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Familiarity breeds progeny: sociality increases reproductive success in adult male ring-tailed coatis (*Nasua nasua*)

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Abstract

The ring-tailed coati (*Nasua nasua*) is the only coati species in which social groups contain an adult male year round, although most males live solitarily. We compared reproductive success of group living and solitary adult male coatis to determine the degree to which sociality affects reproductive success. Coati mating is highly seasonal and groups of female coatis come into oestrus during the same 1–2 week period. During the mating season, solitary adult males followed groups and fought with the group living male. This aggression was presumably to gain access to receptive females. We expected that high reproductive synchrony would make it difficult or impossible for the one group living male to monopolize and defend the group of oestrous females. However, we found that group living males sired between 67–91% of the offspring in their groups. This reproductive monopolization is much higher than other species of mammals with comparably short mating seasons. Clearly, living in a group greatly enhanced a male's reproductive success. At the same time, at least 50% of coati litters contained offspring sired by extra-group males (usually only one offspring per litter); thus, resident males could not prevent extra-group matings. The resident male's reproductive advantage may reflect female preference for a resident male strong enough to fend off competing males.

Keywords: coati, extra-pair paternity, mating success, *Nasua nasua*, paternity, reproductive skew, reproductive synchrony, sociality

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Introduction

Animals are predicted to live in groups if the benefits of group living exceed costs (Krause and Ruxton 2002). These costs and benefits of sociality can differ according to sex, leading to sexual segregation in some species (Conradt 1998; Ruckstuhl & Neuhaus 2002). Coatis (*Nasua spp.*) show strong patterns of sexual segregation: adult females live in groups while adult males typically live alone (Kaufman 1962; Smythe 1970; Russell 1982; Gompper & Krinsley 1992; Gompper 1995). By living alone, adult male coatis increase their foraging success but live under increased predation risk and in some cases have higher ectoparasite loads (Gompper 1996, 2004; Hass & Valenzuela 2002). Unlike the Central American species (*Nasua narica*), South American ring-tailed coati (*Nasua nasua*) social groups typically contain one adult male throughout the year, while other adult males live alone after dispersing from their natal group at 2 years of age (Alves-Costa *et al.* 2004; Resende *et al.* 2004, Hirsch 2007a,b; Costa *et al.* 2009; Olifiers *et al.* 2009). The presence of adult males in social groups could have important effects on the mating system and distribution of reproduction within and between groups of ring-tailed coatis.

In both coati species, adult males violently fight each other for access to receptive females during the short mating season (Kaufman 1962, Booth-Binczik *et al.* 2004, Hirsch 2007a). If an adult male is already associated with

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a social group, it may gain priority access to receptive females during the mating season. Because groups of adult female coatis are able to exclude individual adult males from dense food patches, females should be able to evict unwanted adult males from their group (Gompper 1996; Hirsch 2007b). Despite this ability, females in most ring-tailed coati groups allow a male to enter their group, even when male sociality does not appear to benefit the group as a whole. No examples of adult male parental care, such as protection from predators or food provisioning, have been observed in ring-tailed coatis (Di Blanco & Hirsch 2006; Hirsch 2007a,b). It is plausible that male sociality is a function of female choice. If this is true, one could predict that within-group males should have higher reproductive success compared to solitary males.

During the short 1–2 week mating season, an influx of solitary male ring-tailed coatis typically enters and follows the social group (Hirsch 2007a). Similar social-mating pattern has been found in some primate species such as patas (*Erythrocebus patas*) and blue monkeys (*Cercopithicus mitus stuhlmanni*) (Ohsawa *et al.* 1993; Cords 2000, 2002; Mugatha *et al.* 2006). Within-group male coatis often spend several hours per day chasing and fighting; these solitary males and adult males usually lose weight and receive numerous injuries during the mating season (Binzcik 2006; Hirsch 2007a). Because all within-group adult female coatis are simultaneously in oestrus, sequential mate guarding should be difficult or impossible; thus, reproductive skew should be low (Cant 1998; Reeve *et al.* 1998; Nunn 1999). High reproductive synchrony has been linked to low reproductive skew in multi-male mating systems and to increase extra-pair paternity in single-male mating systems (Stutchbury & Morton 1995; Stutchbury 1998; Westneat & Stewart 2003; Isvaran & Clutton-Brock 2007; Ostner *et al.* 2008). It has been hypothesized that reproductive synchrony functions to increase female mate choice and reduce the possibility that males can monopolize female reproduction (Emlen & Oring 1977; Stutchbury 1998; Ostner *et al.* 2008).

The social system of ring-tailed coatis differs with respect to many studies of reproductive skew and extra-pair paternity because coatis have one adult male per group and several females. In many mammals, the number of adult males in a group is highly correlated with the number of adult females and their degree of reproductive synchrony (Nunn 1999). Ring-tailed coati groups in Iguazu, Argentina, contain one adult male and 1–10 adult females year round; therefore, there is no possible link between the number of adult males and females in a group during most of the year. In this respect, ring-tailed coatis resemble harem groups (Heckel *et al.* 1999; Pemberton *et al.* 2002; Fabiani *et al.* 2004). To our knowledge, no examples of multiple adult males coexisting in a coati group outside the mating season have been reported. When group living males encounter solitary males, they usually fight them off; thus, coati groups may be limited to one adult male because of male–male aggression. Even though coatis do not exhibit a mating system that exactly replicates these extensively modelled systems, studies of other species can be used to construct hypotheses concerning reproductive success in ring-tailed coatis. The primary goal of this paper is to test the extent to which three nonmutually exclusive factors determine male reproductive success in ring-tailed coatis.

1 Do social males have higher reproductive success than solitary males?
If adult male coatis live in social groups year round to increase access to mates during the mating season, the number of offspring sired by social males should be higher than solitary males.

2 Do high levels of reproductive synchrony lead to low reproductive skew?
Reproductive synchrony should limit the degree to which a group living male can monopolize mating. Judging by comparable studies of other mammal species, the ring-tailed coatis' short mating season should prevent group males from siring most of their group's young (Isvaran & Clutton-Brock 2007; Ostner *et al.* 2008). To determine predicted values of within-group paternity in ring-tailed coatis, we looked at previous studies of mammal species that live in one-male or harem groups and exhibit short mating seasons (<2 months). Species that formed temporary harem breeding groups had between 40% and 75% within-group paternity (Le Boeuf and Reiter 1988, Hoelzel *et al.* 1999, Fabiani *et al.* 2004, JM Pemberton *et al.* unpublished data cited in Isvaran & Clutton-Brock 2007). In species that form more permanent social groups, within-group males sired between 30 and 50% of offspring (Heckel *et al.* 1999, Heckel *et al.* 2003, Ohsawa *et al.* 2003, Dechmann *et al.* 2005, Hatcher 2007). We therefore predict that the resident male should sire roughly 30–50% of its group's offspring.

3 Does the ratio of males to group living females influence reproductive skew?
As the number of females in a coati group increases, the number of satellite adult males following the group during the mating season should increase, and the ability of the lone within-group male to defend females and monopolize matings is predicted to decline.

Methods

The study was conducted in Iguazu National Park, Argentina (54°W, 26°S), between July 2002 and Decem-

ber 2004. A total of 150 coatis were captured in 32 × 10 × 12 inch Tomahawk or similar traps, immobilized with Ketamine and Xylazine and fitted with unique combinations of multicoloured ear tags for individual identification (Rototag ear tags, Dalton Co.). A small plug of skin tissue was punched out during ear tagging, and the tissue was stored in 10% DMSO saline solution. Samples were kept at room temperature between the date of capture and January 2005. The samples were stored in a −80 °C freezer from January 2005 until DNA extraction in August 2007.

Genetic sampling focused on four habituated social groups with overlapping home ranges (Hirsch 2007a). Demographic data and group censuses were typically taken at least once a month per group between June 2002 and December 2004. In this population, group sizes ranged from 8 to 65 individuals and group per years included in the paternity analyses ranged from 8 to 54; PQ 2002 = 8, 2003 = 15, GR/PSG 2002 = 54, PSG 2003 = 12, 2004 = 29, SF 2002 = 25 (Hirsch 2007a,b). In Iguazu, pregnant coatis gave birth to an average of approximately 4.5 offspring per year (range 2–7; Hirsch 2007a). All adult females in the study groups were sexually receptive during the mating season and appeared pregnant before the groups disbanded in the nesting season. Differences between the number of mated females and number of females with offspring were typically because of 100% mortality within a litter or the death of the mother.

During some years, it was possible to trap and sample every individual in a group, while in other years extensive sampling of some groups was not possible. All adult females and living offspring were captured in a total of five group years (PQ 2002, 2003, PSG 2002, 2003, SF 2002). The juveniles present in these groups were all born in October, but were typically not trapped until January to March of the following year (at ∼4–5 months of age); thus, some of the offspring died before we were able to sample them. Late in 2002, five adult females and their juvenile offspring split off from the GR group and formed a new group (PSG group). The 2002 PSG juveniles were sired while the mothers were still part of the larger GR group. During 2004, only 9 of 31 juveniles from the PSG group were captured and sampled.

Adult males, adult females and offspring were sampled in a total of five group mating seasons (PQ 2003, PSG 2002, 2003, 2004, SF 2002). Some males that were temporarily group members outside of the mating season were also sampled. In most cases, social adult males were not related to any adult females in their social group (B. T. Hirsch and J. E. Maldonado unpublished data). Males that were captured and tagged in their natal groups were observed entering neighbouring groups and were never observed residing in their natal group at adulthood (Hirsch 2007a). During the mating season (early-mid August), additional satellite adult males were observed following groups. The number of satellite adult males per coati group during the mating season was defined as the total number of adult males seen within 15 m of the social group while adult females were in oestrous. Because we were not able to simultaneously monitor all social groups and it was difficult or impossible to distinguish between unmarked solitary males, the number of males per group recorded during the mating season was likely an underestimate. We often discovered extra-group males when they fought with other adult males; thus, the number of observed males should have correlated closely with the amount of male–male aggression and presumably with the actual number of males attempting to mate. The maximum number of recognizable males observed within a group during the mating season was five males (SF 2003). Solitary males were also seen outside the mating season. Some of these solitary males were trapped and sampled, while others were not. A total of 11 adult males classified as putative fathers were captured and sampled. In some cases (N = 4), males were trapped as subadults (12–23 months old) in their natal group and later observed to be members of another group after they were fully mature males (typically when 3 years of age or older).

DNA purification was carried out using a Qiagen BioSprint 96 workstation following the protocol for DNA extraction from animal tissues as supplied by the manufacturer. All individuals were genotyped at 15 microsatellite loci (Ma3, Davis & Strobeck 1998; Pfl2, Pfl8, Pfl9, Kays *et al.* 2000; PLOT-01, PLOT-04, Fike *et al.* 2007; PLM12, PLM13, Siripunkaw *et al.* 2007; F03, H03, E05, H07, A08, F02, D03, Molecular Ecology Resources primer development consortium 2010). The polymerase chain reaction mixtures (25 μL) were composed of 1.5 μL template DNA, 2.5 μL Gold PCR Buffer, 3 μL $MgCl_2$, 2.5 μL dNTP's, 2 μL BSA, 2 μL Betaine, 1 μL fluorescently labelled forward and reverse primers, 0.15 μL Ampli*Taq* Gold DNA polymerase (Applied Biosystems) and 9.35 μL H_2O. In cases where reactions did not yield a product, the reaction was repeated with larger quantities of DNA (2–3 μL per reaction). Because of poor amplification, all PLM12 primer reactions contained 3 μL of stock DNA. Primers specifically designed for *Nasua nasua* (F03, H03, E05, H07, A08, F02, D03) with the same annealing temperature were multiplexed in the same PCR using 0.2–0.6 μL of each primer. PCRs began with an extended denaturation of 96 °C for 9 min, followed by 95 °C denaturation cycle for 45 s, a 45 s annealing cycle and then a 72 °C extension cycle for 45 s (annealing temperatures in Table 1). The last

Table 1 The 15 microsatellite loci used to determine paternity. A total of 149 individuals were typed. Temp equals annealing temperature in the PCR. Hobs and Hexp represent observed and expected Heterozygosity. Significant deviations from the Hardy–Weinberg equilibrium are indicated by asterisks. Locus-specific exclusion probabilities for the second parent are reported in the last column

	Temp	No. of alleles	Size	Ho	He	HW	Fnull	Exclusion
Ma3	58	3	153–157	0.557	0.498	NS	−0.058	0.806
Pfl2	56	2	148–150	0.154	0.218	**	0.170	0.903
Pfl8	57	5	194–202	0.497	0.492	NS	−0.026	0.723
Pfl9	53	5	205–217	0.584	0.663	**	0.067	0.614
PLOT-01	64	3	155–159	0.416	0.414	NS	−0.005	0.833
PLOT-04	64	5	333–347	0.685	0.698	NS	−0.003	0.546
PLM12	54–57	7	217–229	0.711	0.744	NS	0.023	0.500
PLM13	58	3	102–108	0.664	0.559	NS	−0.089	0.705
F03	60	5	109–119	0.423	0.396	NS	−0.038	0.777
H03	59	4	114–126	0.510	0.520	NS	0.014	0.733
E05	60	2	148–150	0.040	0.065	NS	0.213	0.969
H07	59	5	159–173	0.154	0.145	NS	−0.031	0.927
A08	59	7	213–225	0.718	0.736	NS	0.017	0.309
F02	58	2	203–205	0.564	0.501	NS	−0.061	0.813
D03	58	5	259–269	0.584	0.587	NS	0.003	0.655

three 45 s steps were then repeated 34 times, followed by a final 72 °C extension cycle of 10 min. For PLM12, we used a modified touchup PCR program. The initial 9-min 96 °C denaturation cycle was followed by a 1-min 95 °C denaturation cycle, then a 1-min annealing cycle, followed by a 72 °C extension cycle for 1 min. The annealing cycle started at 54 °C, then was raised one degree each step until the last step reached 57 °C. This cycle was repeated 15 times and then ended with a final 72 °C extension cycle of 10 min.

Products were electrophoresed through an ABI 3130xl genetic analyzer (Applied Biosystems, Inc., Foster City, CA.). Alleles were sized by comparison with concurrently run dye-labelled DNA size standards. Fragment size analysis was performed using the GeneMapper® software (Applied Biosystems), and each genotype was confirmed by visual inspection of the electropherograms. All samples were amplified and genotyped at least two times for each locus. Replicate genotyping was carried out to minimize problems associated with allelic dropout and misclassification of genotypes. If the initial two genotypes derived from a sample did not match, that sample was run two more times and the genotype was determined using a consensus of all four samples. We used the CERVUS 3.0 (Kalinowski *et al.* 2007) computer program to calculate whether the 15 loci conformed to Hardy–Weinberg equilibrium (Table 1). Two alleles that were not in Hardy–Weinberg equilibrium were included in the analysis because it was determined that their inclusion would not lead to an overestimation of within-group male paternity. Given that most alleles deviate from Hardy–Weinberg because of allelic dropout or null alleles and that these two alleles (Pfl2 and Pfl9) had null frequency values of 0.17 and 0.067, respectively, we believe there were no major issues with including these alleles in the analyses (Dakin & Avise 2004). In addition, there were no allele mismatches at these two loci between known mother–offspring pairs, which is evidence for a low frequency of allelic dropout at these loci. Tests for linkage disequilibrium were implemented in GENEPOP 4.0.10, and no statistically significant evidence for linkage disequilibrium between pairs of loci was found.

We used CERVUS 3.0 to determine paternity and maternity assignments of 76 juvenile coatis. Maternity was assigned using a total evidence approach, combining behavioural data (grooming rates between mothers and potential offspring) and genotyping (Prodohl *et al.* 1998; Slate *et al.* 2000). In the three cases where genetically assigned maternity did not match the mother predicted by grooming data, we examined LOD scores (combined likelihood ratios of parental assignment) and allele mismatches between the offspring and the predicted mother. In all three cases, the mother predicted using grooming data had a positive LOD score and no allele mismatches; so, we used the behavioural data to determine maternity in these cases, and not the mother assigned by CERVUS.

Paternity was calculated using trio LOD scores with known mothers. To simulate the expected probability of correctly determining the father at random from the Iguazu population, it was assumed that half of the adult

coatis in the population were sampled. This estimate was derived from the literature on adult sex ratios in *Nasua narica*, where an average of 5.63 males per social group has been reported (range 2.5–14)(Kaufman 1962; Russell 1979, Gompper *et al.* 1997; Hass 2002; Hass & Valenzuela 2002; Booth-Binczik *et al.* 2004; McColgin 2006). Given that a total of four groups and 11 adult males were captured and sampled in Iguazu, a 50% adult male capture rate was determined to be a reasonable estimate. The combined exclusion probability for the second parent was 0.993. Both relaxed and strict trio LOD estimates were calculated based on a simulation of 10 000 offspring with 15 loci and 2.75% mistyped loci (80% critical trio LOD = 0.00, strict 95% critical trio LOD = 2.12). The percentage of mistyped loci entered into the model was based on the observed frequency derived from CERVUS. In cases where the within-group male was known and no father was assigned, it was assumed that the offspring was sired by an extra-group male. Original least square (OLS) regressions were calculated to determine whether the percentage of within-group paternity per year was related to the number of adult females, number of pregnant females, number of males and male/female ratio (JMP 5.1.2; SAS Institute). We also ran these analyses with the percentage of multiple paternity litters as the dependent variable. Because the dependent variables were percentages, we logodds transformed the data before running the analyses to better conform to assumptions of normality.

Results

Likelihood analyses resulted in paternity assignments for 42 of the 74 typed offspring with 95% confidence (56.8% assignment) and 59 of 74 at 80% confidence (79.7% assignment)(Table 2). Of these assigned offspring, five were assigned to an extra-group male (offspring: AK, AE, AM, CU, and c10). If offspring were sired by adult males that were never sampled, using only assigned offspring would lead to an overestimate of within-group paternity (40 of 42 = 95.2% within-group male paternity). If all offspring who were not assigned to the within-group male using the 80% or 95% probability are classified as extra-group offspring, the percentage of within-group paternity ranged between 66.7% and 91.3% using 80% confidence and 44.4–66.7% with 95% confidence. We regard the 95% confidence results as the absolute minimum level of within-group paternity. Because males assigned at the 80% level but not at the 95% level often had zero allele mismatches between father and offspring ($N = 5$) and had at most one mismatch, we regard the 80% criteria as the most robust measure of paternity for this study.

The proportion of within-group paternity (using the 80% assignments) was not correlated with the number of adult females or adult females with living offspring from that group year (OLS regression: number of females; $F_{1,5} = 0.215$, slope = −0.096, $P = 0.675$, number of mothers; slope = −0.073, $F_{1,5} = 0.118$, $P = 0.754$). Within-group paternity was also not significantly correlated with the number of males observed with the group during the mating season or the ratio of observed males to within-group females, but the effect slopes were in the predicted negative direction in both cases (OLS regression: number of males; slope = −0.577, $F_{1,5} = 4.650$. $P = 0.120$, male-female ratio; slope = −5.067, $F_{1,5} = 0.537$, $P = 0.083$).

Multiple paternity was found in at least 9 of 17 litters (53%). During some group years, juveniles were trapped several months after the birth season and several juveniles probably died before being sampled (details in: Hirsch 2007a). If paternity analyses are restricted to 2003, when almost all of the litters were completely sampled, four of eight litters had more than

Table 2 The percentage of offspring fathered by within-group males versus extra-group males. The number of mated females represents the number of adult females in the group during the mating season that could have mated. The number of mothers includes females whose offspring survived the nesting season. Males per group were calculated based on the number of social and extra-group males observed within 15 m of the social group during the mating season. Juveniles that died before being captured and sampled for DNA were not included in the table

						# Fathered within-group		% Within-group paternity	
Group	Year	# Mated ♀	# Moms	# Males	# Offspring	95%	80%	95%	80%
PQ	2003	5	5	1	23	13	21	0.565	0.913
PSG	2002	9	2	2	6	4	5	0.667	0.833
PSG	2003	5	3	1	15	9	12	0.600	0.800
PSG	2004	7	5	3	9	4	6	0.444	0.667
SF	2002	≥6	6	2	12	9	9	0.750	0.750
Total					**65**	**39**	**55**	**0.600**	**0.815**

Table 3 Paternity assignments for six coati group years. Year indicates the year of birth of the offspring

Offspring	Mother	Pair AM	Pair LOD	Candidate father	Group male	Pair AM	Pair LOD	Trio AM	Trio LOD	Trio Δ LOD	Within-group male
PQ 2002											
AA	AY	2	−3.961	VI	?	1	−1.245	4	−2.967	5.135	?
AK	AY	0	1.661	VI	?	1	−0.444	1	1.810	11.644	No
LW	AY	0	2.617	VI	?	1	−0.823	2	−2.981	5.801	?
SB	AY	1	−0.721	OB1	?	2	−3.882	3	−3.470	0.417	?
PB	GZ	1	−0.843	VI	?	1	−2.090	3	−3.420	5.287	?
PU	GZ	0	6.070	TV	?	1	−2.494	2	−2.082	1.089	?
CC	MA	0	7.535	TV	?	2	−6.636	2	−4.448	0.112	?
CL	MA	0	7.736	VI	?	1	−0.706	1	−2.251	5.369	?
TC	MA	0	3.590	EH	?	3	−6.234	4	−8.604	0.406	?
PQ 2003											
AD	(AN)	0	0.343	OB1	OB1	0	3.876	0	4.264	9.378	***
JK	(AN)	0	1.402	OB1	OB1	0	4.602	0	6.367	13.518	***
OV	(AN)	0	−0.840	OB1	OB1	0	2.676	1	0.645	1.177	*
RR	(AN)	0	−0.430	OB1	OB1	0	4.049	1	4.077	11.118	***
DI	AY	0	2.163	OB1	OB1	0	2.388	2	0.125	2.118	*
GD	AY	0	3.290	OB1	OB1	0	2.715	0	5.644	10.815	***
RQ	AY	0	1.976	MD	OB1	2	−6.194	2	−2.927	1.886	No
SV	AY	0	4.661	OB1	OB1	0	0.677	1	0.724	3.219	*
ED	DA	0	2.428	OB1	OB1	0	0.275	0	4.829	9.674	***
OZ	DA	0	2.172	OB1	OB1	0	1.551	1	4.218	10.894	***
RY	DA	0	1.512	OB1	OB1	1	−1.652	2	0.191	8.705	*
SZ	DA	0	4.969	OB1	OB1	0	0.275	0	4.876	9.725	***
AL	GZ	0	−0.283	OB1	OB1	1	−0.032	2	0.822	13.843	*
JF	GZ	0	4.483	OB1	OB1	0	−0.282	1	0.689	5.162	*
LO	GZ	0	−0.226	OB1	OB1	0	1.383	1	4.534	14.645	***
MM	GZ	0	1.864	OB1	OB1	0	1.716	1	4.164	11.901	***
OG	GZ	0	0.341	OB1	OB1	0	2.898	1	5.234	15.489	***
RX	GZ	0	3.108	OB1	OB1	0	1.383	0	6.757	14.460	***
SN	GZ	0	3.383	OB1	OB1	0	2.222	1	4.307	7.734	***
AE	MA	0	5.022	DaMale	OB1	1	−1.745	1	2.242	3.646	No
GL	MA	0	4.937	OB1	OB1	1	−2.455	1	0.686	5.867	*
TL	MA	0	5.507	OB1	OB1	0	1.324	0	4.738	11.138	***
VL	MA	0	3.586	OB1	OB1	0	3.479	0	7.313	12.640	***
PSG 2002											
JS	GH	0	4.228	VI	VI	0	2.172	0	5.228	13.062	***
SX	GH	0	3.369	VI	VI	2	−4.760	2	−2.350	2.562	No
TM	GH	0	3.067	VI	VI	0	1.593	0	4.482	12.925	***
BS	PS	0	0.879	VI	VI	0	1.902	0	5.779	12.097	***
DM	PS	0	2.413	VI	VI	0	1.848	0	5.239	10.599	***
KG	PS	0	2.713	VI	VI	1	−1.660	1	1.113	11.009	*
PSG 2003											
AS	CM	0	5.447	VI	VI	0	3.045	0	3.833	12.355	***
CV	CM	1	0.396	VI	VI	1	−0.557	1	3.424	11.121	***
IB	CM	0	4.313	VI	VI	1	1.461	1	2.552	0.243	***
KH	CM	0	4.880	VI	VI	0	0.621	1	1.155	0.443	*
ZS	CM	0	3.674	VI	VI	0	3.852	0	6.373	16.337	***
AM	GH	0	7.093	VV	VI	1	−0.022	1	1.211	5.739	No
BJ	GH	0	2.818	VI	VI	0	0.140	1	2.910	12.320	***
BO	GH	0	2.718	VI	VI	0	2.245	0	5.570	13.461	***
DH	GH	0	3.382	VI	VI	0	2.773	0	5.938	16.409	***
ES	GH	0	4.319	VI	VI	1	−2.761	1	0.599	3.849	*
BK	NY	0	1.483	VI	VI	1	−0.752	1	0.497	3.226	*
BM	NY	1	1.847	VI	VI	1	−0.638	2	−0.476	0.272	No
IP	NY	0	1.245	OB1	VI	1	0.345	2	−1.866	4.030	No

Table 3 (Continued)

Offspring	Mother	Pair AM	Pair LOD	Candidate father	Group male	Pair AM	Pair LOD	Trio AM	Trio LOD	Trio Δ LOD	Within-group male
RO	NY	1	1.830	VI	VI	0	0.218	1	2.771	8.009	***
RS	NY	0	3.811	VI	VI	0	0.894	0	2.772	1.669	***
PSG 2004											
c1	BS	0	2.907	VI	VI	0	3.917	0	2.301	1.037	***
c9	CM	0	2.521	VI	VI	0	1.955	0	2.464	3.790	***
c10	JW	0	6.033	BF	VI	0	5.212	0	7.920	9.588	No
c2	JW	0	6.416	VI	VI	0	2.459	0	5.435	16.184	***
c5	PS	0	1.532	VI	VI	1	−2.757	1	0.189	2.369	*
c6	PS	0	2.395	MD	VI	2	−4.266	2	−3.388	0.178	No
c7	PS	0	0.792	VI	VI	0	1.845	0	5.369	10.813	***
c3	SX	0	3.160	VI	VI	2	−4.157	2	−3.027	3.990	No
c8	SX	0	1.519	VI	VI	1	−0.918	1	0.473	0.700	*
SF 2002											
KK	BR	0	3.629	WW	WW	0	4.046	1	3.928	7.482	***
MH	BR	0	0.956	WW	WW	0	4.931	1	4.726	7.106	***
CU	EK	0	3.889	IK	WW	1	−1.813	2	0.181	3.992	No
LS	EK	1	0.222	MD	WW	2	−4.130	3	−3.782	1.652	No
BT	LD	0	2.317	WW	WW	0	6.930	1	5.613	12.078	***
RW	MN	0	4.494	MD	WW	2	−2.194	4	−7.480	0.492	No
SR	MN	1	1.105	WW	WW	0	3.691	2	3.600	6.641	***
JL	MS	0	0.377	WW	WW	0	6.579	2	5.005	14.791	***
MG	SL	0	2.071	WW	WW	0	6.696	1	6.372	8.858	***
PK	SL	0	5.579	WW	WW	0	2.333	0	4.361	2.352	***
TR	SL	0	2.072	WW	WW	0	4.457	1	4.166	7.664	***
ZO	SL	1	2.694	WW	WW	0	2.647	2	2.207	4.538	***

AM, number of allelic mismatches. Group males were observed to be incorporated into the social group during the mating season. ***Strict 95% confidence, *relaxed 80% confidence. ? indicates unknown individual.

one father. In seven cases where multiple paternity was detected, only one offspring in the litter was fathered by a solitary male (Table 3). In one case, two of five offspring in a litter were sired by extra-group male(s) (female NY during 2003). We were not able to determine whether the same solitary male fathered more than one offspring in the same group or any other group during the same mating season. This might have occurred, but this was not possible to confirm without a complete sampling of potential fathers. There were no significant correlations between group size, the number of females or the male/female ratio on the percentage of multiple litters in a group (all P values 0.888). The relatively high levels of multiple paternity are evidence that most females were mating with multiple males.

Discussion

Do social males have higher reproductive success than solitary males?

Groups of ring-tailed coatis generally had low levels of extra-group paternity, even though many litters had one offspring fathered by an extra-group male. Within-group paternity was between 66.7% and 91.3% per group/year using the relaxed 80% probability. No solitary male sampled in this study came close to approaching the reproductive success of the social males. All five offspring assigned to extra-group males at the 80% confidence level were assigned to different fathers (VI, DaMale, VV, IK and BF) and there was no evidence that any one extra-group male sired large numbers of offspring (Table 3). Because of the high degree of breeding synchrony between groups at the study site, it would be difficult or impossible for a solitary male to mate with enough females from different groups to achieve similar or greater mating success than social males. This result is strong evidence that social males have higher reproductive success than solitary males.

Do high levels of reproductive synchrony lead to low reproductive skew?

Levels of mating success for the social males were higher than predicted for a species with high reproductive synchrony and ample opportunities for extra-group copulations (we predicted values ≤50%). Two recent

studies using phylogenetic comparisons found that reproductive skew was lower and extra-group paternity higher in populations with greater reproductive synchrony (Isvaran & Clutton-Brock 2007, Ostner *et al.* 2008). This relationship is consistent with incomplete control models of reproductive skew which predict that a main factor driving reproductive skew is the ability of dominants to monopolize access to females and prevent other males from mating with them (Altmann 1962; Cant 1998; Clutton-Brock 1998; Reeve *et al.* 1998). Short reproductive seasons generally lead to a high degree of overlap in female oestrous periods, which means that dominant or within-group males must defend more than one female at the same time (but see Wimmer & Kappeler 2002). Current models of reproductive skew cannot explain the reproductive success of group living male ring-tailed coatis.

Does the number females and males influence reproductive skew?

An increase in the number of females that are simultaneously in oestrus should lead to a decrease in male monopolization and reproductive skew (Nunn 1999; Isvaran & Clutton-Brock 2007, Ostner *et al.* 2008). A trend was found that within-group paternity decreased as the number of male to female coatis increased, but this was not statistically significant, which was likely because of the low sample size ($n = 5$ group years). During the mating season, adult males often engaged in vicious fights for access to adult females. At the end of the mating season, adult males typically had noticeable weight loss and severe cuts and wounds on their body. Even though within-group males sired the majority of offspring, multiple paternity was found in a minimum of 50% of litters. These litters, however, normally contained only one offspring of an extra-group male. Many females engaged in extra-group copulations, suggesting that the resident male could not prevent such matings. Yet these matings did not lead to high levels of extra-group paternity: did adult females choose to mate with resident males when they were most likely to conceive?

Mechanisms leading to high mating success in social male coatis

The mechanisms that led to high reproductive success in social male coatis are not clear. Social males may try to outcompete solitary males using sperm competition, which should result in coatis having large testes compared to other mammals (Parker *et al.* 1997; Soulsbury 2010). Even after considering that male coatis exhibit larger testicular volumes during the mating season, the relative testicular volume in coatis is not larger than average for carnivores (Binzcik 2006; Iossa *et al.* 2008). In general, coati copulations were not brief and pairs were observed to mate for more than 55 min, which is similar to *Nasua narica* (Hass & Roback 2000). This behaviour could be related to induced ovulation, although it is not known if coatis are induced or spontaneous ovulators (Hass & Roback 2000; Lariviere & Ferguson 2002, Lucero *et al.* 2007; Iossa *et al.* 2008). These lengthy copulatory bouts likely make sneaky mating more difficult and increase the probability of mating interruption. If within-group males are able to mate with females at will, they should have a lower risk of being interrupted and can copulate with females for the sufficient length of time needed to induce ovulation. Alternatively, extra-group males that need to fight the social male for access to females may not be able to mate at will. This hypothesis is complicated by observations that females often leave their group to mate with extra-group males, which has also been observed in *N. narica* (Hass & Roback 2000; Booth-Binczik *et al.* 2004). By leaving their group, females are able to mate with extra-group males and lower their risk of being interrupted. If ring-tailed coatis are spontaneous ovulators, within-group males may be able to determine the time of ovulation from olfactory cues. Because within-group males have more contact with adult females, it is possible that they have better knowledge about the ideal time for reproduction and are able to outcompete extra-group males using these cues. Alternatively, females may be able to choose when they mate with various males and the high reproductive success of social males could result largely from female mate choice.

There are strong reproductive benefits to sociality in male ring-tailed coatis, although the exact mechanisms for this are unclear. It is also uncertain why adult males are found in groups year round. Presumably, adult males can only enter coati groups if females allow it. When the mating season starts, adult females may have already chosen a highly desired adult male to enter their group. The exact traits that are desired or selected for by adult females are unclear, but it appeared that within-group males were larger and better fighters than extra-group males. Because adult males typically fight when they meet, social males may have their competitive ability tested several times a year outside the mating season. If resident social males are chiefly responsible for excluding other adult males from social groups, this aggression would limit the number of social males in the population. It is notable that no coati groups have been observed with more than one adult male simultaneously living in the group outside the mating season. It seems plausible that adult male brothers or other close kin could form a coalition to enter

and remain in a social group, but this has never been observed. Adult males are typically extremely aggressive towards each other year round and this extreme antagonism may make it impossible for coatis to form multi-male groups. If only the best fighters can be social, sociality may serve as a signal of male fitness. Females may preferentially mate with these well-tested adult males, or mate with social males closer to the time of ovulation. Social males may be more knowledgeable of group movement patterns and female reproductive status than solitary males. This could give social males an advantage over their competitors.

Even though social males have higher reproductive success compared to extra-group males, this sociality comes at a cost. Social adult males are often excluded from defensible food patches (Gompper 1996; Hirsch 2011a,b). Also, the cost of fighting other adult males is visible in the form of numerous injuries and pronounced weight loss during the breeding season. Presumably, these costs are outweighed by the increased reproductive success documented by our study, although it is not known whether asocial males have longer lifespans. It is also unclear how and why species level differences in coati male sociality arose.

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