RESEARCH ARTICLE

Group Size and Composition Influence Male and Female Reproductive Success in Black Howler Monkeys (*Alouatta pigra*)

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It has been argued that grouping patterns might influence the reproductive performance of individuals. Increasing group size results in greater travel costs and competition over depletable food resources, which could lead to reduced individual reproductive success. However, in groups with an increasing number of males, female reproductive success is predicted to augment because larger male groups might better protect immatures from infanticidal attacks. In contrast, male reproductive success is predicted to decrease with number of males in a group because fertilization cannot be shared between males. In this paper, we test these predictions on the Mesoamerican black howler monkey (*Alouatta pigra*) with data on group size and composition for 120 groups from eight populations of black howler monkeys existing in eight protected forests in Mexico and Guatemala. Male and female reproductive success were calculated as a deviation of the observed number of infants (or immatures) from the expected number of infants (or immatures), relative to the number of males and females in a group. Results indicate that both male and female reproductive success decreased with group size. Male reproductive success decreased with an increasing number of males in a group and with increasing proportion of males relative to females in a group. Decreased female reproductive success was associated with increasing number of females in a group, and female reproductive success had a tendency to increase with increasing number of males in a group. These results suggest that in black howler monkeys, living in larger groups might negatively affect the reproductive success of each member. Our findings are similar to those reported for a population of a sister species, *Alouatta palliata,* living in larger groups. Am. J. Primatol. 70:1–7 2008.   © 2008 Wiley-Liss, Inc.

Key words: reproductive success; sex ratio; group size; black howler monkeys; *Alouatta pigra*; Mesoamerican primate

INTRODUCTION

Several primate species live in permanent cohesive social units when the benefits of group living (enhanced foraging efficiency and predator avoidance) exceed the costs (increased travel costs and within-group feeding competition) [Chapman & Chapman, 2000; Janson & Goldsmith, 1995; Silk, 2007]. The size and composition of groups might influence the reproductive performance of individuals [Silk, 2007]. For example, with increasing group size and therefore increasing travel costs and competition over depletable food resources, individual reproductive success is predicted to decrease [Chapman & Chapman, 2000; Ryan et al., in press]. This should particularly affect female reproductive success, which is highly dependent on access to food resources [Snaith & Chapman, 2007].

However, some folivorous primates live in small groups, despite low or absent competition over undepletable food resources [Chapman & Pavelka, 2005; but see Snaith & Chapman, 2007]. Here, social factors are suggested to play an important role in group structure leading to decreased individual reproductive success with increasing group size [Chapman & Pavelka, 2005]. For example, for some species of langurs (*Presbytis* spp.) and howler monkeys (*Alouatta seniculus*), larger groups of females form a more attractive target for male take-over attempts. These events might be accompanied with infanticide leading to decreased female reproductive success compared with groups with

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fewer females [Crockett & Janson, 2000; Treves & Chapman, 1996; van Schaik & Janson, 2000].

By contrast, individual reproductive success could increase with increasing group size. For example, male red howler monkeys form coalitions to attempt to jointly take over established groups and gain access to females. These coalitions are more likely to succeed than are solitary males in taking over an established multimale group [Pope, 1990, 2000]. If successful, the newly resident males cooperatively defend their group against other coalitions of males in neighboring groups or migrating males that try to take over their group [Pope, 1990, 2000]. During take-over attempts, infanticide has been observed or inferred to occur [see review in Crockett, 2003]. Hence, with an increasing number of males in a group, female reproductive success is predicted to increase because larger male groups might better protect immatures from infanticidal attacks [Treves, 2001]. Alternatively, even though males may benefit from the presence of other males, male reproductive success could decrease with an increasing number of males in a group, if fertilization cannot be shared between coalitionary males [Ryan et al., in press].

The folivore–frugivorous howler monkeys (Alouatta spp.) are good models to investigate the influence of group size and composition on individual reproductive success because they show great variability in group size and composition between species, populations, within populations, and over time [Di Fiore & Campbell, 2007; Treves, 2001]. The two most studied howler monkey species, the red howler monkey (A. seniculus) and the mantled howler monkey (A. palliata), show remarkable differences in their grouping patterns and social behavior [Di Fiore & Campbell, 2007]. In contrast, little is known about the Mesoamerican black howler monkey (A. pigra), but its group size and composition and social system appear to be similar to those of the red howler monkey. Recent phylogenetic and biogeographic studies indicate that the black howler monkey forms a sister clade with the mantled howler monkey [Cortés-Ortiz et al., 2003; Ford, 2006]. Thus, investigating black howler monkeys is important to address evolutionary and ecological questions about the nature of the social diversity of howler monkeys.

The black howler monkey lives in small groups averaging six individuals and both males and females disperse [Van Belle & Estrada, 2006; Van Belle, unpublished data]. Males form coalitions to take over female groups and defend them and their offspring against other take-over attempts [Horwich et al., 2000; Van Belle, unpublished data]. Female reproductive positions in a group seem to be limited, and groups contain no more than five females [Van Belle & Estrada, 2006]. Considering the recent availability of demographic data for several populations of the black howler monkey, in this paper we tested the

predictions set forth above regarding the effect of group size and composition on male and female reproductive success in this howler monkey species. Based on the analyses formulated in Treves [2001] and Ryan et al. [in press], we analyzed data on group size and composition for 120 groups in eight populations of black howler monkeys existing in eight protected forests. These sites have been under protection for more than 4–6 decades, and the black howler populations found within each site are assumed to be demographically and ecologically stable [Van Belle & Estrada, 2006].

METHODS
Sites and Data Collection

Between 2000 and 2003, population surveys of black howler monkeys (A. pigra) were conducted in eight sites located in protected forest reserves in southern Mexico (El Tormento Forest Reserve, Calakmul Biosphere Reserve, Palenque National Park, Yaxchilán National Monument, Montes Azules Biosphere Reserve, and Reforma Community Reserve near Rio Lacantun) and in northern-central Guatemala (Municipal Reserve Salinas Nueve Cerros, Lachuá ecoregion, and Tikal National Park; Fig. 1, Table I).

At each site, we determined the relative location of all groups, defined as a social unit having at least one adult male and one adult female, living in the study area (Table I). This was accomplished using early morning (05:00–07:00 hr) triangulation of their morning choruses and subsequent ground surveys [Estrada et al., 2004; Van Belle & Estrada, 2006; and references therein]. Each group was followed and counted repeatedly until a consensus of group size and age and sex composition was reached. Groups were searched for on subsequent days to confirm their composition and approximate location to reduce the probability of counting a group more than once. Individual howler monkeys in groups were classified as infants (clinging ventrally or dorsally to mother), juveniles (independent of mother and 1/4–1/2 the size of adults), and adults (all large and robust individuals) [Izawa et al., 1979]. The sex of adults and juveniles could be reliably determined. The research reported here complied with protocols approved by the Mexican environmental agencies (SEMARNAT) and the Guatemalan ministry of environment and natural resources (MARN). In both cases protocols adhered to the legal requirements of the countries of Mexico and Guatemala.

Mean ($\pm$SE) size for the 120 groups was 6.57 ± 1.20 individuals, with on average 2.07 ± 0.41 adult males, 2.26 ± 0.33 adult females, 1.28 ± 0.48 juveniles, and 0.96 ± 0.44 infants. The mean adult sex ratio in a group was 1.36 ± 0.20 females per male, and groups had on average 1.10 ± 0.39 immatures per
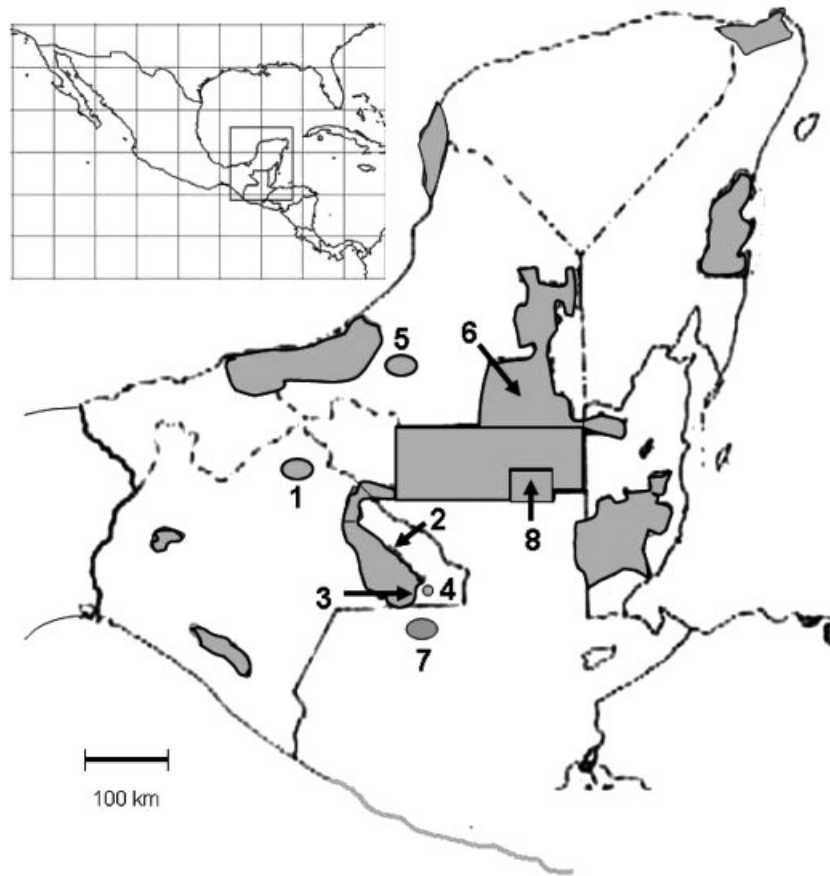
Fig. 1. Map of southern Mexico, Belize, and northern Guatemala showing the locations of the eight protected forests studied. In Mexico: 1, Palenque National Park; 2, Yaxchilán National Monument; 3, Montes Azules Biosphere Reserve; 4, Reforma Community Reserve; 5, El Tormento Forest Reserve; 6, Calakmul Biosphere Reserve. In Guatemala: 7, Municipal Reserve Salinas Nueve Cerros, Lachuá ecoregion; 8, Tikal National Park. The shaded areas indicate the system of national protected areas in southern Mexico, Belize, and northern Guatemala.

TABLE I. Reserve Area, Study Area, and Basic Demographic Features of the Black Howler Populations of the Study Sites Investigated

Site	Reserve area (ha)	Study area (ha)	N	AM	AF	IMM	Group size
El Tormento	1,400	1,400	26	1.77	2.46	2.42	6.65
Calakmul	700,000	400	8	2.50	2.25	2.75	7.50
Palenque	1,771	600	19	2.05	1.91	2.71	6.74
Yaxchilán	2,700	100	8	2.75	2.00	1.88	6.63
Montes Azules	300,000	836	13	1.83	2.31	1.38	5.54
Reforma	1,700	450	12	1.75	2.33	1.00	5.08
Lachuá	850	850	24	1.58	1.92	2.08	5.58
Tikal	57,600	500	10	2.30	2.90	3.60	8.80

Study area refers to the area encompassed by our surveys at each site. N, number of groups encountered in the study area; AM, mean number of adult males in a group; AF, mean number of adult females in a group; IMM, mean number of immatures in a group. (See Tables III and IV in Van Belle and Estrada [2006] for more details on demographic features of these populations).

adult female or 0.65 ± 0.28 juveniles and 0.46 ± 0.16 infants per adult female [Table I; for more details see Tables III and IV in Van Belle & Estrada, 2006].

Data Processing and Statistics

To compare across groups in a population, male and female reproductive success was calculated as the deviation of the observed number of infants (or immatures) from the expected number of infants (or immatures), relative to the number of males and females in a group. Following Treves [2001; equations (1) and (2)], female reproductive success based on the number of infants in group i (F_{INF}) = observed number of infants in group i–(population mean

infants per female * number of females in group i). Female reproductive success based on the number of immatures in a group (F_{IMM}), male reproductive success based on the number of infants in the group (M_{INF}), and the number of immatures in the group (M_{IMM}) were calculated similarly. We assumed that the number of infants in a group represents the recent birth rate and infant survival rate in that group. The number of immatures reflects the accumulated survival rate of infants and juveniles in that group. It also reflects the retention rate of juveniles in their natal group, assuming that the juveniles were born in these groups and have not immigrated from other groups [see Treves, 2001 for an extensive discussion on these assumptions].

To test for a relationship between male and female reproductive success and number of males, number of females, number of adults, sex ratio in a group, and group size, we calculated, per population, the slope of the regression of reproductive success of males and females (F_{INF}, F_{IMM}, M_{INF}, M_{IMM}) on the number of adult and subadult males (M), the number of adult and subadult females (F), the number of adults and subadults (A), the sex ratio residual (S), and group size residual [G; Ryan et al., in press; Treves, 2001]. To avoid spurious significant correlations resulting from number of females appearing on both axes of the analysis when calculating simple sex ratio (M/F), we proceeded as Treves [2001] recommended. S was calculated as the residual of the regression of the number of males on the number of females per group. Furthermore, to control for the correlation between group size and the number of infants or immatures, we followed Ryan et al. [in press] and calculated G as the residual of the regression of the number of infants (or immatures) on group size.

A one-sample T-test was used to calculate whether the mean slopes across the eight populations were significantly different from zero. The significance value was set at $P \leq 0.010$ after a Bonferroni correction. Statistical analyses were conducted in SPSS 12.0 Windows.

RESULTS

Both male and female reproductive success decreased with group size (M_{INF}: mean slope = -0.183, $T = -5.04$, $P = 0.001$; M_{IMM}: mean slope = -0.581, $T = -10.06$, $P = 0.000$; F_{IMM}: mean slope = -0.618, $T = -0.62$, $P = 0.001$; Fig. 2).

Male reproductive success (M_{IMM}) decreased with increasing number of males in a group (mean slope = -0.675, $T = -3.44$, $P = 0.010$; Fig. 2a) and with an increasing proportion of males relative to females in a group (mean slope = 0.753, $T = -4.01$, $P = 0.005$; Fig. 2a).
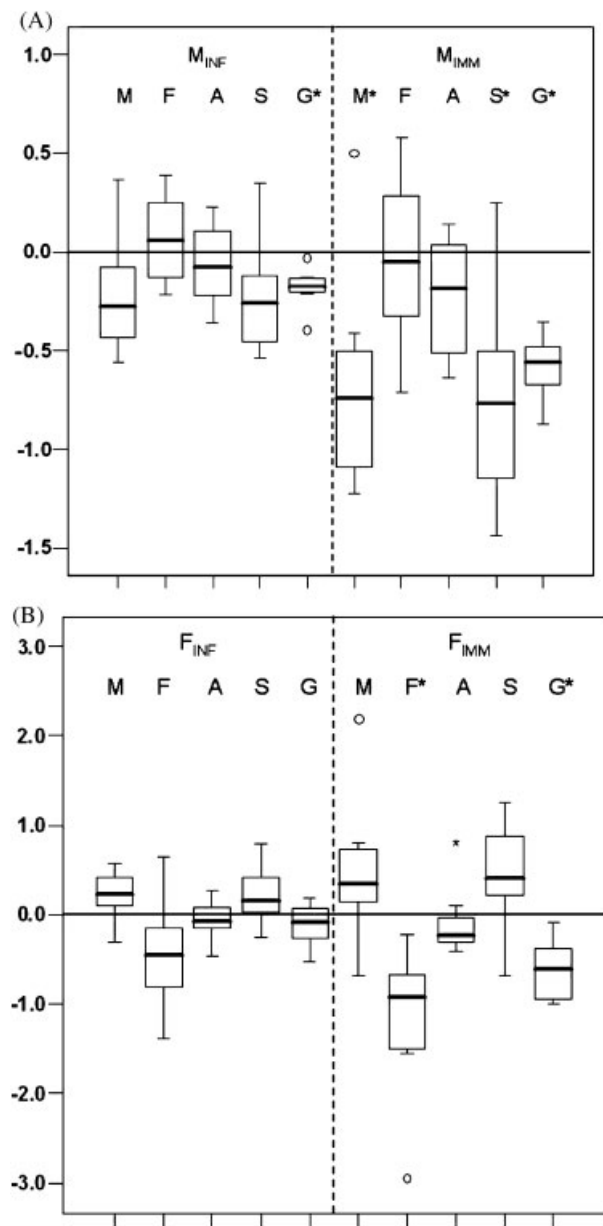

Fig. 2. Box plots indicating the distribution of slopes of the regression of (**A**) male (M_{INF} and M_{IMM}) and (**B**) female reproductive success (F_{INF} and F_{IMM}) on the number of adult and subadult males (M), the number of adult and subadult females (F), the number of adults and subadults (A), sex ratio residual (S), and group size residual (G) for the eight populations. See text for calculations. The asterisks next to M, F, S, and G indicate significant difference.

The highest mean slope (-1.171) was obtained from regressing F_{IMM} on F indicating a decrease in female reproductive success with increasing number of females in a group ($T = -3.95$, $P = 0.006$; Fig. 2b). Female reproductive success (F_{INF}) had a tendency to increase with an increasing number of males in a group, but this was not significant after a Bonferroni correction (mean slope = 0.265, $T = 2.37$, $P = 0.050$; Fig. 2b).

DISCUSSION

First, we want to point out that our data set represents demographic snapshots of populations experiencing demographic fluctuations and that the eight populations investigated here were most likely at different demographic stages [Van Belle & Estrada, 2006]. With this in mind, the results of our analyses suggest that in black howler monkeys, living in large groups might negatively affect the reproductive success of each member, as has been proposed previously for this and other primate species [Horwich et al., 2001; Ryan et al., in press; Silk, 2007; Treves, 2001; van Schaik, 1983]. For both black howler males and females, reproductive success decreased with group size. Such reduced reproductive success may impose a limit on group size in black howler monkeys. Similar results were found for a single mantled howler population in Panama where 23 years of demographic data were analyzed [Ryan et al., in press]. Despite reduced reproductive success, mantled howler monkeys typically live in larger groups of on average 13.8 individuals with three or more adult males and up to nine or more adult females [Di Fiore & Campbell, 2007]. Other selective forces (e.g., infanticide) might affect mantled howler monkeys differently making living in larger groups more advantageous differently or less costly [see Knopff & Pavelka, 2006].

For black howler males, our results indicated that male reproductive success decreased with an increasing number of adult males in a group and an increasing number of adult males per female in the group but was not influenced by the number of females and number of adults. On the basis of similarities in grouping patterns (e.g., small group size) and social system (e.g., male coalitions) between black howler monkeys and red howler monkeys, it is assumed that partitioning of reproduction among black howler males may be highly skewed [Horwich et al., 2000]. Paternity studies in red howler monkeys revealed that the dominant male sired most, if not all, offspring conceived during his tenure [Pope, 1990]. Although male reproductive success decreases with group size and number of males in black howler monkeys, dominant males might benefit from the presence of subordinate males, as observed in red howler monkeys [Pope, 1990, 2000]. Howler males may form coalitions to gain superior competitive ability over extra-group males taking over their group and thus deterring infanticide [Pope, 2000]. Therefore, reproductive success for dominant males can be higher in multimale groups than in one-male groups, as observed in red howler monkeys [Pope, 1990; also see Robbins, 1995]. Subordinate males could gain inclusive fitness when they are related to the dominant male. In red howler monkeys, dominant males had longer tenures when their coalitionary males were kin compared with non-kin resident males [Pope, 2000]. In black howler monkeys, subordinates presumably related to the dominant male were more likely to aid the dominant male with group defense through mutual howling compared with presumable unrelated subordinates [Kitchen et al., 2004].

For black howler monkey females, our results demonstrated that female reproductive success decreased with an increasing number of females in a group but was not influenced by the number of males, number of adults, and sex ratio residual. This corroborates the idea of limited female breeding positions in groups of black howler monkeys, as has been suggested earlier [Crockett & Janson, 2000; Jones, 2004]. Black howler groups have on average 2.26 adult females with no more than five adult females [Van Belle & Estrada, 2006]. Similarly, red howler monkey groups contain on average three and no more than five adult females [Di Fiore & Campbell, 2007]. In both red howler and black howler monkeys, migrating females are actively prevented by resident females from entering established groups [Brockett et al., 2000; Pope, 1998]. In red howler monkeys, groups with more females attract more often extra-group males attempting to take over the group and ousting resident males compared with groups with fewer females. Infanticide may occur during these take-over attempts, which could reduce female reproductive success in larger female groups [Brockett et al., 1999; Crockett & Janson, 2000]. This could possibly be offset by multiple resident males forming coalitions to defend females and their offspring against infanticidal male take-overs [Pope, 2000; Treves, 2001]. Our results did not reveal a significant increase in female reproductive success with increasing number of males in a group; however, there was a general tendency in this direction (mean slope = 0.265, $P = 0.050$).

A recent review of the ecological constraint models questioned the widely accepted assumption that folivorous primates do not encounter within-group feeding competition [Snaith & Chapman, 2007]. These authors indicated that in many folivorous primate species, females experienced reduced reproductive success with an increasing number of females in a group, suggesting that feeding competition played an important role in the reproductive success of folivorous primate females, as has been widely accepted for frugivorous primates. However, Knopff and Pavelka [2006] concluded from a study of three black howler groups in Monkey River, Belize, that the large group did not experience increased feeding competition compared with two smaller groups.

In contrast to Treves [2001], our results did not reveal a significant increase in female reproductive success with increasing proportion of males in a group. Because Treves averaged slopes across 26 populations of five howler monkey species, including black howler monkeys, with distinct social systems

and grouping patterns, he might have generalized patterns not seen in all howler monkey species. Our results on black howler monkeys are similar to the findings of Ryan et al. [in press] of a mantled howler population in Panama. Despite the differences in grouping patterns between mantled howler and black howler monkeys, in both species female reproductive success decreased with an increasing number of females in a group, and male reproductive success declined with the number of males in a group [Ryan et al., in press]. Male and female reproductive success in both species might be affected similarly by group size and composition; however, proximate mechanisms (e.g., infanticide risk, dispersal patterns, mating system) might be distinct between these two species.

Our study has shown how male and female reproductive success might be influenced by group size and composition in Mesoamerican black howler monkeys. This approach parallels that of Treves [2001] and Ryan et al. [in press], where proxies (based on relatively easily collected demographic data) of individual reproductive success also suggest differences and similarities between howler monkey species. To further our understanding of the diversity of howler monkey sociality and grouping patterns, we need multipopulation demographic data, long-term monitoring of the dynamics of demographic changes in focal populations as well as behavioral data on social and reproductive patterns and dynamics of different howler monkey species and populations [Strier, 2003]. These data should be paralleled by information on paternity and kin relationships [Chapais & Berman, 2004].

REFERENCES

Brockett RC, Horwich RH, Jones CB. 1999. Disappearance of infants following male takeovers in the Belizean black howler monkey (Alouatta pigra). Neotropical Primates 7:86–88.

Brockett RC, Horwich RH, Jones CB. 2000. Female dispersal in the Belizean black howling monkey (Alouatta pigra). Neotropical Primates 8:32–34.

Chapais B, Berman CM. 2004. Kinship and behavior in primates. New York: Oxford University Press. 507p.

Chapman CA, Chapman LJ. 2000. Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in groups. Chicago: University of Chicago Press. p 24–41.

Chapman CA, Pavelka MSM. 2005. Group size in folivorous primates: ecological constraints and the possible influence of social factors. Primates 64:1–9.

Cortés-Ortiz L, Bermingham E, Rico C, Rodríguez-Luna E, Sampaio I, Ruiz-García M. 2003. Molecular systematics and biogeography of the Neotropical monkey genus, Alouatta. Mol Phylogenet Evol 26:64–81.

Crockett CM. 2003. Re-evaluating the sexual selection hypothesis for infanticide by Alouatta males. In: Jones CB, editor. Sexual selection and reproductive competition in primates: new perspectives and directions. American society of primatology: special topics in primatology, Vol. 3. Norman: The American Society of Primatologists. p 327–365.

Crockett CM, Janson CH. 2000. Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In: van Schaik CP, Janson CH, editors. Infanticide by males and its implications. Cambridge: Cambridge University Press. p 75–98.

Di Fiore A, Campbell CJ. 2007. The atelines: variation in ecology, behavior, and social organization. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. New York: Oxford University Press. p 155–185.

Estrada A, Luecke L, Van Belle S, Barruetta E, Rosales-Meda M. 2004. Survey of black howler (Alouatta pigra) and spider (Ateles geoffroyi) monkeys in the Mayan sites of Calakmul and Yaxchilán, Mexico and Tikal, Guatemala. Primates 45:33–39.

Ford SM. 2006. The biogeographic history of Mesoamerican primates. In: Estrada A, Garber PA, Pavelka MSM, Luecke LG, editors. New perspectives in the study of Mesoamerican primates: distribution, ecology, and conservation. New York: Springer. p 81–114.

Horwich RH, Brockett RC, Jones CB. 2000. Alternative male reproductive behaviors in the Belizean black howler monkeys (Alouatta pigra). Neotropical Primates 8:95–98.

Horwich RH, Brockett RC, James RA, Jones CB. 2001. Population structure and group productivity of the Belizean black howling monkey (Alouatta pigra). Primate Rep 61:47–65.

Izawa K, Kimura K, Samper-Nieto A. 1979. Grouping of the wild spider monkeys. Primates 20:503–512.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol 6:326–336.

Jones CB. 2004. The number of adult females in groups of polygynous howling monkeys (Alouatta spp.): theoretical inferences. Primate Rep 68:7–25.

Kitchen DM, Horwich RH, James RA. 2004. Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: experimental evidence for the effect of intra-group male relationships and age. Behaviour 141:703–723.

Knopff KH, Pavelka SMS. 2006. Feeding competition and group size in *Alouatta pigra*. Int J Primatol 27: 1059–1078.

Pope TR. 1990. The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. Behav Ecol Sociobiology 27:439–446.

Pope TR. 1998. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). Behav Ecol Sociobiol 48: 253–267.

Pope TR. 2000. The evolution of male philopatry in Neotropical monkeys. In: Kappeler PM, editor. Primate males. Cambridge: Cambridge University Press. p 219–235.

Robbins MM. 1995. A demographic analysis of male history and social structure of mountain gorillas. Behaviour 132:21–47.

Ryan SJ, Starks PT, Milton K, Getz WM. In press. Intersexual conflict and group size in mantled howler monkeys: a 23-year evaluation. Int J Primatol.

Silk JB. 2007. The adaptive value of sociality in mammalian groups. Phil Trans R Soc B 362:539–559.

Snaith TV, Chapman CA. 2007. Primate group size and interpreting socioecological models: do folivores really play by different rules? Evol Anthropol 16: 94–106.

Strier KB. 2003. Primatology comes of age: 2002 AAPA luncheon address. Yearbook Phys Anthropol 46:2–13.

Treves A. 2001. Reproductive consequences of variation in the composition of howler monkey (*Alouatta* spp.) groups. Behav Ecol Sociobiology 50:61–71.

Treves A, Chapman CA. 1996. Conspecific threat, predation avoidance, and resource defense: implications for grouping in langurs. Behav Ecol Sociobiol 39:43–53.

Van Belle S, Estrada A. 2006. Demographic features of *Alouatta pigra* populations in extensive and fragmented forests. In: Estrada A, Garber PA, Pavelka MSM, Luecke LG, editors. New perspectives in the study of Mesoamerican primates: distribution, ecology, and conservation. New York: Springer. p 121–142.

van Schaik CP. 1983. Why are diurnal primates living in groups? Behaviour 87:120–144.

van Schaik CP, Janson CH. 2000. Infanticide by males and its implications. Cambridge: Cambridge University Press. 569p.