see Harcourt 1989). We followed Nöe (1986) and defined coati coalition support as a single, short, cooperative event such as two individuals jointly attacking a third individual. The extent to which these ephemeral coalitions may reflect long-term alliances is beyond the scope of this study.

When coalition support occurred, the identification of the coalition members was recorded, and the individuals giving and receiving aid were noted. Coati agonistic disputes can be extremely complex and occur rapidly. Often a dispute between two individuals escalated within 5–10 s to involve several discrete groups of band members. These situations were difficult to record thoroughly; thus we primarily focused analyses on disputes involving agonistic events with one or two small coalitions, each made up of three or fewer individuals. Data on cooperation during conflicts were analysed only when all adult band members were present.

RESULTS

Segregation and Linkage

Because large, known sibships from the BCI population were not available for analysis, we examined patterns of restriction fragment inheritance in the outbred Granby and inbred Fossil Rim families. Restriction fragments revealed separately by Jeffreys 33.15 and 33.6 probes did not overlap in position (no two bands co-segregated) in any individual; thus the two probes appeared to hybridize to different loci. Therefore, data from both probes were combined in subsequent analyses. In the Granby family, 69 fragments were found in 8 individuals, including one unique band in an offspring, presumably a mutation, that was excluded from further analyses. Of 68 fragments, the male and the female parent had 46 fragments each. Excluding 24 fragments shared by both parents, 44 fragments were examined for segregation bias. No fragment was found in all of the male offspring but in none of the female offspring. Therefore, none of the variable DNA fragments is linked to the Y chromosome. Of the 44 variable fragments, with one exception, none was found in all offspring; hence they must be heterozygous in the parents. The exception, found in a mother and all her offspring, may be a maternal homozygote. The probability that any one of 44 fragments would appear homozygous by chance, however, is $0.5^{\text{no. of offspring}} \times 44 = 0.7$, and the chance that any one of 22 maternal fragments (those not occurring in the father) would appear homozygous by chance is 0.4 (Hanotte et al. 1992). The autoradiograph density of fragments was not different between the female and her offspring, suggesting that she was heterozygous at the locus. For the 44 fragments found in only one parent, the mean transmission frequency to offspring was 0.48, near the expected value of 0.5 assuming the parent was heterozygous and the fragment unlinked.

Fingerprint Similarity in Captive and Wild Populations

Fingerprint similarity varied with the level of genetic relatedness (Fig. 1). In the Granby Zoo family, the average fingerprint similarity between parents and offspring and between siblings was 72.8 (range=66.7–79.5; 95% C.I.= ± 11.6). Granby parents were presumed to be unrelated based on breeding records, and their relatively low similarity value ($S=52.2$) supported this assumption. For the Fossil Rim family, the average fingerprint similarity between parents and offspring and between siblings was 82.4 (range=76.9–88.9; 95% C.I.= ± 10.2). The value of similarity for the parents of the Fossil Rim family was 72.3, consistent with the suggestion that the pair might be siblings (Hampton 1990; B. Williams, personal communication; see Methods). This conclusion is also suggested by the higher mean similarity value of the Fossil Rim family compared with the Granby Zoo family. Of 100 random subsamplings of the pooled data, none had a difference as great as that observed. The mean ± SD number of fragments was 44 ± 3.6 (range=38–49) for the Granby Zoo family and 39.6 ± 2.6 (range=36–43) for the Fossil Rim family.

On BCI, eleven mother–offspring dyads from four bands were identified; the average fingerprint similarity of these dyads was 81.5 (range=72.0–88.0; 95% C.I.= ± 11.4; Fig. 1). This mean similarity value was not significantly different from the mean of 82.4 for the inbred offspring of the Fossil Rim family. Of 100 random subsamplings of the pooled data, 56 had a difference as great as that observed. The mean similarity value is considerably higher than the values of 72.8 for the offspring of the Granby Zoo family, however; of 100 random subsamplings of the pooled data, none had a difference as great as that observed. The discrepancy may reflect local inbreeding in the BCI population, or that the founders of the Granby Zoo family were from genetically distinct populations, and highlights the importance of a within-population calibration for relatedness values of 0.5 (Jones et al. 1991; Packer et al. 1991).

To estimate values of similarity of unrelated individuals we compared fingerprints of individuals from BCI to a nearby mainland population

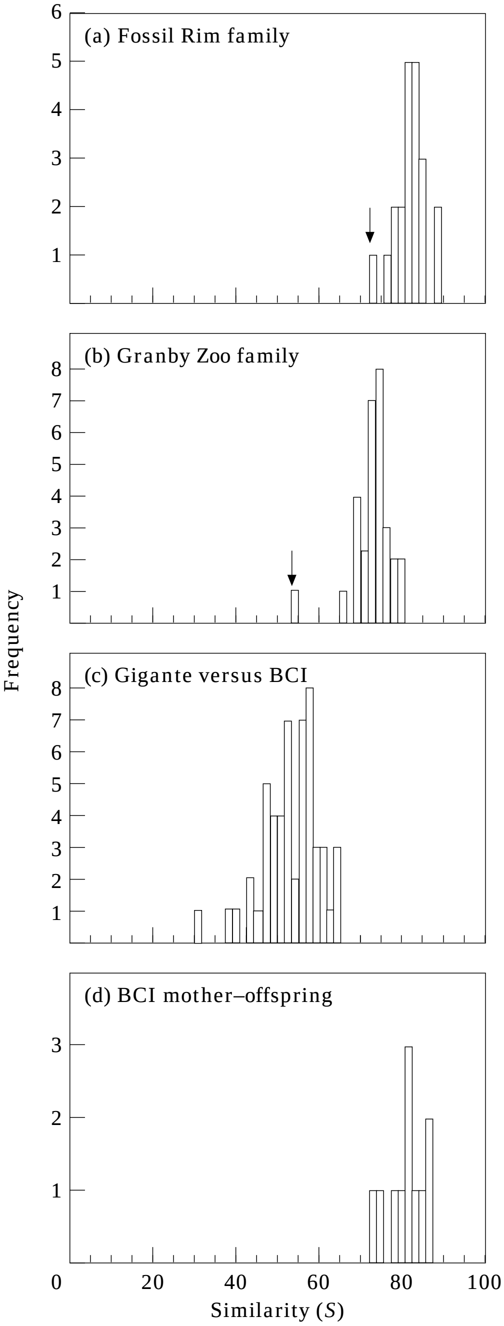


Figure 1. Frequency distributions of fingerprint similarity values for individuals from two captive families and wild coati populations. Arrows indicate similarity of parents. (a) Fossil Rim family ($N=7$ individuals and 21 relationships). The parents are probably siblings, and thus the offspring are inbred. (b) Granby Zoo family ($N=8$ individuals and 28 relationships). Parents are thought to be unrelated. (c) Comparison of unrelated individuals from Barro Colorado island and Gigante peninsula ($S_g=52.7$; 95% C.I.=15.3; range=29.9–65.0; $N=53$ relationships). Individuals are considered unrelated because of the difference in geographical locality. (d) Mother–offspring dyads from Barro Colorado island ($S_g=81.5$; 95% C.I.=11.4; range=72.0–88.0; $N=11$ relationships).

Table II. Reproductive success of marked 1992 putative breeding males (observed with the band during the mating season) for three habituated bands

	Number of offspring sampled				Success of 1992 males		
Band	1990	1991	1992	Number of 1992 putative breeding males	Probable father of 1992 offspring?	Father of 1990–1991 offspring?	Possible fathers of other offspring identified?
KL	n/a*	2 of 3	1 of 1	2	No	No	No
X	1 of 2	4 of 8	3 of 7	1	Yes (1 of 3)	No	Yes (2 of 4 from 1991)†
T	3 of 4	1 of 1	1 of 5	2	No	No	Yes (1 of 3 from 1990)

Columns indicate the band, the number of offspring sampled from the band (1990–1992), the number of males monopolizing access to the band in 1992, and the success of the putative males in fathering these offspring.
*KL band resulted from a fission event in late 1990 or early 1991.
†The two offspring for whom paternity was identified were probably fathered by different males (see text).

from Gigante peninsula. The average fingerprint similarity of these inter-population dyads was 52.7 ($N=53$; range=29.9–65.0; 95% C.I.= ± 15.3; Fig. 1). The distribution of supposed unrelated individuals and individuals related as siblings or parent–offspring, from both captive and wild populations, do not overlap (Fig. 1). Consequently, we defined unrelated individuals as those less than one standard error above the mean of the mainland–island comparisons ($S<60.5$). Dyads with the value of 60.5 and lower should not be related as siblings or parent–offspring, as suggested by the distribution of $r=0.5$ dyads in the BCI population and in the captive colonies (Fig. 1). Similarly, we defined highly related dyads (those related as parent–offspring or siblings) as having similarity values greater than one standard error below the BCI parent–offspring mean ($S>75.7$). Finally, we defined a category of slightly related dyads to include those between 1 and 1.96 standard errors below the BCI parent–offspring mean ($70.1<S<75.7$). This category includes some individuals that are related as parent–offspring and siblings; 0% of Fossil Rim and 18.2% of BCI mother–offspring dyads fall within this range. Therefore, this grouping probably includes some highly related dyads ($r=0.5$) as well as more distantly related individuals. Some unrelated individuals might be included as well, although none of our unrelated comparisons from the mainland fall within this range. Dyads with similarity values falling between the unrelated and the slightly related categories ($60.5<S<70.1$) were not classified.

Paternity

Field behavioural observations of bands suggested that social structure during the breeding season resembled a harem system, with one or two males monopolizing access to band females (Kaufmann 1962; Gompper 1994). In 1992, observations were made on the males consorting with five bands. Unknown, unmarked males consorted with two of these bands. The other three bands consorted with marked individuals, allowing parental exclusion techniques to be used to test the hypothesis that time spent by putative fathers with females is indicative of breeding success.

The monopolization of a band by a male did not accurately predict paternity (Table II). The putative breeding males were excluded from paternity for four of five 1992 offspring. For the one exception the successful breeding male could not have fathered all the band offspring. In addition, none of the marked males observed with the band in 1992 were the fathers of 11 sampled offspring born in 1990 or 1991. In several instances, other sampled males could not be excluded from paternity (Table II), but a single male was never identified as a possible father of all band offspring. In the X band in 1991, two probable sires were identified. These males did not father all the offspring, indicating that at least three males may have gained paternity in 1991 (Table II).

Relatedness within Bands

Most bands showed high overall mean similarity. Of the 19 band-years for which mean

Table III. Number of individuals sampled per band and mean similarity coefficients (S_g) for all individuals, for individuals who were in the band at the same time, and for individuals in a band during a given year

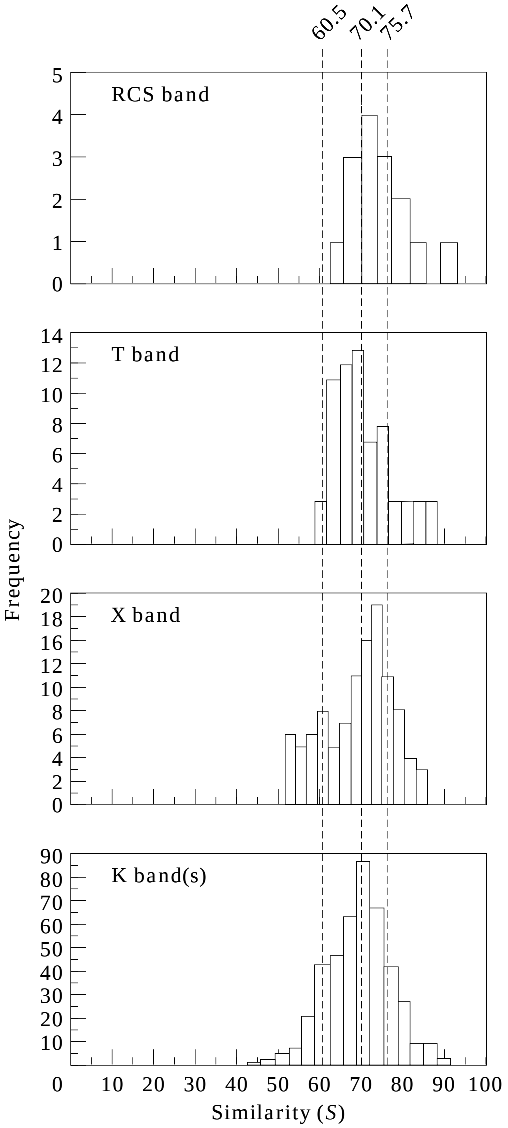
Band	Number coatis (all years)	Number coatis sampled*	S_g (all years)	S_g (overlapping tenure†)	S_g (1989)	S_g (1990)	S_g (1991)	S_g (1992)	S_g (1993)
T	21	12	70.6 (12, 66)	71.7 (12, 45)	67.9 (8, 28)	77.6 (5, 10)	77.8 (6, 15)	85.6 (2, 1)	85.6 (2, 1)
X	37	20	69.4 (20, 106)	69.2 (20, 99)	Unknown	65.2 (10, 32)	67.2 (15, 67)	67.4 (15, 67)	65.5 (12, 43)
K	34	28	70.8 (28, 321)	70.8 (28, 314)	72.5 (21, 176)	70.2 (26, 263)	n/a	n/a	n/a
KPLT	33	7	64.3 (7, 17)	65.7 (7, 15)	n/a	n/a	71.5 (6, 11)	75.0 (5, 7)	65.4 (5, 10)
KL	26	13	74.6 (13, 60)	74.6 (13, 60)	n/a	n/a	74.6 (13, 60)	72.8 (5, 10)	71.2 (2, 1)
KB	20	7	75.1 (6, 21)	75.1 (6, 21)	n/a	n/a	n/a	75.1 (6, 21)	74.3 (5, 15)

Values in parentheses are number of individuals sampled (and thus used in calculating S values) and the number of relationships examined among these individuals.*

*Not all potential relationships were determined due to low DNA quantity for some individuals.

†Individuals in the band at the same time.

similarity coefficients were calculated (Table III), four were in the range of highly related individuals and nine were slightly related. Approximately half the dyads within bands were classified as highly and slightly related (S>70.1; Fig. 2). The six individuals sampled from band RCS had a mean similarity of 74.2, indicating average dyads were composed of slightly related individuals (Fig. 2). None of the RCS individuals examined were unrelated, and 40% of RCS relationships were categorized as highly related. Similarly, band K had high mean similarity among individuals (Fig. 2). Band X consistently had mean similarity of less than 70.1, however, suggesting the presence of unrelated individuals (Table III). Four (T, X, K and KPLT) of the six extensively sampled bands also included individuals that were unrelated to one another (S<60.5), although some of these individuals were related to other band members. Three bands (K, KL, KPLT) contained individuals unrelated to all adult and subadult band members. Similarly, band X had one female who was unrelated to nine of 11 adult and subadult females.



Although the mean relatedness of all bands over all years was generally high, the variance in relatedness was often large within bands (e.g. the variance in similarity values of band X; Fig. 2). One adult female (#1) in band X had a similarity value of less than 60.5 to all other adult and subadult band members except two, one of which had a low similarity value of 60.6 and the other a value of 71.0. A second female (#4) was unrelated to three adults and subadults, was slightly related to only one individual, and was not highly related to any band members. Over all years, 11 of the 66 similarity values of adult and subadults fell below 60.5; thus 16.7% of the dyads involved unrelated individuals. Thirteen comparisons were above 75.7, delineating 19.7% of the relationships of these band members as highly related. When juveniles are included, 16.0% of dyads (N=106) involved unrelated individuals, and 23.6% involved highly related individuals (Fig. 2).

Because the size of bands varies greatly within and between years (Table I) we expected that mean relatedness would also vary. For example, over 5 years, similarity values for adults and subadults within T band indicate that the average dyad was slightly related (S_g=70.6; Table III).

Figure 2. Distributions of similarity values for all individuals found in four bands during all years of band observation. K band(s) include individuals from several bands during 1991–1993 (Table I). Mean similarity, number of individuals examined and number of relationships plotted for each band are as follows: RCS band: 74.2, 6, 15; T band: 70.6, 12, 66; X band: 69.4, 20, 106; K band(s): 69.4, 33, 428. For X and K bands, relationships do not include all possible comparisons of individuals due to limited DNA quantities for several individuals. Dashed lines indicate limits for highly related, slightly related and unrelated categories.

Table IV. Adult female band members classified as either unrelated or related to most other adult and subadult band members. Individuals are listed by band and year(s) of study

Band (years)	Unrelated female	Related females	Context
X (1991–1993)	#1 (adult when trapped in 1991)	#2, #18, #19, #26 (all adults in 1991; #19 died in late 1991)	#1 probably migrated into band in late 1980s; alive in 1993
K (1989)	fk18 (adult when trapped in 1989)	fk7, fk14, y2b, y6y, y4y, y5b (all adults in 1989)	Source of fk18 unknown; died in Dec. 1989
KL (1991–1992)	#36 (adult in 1991)	fk8, #56, y3g (all adults in 1991)	Source of #36 unknown; possible immigrant; disappeared early 1992
KPLT (1992–1993)	y28b (adult when trapped in 1992)	y2b, y6y, y4y, y5b (all adults in 1993)	y28b migrated into band in late 1992; alive in 1993)
Total	$N=4$	$N=13$	

Context indicates the origin, if known, based on field observations, and the most recent observations of the unrelated female.

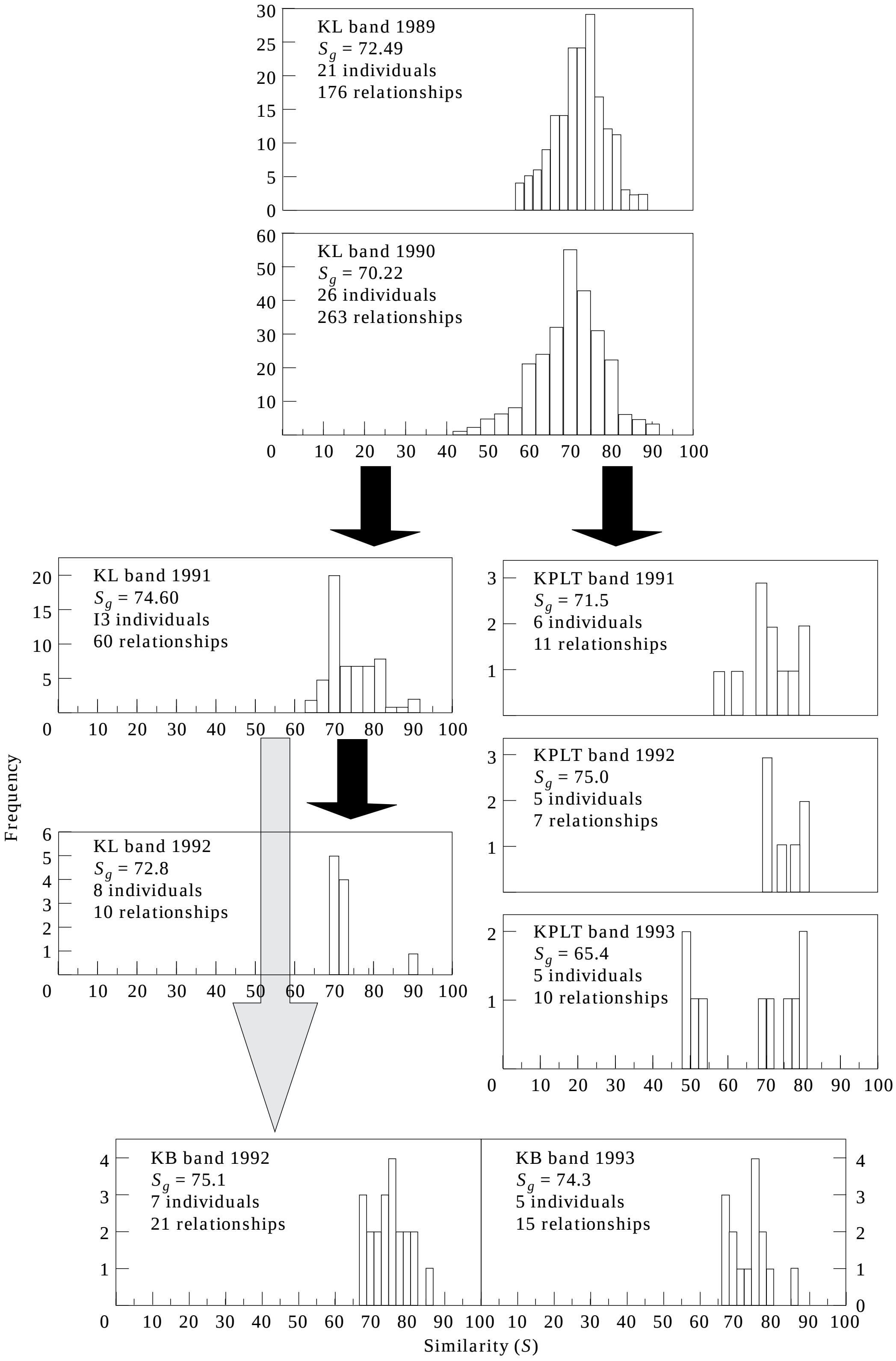
Many of these individuals, however, were not simultaneously in the band during any particular year due to deaths, emigrations and age-class differences. Thus, in 4 of the 5 years, the average dyad in the T band was highly related (Table III). During any one year, the proportion of examined relationships within the T band deemed highly related ($S>75.7$) was 2 of 28 in 1989 (6 of 28 slightly related), 6 of 10 in 1990 and 9 of 15 in 1991. Two dyads, one involving individuals not in the band during the same year, had similarity values below 60.5. The K band and its descendant bands (KPLT, KL, KB) showed a similar pattern of high mean relatedness and high variance in similarity (Fig. 2). The distribution of relatedness also changed greatly from year to year as fission and migration events occurred (Fig. 3; Table III). In 1989 and 1990 the K band contained 21 and 26 individuals, respectively, with a mean similarity value of 72.5 in 1989 and 70.2 in 1990. During this period, 6.8–6.5% of dyads had similarity values less than 60.5. This percentage would have been larger if the two individuals who accounted for four of the 12 similarity coefficients less than 60.5 in 1989 had not died. In 1991, K band fissioned into bands KPLT and KL. Consequently, descendant band KL had no unrelated dyads, and KPLT had many fewer unrelated dyads than its parental band. In 1993, a female immigrated into band KPLT, such that four of 10 relationships between the core individuals involved unrelated dyads. Band KL subsequently fissioned again in 1992 into bands KB and KL, and relatedness between these bands remained high for 1992 and 1993 (Fig. 3).

Time Spent Alone

One adult female in each of four bands was identified as unrelated to all or most other band members (Table IV). Three of these four females were suspected to be immigrants, based on field observations or high fingerprint similarity to individuals in other bands (Gompper 1994). The source of the fourth female was unknown. Behavioural and ecological parameters of these four females were compared with 13 highly related adult females selected from the same bands during the same year(s). Observations on four of these highly related females were made during two disparate periods (see below). Consequently, we had 17 non-independent pair-wise comparisons between related and unrelated females.

Among adult band members, unrelated females were significantly more likely to be alone than were females with close kin (tied $Z=-3.030$; tied

Figure 3. Histograms representing changes in fingerprint similarity distributions among individuals in a band that underwent two fission events over 5 years. Band K split in 1991 into bands KPLT and KL. KL split in 1992, giving rise to band KB. Each histogram represents relationships of all sampled band members during a particular year. Individuals who joined a band for brief periods (less than 3 months) are excluded.


KL band 1989
S_g = 72.49
21 individuals
176 relationships
KL band 1990
S_g = 70.22
26 individuals
263 relationships
KL band 1991
S_g = 74.60
I3 individuals
60 relationships
KPLT band 1991
S_g = 71.5
6 individuals
11 relationships
KPLT band 1992
S_g = 75.0
5 individuals
7 relationships
KL band 1992
S_g = 72.8
8 individuals
10 relationships
KPLT band 1993
S_g = 65.4
5 individuals
10 relationships
KB band 1992
S_g = 75.1
7 individuals
21 relationships
KB band 1993
S_g = 74.3
5 individuals
15 relationships
Frequency
Similarity (S)
0 10 20 30 40 50 60 70 80 90 100

$P=0.0024$). As a group, unrelated females were observed alone in 35.9 ± 7.0% of sightings compared with 5.2 ± 2.0% for the related females. This may be an underestimate of the time spent alone by unrelated females, because solitary individuals are more likely to be overlooked by an observer. In contrast, groups are more often observed in the forest due to their noisier movements, wider distribution on the forest floor, and more vocal behaviour.

The 13 related females include four individuals (individuals y2b, y6y, y4y and y5b) examined twice during different years (1989 and 1992; Table IV). Treating these repeated measures as independent could lead to a 'pooling' problem (Machlis et al. 1985; Leger & Didrichsons 1994). If, however, we excluded data collected on these four females from either 1989 or 1993 from the analysis, unrelated females were still significantly more likely to be found alone (excluding 1989: $U=2$; $U'=46$; tied $Z=-2.741$; tied $P=0.0061$; excluding 1993: $U=0$; $U'=48$; tied $Z=-3.111$; tied $P=0.0019$). Related females were alone for 7.0 ± 2.5% of observations excluding 1989 and 3.2 ± 1.4% of sightings alone excluding 1993.

Individual unrelated females were alone in 17.2% ($N=34$ observations), 33.3% ($N=6$), 42.9% ($N=7$) and 50.0% ($N=16$) of observations. In contrast, although one related female was observed alone in 25% of sightings, 8 of 16 related females were never alone (13.4 ± 9.1 observations per female; range=4–34). These patterns held within all four examined bands. For example, KPLT band females were seen alone on 14 occasions. Eight of these sightings involved unrelated adult female y28b (Fig. 4). Two of the related females were never seen alone in either 1993 (as KPLT band; Fig. 4) or in 1989 (as K band). The proportion of related adult females not observed alone in 215 individual sitings (Table IV) was 2 of 4, 2 of 4, 5 of 6, and 1 of 3 for bands X, KPLT, K, and KL, respectively.

	y2b	y6y	y28b	y4y	y5b
y2b					
y6y	77.9				
y28b	52.5	50.0			
y4y	69.4	80.9	47.6		
y5b	81.1	74.9	47.5	71.1	

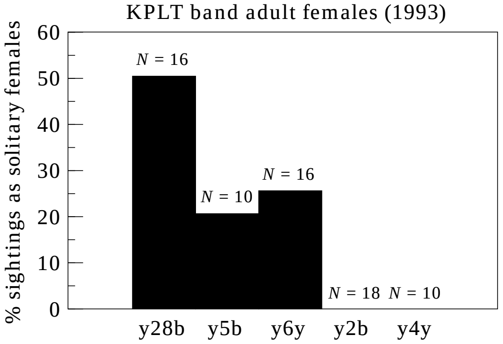


Figure 4. Fingerprint similarity values for the five sampled adult females from KPLT band during 1993 and the proportion of sightings of these individuals as solitary females. For example, unrelated female y28b was solitary for eight of 16 observations.

Coalition Formation and Aggression

For three of the four bands (X, KL, and KPLT bands; Table IV), detailed behavioural data were collected on the interactions of the related and unrelated adult females. During conflict situations individuals received aid in 68.3 ± 5.8% of occasions. Related females were significantly more likely than unrelated females to receive support. Related females ($N=10$) received support in 78.6 ± 2.5% of conflicts ($N=188$ conflicts; range=65.0–92.9%), while the three unrelated females received support in 34.0 ± 3.0% of conflicts ($N=44$ conflicts; range=30.8–40.0%) ($U=0$; $U'=30$; tied $Z=-2.539$; tied $P=0.0111$). The ratio of the number of times an individual gave assistance to the number of times an individual received assistance was 1.3 for all individuals, regardless of relatedness. The three unrelated females had ratios of 2.0, 2.7 and 3.5. All related females had ratios of less than 1.2. The mean ratio differed significantly between related and unrelated females ($U=0$; $U'=30$; tied $Z=-2.550$; tied $P=0.0108$).

As a group, unrelated females received the majority of aggression. Of 80 aggressive incidents between individuals listed in Table IV, 42 (53%) were directed by related females towards unrelated females. Eighteen events would be expected if aggression were apportioned regardless of relatedness. A typical pattern of aggression between band members is shown in Table V. Three of the four related females directed more than 57% of their aggression towards unrelated female y28b.

Table V. Instigators and recipients of aggression between KPLT band adult females in 1993

Aggression instigator	Aggression recipient				
	y2b	y6y	y4y	y5b	**y28b**
y2b	—	0	0	2	6
y6y	0	—	1	2	4
y4y	2	0	—	1	9
y5b	1	1	1	—	1
y28b	2	1	1	1	—

Values refer to the number of agonistic events in which each individual was involved. Individual in bold was unrelated to all other band adult females.

DISCUSSION

Genetic Relatedness

Coati bands are not nuclear families, but rather are extended families often containing some unrelated individuals. Within-band variance in relatedness was high, and unrelated individuals were found in four of the six intensively studied bands. Thus, despite relatively high mean relatedness, coati bands have a characteristically high variance in relatedness. This diversity of relatedness coefficients within bands emphasizes the difficulty of invoking a single evolutionary mechanism to explain the maintenance of coati social or cooperative behaviours. Specific cooperative behaviours may be maintained by a variety of mechanisms (e.g. kin selection, reciprocity, manipulation, group selection), depending on the relatedness of the individuals involved. Given the long-term persistence of unrelated individuals in coati bands, reciprocal altruism, as originally hypothesized by Russell (1979, 1983), may indeed be a valid mechanism for maintaining coati sociality.

Our findings of high variance in relatedness between coati band members are consistent with those of other genetic studies of group-living carnivores (Gompper & Wayne 1996). For example, 42% of individuals in male lion, *Panthera leo*, coalitions are unrelated (Packer & Pusey 1983; Packer et al. 1991). Lehman et al. (1992) found that wolf, *Canis lupus*, packs from several populations often contained individuals unrelated to the dominant breeding pair. Thus, although wolf packs are dominated by highly related individuals, they are not necessarily family units consisting of a mated pair and their offspring. Interestingly, unrelated coatis were more likely to occur in large than small bands.

A common problem revealed by genetic studies of carnivores and other taxa is that behavioural observations may not always provide accurate assessments of paternity (e.g. Burke 1989; Birkhead et al. 1990; Westneat 1993; Xia & Millar 1991; Keane et al. 1994). Our genetic analyses of coati bands revealed a similar lack of predictability. Female coatis were apparently able to breed with alternative mates despite being guarded by a single male. Most solitary adult males sighted within the home range of bands were marked and habituated. These solitary males were probably related to band females, however (Gompper 1994, 1996), and during the breeding season unmarked males were often sighted within 100 m of bands. Social structure in the breeding season resembled a harem system, with males monopolizing access to band females, chasing away other males, travelling with the group and grooming band members. Yet the genetic analyses showed that these males were rarely successful at monopolizing reproduction. Females often temporarily left the band during the mating period (M. E. Gompper, personal observation). Therefore, although males attempted to restrict access to females in the band, the mating system is none the less promiscuous. More study is needed to better document this pattern and to discern the benefits males receive by attempting to guard access to females.

Our genetic results revealed two other features of the mating system in coatis. First, genetic analyses showed that several males may mate with the females of a band. This pattern is consistent with results of several other carnivore studies (e.g. Gompper & Wayne 1996). A second feature is the absence of temporal continuity of fathers. Although the number of identified fathers is relatively small, and additional study is needed, none of our sampled males fathered offspring in consecutive years within a given band. This observation contrasts with that of the long-term mate fidelity identified in grey seals, *Halichoerus grypus* (Amos et al. 1995). Both factors contribute to the high variance in relatedness typical of coati bands. Variability in female mate choice and lack of temporal continuity may prevent inbreeding in coati populations resulting from the rigid philopatry of females who may breed within 2 years of birth (Russell 1982; Packer et al. 1991).

Kinship and Behaviour

Our results show that unrelated and related individuals within coati bands differ in how much they benefit from group living. Unrelated females spend more time alone and receive more aggression than their related counterparts. Compared with band members with close kin, unrelated females also receive less coalition support and have an increased ratio of the support given to that received. Thus, kinship of band members must be measured to understand fully the variation in behaviour of group-living coatis as well as to identify the benefits or costs of group living.

Adult females who leave a group to temporarily forage alone incur additional costs, including lack of access to high quality food patches, increased parasite loads and presumably increased predation risks (Russell 1982; Burger & Gochfeld 1992; Gompper 1994, 1996). None the less, all unrelated adult females were observed alone, averaging 36% of all sightings. In contrast, most related females were never observed alone. This difference between related and unrelated females suggests that the benefits of remaining with other band members are marginal and may be outweighed by the costs of aggressive interactions or lack of coalition support. Unrelated females received most of the aggression within coati social groups, which often occurred during fruit foraging (Gompper 1994, 1996). Females leaving the group might temporarily reduce the impact of aggressive competitors, and perhaps simultaneously decrease foraging competition from other band members (Gompper 1994, 1996).

Coalition formation is central to coati sociality. Coalitions are most apparent during conflict situations, for example during feeding competition or agonistic encounters with solitary adult males or potential predators such as *Cebus* monkeys and large snakes (Janzen 1970; Russell 1981b; Gompper 1996, personal observation). Within bands, agonism is characterized by support for kin over non-kin. Among primate species, coalition formation is common, and genetic relatedness often plays a fundamental role in structuring coalitions (e.g. references in Harcourt & de Waal 1992). Harcourt (1989) suggested that examples of alliance or coalition formation among non-primates are rare partly because researchers do not look for them. Among carnivores, coalitions have previously been reported only among grey wolves (Mech 1970; Jenks 1988) and spotted hyaenas, *Crocuta crocuta* (Zabel et al. 1992; Smale et al. 1995). Harcourt (1989) proposed that species such as the coati, living in large stable social groups and feeding on patchy resources, are likely to cooperate in contest support. This study confirms the existence of coalition support in coatis and indicates that an individual without close kin will receive this benefit of group living less often. None the less, unrelated females do gain some coalition support. Butovskaya (1993) suggested that, among species with loose social hierarchies, there is a tendency towards cohesive relationships within all social categories. This may apply to coatis, because no dominance hierarchy has been observed between band members.

Why unrelated females should give more support than they receive is an intriguing question. One possible parallel may occur in dwarf mongooses (Creel & Waser 1994), in which unrelated females are younger than or subordinate to related females and are waiting in the demographic queue for reproductive benefits. Unlike dwarf mongooses, however, there is no evidence of dominance hierarchies or reproductive suppression in coati bands. In fact, several of the unrelated females (#1; fk18, #36) were apparently older than some of the related females, and two (#1 and #36) of the four unrelated females did breed, although less often than did the related band members (Gompper 1994). Any conclusions about reproductive fitness in unrelated and related individuals are premature, because the data on reproduction by unrelated females do not represent lifetime reproductive success; increased sample sizes are needed as well as additional data on litter size and survival of offspring. Also, no attempt has been made to quantify inclusive fitness which, as in other social carnivores (Packer et al. 1991; Creel & Waser 1994; Keane et al. 1994), may be substantial.

This and other studies have shown that female coatis gain some benefits and avoid some costs by living in groups (Russell 1979, 1981b, 1983; Gompper 1994, 1996) and that unrelated females do not gain the full benefits of band life. As group members, unrelated females receive increased aggression and decreased coalition support, as well as increased parasite loads and increased feeding competition from other band members (Gompper 1994, 1996). None the less, unrelated females remain with bands. We hypothesize that unrelated females may join groups to gain only minor immediate benefits, such as access to fruit patches. When those minor benefits cease to exist, for example during the birthing season when parous females temporarily leave the band or when feeding competition within a band is high, a female may spend more time alone. During most of the year, however, marginal benefits resulting from living in a band may maintain group living by unrelated females despite the costs. By remaining with the band and accepting these costs, unrelated females may also eventually obtain major benefits of group living, such as the production of additional young and the cooperative care and protection of offspring.

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REFERENCES

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49,** 227–267.

Amos, B., Twiss, S., Pomeroy, P. & Anderson, S. 1995. Evidence for mate fidelity in the gray seal. *Science*, **268,** 1897–1899.

Amos, W., Twiss, S., Pomeroy, P. P. & Anderson, S. S. 1993. Male mating success and paternity in the grey seal, *Halichoerus grypus*: a study using DNA fingerprinting. *Proc. R. Soc. Lond. Ser. B*, **252,** 199–207.

Birkhead, T. R., Burke, T., Zann, R., Hunter, F. M. & Krupa, A. P. 1990. Extra-pair paternity and intraspecific brood parasitism in wild zebra finches *Taeniopygia guttata*, revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.*, **27,** 315–324.

Bruford, M., Hanotte, O., Brookfield, J. F. Y. & Burke, T. 1992. Single-locus and multilocus DNA fingerprinting. In: *Molecular Genetic Analysis of Populations: A Practical Approach* (Ed. by A. R. Hoelzel), pp. 225–269. Oxford: IRL Press.

Burger, J. & Gochfeld, M. 1992. Effect of group size on vigilance while drinking in the coati, *Nasua narica* in Costa Rica. *Anim. Behav.*, **44,** 1053–1057.

Burke, T. 1989. DNA fingerprinting and other methods for the study of mating success. *Trends Ecol. Evol.*, **4,** 139–144.

Burke, T. & Bruford, M. W. 1987. DNA fingerprinting in birds. *Nature, Lond.*, **327,** 159–152.

Butovskaya, M. 1993. Kinship and different dominance styles in groups of three species of the genus *Macaca* (*M. arctoides*, *M. mulatta*, *M. fascicularis*). *Folia Primatol.*, **60,** 210–224.

Caro, T. M. 1994. *Cheetahs of the Serengeti Plains*. Chicago: University of Chicago Press.

Clutton-Brock, T. H. 1989. Mammalian mating systems. *Proc. R. Soc. Lond. Ser. B*, **236,** 339–372.

Connor, R. C., Smolker, R. A. & Richards, A. F. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc. natn. Acad. Sci. U.S.A.*, **89,** 987–990.

Creel, S. R. & Waser, P. M. 1994. Inclusive fitness and reproductive strategies in dwarf mongooses. *Behav. Ecol.*, **5,** 339–348.

Croat, T. B. 1978. *Flora of Barro Colorado Island*. Stanford, California: Stanford University Press

Dietz, E. J. 1983. Permutation tests for association between two distance matrices. *Syst. Zool.*, **32,** 21–26.

Emlen, S. T. 1991. Evolution of cooperative breeding in birds and mammals. In: *Behavioural Ecology* (Ed. by

J. R. Krebs & N. B. Davies), pp. 301–337. Oxford: Blackwell.

Emlen, S. T. 1995. An evolutionary theory of the family. *Proc. natn. Acad. Sci.*, **92,** 8092–8099.

Gentry, A. H. (Ed.)1990. *Four Neotropical Rainforests*. New Haven, Connecticut: Yale University Press.

Gilbert, D. A., Lehman, N., O'Brien, S. J. & Wayne, R. K. 1990. Genetic fingerprinting reflects population differentiation in the California Channel Island fox. *Nature, Lond.*, **334,** 764–767.

Gilbert, D. A., Packer, C., Pusey, A. E., Stephens, J. C. & O'Brien, S. J. 1991. Analytical DNA fingerprinting in lions: parentage, genetic diversity, and kinship. *J. Hered.*, **82,** 378–386.

Gittleman, J. L. 1989. Carnivore group living: comparative trends. In: *Carnivore Behavior, Ecology, and Evolution* (Ed. by J. L. Gittleman), pp. 183–207. Ithaca, New York: Cornell University Press.

Gompper, M. E. 1994. The importance of ecology, behavior, and genetics in the maintenance of coati (*Nasua narica*) social structure. Ph.D. dissertation, University of Tennessee.

Gompper, M. E. 1995. *Nasua narica*. *Mamm. Sp.*, **487,** 1–10.

Gompper, M. E. 1996. Foraging costs and benefits of coati (*Nasua narica*) sociality and asociality. *Behav. Ecol.*, **7,** 254–263.

Gompper, M. E. In press. Population ecology of the white-nosed coati (*Nasua narica*) on Barro Colorado Island, Panama. *J. Zool., Lond.*.

Gompper, M. E. & Krinsley, J. S. 1992. Variation in social behavior of adult male coatis (*Nasua narica*) from Panama. *Biotropica*, **24,** 216–219.

Gompper, M. E. & Wayne, R. K. 1996. Genetic relationships among individuals within carnivore societies. In: *Carnivore Behavior, Ecology, and Evolution* Vol. 2 (Ed. by J. L. Gittleman), pp. 429–452. Ithaca, New York: Cornell University Press.

Hampton, G. 1990. New coati facility opened at Fossil Rim Wildlife Center. *AAZPA Communique*, October, 23.

Hanotte, O., Bruford, M. W. & Burke, T. 1992. Multilocus fingerprints in gallinaceous birds: general approach and problems. *Heredity*, **68,** 481–494.

Harcourt, A. H. 1989. Social influences on competitive ability: alliances and their consequences. In: *Comparative Socioecology* (Ed. by V. Standen & R. A. Foley), pp. 223–242. Oxford: Blackwell Scientific Publications.

Harcourt, A. H. 1992. Coalitions and alliances: are primates more complex than non-primates? In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 445–471. Oxford: Oxford University Press.

Harcourt, A. H. & de Waal, F. B. M. (Eds) 1992. *Coalitions and Alliances in Humans and Other Animals*. Oxford: Oxford University Press.

Janzen, D. H. 1970. Altruism by coatis in the face of predation by *Boa constrictor*. *J. Mamm.*, **51,** 387–389.

Jeffreys, A. J., Wilson, V. & Thein, S. L. 1985a. Hypervariable 'minisatellite' regions in human DNA. *Nature, Lond.*, **314,** 67–73.

Jeffreys, A. J., Wilson, V. & Thein, S. L. 1985b. Individual-specific 'fingerprints' of human DNA. *Nature, Lond.*, **316,** 76–79.

Jenks, S. 1988. Behavioral regulations of social organization and mating in a captive wolf pack. Ph.D. dissertation, University of Connecticut.

Jones, C. S., Lessells, C. M. & Krebs, J. R. 1991. Helpers-at-the-nest in European bee-eaters (*Merops apoaster*): a genetic analysis. In: *DNA Fingerprinting: Approaches and Applications* (Ed. by T. Burke, G. Dolf, A. J. Jeffreys & R. Wolff), pp. 169–192. Basel: Birkhaüser Verlag.

Kaufmann, J. H. 1962. Ecology and social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. *Univ. Calif. Publ. Zool.*, **60,** 95–222.

Kays, R. W. & Gittleman, J. L. 1995. Home range size and social behavior of kinkajous (*Potos flavus*) in the Republic of Panama. *Biotropica*, **27,** 530–534.

Keane, B., Waser, P. M., Creel, S. R., Creel, N. M., Elliot, L. F. & Minchella, D. J. 1994. Subordinate reproduction in dwarf mongooses. *Anim. Behav.*, **47,** 65–75.

Leger, D. W. & Didrichsons, I. A. 1994. An assessment of data pooling and some alternatives. *Anim. Behav.*, **48,** 823–832.

Lehman, N., Clarkson, P., Mech, L. D., Meier, T. J. & Wayne, R. K. 1992. A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA. *Behav. Ecol. Sociobiol.*, **30,** 83–94.

Leigh, E. G., Jr, Rand, A. S. & Windsor, D. M. (Eds) 1982. *The Ecology of a Tropical Forest*. Washington, D.C.: Smithsonian Institution Press.

Lynch, M. 1990. The similarity index and DNA fingerprinting. *Molec. Biol. Evol.*, **7,** 478–484.

Lynch, M. 1991. Analysis of population genetic structure by DNA fingerprinting. In: *DNA Fingerprinting: Approaches and Applications* (Ed. by T. Burke, G. Dolf, A. J. Jeffreys & R. Wolff), pp. 113–126. Basel: Birkhäuser Verlag.

Machlis, L., Dodd, P. W. D. & Fentress, J. C. 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. *Z. Tierpsychol.*, **68,** 201–214.

Mech, L. D. 1970. *The Wolf*. Garden City, New York: Natural History Press.

Nöe, R. 1986. Lasting alliances among adult male savannah baboons. In: *Primate Ontogeny, Cognition, and Social Behaviour* (Ed. by J. G. Else & P. C. Lee), pp. 381–392. Cambridge: Cambridge University Press.

Packer, C. & Pusey, A. E. 1983. Cooperation and competition within coalitions of male lions: kin selection or game theory. *Science*, **221,** 1191–1193.

Packer, C., Gilbert, D. A., Pusey, A. E. & O'Brien, S. J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature, Lond.*, **351,** 562–565.

Reeve, K. K., Westneat, D. F. & Queller, D. C. 1992. Estimating average within group relatedness from DNA fingerprints. *Molec. Ecol.*, **1,** 223–232.

Rood, J. P. & Nellis, D. W. 1980. Freeze marking mongooses. *J. Wildl. Mgmt*, **44,** 500–502.

Russell, J. K. 1979. Reciprocity in the social behavior of coatis (*Nasua narica*). Ph.D. dissertation, University of North Carolina.

Russell, J. K. 1981a. Patterned freeze-brands with canned freon. *J. Wildl. Mgmt.*, **45,** 1078.

Russell, J. K. 1981b. Exclusion of adult male coatis from social groups: protection from predation. *J. Mamm.*, **62,** 206–208.

Russell, J. K. 1982. Timing of reproduction by coatis (*Nasua narica*) in relation to fluctuations in food resources. In: *The Ecology of a Tropical Forest* (Ed. by E. G. Leigh Jr, A. S. Rand & D. M. Windsor), pp. 413–431. Washington, D.C.: Smithsonian Institution Press.

Russell, J. K. 1983. Altruism in coati bands: nepotism or reciprocity? In: *Social Behavior of Female Vertebrates* (Ed. by S. K. Wasser), pp. 263–290. New York: Academic Press.

Smale, L., Holekamp, K. E., Weldele, M., Frank, L. G. & Glickman, S. E. 1995. Competition and cooperation between litter-mates in the spotted hyaena, *Crocuta crocuta*. *Anim. Behav.*, **50,** 671–682.

Southern, E. M. 1975. Detection of specific sequence among DNA fragments separated by gel electrophoresis. *J. molec. Biol.*, **98,** 513–517.

Vehrencamp, S. L. 1979. The roles of individual, kin, and group selection in the evolution of sociality. In: *Handbook of Behavioral Neurobiology* (Ed. by P. Marler & J. G. Vandenburgh), pp. 351–394. Plenum: New York.

de Waal, F. B. M. & Harcourt, A. H. 1992. Coalitions and alliances: a history of ethological research. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 1–19. Oxford: Oxford University Press.

Wayne, R. K., Gilbert, D. A., Lehman, N., Hansen, K., Eisenhawer, A., Girman, D., Peterson, R. O., Mech, L. D., Gogan, P. J. P., Seal, U. S. & Krumenaker, R. J. 1991. Conservation genetics of the endangered Isle Royale gray wolf. *Conserv. Biol.*, **5,** 41–51.

Westneat, D. F. 1993. Polygyny and extrapair fertilizations in eastern red-winged blackbirds (*Agelaius phoeniceus*). *Behav. Ecol.*, **4,** 49–60.

Wetton, J. H., Carter, R. E., Parkin, D. T. & Walters, D. 1987. Demographic study of a wild house sparrow population by DNA 'fingerprinting'. *Nature, Lond.*, **327,** 147–149.

Wilkinson, G. S. 1988. Reciprocal altruism in bats and other mammals. *Ethol. Sociobiol.*, **9,** 85–100.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75,** 262–300.

Wrangham, R. W. 1986. Evolution of social structure. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 282–296. Chicago: University of Chicago Press.

Wright, S. 1922. Coefficients of inbreeding and relationship. *Am. Nat.*, **56,** 330–338.

Wright, S. J., Gompper, M. E. & DeLeon, B. 1994. Are large predators keystone species in Neotropical forests? The evidence from Barro Colorado Island. *Oikos*, **71,** 279–294.

Xia, X. & Millar, J. S. 1991. Genetic evidence of promiscuity in *Peromyscus leucopus*. *Behav. Ecol. Sociobiol.*, **28,** 171–178.

Zabel, C. J., Glickman, S. E., Frank, L. G., Woodmansee, K. B. & Keppel, G. 1992. Coalition formation in a colony of prepubertal spotted hyenas. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 113–135. Oxford: Oxford University Press.