

RESEARCH ARTICLE

Male Reproductive Strategies in Black and Gold Howler Monkeys
(*Alouatta caraya*)LUCIANA I. OKLANDER^{1,2,3*}, MARTIN KOWALEWSKI^{1,4}, AND DANIEL CORACH^{1,3}¹CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina), Puerto Iguazú, Misiones, Argentina²IBS (Instituto de Biología Subtropical), Facultad de Ciencias Forestales, Universidad Nacional de Misiones, Puerto Iguazú, Misiones, Argentina³SDHG (Servicio de Huellas Digitales Genéticas), Facultad de Farmacia y Bioquímica, Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, Argentina⁴EBCo-MACN (Estación Biológica Corrientes, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'), Corrientes, Argentina

Behavioral and demographic factors such as group size, social structure, dispersal patterns, and mating systems affect male reproductive success. In the present study, we analyze the relationship between social structure, genetic relatedness of adult males and offspring paternity in one population of *Alouatta caraya* inhabiting a continuous forest in Northern Argentina. After 14 months of behavioral studies and genotyping 11 microsatellites, we found that dominant or central males achieved greater mating success and fathered all the offspring conceived during our study in two multimale–multifemale groups (both including three adult males). Although skewed toward the dominant males, females copulated with almost all resident males and with extra group males. We found significantly fewer agonistic interactions between adult males in the group with fewer females and where males were more genetically related to each other (average relatedness $r = 0.237$; 0.015 int/ind/hr vs. $r = 0.02$; 0.029 int/ind/hr). Paternity was also analyzed in two other neighboring groups which also showed strong skew to one male over a 2-year period. These results reveal that even though female black and gold howlers mate with many males, infants are typically fathered by one dominant male. *Am. J. Primatol.* 76:43–55, 2014. © 2013 Wiley Periodicals, Inc.

Key words: *Alouatta*; dominance hierarchies; reproductive success; microsatellites; population genetics

INTRODUCTION

Sexual selection theory predicts that males will compete actively for access to females and fertilizations, as females are usually a limited resource [Clarke et al., 2009; Paul, 2002; Smuts & Smuts, 1993; Trivers, 1972]. This may result in male–male relationships characterized by competition, intolerance, and dominance hierarchies [Cowlshaw & Dunbar, 1991; Kappeler & van Schaik, 2002; van Hooff, 2000; Wang & Milton, 2003]. Although fertilizations cannot be shared among males, increasing social tolerance among resident males is possibly related to benefits derived from indirect inclusive fitness and/or male–male negotiation of favors (i.e., reproductive benefits for support given during intergroup encounters or collective defense of resident males) [Garber & Kowalewski, 2011; Silk, 2006]. In general, kin relationships may influence the degree of agonistic behavior between individuals [Chapais et al., 2001].

In *Alouatta caraya*, as in many New World primate species, several adult males may co-reside in the same social group (*A. caraya* [Kowalewski &

Garber, 2010], *Brachyteles hypoxanthus* [Strier et al., 2002]; *Ateles paniscus* [Symington, 1990]; *Alouatta palliata* [Wang & Milton, 2003]). However, *Alouatta* males usually engage in inter- and intra-group competition for resident females especially during female fertile periods [Di Fiore et al., 2011; van Belle et al., 2008]. In the present study, we analyze male social structure and genetic relatedness in one population of *A. caraya*. Specifically, we

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*Correspondence to: Luciana I. Oklander, Bertoni 85, Puerto Iguazú, Misiones, Argentina. E-mail: lulaok@gmail.com

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investigate the relationship between male dominance hierarchies, mating success and reproductive success in multimale groups of black and gold howler monkeys.

In most multimale/multifemale primate groups, promiscuous copulation occurs, with a pronounced skew in male mating success as a function of dominance rank or central position [Cowlshaw & Dunbar, 1991; Paul, 1997; Pope, 1990; van Belle et al., 2009]. Therefore, the maintenance of social dominance hierarchies and/or central positions is expected to play an important role in the access to fertile females [Altmann, 1962; Boesch et al., 2006; Constable et al., 2001; De Ruiter & van Hooff, 1993; Dixson, 1998; Jones, 1985; Ryan et al., 2008]. Although mating success is often correlated with dominance in multimale groups, mating success is not necessarily translated directly into male reproductive success or paternity success [Altmann et al., 1996; Constable et al., 2001]. Therefore, to test hypotheses on reproductive skew, the relationship between social dominance hierarchies/male centrality and paternity success, it is necessary to combine behavioral and genetic studies. These types of studies have been successful in several primate species and, in general, have demonstrated a positive correlation between high male rank and paternity (e.g., *Papio cynocephalus* [Altmann et al., 1996], *Pan troglodytes* [Constable et al., 2001], *Pan paniscus* [Gerloff et al., 1999], *Cercocebus torquatus* [Gust et al., 1998], *Semnopithecus entellus* [Launhardt et al., 2001], *Alouatta arctoidea* [Pope, 1990]). However, studies in macaques suggest that there is no direct relationship between dominance and paternity and it may be greatly diminished in species with weak hierarchies or centrality [Paul, 2004].

Both sexes of *Alouatta* typically disperse from their natal social groups but often at different ages [Crockett & Pope, 1993; Glander, 1980; Oklander et al., 2010; Rumiz, 1990]. In this regard, many individuals are likely to spend a large portion of their adult lives in groups without close kin [Di Fiore et al., 2011]. Previous studies showed that most adult individuals of the study population that belong to the same group are not closely related (average r within groups $r = 0.118$), but in some groups females related as sisters or half-sisters and males related as brothers or half-brothers were found [Oklander et al., 2010].

In Argentina, *A. caraya* shows differences in density and social organization in different types of habitat such as fragmented, gallery, and flooded forests. Multimale groups are present at higher frequencies in flooded and continuous forests than in fragmented and gallery forests [Kowalewski & Zunino, 2004; Rumiz, 1990]. In our study population, the average number of adult males per group was 2.1 ± 0.7 (range 1–3), and the average number of adult females was 3.1 ± 0.9 (range 2–4) [Oklander et al., 2010]. These groups frequently engaged in

intergroup encounters (almost twice a day), making the support of other resident males a potentially important benefit to trade for access to females [Garber & Kowalewski, 2011; Kowalewski, 2007]. Black and gold howler male tenure in this species is relatively short (4 ± 1 years [Kowalewski & Garber, 2010]). Solitary males or male coalitions may try to enter in a group by confronting the resident central male who can defend the group with the support of other resident males [Kowalewski, 2007; Oklander, 2007]. If a new male enters in a group, the event is usually followed by infanticide [Pavé et al., 2012]. We also witnessed, in one occasion, a resident male taking over the group displacing the central male [Kowalewski, 2007; Oklander, 2007]. *Alouatta caraya* females at our study site engage in fertile (during ovulation) and non-fertile copulations (e.g., during gestation and lactation) with resident and non-resident males [Kowalewski & Garber, 2010] and births occurred throughout the year [Kowalewski & Zunino, 2004]. Conspicuous behavior during females' fertile periods, such as mate guarding, characterize short periods of high within-group male–male interference (e.g., persistent following of a female at close range for 2–3 days [Kowalewski & Garber, 2010]).

The present study combines behavioral studies over 14 months and genetic analyses in multimale–multifemale groups of black and gold howler monkeys in order to determine male (1) dominance hierarchies (2) relatedness within groups (3) mating success, and (4) paternity success. Based on previous observations of mate guarding and asynchronous births within groups [Kowalewski, 2007; Kowalewski & Garber, 2010; Kowalewski & Zunino, 2004; Oklander, 2007], we predict that there will be a male dominance hierarchy in which higher ranked/central males will father most of the offspring in their resident group. We expect that higher ranked/central males will obtain most of the matings, however we also predict that alpha males will not monopolize copulations because: (1) dominant males allow lower ranking males to copulate in order to gain support during intergroup encounters and male incursion attempts and/or (2) risk of infanticide, and the fact that females copulate during gestation and lactation, suggests that females might choose to mate with subordinate males in order to confuse paternity [Garber & Kowalewski, 2011; Kowalewski & Garber, 2010; Oklander et al., 2010]. We also expect that closely related males will have lower levels of male–male agonistic interactions indicating greater male–male tolerance within groups.

METHODS

Study Site

We studied black and gold howler groups inhabiting flooded forests of the “Brasilera” Island located at $27^{\circ} 20' S$, $58^{\circ} 40' W$, near the confluence of

the Paraná and Paraguay rivers, in the northeast of Chaco Province, Argentina. The island has an area of 292 ha, is characterized by a subtropical climate (average annual temperature: 21.6°C, annual rainfall average: 1,200 mm, Servicio Meteorológico Nacional) and does not contain any permanent human settlements. The continuous forest allows the coexistence of multimale and multifemale black and gold howler groups that overlap home ranges up to 60–75% [Oklander et al., 2010]. A more complete description of the site and location of study groups are provided elsewhere [Kowalewski & Garber, 2010; Kowalewski & Zunino, 2004].

Behavioral Studies

We conducted behavioral studies on two multimale groups (Group G and Group X). Group G had ten individuals, and Group X had nine. One infant was born in each group during the study and one more was born in Group X after the end of the study (Table I). Both groups had three adult males. Group G had four adult females and three juveniles, while Group X had two adult females and four juveniles (Table I). Individuals were classified by age-sex classes following Rumiz's criteria [1990]. Members

TABLE I. Composition of Study Groups

Age class	Sex	Name	Focal hours per sampling period	Total focal hours (five sampling periods)	
Group G	Adult	Male	Marley ^a	70	350
			Jose ^a	70	350
			Quique ^a	70	350
	Adult	Female	Lola	0	0
			Orejas ^a	0	0
			Tamara	0	0
			Monga	0	0
	Juvenile	Male	Hermoso	0	0
			Julio ^a	0	0
			Alf ^a	0	0
Infant		Turko ^{a,b}	0	0	
Group X	Adult	Male	Gatti ^a	70	350
			Chao ^a	70	350
			Jesus ^a	70	350
	Adult	Female	Josefa	0	0
			Ana ^a	0	0
	Juvenile	Male	Primo ^a	0	0
			Toby	0	0
			Lisa	0	0
	Infant		Gorda ^a	0	0
			Cozi ^{a,c}	0	0
Bz ^{a,d}			0	0	

^aSampled individuals.

^bBorn May 2002.

^cBorn April 2002.

^dBorn after the end of the study in February 2003.

of the groups were habituated and marked with color anklets and ear tags.

We collected behavioral data over a 14-month period running from September 2001 to October 2002, during five separated sampling periods of 2 weeks to obtain information across the four seasons (Summer 2002, Autumn 2002, Winter 2002, and Spring 2001 and 2002).

Behavioral data were derived using a continuous focal sampling technique [Altman, 1974] on each adult male over a 30 min period throughout the day in the five sampling periods. These focal samples represent 2,100 hr of observation (Table I). We recorded the focal male's activity (e.g., grooming, feeding, resting, moving, dyadic agonistic interactions and copulations) and the identity of all neighbors within 5 m. We discarded focal samples if we lost visible contact with the individual for more than 5 min. The following dyadic agonistic interactions between each adult male and all members of their group were recorded:

Aggressive interaction: physical assault, threats, chases, fights, wrestling and howling.

Supplantation: when an animal retreats at the approach of another animal and the other animal occupies the space previously occupied by the retreating animal [Whitten, 1983].

Avoidance: Seemingly voluntary movement taken by some individuals in order to avoid other individuals. The approaching animal did not occupy the space of the retreating animal.

For all these interactions, we recorded the direction (actor-recipient) to determine the relative position of each individual in the hierarchy. The repeated pairwise encounters in 5-min segments were considered as a single agonistic interaction.

We recorded the number of copulations that each male achieved in every sampling period. Copulation was scored when we observed a mounting, intromission, and a thrusting sequence [Jones, 1985; Kowalewski & Garber, 2010; Strier, 1997]. Information on the behavioral contexts in which matings occurred was obtained from the focal sampling and with ad libitum notes (Table II). Each adult male was being sampled by a different observer simultaneously: therefore we are confident that we recorded all copulation events within groups during each sampling period.

Data Analysis

Dominance hierarchies

Dominance relationships develop from repeated contests within dyads [Drews, 1993; Wittig & Boesch, 2003]. Dominance rank among males was determined by means of dyadic interaction matrices made with pooled focal observation data for each season [Altman, 1974; Lehner, 1996]. Separate matrices were constructed for each sampling period

TABLE II. Detailed Copulation Events in Each Group and Season

Season	Date	Male	Female	Mutual pre-copulatory grooming	Male neighbors within 5 m	Mate guarding	Aggression between males	
Group G								
Spring 1	12/09/2001	Marley	Tamara	x	No			
	12/09/2001	Marley	Tamara		No	x		
	13/09/2001	Jose	Tamara	x	No			
	15/09/2001	Marley	Orejas		No			
	17/09/2001	Marley	Orejas		No			
	17/09/2001	Marley	Orejas		No			
	18/09/2001	Quique	Tamara		No			
	18/09/2001	Marley	Orejas		No			
	18/09/2001	Marley	Orejas	x	Jose	x		
	18/09/2001	Marley	Orejas		No	x	x vs. Quique	
	19/09/2001	Quique	Tamara		No			
Summer	07/01/2002	Marley	Tamara		No			
	08/01/2002	Marley	Tamara	x	No			
	08/01/2002	Marley	Tamara	x	No			
	08/01/2002	Jose	Monga	x	No			
	11/01/2002	Marley	Lola		No	x	x vs. Jose	
	11/01/2002	Marley	Lola		No			
	12/01/2002	Marley	Lola		No			
	13/01/2002	Quique	Monga		No			
	15/01/2002	Quique	Lola		No			
	15/01/2002	Quique	Lola		No			
	15/01/2002	Quique	Lola		No			
	16/01/2002	Jose	Tamara		No			
	16/01/2002	Marley	Lola		No			
	Autumn	27/03/2002	Quique	Tamara	x	No		
		29/03/2002 ^a	Quique	Tamara		No	x	x vs. Marley
29/03/2002 ^b		Marley	Orejas		No			
29/03/2002 ^{a,b}		Marley	Tamara	x	No			
Winter	31/03/2002	Marley	Tamara		No			
	28/07/2002	Jose	Lola		Quique			
	30/07/2002	Quique	Lola		No	x	x vs. Jose	
Spring 2	30/07/2002	Marley	Orejas		No	x		
	30/07/2002	Marley	Orejas		No			
	05/10/2002	Marley	Monga		No			
	06/10/2002 ^a	Quique	Monga		No	x	x vs. Marley	
	06/10/2002 ^a	Marley	Monga		No	x	x vs. Quique	
	06/10/2002 ^a	Marley	Monga		No			
	09/10/2002	Marley	Lola		No			
	10/10/2002	Marley	Lola		Jose			
10/10/2002	Marley	Lola	x	No				
11/10/2002	Marley	Lola	x	No				
12/10/2002	Jose	Tamara	x	No				
Group X								
Spring 2	11/09/2001	Gatti	Ana		No			
	11/09/2001	Gatti	Ana	x	No			
Summer	07/01/2002 ^a	Chao	Josefa	x	No			
	07/01/2002 ^a	Chao	Josefa	x	No			
	07/01/2002 ^a	Gatti	Josefa		No			
	09/01/2002	Gatti	Ana		No			
	08/01/2002	Chao	Tamara		No			
	08/01/2002	Chao	Tamara		No			
	08/01/2002	Gatti	Orejas		No			
	09/01/2002	Gatti	Orejas		No			

TABLE II. Continued

Season	Date	Male	Female	Mutual pre-copulatory grooming	Male neighbors within 5 m	Mate guarding	Aggression between males
Winter	24/07/2002	Chao	Josefa		No		
	24/07/2002	Chao	Josefa		No		
	25/07/2002	Gatti	Josefa		No		
	26/07/2002	Gatti	Josefa		No		
	27/07/2002	Chao	Josefa		No		
	28/07/2002	Chao	Josefa		No		
Spring 2	04/10/2002	Gatti	Josefa		No		
	05/10/2002	Gatti	Josefa		Jesus		
	05/10/2002	Gatti	Josefa	x	No		
	06/10/2002	Gatti	Tamara		No		

Bold: extra-group copulations.

^aTwo males copulating with the same female on the same day.

^bOne male copulating with two females on the same day.

to detect the possibility of rank reversal during the study.

From the interaction outcomes we calculated a dominance index (DI) [Lehner, 1996], which measures an individual's success with different opponents.

$$DI = \frac{\sum W_i/T_i}{N}$$

where: N = total no. of opponents, W_i = no. of wins in interactions with opponent "i", T_i = total no. interactions with opponent "i."

Dominance rank was established following the DI. The male with the highest DI within a social group was considered the alpha or central male of the group. Dominance linearity was determined by using Landau's index (h') [Lehner, 1996], and improved index of linearity (h') because tied dyads are admitted in this test [de Vries, 1995]. A linearity index ≥ 0.9 was indicative of a strong linear hierarchy [Martin & Bateson, 1986].

Access to receptive females

We used Kruskal–Wallis tests to compare the number of copulations obtained by each male rank within groups. For all statistical tests, the P -level was set at 0.05. Dominance rank and number of copulations obtained are presented in Table III. Detailed copulation events are described in Table II.

Genetic Studies

We had captured, obtained tissue samples and genotyped individuals from seven groups and two solitary individuals living in the continuous forest of the "Brasileria" Island ($n=48$, 23 males and 25 females (34A, 5SA, 9J) as described in Oklander et al. [2007, 2010].

A small fragment of epithelial ear tissue (approximately 3 mm in diameter) was obtained using small surgical scissor for DNA extraction

from each animal. Tissue samples from captured individuals and corpses found in the study sites were preserved at room temperature in solid NaCl [Oklander et al., 2004] until the DNA extraction in the laboratory. During the study period, we gathered additional stool samples from five infants (Table IV). Two different stool samples from each individual were non-invasively collected immediately after defecation and also preserved at room temperature in solid NaCl.

Most individuals of the groups studied (Groups G and X) were genotyped (Table I), as well as two solitary individuals, and individuals from five other neighboring groups. Therefore by genotyping individuals from many groups, we increased the probability of encountering parents of infants and juveniles.

This study complies with current Argentine laws and was conducted with permission from the National Resources Board, Fauna and Flora Department, Corrientes Province, Argentina. This research also adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

Laboratory Procedures

A total of 53 individuals were genotyped in this study (48 from tissue and 5 from stool samples). Genomic DNA was extracted from ear tissue using standard SDS/Proteinase K digestion followed by phenol–chloroform organic extraction [Sambrook et al., 1989]. DNA was also extracted from stool samples of infant individuals using the Guanidinium Thiocyanate-Silica [Boom et al., 1990] procedure, already tested in *A. caraya* [Oklander et al., 2004]. For these samples we used a multiple tubes procedure: five DNA extractions were carried out at the same time for every fecal sample including negative controls. These five extractions were then pooled to

TABLE III. Rank of Adult Males in the Groups and Number of Copulations Achieved in Each Season

Male	Spring 1			Summer			Autumn			Winter			Spring 2									
	DI	Rank	Copul.	DI	Rank	Copul.	DI	Rank	Copul.	DI	Rank	Copul.	DI	Rank	Copul.							
			Copul./total copul.			Copul./total copul.			Copul./total copul.			Copul./total copul.			Copul./total copul.							
Marley	0.71	1	8	0.73	1	7	0.54	1	3	0.60	1	2	0.73	1	2	0.50	1	7	0.78	1	7	
Jose	0.52	2	1	0.09	3	2	0.15	2	0	0.00	2	1	0.71	2	1	0.25	2	1	1	0.11	2	1
Quique	0.43	3	2	0.18	2	4	0.31	3	2	0.40	3	1	0.66	3	1	0.25	3	1	1	0.11	3	1
Total copul.			11			13			5			4			4			9				9
Gatti	0.85	1	2	1.00	1	2	0.50	1	0	0.00	1	0	0.80	2	2	0.33	2	2	3	1.00	3	3
Chao	0.47	2	0	0.00	2	2	0.50	2	0	0.00	2	0	0.82	1	4	0.67	1	4	0	0.00	3	0
Jesus	0.37	3	0	0.00	3	0	0.00	3	0	0.00	3	0	0.37	3	0	0.00	3	0	0	0.00	2	0
Total copul.			2			4			0			0			6			3				3

use as template for PCR [Taberlet et al., 1996]. Nuclear DNA concentration from these samples was not quantified. To prevent possible contamination, the extraction procedure was performed in a separate room dedicated only to DNA extraction from forensic samples, hair, and feces. Extractions were performed in a laminar flow hood with negative pressure. We used aerosol resistant pipettor tips for all DNA extractions and PCR preparations and all plasticware was disposable.

Microsatellites have proven to be an extremely valuable tool for the studies of population genetics and mating systems, among others, in a wide range of organisms [Zane et al., 2002]. For each sample, we amplified 11 microsatellites characterized for *A. caraya*: AC14, AC17, AC45, TGMS1, TGMS2, D5S117, D8S165, D17S804, LL1110, LL1118, LL157 [Di Fiore & Fleischer, 2004; Tomer et al., 2002]. These microsatellites were already screened for this population in Oklander et al. [2007]. All loci were in Hardy-Weinberg equilibrium and mean observed heterozygosity was 0.54 (range 0.146–0.792) [Oklander et al., 2007]. These markers provide an exclusion power for parentage analysis of 0.922 when neither parent is known and 0.992 when one parent is known [Oklander et al., 2007].

Genotyping PCR reactions were performed in final volumes of 25 µl using 5–10 ng of DNA template in the case of tissue samples or 5 µl of the extraction pool in stool samples and included 20 mM Tris-HCl, 50 mM KCl, 1.5 mM MgCl₂, 0.2 mM each dNTP, 1 U Taq DNA polymerase (InBio Highway, Tandil, Argentina), 1 pmol of each forward primer bearing an M13 tail, 4 pmol of each reverse primer, and 4 pmol of M13 labeled with a fluorescent dye (6-FAM) on its 5' end [Oklander et al., 2007; Schuelke, 2000]. Allele sizes of PCR products were determined using an ABI Prism Genetic Analyzer 310 (Life Technology, Foster City, CA) and the softwares Gene Scan and Genotyper were used to score the allele sizes, using GS-500 TAMRA as size standard (Life Technology). In the case of DNA extracted from stool samples, PCR was run three times to minimize possible genotyping errors due to allelic dropout [Surridge et al., 2002; Taberlet et al., 1996]. We recorded an allele only if it was observed at least twice. Homozygous genotypes were replicated four additional times each, scored from the two separate fecal samples per individual. All amplification assays included negative controls.

Genetic Relatedness

We used KINGROUP 2-101202 [Konovalov et al., 2004] to estimate genetic relatedness (*r*) between the adult males of the behaviorally studied groups by means of Queller and Goodnight [1989] and Wang [2002] estimators. Average *r* (estimated by Queller & Goodnight [1989]) for each sex and both

TABLE IV. Maternity and Paternity of Infants and Juveniles

Individual	Age	Sex	Group	Mother	Mother confidence (%)	Father	Father confidence (%)	Trio confidence mother unknown (%)	Trio confidence mother known (%)
Turko ^a	I		G	Orejas	99	Marley	95	99	99
Julio	J	M	G	Orejas	99	Jose	90	99	99
Alf	J	M	G	Not sampled	—	Jose	99	—	—
Cozi ^a	I		X	Not sampled	—	Gatti	99	—	—
Bz ^a	I		X	Ana	95	Gatti	99	90	99
Primo	J	M	X	Not sampled	—	M207	90	—	—
Gorda	J	F	X	Not sampled	—	M207	95	—	—
INF53 ^a	I		NF	H20C	90	M23	99	95	99
INF56 ^a	I		NF	H26C	99	M23	99	99	99
M25	J	M	NF	H20C	99	M17 ^b	99	95	99
Mireya	J	F	LR	China	99	TomX	99	99	99
Milica	J	F	LR	China	99	TomX	95	90	99
Lila	J	F	LR	Not sampled	—	Mazzi	99	—	—
Migui	J	F	LR	Chile	99	Mazzi	99	99	99

Includes: age, sex, group, father, mother, mother/father, and trio confidence level.

^aFecal samples, tissue samples for the remaining individuals.

^bExtragroup father.

sexes pooled within groups of this population were previously published in Oklander et al. [2010].

We performed a rarefaction analysis to determine the change in relatedness estimates with additional loci. For this we used the 11 loci, Queller and Goodnight's r , and the web-based software RERAT [Schwacke et al., 2005]. Rarefaction analysis showed that with each additional locus, both the mean difference and variance between estimates of relatedness decreased dramatically (Fig. 1). Calculated relatedness values did not change significantly after the inclusion of the eighth loci, indicating that the 11 loci used here were sufficiently polymorphic for relatedness calculations. A total of 10,000 permutations were used to generate these data.

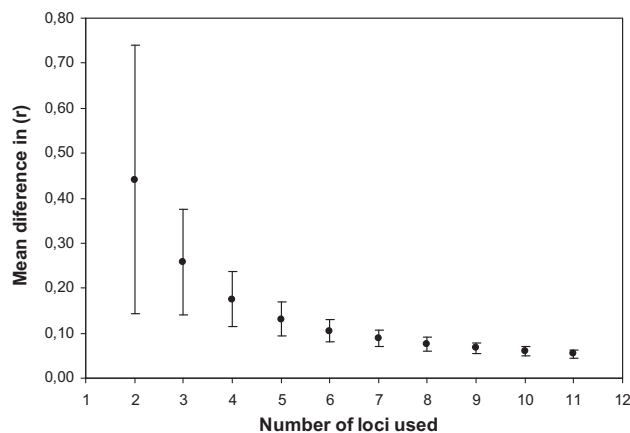


Fig. 1. Rarefaction analysis between the number of loci used in *Alouatta caraya* and the resultant Queller and Goodnight [1989] estimate of relatedness. Each point represents the mean difference between current estimate of relatedness and the one previous to it; the bars represent the standard deviation.

We generated likelihood relationship-hypotheses for intra-group male dyads using KINGROUP 2.101202 [Konovalov et al., 2004]. This program compares the likelihoods of different relationship categories between two individuals, based on simulations and genotypic data. Significance level of the obtained ratio in KINGROUP was calculated by simulating 1,000 pairs of individuals. We rejected the alternative hypothesis if P was ≤ 0.05 .

Paternity and Maternity Analysis

We analyzed paternities and maternities of five infant and nine juvenile individuals from four groups. Two of these groups were under behavioral study (Groups G and Group X), and the other two were neighboring groups of the study groups (Groups LR and NF; Table IV).

Two infants were conceived and born during the behavioral study (Groups G and X), and one more infant was born in Group X a few months after the end of the study. Gestation length for *A. caraya* is estimated between 152 and 195 days [Di Fiore et al., 2011; Kowalewski & Garber, 2010]. Therefore, the infant born in April 2002 was most probably conceived in November 2001, the one born in May 2002 was conceived in December 2001, and the one born in February 2003 was conceived in September 2002, therefore this last infant was also conceived during the study (Table I).

Maternity was known for the two first infants because we observed mother-offspring associations during the behavioral monitoring. Nevertheless, we ran a maternity analysis to test for any possible inconsistency. We ran maternity and paternity tests with and without known mothers. For this analysis

we considered all adult individuals sampled and alive at the moment of conception as potential fathers and mothers. An adult individual was assigned as father/mother if it was the only male/female with no genetic mismatches with a given offspring, and the paternity/maternity assignment was supported at the 90% confidence level by the maximum likelihood method employed in CERVUS 3.0 [Kalinowski et al., 2007]. We generated confidence levels with CERVUS strict 99%, relaxed 95% and 90% using 100,000 simulations and the following parameters: 70% of candidate parents sampled for maternity (17), 90% of candidate parents sampled for paternity (17), 90% of loci typed, and a typing error rate of 0.01 in both cases (Table IV).

RESULTS

Agonistic Interactions

The total number of agonistic interactions used to construct social dominance hierarchies was 303 for Group G and 140 for Group X. The rate of agonistic interactions during the study was one every 3.5 hr for Group G (0.029 int/ind/hr) and one every 7.5 hr for Group X (0.015 int/ind/hr). Therefore, in the group with more females, males interact agonistically with each other more frequently. The rates of agonistic interactions (int/ind/hr) for each male dyad for group G were: Marley–Quique = 0.094, Marley–Jose = 0.063, Jose–Quique = 0.04, and for group X: Gatti–Chao = 0.038, Gatti–Jesus = 0.014, Chao–Jesus = 0.003.

Landau's index h (or h') showed a value of $h = 1$ in the five sampling periods for both groups, suggesting a linear hierarchy between males in each group. However, the dyadic interaction matrices showed that there have been changes in male hierarchies during the study in both groups (Table III). Group X exhibited a rank reversal between the first (Gatti) and second (Chao) ranked males, followed by two rank reversals in which the original alpha (Gatti) regained his rank, the third-ranked male (Jesus) moved into second, and Chao (the challenger) became peripheral (observed in 80% of focals at more than 20 m from all the members of his group), leaving the group entirely shortly after the study. Group G only exhibited a rank reversal between the second and third ranked males, followed by a reversal back to their original ranks, where they remained through the end of the study.

Access to Receptive Females

We observed a total of 42 intra-group copulations in Group G, and 15 in Group X during all the study (Tables II and III) and five extra group copulations. Two or more mating events took place on the same day in 69% of the cases in Group G and 60% in Group X (Table II). With the exception of female Orejas, that copulated only with the alpha male, all males and

females copulated with each other at least once in group G. In group X, Gatti, that was alpha during most of the study, copulated with both intra-group and with two extra-group females, whereas Chao, who ranked second during most of the study, copulated with only one intra-group female and one extra-group female. Only female Josefa mated with both resident males. Unlike group G, the lowest ranking male (Jesus) obtained zero copulations (Table III).

Behavior sampling dates during seasons do not exactly match the estimated month of conceptions or births estimated in this study. However, the female that gave birth in May 2002 (Orejas) copulated six times in the previous spring with the most plausible father (Tables II and IV). Both groups showed significant differences between male rank and number of copulations in the five sampling periods [Group G: Kruskal–Wallis test: H ($df = 2$, $N = 42$) = 7.30, $P = 0.02$; Group X Kruskal–Wallis test: H ($df = 2$, $N = 15$) = 5.18, $P = 0.03$]. The alpha males, identified from the analysis of dyadic interaction matrices in each period, copulated more than the other males. Alpha males accounted for 64% of copulations in Group G and 73% in Group X.

Our review of the context of copulations yields a number of qualitative results: (1) In both study groups, copulations mostly occurred at more than 5 m from the other resident adult males; moreover, whenever an additional adult male was seen within 5 m of a mating couple, this male never was the dominant male; (2) In group G, but not in group X, we observed mate guarding and agonistic interactions associated with copulations; (3) We detected more promiscuous copulation between multiple males and females during the summer session, when the rank between the two subordinate males was reversed in group G; (4) We registered five extra-group copulations between the females of group G with males of group X; four of these took place during the summer session when the ranks of the two subordinate males were reversed in group G; (5) We never saw females explicitly soliciting copulation (tongue flicking, presenting, approaching the male), but we recorded cases of pre copulatory grooming (Table II) and copulation attempts from the resident males that were rejected by females in both groups (data not available); (6) There are two distinct patterns of copulations for females: a female may either repeatedly copulate with the same male during the same and/or consecutive days (e.g., Orejas and Marley during Spring 1), or she may copulate only once or twice with a male, separated by one or more days (e.g., Monga during summer and Lola during winter); mate guarding occurred only in the former context in group G; (7) Some females are more promiscuous than others: for example, Tamara had the most matings, spread across more males, than any other

female in group G, and she also copulated with two males from group X; (8) Females were seen to mate while they are pregnant (e.g., Josefa during the summer, Orejas during the autumn); (9) In group X, Josefa mated twice with Chao and once with Gatti during the summer session when she was pregnant with Gatti's infant. During the winter, when Chao and Gatti's ranks were reversed and Josefa was nursing a 3-month-old infant (an age that is highly vulnerable to infanticide), she mated repeatedly over a 5-day period with both males (twice with the infant's father and four times with Chao, who is now alpha). None of these copulations were contested (no mate guarding, no aggression), which strongly suggest that the distribution of matings during these sessions was Josefa's choice. It would also support an infanticide aversion tactic as incentive; (10) Finally, we never observed any forced copulations, injuries or cases of sexual coercion by males.

Paternity of Infants and Juveniles From Studied and Neighboring Groups

The alpha male in Group G (Marley) was the only male with no genetic mismatches with the only infant born during the study in this group, and therefore the only possible father (Table IV). In Group X, Gatti was the alpha male during the sampling periods when conception of the two infants studied was most plausible (Spring 2001 and Spring 2002), and he was also the only adult male not excluded from paternity for this infant (Table IV).

When analyzing the paternity of juvenile individuals older than 2 years at the beginning of the study (Group G: Julio and Alf, Group X: Primo and Gorda) we found that they were not sired by the alpha-ranking males during the study (Table IV). In the case of Group G, two male juveniles were descendants of the β male in the hierarchy during the behavioral study (Jose). Similarly, in Group X, we found two juveniles (Primo and Gorda) that were sired by a former male member of group X that we found dead prior to this study (M207; Table IV).

We analyzed paternities and maternities of two neighboring groups (LR and NF), that were not followed intensively, but visited regularly for population studies [Kowalewski, 2007; Kowalewski & Zunino, 2004]. Group LR had two juveniles of approximately 3 years old (Lila and Migui), sired by one male (Mazzi) and two smaller juveniles, but clearly not twins because of differences in their sizes (Mireya and Milica), sired by another male of the same group (TomX). When we analyzed the Group NF we found one juvenile male (M25) approximately 2 years old sired by a male from another group (M17 from Group V) and two infants sired by a resident male (M23; Table IV).

Relatedness Between Adult Males of the Groups Studied Behaviorally

We analyzed two different relatedness coefficients (r) between the adult males of the Groups G and X. The estimated pairwise relatedness among males of Group G was: Jose–Marley $r = 0.054$; Jose–Quique $r = -0.263$; Quique–Marley $r = 0.006$ for the estimator of Queller & Goodnight [1989]; and Jose–Marley $r = 0.054$; Jose–Quique $r = -0.202$; Quique–Marley $r = -0.192$ for the estimator of Wang [2002] estimators. In all cases, dyadic relatedness coefficients show that males are unrelated in this group. While for Group X were: Gatti–Jesus $r = 0.385$; Gatti–Chao $r = 0.316$; Chao–Jesus $r = -0.258$ for the estimator Queller & Goodnight [1989] estimator; and Gatti–Jesus $r = 0.374$; Gatti–Chao $r = 0.368$; Chao–Jesus $r = -0.275$) for the Wang [2002] estimator. Likelihood relationship-hypotheses showed only one dyad could be compatible with full-siblings or father/son (Gatti–Jesus) in group X. Relatedness coefficients suggest that Gatti is related to both males but Jesus and Chao are not related to each other. This pattern may be possible if Jesus was the father of Gatti, and Chao was Gatti's half brother through his mother, or if Gatti was a half brother to both Jesus and Chao via different parents. Therefore we consider these coefficients as a rough index of relative degree of relatedness, rather than exact indicators.

Overall these results show higher relatedness between adult males in the group that showed a lower number of agonistic interactions.

DISCUSSION

Dominance and Relatedness

Our results indicate that males of *A. caraya* in our study groups ranked following a linear order. Groups experienced reversions for short periods of time, which suggests that subordinate males in multimale groups may attempt to “escalate” in these hierarchies. In this study agonistic interactions were scarce, a trend shown in this and other howler species. Previous studies showed in *A. caraya* 0.019 int/ind/hr [Bicca-Marques, 1993], and in *A. palliata*; male–male = 0.018 int/ind/hr, male–female = 0.049 int/ind/hr [Wang & Milton, 2003]. The low level of agonistic interactions is possibly related to the high costs imposed by physical aggression that may result in the death of males [Dias et al., 2010], thus, the predominant behaviors in male–male howler relationships involve low physical risk [Dias et al., 2008; Garber & Kowalewski, 2011; Preuschoft & van Schaik, 2000; van Belle et al., 2008; Wang & Milton, 2003]. Nevertheless, intense forms of aggression have been reported for howlers (*Alouatta arctoidea* [Crockett & Pope, 1988], *A. palliata* [Cristóbal-Azkarate et al., 2004; Dias et al., 2010]).

This study analyzed two groups with three adult males each, but with different numbers of adult females (2 vs. 4). We found that males participated in a greater number of agonistic interactions with each other in the group with higher number of females (0.029 int/ind/hr vs. 0.015 int/ind/hr). Males may behave more aggressively towards each other when the number of females to monopolize increases. This research shows that agonistic interactions among males possibly depend on the number of females in the groups studied. However, we only collected data on two groups and in order to corroborate this finding it would be necessary to study several groups with different female group size.

Additionally, we explored the association between male–male agonistic interactions and male–male degree of relatedness. Our results indicate that at least one male dyad is closely related as full-siblings or father-son in the group that showed fewer agonistic interactions between males. Therefore their relatedness could also explain greater male–male tolerance. Several observations in primates indicate that behaviors vary depending on the degree of kinship. Among Japanese macaques, for example, the frequency of support in agonistic interactions [Chapais et al., 2001] and feeding tolerance in defensible food sources [Belisle & Chapais, 2001] decrease among individuals that are not closely related. In howlers, studies on *A. arctoidea* [Pope, 1990] suggest higher level of cooperation in behaviors such as howling in related or familiar males.

Although the use of pairwise genetic relatedness indices has been criticized for assessing kinship relations, in our study we were only interested to differentiate related from unrelated males. van Horn et al. [2008] suggested that the success rate of detecting truly unrelated pairs is higher than 96%, thus, we consider that the level of precision in order to differentiate closely related from unrelated males is satisfactory enough.

Mating Success and Paternity Success

Alpha or central males enjoyed greater mating success (average 68.5%, range 64–73%) and fathered all the offspring conceived during our study. However, although higher ranked males participated in more copulations, nearly all adult resident males copulated.

In this *A. caraya* population mating skew was low compared to reproductive skew as was also found in *Cebus capuchinus* [Jack & Fedigan, 2005] and *Elemur fulvus rufus* [Port, 2009]. Our results on the context of copulations showed several cases of male–female mate guarding and male–male aggression prior to copulation in only one group. In the other group studied we never saw these behaviors and therefore female choice would be determinant in copulation distribution in this case. This between

group difference suggests that both females and males play simultaneously different mating strategies and no one completely controls reproduction.

During our study we did not witness dominant males allowing lower ranking males to copulate because all the matings by subordinate males occurred out of the sight of the dominant/central male. However we registered more promiscuous intra and extra-group copulations during a period of non-stability in the male hierarchy in one group and more promiscuous copulations of one female nursing a 3-month-old infant when male ranks were reversed in the other group. These behaviors support our second prediction that alpha males do not monopolize copulations because females choose to mate with subordinate males in order to confuse paternity and decrease infanticide risk.

Theoretical models of reproductive skew describe a framework for explaining how reproduction is distributed among members of a social group [Kutsukake & Nunn, 2006; Reeve & Keller, 2001]. Bradley et al. [2005] investigated paternity in 48 offspring from four gorilla groups (*Gorilla beringei beringei*) and found that both dominant males and secondary males fathered offspring and were unrelated, and that extra-group males did not father any offspring. They suggested that their results are explained by a tug-of-war model where both top and secondary ranked males compete over the access to fertile females, and that silverbacks cannot control the mating access to resident females. Another study on male reproduction on redfronted lemurs (*Eulemur fulvus rufus*), which social organization is characterized by a high number of males, indicated a reproductive skew toward dominant males (71% of 49 offspring in one population) [Kappeler & Port, 2008]. However, skew models fail to support the finding, and the number of females best predicted how reproduction was distributed.

Within skew models, transactional model assumption that one individual completely controls reproduction is likely to be violated, while tug-of-war models do not sufficiently incorporate individuals' options outside the group [Port & Kappeler, 2010]. Our present and previous research on *A. caraya*, shows that a central/dominant male tries to control reproduction by mate guarding receptive females, but is unable to monopolize access to females from either resident or extragroup males, as females can escape from male control. These behaviors reveal the need to reformulate models that give full control of mating access to males [Kutsukake & Nunn, 2009]. The classic priority of access model [Altmann, 1962] explains only proximate patterns of skew [Port & Kappeler, 2010], but proposes a decrease in reproductive skew when the number of females, or their estrous synchronicity increases [Boesch et al., 2006; Bradley et al., 2005; Kutsukake & Nunn, 2009]. Although our females do not seem to synchronize

estrus (we still lack data on hormone profiles), we found a trend of decreasing male mating skew in the group with more females. In general, skew models fail to support our findings [see Kutsukake & Nunn, 2006]. Our results in black and gold howler suggest that there is not a unique model that may explain reproductive skew in this population and indicate the existence of a continuum of dynamic responses (from aggression to leaving the group) that subordinate males express depending on the particular group situation. Several factors are involved in male access to females including kinship relationship between males, numbers of resident and non-resident male competitors, number of resident females, female choice, degree of breeding seasonality, and history and demographic characteristics of the study population [Altmann et al., 1996; Cowlishaw & Dunbar, 1991; Jones et al., 2008]. Further studies on female mate selection and female hormone profiles in this species will shed light into the underlying relationship between male behavior and reproductive success.

Molecular Determination of Paternity

We already mentioned that paternity tests revealed that alpha males fathered all infants conceived during the study. However, when analyzing the paternity of juveniles between 2 and 3 years old from the same groups, we found that they were not sired by the alpha males during the study period, but by a different male. In Group G, the assigned father of juveniles was Jose (which was a subordinate male during all the study), whereas in Group X the assigned father was a male that was found dead before starting the study.

The same pattern of differences in paternity was found in two other groups where one male sired infants or small juveniles, while another male sired older juveniles. In Group NF, the assigned father of the older juveniles was an extra-group male, while in Group LR it was another male from the same group. The case of extra-group paternity could be explained either due to extra-group mating or rapid male turnover in groups. This finding agrees with behavioral data indicating high degree of female extra-group promiscuity in the same population and short periods of male tenure [Kowalewski & Garber, 2010].

Our results suggest a temporary monopolization of paternity for 1–2 years in the four groups studied, as individuals from the same age in any group were fathered by a single male. In all cases our results indicate that one male tends to monopolize paternity for a period of time, usually during his tenure as alpha or central male. In this regard, keeping the central position in a group offers significant advantages in terms of achieving reproduction. In this study we detected reversals in hierarchy in both groups, resulting in unstable affiliative-agonistic

within group male relationships. This weak stability of male's position in the hierarchy and its relationship with female fertilization results in males needing to escalate towards the central position within a multimale group. In other species of howlers, such as *A. pigra*, several changes in male group membership over a relatively short period of time have been observed (seven changes in 6 months [van Belle et al., 2008]). Changes in male group membership sometimes escalated to physical aggression, causing bloody and lethal wounds involving high potential costs for both males [Horwich et al., 2000; van Belle et al., 2008].

Altogether, our results suggest that males need to compete intensely to stay in the alpha or central position of the group and that this position enables them to monopolize paternity for a period of time. Traditional skew models seem to be weak to explain our study groups behavior, in this regard we need to construct more complex models [Port & Kappeler, 2010] while considering a combination of factors such as central male control of paternity, resident related and non-related resident males, frequency of resident male support during intergroup encounter, female mating and reproductive decisions [but see Kutsukake & Nunn, 2006]. We suggest that this interplay of interacting competing sexual strategies implemented by both females and males underlies the social structure and organization of these howler groups.

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