Intragroup genetic relatedness in two howler monkey species (*Alouatta pigra* and *A. palliata*):
Implications for understanding social systems and dispersal

by

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ABSTRACT

Social systems and dispersal patterns impact genetic variation within and between primate groups. Kinship plays a role in shaping social interactions and therefore shapes social systems. However, few studies have used molecular data to describe the degree of genetic relatedness among intragroup individuals. In this study, I analyze genetic relatedness among same-sex intragroup adults in *Alouatta palliata* and *A. pigra*, sister species that have distinct social systems, to test the hypothesis that patterns of intragroup genetic relatedness will also be distinct. Results indicate that in both species, most groups contain closely related same-sex dyads, which was unexpected for *A. palliata* since it has been reported that most juveniles disperse and join groups that do not contain close kin. However, the degree of intragroup relatedness seems to be more variable among *A. pigra* groups, whereas most same-sex adults are closely related in *A. palliata* groups. This suggests that dispersing individuals may use multiple strategies to join groups (i.e., coalition take overs by related males, solitary individuals joining groups that contain close relatives, etc.) or that philopatry is common in these groups. Further study including both long-term observational and genetic data is necessary to determine the degree of variation in intragroup genetic relatedness for both species within and among populations and fitness consequences of various strategies. Ecological and demographic data are also necessary to determine the importance of other factors, especially habitat fragmentation, in determining the degree of relatedness in howler monkey groups.

ACKNOWLEDGEMENTS

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INTRODUCTION

Social interactions and the relationships that result from those interactions (i.e., social structure) and social organization (which describes group size, composition, and cohesion) are inherently linked to mating systems, which together describe the social system of group living species, like primates (Kappeler and van Schaik 2002). Kinship is a factor that affects social interactions, such as nepotism and dominance relationships (Silk 2002), and therefore should affect the formation of social systems. Many studies have addressed the role of kinship in shaping primate social systems, mostly regarding the role of kin selection in cooperative behavior among Old World cercopithecines (Strier 2011), in which females do not disperse from their natal groups (i.e., females are philopatric) (Kawai 1958; Sade et al. 1976). For example, female Japanese macaques spend more time in the proximity of close kin than distant kin (Kurland 1977), and female vervet monkeys respond faster to distress calls that come from close kin (Seyfarth and Cheney 1984). Similarly, rhesus macaque brothers that disperse to the same group associate more closely with each other and are less likely to impinge on one another's reproductive access to females than with non-kin (Vessey and Meikle 1988). Despite the breadth of studies linking kinship to primate social behavior, relatively few have used genetic data to assess the degree of relatedness among individuals in primate groups (Silk 2002; Di Fiore 2009), especially for Neotropical primates. This study addresses this problem by investigating intragroup genetic relatedness for both sexes in two species of howler monkeys (*Alouatta pigra* and *A. palliata*).

In addition to social interactions, dispersal patterns also play an important role in shaping primate social systems. This is because dispersal patterns greatly affect the genetic structure of populations and the determination of genetic relationships among group members, since turnover in group membership can either be attributed to recruitment of natal juveniles into the breeding group, or to immigration of extragroup individuals. Here, dispersal is defined after Howard (1960) as, "the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate." Although in mammals dispersal is most commonly male-biased, primates exhibit a diversity of dispersal regimes: 1) female-biased (*Pan* spp.: Pusey 1980; Eriksson et al. 2006, *Gorilla* spp.: Stokes et al. 2003, *Papio hamadryas*: Hammond et al. 2006), 2) male-biased (*Cebus olivaceus*: Robinson

1988, *Papio cynocephalus*: Altmann et al. 1996, *Colobus vellerosus*: Wikberg et al. 2012), and 3) bi-sexual dispersal (*Aotus*: Fernandez-Duque and Huntington 2002, *Leontopithecus rosalia*: Baker and Dietz 1996, *Alouatta* spp.: Clarke and Glander 1984; Glander 1992; Brockett et al. 2000; Pope 1989).

Traditionally, studies on dispersal have been based on long-term observations of particular groups and populations. However, long-term field studies are often difficult, due to logistics and costs associated with such projects, in addition to dealing with political obstacles (Strier and Mendes 2009). This has resulted in a shortness of these data, particularly for New World monkeys. Genetic data can ameliorate this dilemma by providing an alternative method of study. Over the last decade, molecular methods have been implemented to investigate genetic relatedness among many social vertebrate species in order to understand the extent and implications of kin associations in relation to dispersal patterns (*Parus major*: Van De Casteele and Matthysen 2006; *Passer domesticus*: Vangestel et al. 2011; *Crocuta crocuta*: Watts et al. 2011; delphinids: Möller 2012; *Papio cynocephalus*: Altmann et al. 1996; *Lagothrix poeppigii*: Di Fiore and Fleischer 2005; *A. seniculus*: Pope 1998). Relatedness analysis is also useful to investigate sex-biased dispersal because we can expect mean relatedness to be greater among group members of the philopatric sex than among the dispersing sex (Goudet et al. 2002). Since genetic data are quicker to obtain than observational data to track dispersal in long-lived species, many recent studies have implemented relatedness analysis to infer sex-biases in dispersal (*Pseudotropheus* spp.: Knight et al. 1999; *Egernia cunninghami*: Stow et al. 2001; *Vombatus ursinus*: Banks et al. 2002; *Papio hamadryas*: Hammond et al. 2006).

Primates are an excellent study system for the investigation of the effects of social interactions and dispersal on intragroup genetic relatedness since social systems are very diverse across taxa. Although there are a large number of behavioral studies on Neotropical primates, little has been published regarding the interactive role of dispersal and social interactions in shaping patterns of intragroup genetic relatedness. In the absence of long-term behavioral studies, or where paternity cannot be easily determined exclusively by social interactions among mates, genetic data provide the means to estimate the patterns of genetic relationships among individuals, both within and among groups.

Here, I investigate patterns of within-group genetic relatedness to understand how these patterns may affect our current understanding of the social systems and dispersal patterns of two

species of howler monkeys (*A. pigra* and *A. palliata*). Given their phylogenetic proximity, these species provide a useful model to investigate how dispersal and social structure interact to shape genetic relationships among group individuals because their social systems are distinct and their patterns of dispersal may differ (see below). In this study, I ask specifically, 1) what are the patterns of genetic relatedness among same-sex adults within social groups in these species? 2) How variable is intragroup relatedness among groups in each species and what might account for this variation? and 3) Do these patterns reflect our current understanding of their dispersal and social structure? To do this, I analyze and compare pairwise coefficients of genetic relatedness (r) among adult individuals generated from multilocus microsatellite genotypes.

Study Species

      Alouatta pigra and *A. palliata* are Mesoamerican primates of the family Atelidae. They are sister species that diverged 3 MYA (Cortés-Ortiz et al. 2003). *Alouatta pigra* is restricted to the Yucatan Peninsula in Mexico, Guatemala and Belize (Marsh et al. 2008), while *A. palliata* exists in southern Mexico in the state of Veracruz, Tabasco, Oaxaca, and Chiapas and ranges south through Central America to the west coast of Ecuador and the northwestern tip of Peru (Cuarón et al.2012). In both species, mating systems are polygynandrous, individuals live in uni or multi-male/multi-female groups (Van Belle et al. 2009; Jones 1985, see below for a more detailed description), and dispersal is bisexual (Brockett et al. 2000; Horwich et al. 2000; Van Belle et al. 2008; Glander 1992; Clarke and Glander 2004). Our understanding of the social system of these species has arisen from observations on a few study groups in a few populations. Reports of social structure and dispersal for *A. pigra* have been very limited to incidental observations and only recent studies have started to uncover some of the characteristics of the social interactions in this species (see Van Belle and Estrada 2006, 2008; Van Belle et al. 2008, 2009, 2011, 2012). Most reports of social structure and intergroup movement in *A. palliata* come from a single population in Costa Rica [Hacienda La Pacifica (LP)] (Glander 1980, 1992; Clarke and Glander 1984, 2004, 2010; Clarke 1983, 1990; Clarke and Zucker 1994; Clarke et al. 1998; Zucker and Clarke 1998). This population is one of the few howler monkey populations that have been continuously monitored for multiple generations. Consequently, the information obtained from this population has played a prominent role in the development of our

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understanding of the species-typical social system. However, observations of *A. palliata* populations in Mexico (Dias and Rodríguez Luna 2006, Arroyo-Rodríguez et al. 2008) and on Barro Colorado Island (BCI) in Panama (Carpenter 1934; Wang and Milton 2003) suggest that social systems and dispersal patterns may differ between study sites (see below).

Social Organization and Social Structure

In *A. pigra*, mean group size ranges from 4–9 individuals and groups typically contain 1–2 adult males, 1–3 adult females, and 1–4 immatures (Chapman and Balcomb 1998; Van Belle and Estrada 2006). Uni-male groups can be just as prevalent as multi-male groups in some populations, and seem to be more common in continuous than fragmented forest (Van Belle and Estrada 2006). In contrast, *A. palliata* has the largest group size in the genus, which can range from 6–20+ individuals (see review in Chapman and Balcomb 1998), and can be as large as 45 individuals (Clarke and Zucker 1994). Groups are commonly multi-male/multi-female and usually consist of 2–4 adult males, 2–10 adult females, and 1–10 immatures (Glander 1980; Estrada 1982; Arroyo-Rodríguez et al. 2008; Milton et al. 2009).

There are important differences in social structure among *A. pigra* and *A. palliata*. Intrasexual dominance hierarchies in *A. pigra* are not apparent among adults in a group as they rarely interact with each other (Van Belle et al. 2008; Van Belle et al. 2011). In some multi-male groups, however, evidence suggests that one male is higher ranking than the others. This alpha or central male has tighter associations with group females and participates in the defense of the group (i.e. howling bouts and intergroup interactions) more frequently (Kitchen et al. 2004; Van Belle et al. 2008; Van Belle et al. 2009). Central males are also considered to sire most of the offspring in a group (Van Belle et al. 2009). Among intragroup females, agonistic interactions are very uncommon and their rates of affiliation and degrees of proximity to each other vary among groups (Van Belle et al. 2011). In contrast, at LP, *A. palliata*, is reported to have age-reversed linear dominance hierarchies in both sexes, meaning that higher-ranking individuals are younger than lower-ranking individuals (Jones 1980; Glander 1980; Zucker and Clarke 1998). However, on BCI, intragroup *A. palliata* individuals rarely engage in dominance-related interactions and linear dominance hierarchies could not be discerned by researchers, who were only able to identify alpha males in groups (Carpenter 1934; Wang and Milton 2003). Alpha

males do not have exclusive access to group females, as multiple males in *A. palliata* groups are usually observed to copulate with resident females (Glander 1980; Wang and Milton 2003, Jones and Cortés-Ortiz 1998).

Dispersal and Group Formation

There are very few documented cases of dispersal in *A. pigra* (Brockett et al. 2000; Horwich et al. 2000; Van Belle et al. 2011, 2012). In this species, females disperse as juveniles, sub adults, or adults by traveling alone or with another individual (Horwich et al. 2000; Van belle et al. 2011) and are often met with aggression from resident females, who can act together to prevent their immigration (Van Belle et al. 2011). Immigration of extragroup females and secondary dispersal appear to be rare at the Community Baboon Sanctuary (CBS) in Belize, leading Brockett et al. (2000) to suggest that it may be more common for emigrating females to form new groups. This pattern of female dispersal in which dispersing females form new groups instead of join established groups, is reported for red howler monkeys (*A. seniculus*) (Crockett 1984, Pope 1992). This interpretation is strengthened by recent observations from Van Belle et al. (2011) at Palenque National Park (PNP) in Mexico of immigration attempts of immature *A. pigra* extragroup females (n = 3) into established groups. Group members met these females with varying levels of agonism and their temporary associations only lasted from 14 days to three months. Over the 14-month period of Van Belle et al.'s study, none of these females successfully joined the group.

On the other hand, previous research at LP shows that most *A. palliata* male and female juveniles are forced by nonrelatives to disperse from their natal group at an average age of 21.9 months and 32.8 months, respectively (Glander 1992; Clarke and Glander 2008). After leaving their natal group, juveniles spend a significant amount of time solitary before joining an established group that presumably contains no kin (Glander 1992). According to Glander (1992), transient dispersal (i.e., joining a group for less than 1 year and moving before reproducing there) is common among females in this species, as immigrating females will leave a group if they fail to reach the alpha position (Jones 1980).

In *A. pigra,* male group membership appears to change more frequently than female group membership, which is considered quite stable (Van Belle et al. 2008; Brockett et al. 2000).

Extragroup *A. pigra* males travel alone or in pairs and those that form coalitions are more successful in group takeovers (Van Belle et al. 2008; Horwich et al. 2000). At CBS, Horwich et al. (2000) reported that two coalitions of males expelled resident males during takeovers and that males traveling alone joined groups without expelling resident males (although sometimes single males were also successful in displacing resident males in takeovers). Van Belle et al. (2012) observed two two-male coalitions involved in takeover events at PNP and provide genetic evidence suggesting that in both cases, the males were closely related. At CBS, Horwich et al. (2000) also observed an expelled male and female eventually form a new group.

Although *A. palliata* has been studied for longer than *A. pigra*, only one instance of a male-male coalition takeover has been observed in this species (Dias et al. 2010), which suggests that it occurs less frequently. However, it is unknown whether or not these coalition males were closely related, or the frequency at which this type of event takes place. Immigrating *A. palliata* males attempt to take over a group by defeating the alpha male and will remain solitary if they cannot do so (Glander 1992). Displaced alpha males remain as low-ranking males in the group or as peripheral individuals (Clarke 1983). Although it has been thought that *A. palliata* alpha males had exclusive reproductive access to receptive females (Glander 1980), recent genetic paternity exclusion analysis in the LP population revealed that lower ranking males likely share paternity of group offspring (Ellsworth 2000).

Secondary dispersal (moving between social units after breeding in one) is thought to be rare for both sexes (Glander 1992), but has been reported to occur at a low rate for *A. palliata* at LP and is suggested to be a reproductive strategy in which individuals of both sexes seek to join groups with a more favorable sex ratio (Clarke and Glander 2010; Ryan et al. 2008). Secondary dispersal has not been reported for *A. pigra*. Similarly, sequential dispersal of related individuals to the same group has not been investigated for either species but based on long-term behavioral data, Glander (1992) suggests it does not occur in *A. palliata*. It is unknown what proportion of *A. pigra* juveniles disperse from their natal group, but it seems that most males disperse, Horwich et al. (2000) report no retention of *A. pigra* natal males at CBS. However, retention of *A. palliata* juveniles (males and females) has been observed in Costa Rica and Mexico (Clarke and Zucker 1989; Arroyo-Rodriguez et al. 2008; Clarke and Glander 2008), but philopatry is thought to be rare in this species (Glander 1992; Clarke and Glander 2008).

The above observations of dispersal and social behavior have lead to the assumption that *A. palliata* groups are composed of unrelated adults and their offspring (Glander 1980; Glander 1992; Clarke et al. 1998). On the other hand, given that coalitions of related *A. pigra* males have been reported to take over groups and female immigration is rare, it is fair to presume that *A. pigra* groups contain closely related same-sex adults (see Horwich et al. 2000; Van Belle et al. 2008; Van Belle et al. 2012). Particularly, based on our current knowledge of the social systems in these species, I conjecture that 1) there are two kinds of *A. pigra* groups for females: new and well-established groups, and two types of multimale groups for males: those formed via coalition takeovers and those joined by solitary males. New and well-established *A. pigra* groups should differ in the levels of relatedness between adult females. In new groups, adults are not kin since they form via aggregations of unrelated adults. In well-established groups, relatedness among adult females should be high due to non-random retention of juvenile females. Relatedness among adult males in multimale groups resulting from coalition takeovers should be high, while the degree of relatedness could vary among groups joined by solitary males. 2) Relatedness among intragroup same-sex *A. palliata* adults should be low, as most juveniles of both sexes emigrate and turnover in group membership involves immigration of presumably unrelated individuals.

Hypothesis

Due to reported differences in social structure, social organization and patterns of dispersal, I hypothesize that *A. pigra* and *A. palliata* will have different patterns of genetic relatedness among same-sex intragroup adults.

Predictions (see Table 1)

1. Mean relatedness of adult female dyads in *A. pigra* groups will be highly variable due to likely random sampling in this study that would include both well-established and recently formed groups.

2. Similarly, there should be variation in mean *A. pigra* adult male relatedness among multi-
    male groups due to previous observations of coalitions between related individuals as well as
    solitary males joining established groups.

3. Same-sex adult dyads in *A. palliata* groups should be unrelated and variation among groups
    in mean relatedness between same-sex adults should be low.

METHODS

Sample Collection

Blood and hair samples from 76 *A. pigra* individuals [31 adult females (AF), 26 adult males (AM), 19 immatures (IM)] and 140 *A. palliata* individuals (59 AF, 42 AM, 39 IM) were obtained from 39 wild groups from different location in Mexico and Guatemala. Sampled individuals were captured as described in Rodríguez-Luna and Cortés-Ortiz (1994) between 1998 and 2012. Exact sampling locations are shown in Figure 1. Blood samples were mixed in lysis buffer (Seutin et al. 1991), kept on ice in the field and stored at -20°C after they arrived in the laboratory. Hair samples were stored in paper envelopes, kept at room temperature in the field, and stored at -20°C in the lab.

DNA Extraction and Microsatellite Genotyping

Genomic DNA was extracted from both blood and hair samples for all individuals (except from one infant for which only DNA from hair was extracted) using the QIAGEN DNEasy tissue kit (Qiagen Inc., Valencia, CA). The manufacturer's protocol for animal tissue extractions was executed with the following modifications: step 1) for blood samples: starting volume of 100 μL of whole blood, added to 100 μL buffer ATL, and for hair samples: approximately 15 hair follicles in 100 μL buffer ATL.

All *A. pigra* and *A. palliata* individuals were genotyped at 22 and 19 microsatellite loci, respectively (Table 2). We conducted both single and multiplex reactions to amplify these loci. Singleplex amplifications were preformed in a reaction volume of 10 μL containing 1 μL 10X

buffer, 1 µL dNTPs at 2µM each, 0.8 µL MgCl$_2$ (50mM), 0.25 µL of fluorescently labeled forward primer (10 µM), 0.25 µL unlabeled reverse primer (10 µM), 5.7 µL water, 0.045 µL Platinum taq (Invitrogene), and 1 µL DNA extract. The thermal cycling profile was as follows: initial denaturation of 94 ^{o}C for 2 min, followed by 35 cycles of 94 ^{o}C for 30 s, annealing temperature (see Table 2) for 30 s, 72 ^{o}C for 30 s, followed by a 72 ^{o}C for 10 min. Based on similarities in annealing temperature. I ran multiplex reactions (Table 2) for a number of samples using the QUIAGEN multiplex PCR kit (Qiagen Inc., Valencia, CA), with a total reaction volume of 10 µL. The reaction mix contained 5 µL of 2X Master Mix, 1 µL of 10X primer mix (with each primer concentrated at 2 µM), 1 µL of water, 2 µL of Qsolution, and 1 µL of DNA. PCRs for those loci that were multiplexed followed a thermal cycling profile of 95 ^{o}C for 15 min, followed by 34 cycles of 94 ^{o}C for 30 s, annealing temperature for 30 s, 72 ^{o}C for 45 s, followed by a 60 ^{o}C extension of 30 min. PCR products were electrophoresed on a 2% agarose gel to verify the presence and quality of amplifications in order to determine the appropriate dilutions for genotyping. PCR products were diluted with water according to the intensity of the observed band and added to a mix of fluorescent standard (GS500LIZ) and Hi-Di Formamide (Applied Biosystems) before samples were sent to the University of Michigan DNA Sequencing Core where genotyping was done on an Applied Biosystems DNA sequencer (Model 3730XL). Allele sizes were scored using GeneMarker V 1.5 (SOFTGENETICS) by at least two different researchers. If researchers were unable to agree on a call, the genotype was re-amplified. Several individuals for each locus were genotyped from different PCR reactions more than once to ensure genotype accuracy.

Analyses

Observed and expected heterozygosities, number of alleles per locus, allele frequencies and probability of identity (PI) were calculated in GenAlEx 6.41 (Peakall and Smouse 2006). I used Micro-Checker (Van Oosterhout et al. 2004) to test for evidence of null alleles, scoring errors due to stuttering, and large allele dropout. For both species, none of the loci showed evidence to suggest the presence of any of the above phenomena in my dataset.

I used Arlequin ver 3.5.1.3 (Excoffier and Lischer 2010) to analyze linkage disequilibrium (LD) between pairs of loci and departures from Hardy-Weinberg equilibrium

(HWE) in each species. After implementing a sequential Bonferroni correction to account for multiple comparisons between loci, I found evidence for LD between five pairs of loci for *A. pigra* and seven pairs for *A. palliata*. I cannot be sure of physical linkage between any pair of loci since the location of these microsatellites in the genome is unknown. However, the fact that different loci show LD in these two sister species (API14 and API06 for *A. pigra* and API11, D6S260, TGMS1 and TGMS2 for *A. palliata*) suggests that physical proximity of loci may not be responsible for this observation. Data analysis after removal of genotype data for loci to correct for LD did not produce results different from those of analyses utilizing the entire data set. For both species, several loci showed evidence for deviation from HWE (Table 2). For neutral loci, like microsatellites, deviations from HWE are often caused by the presence of null alleles. Based on my analyses with Micro-Checker, there is no evidence of null alleles in my datasets. However, my samples came from multiple populations that may be genetically structured, which would create a Wahlund effect (Wahlund 1928). Although the presence of LD and deviations from HWE may make estimates of relatedness less accurate, it should do so equally across dyads and thus should not affect interpretation of my results. Therefore, I present results using genotype data for all loci (*A. pigra* n = 22, *A. palliata* n = 19).

Relatedness

To determine which estimator of relatedness is most appropriate for each data set, I compared estimates of relatedness from several estimators using simulated genotypes [100 each of monozygotic twins (r = 1), parent-offspring (r = 0.5), full sibs (r = 0.5), half-sibs (r = 0.25), first cousins, (r = 0.125), and unrelated (r = 0)] against actual values from my data sets in COANCESTRY (Wang 2011). Relatedness coefficients (r) are reported for the estimator that performed best at matching true r-values of the pre-determined dyadic relationships between individuals with the simulated genotypes listed above. The QuellerGt (Queller and Goodnight 1989) estimator performed best for the *A. pigra* data set, while the LynchLi (Lynch 1988; Li et al.1993) and QuellerGt performed equally well for *A. palliata*. The Ritland (1996) estimator performed worst for both species. Here, I report QuellerGt r-value estimates and used those estimates in statistical analyses. To confirm the appropriateness of this estimator, I compared QuellerGt r-values against others estimated by COANCESTRY for known mother-offspring

dyads in each species (n = 4 dyads each, see Figure 2). QuellerGt reliably estimated expected r-values for these dyads (r ≈ 0.5) (see results for more details). After Di Fiore (2009) and Van Belle et al. (2012), I consider closely related dyads to be those that could be related on the order of parent-offspring or half or full siblings (*A. pigra*: r ≥ 0.25; *A. palliata*: r ≥ 0.3) and unrelated dyads to be those with r-values below this threshold. The threshold for closely related dyads is greater in *A. palliata* since the markers used were not as polymorphic and produced a mean value for known mother-offspring dyads that was greater than r = 0.5.

I also used COANCESTRY to test for significant intraspecific differences in mean relatedness between a) intragroup adult males and all possible dyads, b) intragroup adult females and all possible dyads c) intragroup adult males and all possible adult male dyads, d) intragroup adult females and all possible adult female dyads, e) intragroup adult males and intragroup adult females, and f) all possible adult male dyads and all possible dyads, g) all possible adult female dyads and all possible dyads. This analysis was performed by the bootstrapping method, with resampling 1,000 times. For each species, comparisons involving mean relatedness among intragroup adult females were conducted using only genotype data for adult females sampled from groups from which we obtained samples from all adult females present in the group (*A. pigra* n = 9 groups, *A palliata* n = 6 groups). The same criterion was applied for comparisons involving relatedness among intragroup adult males (*A. pigra* = 8 groups, *A. palliata* = 7 groups; Table 3).

Variation within species

To test variation in the degree of relatedness between social groups within each species, I used a one-way ANOVA in R (R Development Core Team 2011). Since within-group variation is lacking when only one same-sex dyad is present, I only included groups in which more than one same-sex adult dyad was present (i.e., when there are more than two adult males or females in the group). For females, I used four groups for each species and for males I used four *A. palliata* groups. I was unable to test variation in mean relatedness of intragroup males between *A. pigra* groups since all study groups had fewer than three adult males.

To investigate whether group size has an effect on the levels of intragroup relatedness, I tested the significance of correlations between the total number of adults in the group as well as

the number of adult individuals of the same and opposite sex in the group and mean intragroup relatedness for each sex in each species using IBM SPSS Statistics 19 (Armonk, NY). Total number of adults in the group served as a proxy for group size here since I do not have accurate data on number of immatures for every group sampled. I visually inspected Q-Q plots and determined that data approximate a normal distribution, so I report Pearson's correlation coefficient (r).

RESULTS

Power of molecular markers

Observed heterozygosity (H_o) per locus in *A. pigra* ranged from $H_o = 0.17$ to $H_o = 0.76$ and averaged at $H_o = 0.51$ across all 22 microsatellite markers and the mean number of alleles per locus (N_a) was 5.05 (Table 2). Probability of identity was very low (PI = 1.0×10^{-14}, $PI_{sib} = 6.1 \times 10^{-7}$) indicating that it is unlikely that two individuals or any two siblings, respectively, in a randomly chosen dyad share the same multilocus genotype. This suggests that the combination of markers used for this study is sufficient to generate a unique genotype for each individual in the sample. Heterozygosity and mean number of alleles per locus were lower among the markers used for *A. palliata* (Mean $H_o = 0.27$ [range $H_o = 0.05$ to $H_o = 0.70$], mean $N_a = 4.74$]. However, probability of identity was very low (PI = 3.1×10^{-8}, $PI_{sib} = 4.6 \times 10^{-4}$), suggesting that although the markers used for *A. palliata* were not as polymorphic as those used for *A. pigra*, their combination is sufficient to distinguish among individuals.

For known mother-offspring dyads (n = 4 for each species), mean QuellerGt relatedness was close to the expected value of r = 0.5 (*A. pigra*: mean r = 0.47, range r = 0.24-0.68, *A. palliata*: mean r = 0.64, range r = 0.32 to r = 0.89; Figure 2). For *A. palliata*, the mean is higher than the expected value for this type of relationship (i.e., ~0.5), but this is not surprising given that many of the markers used for *A. palliata* were not highly polymorphic. Although I report QuellerGt r-values for both species since this estimator also performed well in the simulation studies, I warn that these values are probably slightly inflated for *A. palliata*. This should not be

a problem for the purposes of this study since I am only making within-species comparisons using these values.

Intragroup same-sex relatedness

In both species, relatedness among intragroup same-sex adult dyads for both sexes [intragroup adult male dyads: r_{IM} (*A. pigra*: mean $r_{IM} = 0.16 \pm SE = 0.079$, *A. palliata*: mean $r_{IM} = 0.45 \pm SE = 0.068$), intragroup adult female dyads: r_{IF} (*A. pigra* mean $r_{IF} = 0.25 \pm 0.045$, *A. palliata* mean $r_{IF} = 0.36 \pm 0.066$] was significantly greater than the relatedness among all dyads (r_{all}) (*A. pigra*: mean $r_{all} = -0.008 \pm 0.004$, $p < 0.05$; *A. palliata*: $r_{all} = -0.007 \pm 0.003$, all $p < 0.05$) and than all same-sex adult dyads (r_{AM} and r_{AF}) in the sample (*A. pigra*: $r_{AM} = 0.012 \pm 0.010$, $p < 0.05$, $r_{AF} = -0.005 \pm 0.008$, $p < 0.05$; *A. palliata*: $r_{AM} = 0.010 \pm 0.0003$, $p < 0.05$, $r_{AF} = 0.008 \pm 0.006$, $p < 0.05$) (Figure 3). These results indicate that, in general, groups do not contain a random sample of adult genotypes from the population, but may contain close relatives. Also, for both species, the average coefficient of relatedness among intragroup adult male dyads was not significantly different from that among intragroup adult female dyads (both $p > 0.05$), suggesting that levels of relatedness among intragroup males and females are similar.

Interestingly, when comparing all *A. pigra* adult male dyads (n = 325 dyads, mean $r_{AM} = 0.012$) to all dyads in the species mean (n = 2850 dyads, $r_{all} = -0.008$), adult male dyads are significantly more closely related ($p < 0.05$). Similarly, for *A. palliata*, all adult female dyads (n = 1711 dyads, $r_{AF} = 0.008$) were significantly more closely related than all dyads in that species (n = 9730 dyads, $r_{all} = -0.007$, $p < 0.05$). This is likely an effect of the high statistical power arising from large sample sizes enhancing the ability to detect this slight difference. These results are likely not biologically relevant since relatedness among these dyads is effectively zero. Also, for both species, relatedness among all adult male dyads is not significantly different from that among all adult female dyads.

Intergroup Variation

There was greater variation between groups in the degree of relatedness among intragroup adult males in *A. pigra* than in *A. palliata* (Table 3). Most *A. pigra* groups had only

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two adult males and in some groups they were unrelated (e.g., groups 13 and 20A) while in other groups adult males were very closely related (groups 2 and 10). In group 5, the only three-male group for this species, two males were closely related to each other ($r > 0.25$), while the third appeared to be unrelated to both individuals ($r = 0$ and $r = 0$). As mentioned above, I did not conduct an ANOVA for *A. pigra* males since variation cannot be investigated comparatively within groups.

There were two *A. palliata* groups with more than two adult males (groups 74 and 78). In both groups, all adult male dyads were closely related ($r > 0.3$) and their mean male relatedness did not differ between groups [ANOVA $F(1, 4) = 0.10$, $p = 0.77$)]. Among the two-male *A. palliata* groups ($n = 5$), there was only one in which the adult males were unrelated ($r = -0.14$, group 25). This dyad was in fact the only intragroup adult male dyad that was below $r < 0.3$ for this species. These results indicate that intragroup *A. palliata* males tend to be closely related to each other, but exceptions certainly exist.

Variation between groups in intragroup adult female relatedness was high for both species. In *A. pigra*, relatedness in two-female groups ranges from unrelated (group 12) to closely related (groups C and W). In three-female groups ($n = 4$), the degree of relatedness among pairs of intragroup adult females varied from unrelated ($r = 0$) to closely related ($r = 0.54$). For *A. palliata*, there were two groups that only contained two adult females (groups R and 53). In both cases, these females were very closely related to each other – on the order of mother-daughter or full siblings. There were four *A. palliata* groups in which there were more than two adult females. In two of these groups (A and Y), all females appear to be quite closely related to each other (all $r > 0.3$). The other two groups (25 and B), however, contain a mixture of unrelated and closely related dyads. For both species, ANOVA analysis indicates a significant difference among groups in mean relatedness of intragroup adult females [*A. pigra*: ANOVA $F(3, 14) = 10.1$, $p = 0.001$; *A. palliata*: ANOVA $F(3, 8) = 4.17$, $p = 0.047$]. For both species, number of adults in the group (as well as the number of males and separately the number of females) was not correlated with mean intragroup relatedness among adult males, nor among adult females (Table 4).

DISCUSSION

Alouatta pigra and *A. palliata* are sister species and they are reported as having distinct social systems (Crockett and Eisenberg 1987) and thus, different levels of expected intragroup relatedness are expected (Horwich et al. 2000; Brockett et al. 2000; Glander 1980). However, my results show a convergence in the broader pattern of similar moderate to high mean levels of intragroup relatedness among adults (i.e., most groups contained closely related same-sex adult dyads), especially for females. I did not find a significant difference between males and females in intragroup genetic relatedness in either species, which suggests that there is no sex bias in dispersal. These findings invoke the need for deeper investigation in the dispersal patterns and social interactions in both species, and the role of these factors in shaping intragroup genetic relatedness in howler monkeys.

High levels of relatedness among same-sex adults were unexpected for *A. palliata*. Nevertheless, my results show support for the hypothesis that *A. pigra* and *A. palliata* have different patterns of genetic relatedness among same-sex intragroup adults. Mean intragroup adult male-male relatedness in *A. pigra* groups was variable, with groups including both related and unrelated males, but in *A. palliata* most intragroup males were closely related to each other and only one group had one male dyad that was unrelated (group 25). Also, although mean intragroup adult female relatedness varied among groups in both species, the variation among *A. pigra* groups was much greater and included groups with unrelated, closely related, or a mixture of unrelated and closely related adult females, while *A. palliata* groups contained adult females that were closely related and in only one group, females were not closely related to each other. When analyzing the effect of the number of adults in the group, I found no correlation with intragroup relatedness for either sex. However, since the correlations between number of *A. palliata* adults and mean adult female intragroup relatedness was close to significance (Table 4) and most of the *A. palliata* groups that were sampled completely for females had fewer (i.e., 2 or 3) adult females than what is typical for the species, I analyzed separately correlations including multifemale groups from which not all adult females present were sampled. When including these incomplete groups, mean intragroup adult female relatedness is negatively correlated with number of adults and number of adult males in the group ($r = -0.51$, $p = 0.05$ and $r = -0.53$, $p = 0.04$ respectively), but not with number of adult females ($r = -0.48$, $p = 0.07$). Further analysis

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including more groups and samples from all adults in larger groups are necessary to determine if intragroup relatedness indeed decreases with group size.

Interspecific Contrasts in Genetic Relatedness - Males

Multimale *A. pigra* groups consist of unrelated or closely related adult males, or a combination of both (Table 3), while all but one *A. palliata* group (group 25) exclusively contained closely related adult males. These findings were expected for *A. pigra*, but at odds with my predictions of relatedness patterns among *A. palliata* intragroup adult male relatedness based on previous reports of male recruitment (Glander 1980). Van Belle et al.'s (2012) observation of group takeovers by related males suggest that the degree of relatedness among intragroup *A. pigra* males may be high. This pattern should be different than that among *A. palliata* groups, in which resident males are presumed to be the result of multiple additions of unrelated males over time (Glander 1992). However, Dias et al. (2010) report a coalition of *A. palliata* males taking over a group, though it was not known whether these individuals were related. These observations suggest that at least some *A. palliata* males join groups together, similar to what is typically reported for *A. pigra* males.

On the other hand, the presence of more than one male in a group may not always be the result of a group take-over by a coalition of closely related individuals. For example, Horwich et al. (2000) observed solitary *A. pigra* males joining established groups and living with other resident males. Additionally, multi-male groups may also be formed when juvenile males stay in their natal group until adulthood. However, there is no information available on the proportion of male *A. pigra* juveniles that do not disperse from their natal group. My genetic results suggest that in both species, there may be multiple strategies for males to become group residents, as groups were uni- or multimale and males in multimale groups were sometimes related and sometimes unrelated. This is similar to what Crickett and Eisenberg (1987) report for *A. seniculus*. For example, it is likely that solitary males may take over a group in *A. pigra* [as observed by Horwich et al. (2000)], and I found some uni-male groups with males unrelated to any of the resident females (data not shown). Also, some solitary males may join groups of unrelated males as I found groups with unrelated males in both species, as suggested by Glander (1992) for *A. palliata*, and Horwich (2000) for *A. pigra*. Groups with unrelated males in both

species observed in the present study could have arisen through this strategy or through group take over by coalitions of unrelated males (not yet confirmed with observational data in any of these species). Furthermore, some coalitions of related males taking over established groups (as those reported by Van Belle et al. 2012 for *A. pigra*) may occur in both species, as my data show that males in four out of five two-male groups in *A. palliata* and two out of eight in *A. pigra* were closely related. Finally, some males may remain philopatric (as reported by Clarke and Zucker 1989; Clarke and Glander 2008; Arroyo-Rodríguez et al. 2008), and many intragroup adult male-adult female dyads for both species in my study groups were closely related on the order of mother-son or full sibling relationship (30% in *A. pigra*, 40% in *A. palliata,* data not shown). This latter finding may support male philopatry or the possibility of males joining groups that contain female kin (full sisters). Additionally, when male subadults (~4–6 years old) were present in a complete group, they were always closely related to at least one of the adults in the group (male and/or female). These individuals are past the age of typical dispersal [which is 21.9 months for juvenile male *A. palliata* (Glander 1992)], so if they are philopatric, they should be residing with their parents and/or siblings if they are also still present in the group. Further research including both behavioral observations and genetic analyses is necessary to understand the extent to which each of these strategies is used, as well as the implication of each strategy for the reproductive success of males in the group.

Interspecific Contrasts in Genetic Relatedness - Females

I expected to find high levels of relatedness among adult *A. pigra* females in some (the well-established) groups, and unrelated females in others (the recently formed groups). For *A. palliata*, on the other hand, I expected low levels of relatedness among adult females in all groups. Consequently, I predicted high variation in mean adult female relatedness among *A. pigra* groups and little to no variation among *A. palliata* groups. My results indicate that most groups had closely related adult female dyads in both species (Table 3), but intragroup adult females could be all unrelated to each other (U), all closely related to each other (C), or a mixture of closely related and unrelated dyads (M). In *A. pigra* groups from which all adult females were sampled (n = 9), there was a similar proportion of U (n = 3) and C (n = 4) groups. For *A. palliata* groups where all females were sampled (n = 6), most were C (n = 4) and only one was U. In both

species, most groups that were C or U only had two adult females and groups that had 3+ adult females tended to be M. Although I did not find a correlation between number of adults in complete groups and intragroup relatedness, this suggests that larger groups may tend to have a mixture of closely related and unrelated dyads, especially in *A. palliata*, for which two-female groups are not very typical.

Brockett et al. (2000) provide the only report of female immigration for *A. pigra* into an established group. This instance occurred at CBS and involved a single juvenile female. Where this female came from and whether or not she could have been related to her new group's residents was not known. However, over a 14-month period, Van Belle et al. (2011) did not observe successful female immigration at PNP, but reported temporary associations between extragroup females with established groups. Unfortunately, we do not currently have information on the proportion of *A. pigra* juvenile females that disperse from their natal group, and clearly, further study is necessary to determine the extent to which dispersing females either immigrate into existing groups or establish new groups, and whether individuals immigrating into a group are related to any resident members of the group.

However, if *A. pigra* female dispersal patterns are similar to those among *A. seniculus*, as suggested by Brockett et al. (2000), then dispersing females can be expected to establish new groups with unrelated individuals (Pope 1992). Initially for new groups, it can be expected that genetic relatedness among intragroup females be close to zero. Over time, as reproductively dominant females retain their daughters, prevent other juvenile females from immigrating, and founder females die mean relatedness among adult females should increase until it approaches r = 0.5 (mother-daughter or full sisters). In a population containing groups of mixed ages, this phenomenon would be manifested in high variance in mean intragroup adult female relatedness. Results in the present study (which includes a random sample of groups) do not conflict with this idea as I observed variation between *A. pigra* groups in mean intragroup adult female relatedness (Table 3).

Data from long-term *A. palliata* studies in Costa Rica have suggested that intragroup adults are not related to each other (Glander 1980; Glander 1992; Clarke et al. 1998; Clarke and Glander 2008). My results do not support this expectation as most *A. palliata* groups consisted of closely related adult females or had a mixture of closely related and unrelated adult females. Additionally, most (all but two) subadult females in complete groups were closely related to at

least one adult (male and/or female) in the group. This supports the idea that the proportion of juveniles that remain philopatric may be greater than initially considered for this species (i.e., 6% at LP: Clarke and Glander 2008), that females join groups composed of related individuals (e.g., older siblings that had previously dispersed into the same group), that this may be a variable trait between the Mexican (in this study) and Costa Rican population, and/or that other factors are affecting the levels of dispersal in the Mexican population.

More longitudinal data on group membership and intergroup movements by individuals of both sexes are required to determine the degree of variation in natal recruitment across populations in each species, as rates of philopatry have only been reported for *A. palliata* at LP (Clarke and Glander 2008). Similarly, reports of immigration to groups where kin are already present do not exist for either species, and Glander (1992) did not observe multiple individuals from a group disperse to the same group in 20 years at LP. This population, however, is representative of a very small percentage of the entire range of *A. palliata* and very few subsequent studies have reported dispersal in this species (but see Clarke et al. 1998; Clarke and Glander 2008), and descriptions of dispersal in Mexican populations are sparse (but see Estrada 1982, Mandujano et al. 2004, Arroyo-Rodríguez et al. 2008). It is possible that immigration to groups with close kin occurs, but has not yet been observed due to lack of genetic data to confirm kin relationships among individuals in populations that have not been followed for multiple generations (i.e., pedigrees are not available).

In some instances, it is necessary to use a combination of both genetic and observational data to sufficiently characterize the degree of local relatedness or genetic structure that arises from patterns of dispersal and social interactions (Möller and Beheregaray 2004; Harris et al. 2009; Ribeiro et al. 2012). When genetic data are coupled with observational data, cryptic complexity in social and/or mating systems may be revealed. For example, paternity analysis of genetic relationships among suspected fathers or alpha males and the offspring they help rear, has changed the designation of a mating system from strictly monogamous or polygynous to be more flexible (Goossens et al. 1998; Ellsworth 2000), or has revealed that socially polyandrous females have predominantly monandrous clutches (Moore et al. 2009). Similarly, investigation of intragroup genetic relatedness in primate groups has deepened our understanding of the role of kinship in shaping their social organization and social structure. For example, Bradley et al. (2005) demonstrated that dominant male mountain gorillas share paternity of group offspring

with the second-ranking (unrelated) male and thus the resulting mixture of paternal kin and non-kin offspring in the same group allows for potential nepotistic social interactions in this species. Langergraber et al. (2007) found that although male chimpanzees preferentially affiliate and cooperate with maternal brothers, they do not prefer paternal brothers and most affiliative and cooperative dyads were not closely related. These findings suggest that cooperation among chimpanzee males is not always kin-based. Since howler monkey groups tend to be composed of a mixture of related and unrelated same-sex adult dyads (especially for *A. palliata* females and for *A. pigra* males and females), observational data may reveal similar patterns of association preferences in these species.

Complexity of Social Systems

If *A. pigra* and *A. palliata* are constrained by common ancestry and share a similar social system, we should see no interspecific differences in their social organization, social structure, and mating system. Observational data, however, have suggested that this is not the case (Crockett and Eisenberg 1987). Nonetheless, it is now apparent that high levels of genetic relatedness among intragroup adults may be a common feature in howler monkey social systems (black-and-gold howlers: Oklander et al. 2010; red howlers: Pope 1998, *A. pigra*: Van Belle et al. 2012, present study; mantled howlers: Milton et al. 2009, present study). The high degree of similarity between *A. pigra* and *A. palliata* in moderate to high levels of mean intragroup genetic relatedness presented here may suggest that their social systems are more similar than previously thought or that their distinct patterns of dispersal and social interactions produce similar levels of intragroup relatedness. For example, philopatry among juvenile females may be the most common factor contributing to a high degree of relatedness among adult females in groups of both species. In contrast, coalition takeovers involving related males may be a more common factor driving high adult male relatedness in *A. pigra* groups, while juvenile male philopatry and/or immigration to groups where kin are already present could be responsible for a high degree of male relatedness in *A. palliata* groups.

The variable levels of intragroup relatedness within and between *A. pigra* groups presented here for males and females appear to be consistent with Van Belle et al.'s (2012) findings at PNP. However, the high level of relatedness among intragroup adult males and

females in most *A. palliata* groups along with the low level of intergroup variation in this study contrast with the expectation of low relatedness among adults in this species (Glander 1980, 1992; Clarke et al. 1998). Contrary to my findings, Ellsworth (2000) revealed mean r-values within *A. palliata* groups that did not suggest close kinship among intragroup adult dyads. Confidence in relatedness estimates increases with the number of unlinked loci (Blouin *et al.* 1996), so her results should be interpreted with caution since the number of markers used in Ellsworth's study was low (n = 8), which could affect the power of her results. Using 13 markers, Milton et al. (2009) found closely related adult *A. palliata* males in some groups on BCI but only a single pair of closely related intragroup adult females. These mixed results for *A. palliata* among populations, along with the results presented here, suggest that the degree of intragroup relatedness varies between groups and/or populations for both species. Comparative genetic studies using the same microsatellite markers across populations would be desirable to test this hypothesis.

Intraspecific differences in social structure and dispersal patterns across populations may be responsible for producing variable levels of intragroup genetic relatedness like those presented in this study. Such differences in social systems may in turn be attributed to variation in ecological and demographic factors between habitats (Schradin and Pillay 2005; Streatfeild et al. 2011; Chapman and Rothman 2009). Likewise, dispersal patterns may vary between populations in relation to the distribution of food resources (Henzi et al. 1997; Koenig et al. 1998; Sinha et al. 2005) and to habitat fragmentation (Oklander et al. 2010). In particular, habitat fragmentation has been demonstrated to affect social organization and dispersal in howler monkeys (reviewed in Arroyo-Rodríguez and Dias 2010). Forest connectivity affects rates of dispersal for arboreal primates because movement between forest fragments is more risky since monkeys have to travel across the ground. Therefore, one might hypothesize that philopatry may be more common in fragmented forests than in continuous forests. Oklander et al. (2010) compared genetic structure and intragroup relatedness of *A. caraya* groups between continuous and fragmented forests and found differences between the habitat types. In continuous forest, groups were not genetically differentiated and intragroup adults were not closely related, but in fragmented forest, some groups were genetically differentiated and intragroup adult females were more closely related than adult males suggesting that females are philopatric in the fragmented forest, but not in the continuous forest. Many of the groups sampled in this study live

in very small forest fragments often isolated by pasturelands for cattle. In contrast, most *A. palliata* groups at the LP population are connected via forest corridors (see map in Glander 1992) and BCI has not been altered much by humans since its inception and was deemed a nature reserve in 1923. Differences in the degree of forest fragmentation between habitats at LP, BCI, and this study may account for the greater prevalence of closely related dyads in this study due to higher rates of philopatry.

The degree of intraspecific variation in social systems and dispersal patterns within and between howler monkey populations remains to be described, but the results presented here demonstrate that in both *A. pigra* and *A. palliata* there is intraspecific variation between groups in the levels of genetic relatedness among same-sex adults. These intraspecific differences, along with the seemingly similar patterns of intragroup relatedness between species with distinct social systems demonstrate the complexity of interactions between habitat, demography, social interactions and dispersal patterns that shape patterns of genetic relatedness in howler monkey groups.

Conclusions

I present evidence for intraspecific variation in the degree of intragroup genetic relatedness for both sexes in *A. pigra* and *A. palliata*. However, most groups of both species contained closely related same-sex adult dyads. My results are congruent with expected levels of intragroup relatedness that would arise if patterns of *A. pigra* dispersal and social interactions follow our current understanding. To determine if relatedness indeed differs among group types in this species, genetic data must be paired with long-term behavioral and demographic data to confirm hypothesized modes of group formation and to compare time since group establishment and male immigration strategies with intragroup relatedness. However, my results are not consistent with the expectation of low levels of relatedness in *A. palliata* groups based on observations of juvenile emigration, and indicate that howler monkey social systems are more complex than previously suggested. Additional long-term demographic, behavioral, genetic, and ecological data from multiple populations are necessary to determine the factors that influence the degree of genetic relatedness in the social systems of these species.

Table 1. Predictions of the degree of intragroup relatedness among same-sex dyads for each species based on observational data.

Species	Degree of relatedness	
	AFAF	**AMAM**
A. pigra	Variable across groups: Unrelated ($r \leq 0.25$) in new groups. Closely related ($r \geq 0.25$) in well-established groups.	Variable across groups: Closely related ($r \geq 0.30$) in coalition-formed groups. Variable in solitary joined groups.
A. palliata	Unrelated ($r \leq 0.25$), low intergroup variation	Unrelated ($r \leq 0.30$), low intergroup variation

AFAF = adult female-adult female dyads, AMAM = adult male-adult male dyad.

Table 2. PCR conditions and variability for the microsatellite markers used for both species.

Locus	Species	Apm Multiplex	T °C [*Api*/(*Apm* multiplex)*Apm* single]	Na (*Api/Apm*)	Ho (Api/Apm)	He (Api/Apm)	Dev. HWE? (Api/Apm)	Source
AP68	*Api, Apm*	2	50/(53)50	6/4	0.65/0.06	0.53/0.05	***/ns	Ellsworth and Hoelzer 1998
AP74	*Api*	na	52/na	4/na	0.41/na	0.35/na	ns/na	Ellsworth and Hoelzer 1998
D5S111	*Api*	na	60/na	5/na	0.20/na	0.19/na	***/na	Research genetics (for all MapPairs)
D6S260	*Api, Apm*	na	53/53	7/7	0.72/0.40	0.57/0.32	ns/***	Research genetics (for all MapPairs)
D14S51	*Api, Apm*	na	53/55-60	3/5	0.60/0.21	0.44/0.23	ns/***	Research genetics (for all MapPairs)
D17S804	*Api*	na	60/na	6/na	0.53/na	0.4/na	**/na	Research genetics (for all MapPairs)
PEPC8	*Api, Apm*	na	46/46	5/4	0.48/0.11	0.4/0.08	ns/ns	Escobar-Paramo 2000
AB20	*Api, Apm*	na	67/na	8/4	0.570.07	0.57/0.06	***/ns	Goncalves et al. 2004
APM1	*Api, Apm*	7	64/(64)64	5/6	0.69/0.37	0.55/0.31	ns/***	Cortés-Ortiz et al. 2010
APM4	*Api, Apm*	7	65/(64)64	4/8	0.33/0.38	0.42/0.44	***/***	Cortés-Ortiz et al. 2010
AB06	*Api, Apm*	na	60/(55)55	4/5	0.49/0.15	0.41/0.13	ns/***	Goncalves et al. 2004
AB07	*Api, Apm*	na	60/60	2/2	0.49/na	0.43/0.31	ns/ns	Goncalves et al. 2004
AB12	*Api*	na	65/na	4/na	0.51/na	0.47/na	**/na	Goncalves et al. 2004
AB16	*Api*	na	65/na	3/na	0.36/na	0.3/na	***/na	Goncalves et al. 2004
AB17	*Api*	na	60/na	7/na	0.76/na	0.59/na	ns/na	Goncalves et al. 2004
APM9	*Api*	na	55/na	5/na	0.56/na	0.46/na	***/na	Cortés-Ortiz et al. 2010
API06	*Api, Apm*	3	55/(55)55	6/4	0.58/0.12	0.52/0.11	*/***	Cortés-Ortiz et al. 2010
API07	*Api, Apm*	3	50/(55)50	6/3	0.59/0.47	0.48/0.39	ns/ns	Cortés-Ortiz et al. 2010
API08	*Api*	na	55/na	5/na	0.63/na	0.57/na	ns/na	Cortés-Ortiz et al. 2010
API09	*Api*	na	60/na	6/na	0.33/na	0.48/na	***/na	Cortés-Ortiz et al. 2010
API11	*Api, Apm*	4	55/(55)55	3/4	0.17/0.08	0.13/07	ns/***	Cortés-Ortiz et al. 2010
API14	*Api, Apm*	4	55/(55)55	7/3	0.6/0.05	0.49/03	***/ns	Cortés-Ortiz et al. 2010
1110	*Apm*	5	na/(53) 54	na/2	na/0.21	na/0.22	na/ns	Di Fiore and Fleischer 2005
157	*Apm*	5	na/(53) 54	na/8	na/0.7	na/0.57	na/***	Di Fiore and Fleischer 2005

Table 2, cont.

Locus	Species	*Apm* Multiplex	T °C [*Api*/(*Apm* multiplex)*Apm* single]	Na (*Api*/*Apm*)	Ho (Api/Apm)	He (Api/Apm)	Dev. HWE? (Api/Apm)	Source
AC45	*Apm*	na	na/65	na/10	na/0.5	na/0.58	na***	Oklander et al. 2007
1118	*Apm*	2	na/(53) 52	na/4	na/0.06	na/0.08	na/***	Di Fiore and Fleischer 2005
TGMS1	*Apm*	8	na/60	na/3	na/0.32	na/0.25	na/***	Tomer et al. 2002
TGMS2	*Apm*	8	na/60	na/4	na/0.48	na/0.37	na/***	Tomer et al. 2002

Apm = *A. palliata*, *Api* = *A. pigra*, na = locus not amplified for species, T °C = annealing temp, Na = number of alleles, Ho = observed heterozygosity, He = expected heterozygosity, Dev HWE? = test for significant deviation from HWE: ns=not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 3. QuellerGt estimates of the coefficient of relatedness (r) for all same-sex intragroup dyads in all complete groups sampled in this study.

Group	n AM	n AF	r1	r2	r3	r4	r5	r6	Mean r
A. palliata									
Females									
A	1	4	0.51	0.42	0.64	0.43	0.88	0.57	0.58
25	2	4	0.05	-0.14	-0.20	0.26	0.20	-0.03	0.02
B	1	3	0.47	0.01	0.26				0.25
Y	1	3	0.60	0.33	0.45				0.46
R	1	2	0.85						0.85
53	1	2	0.66						0.66
Males									
74	3	10	0.61	0.45	0.56				0.54
78	3	2	0.69	0.45	0.38				0.51
14	2	5	0.58						0.58
25	2	4	-0.14						-0.14
26	2	2	0.61						0.61
77	2	1	0.31						0.31
80	2	8	0.49						0.49
A. pigra									
Females									
4	1	3	0.50	0.33	0.54				0.46
5	3	3	0.29	0.00	0.00				0.10
10	2	3	0.46	0.15	0.22				0.28
1	2	3	0.14	0.03	0.23				0.13
10A	2	2	0.20						0.20
W	1	2	0.49						0.49
12	1	2	-0.03						-0.03
C	1	2	0.43						0.43
11	2	2	0.29						0.29
Males									
5	3	3	0.58	-0.14	-0.05				0.13
1	2	3	0.11						0.11
2	2	1	0.53						0.53
3	2	1	0.17						0.17
20A	2	1	0.02						0.02
10	2	3	0.30						0.30
11	2	2	0.19						0.19
13	2	1	-0.09						-0.09

n AM = number of adult males, n AF = number of adult females, r1, r2, etc. = dyadic r-value, mean r = mean intragroup relatedness among dyad types.

Table 4. Tests for significant correlations between group composition categories and mean intragroup relatedness were not significant.

Correlation	r ~ n adults	r ~ n AM	r ~ n AF
A. pigra			
AFAF			
Pearson's *r*	-0.36	-0.47	-0.1
p	0.34	0.21	0.79
AMAM			
Pearson's *r*	-0.01	-0.15	0.07
p	0.98	0.70	0.87
A. palliata			
AFAF			
Pearson's *r*	-0.78	-0.74	-0.69
p	0.07	0.10	0.13
AMAM			
Pearson's *r*	0.21	0.47	0.15
p	0.66	0.28	0.75

n adults = number of adults, n AM = number of adult males, n AF = number of adult females, r = mean intragroup relatedness
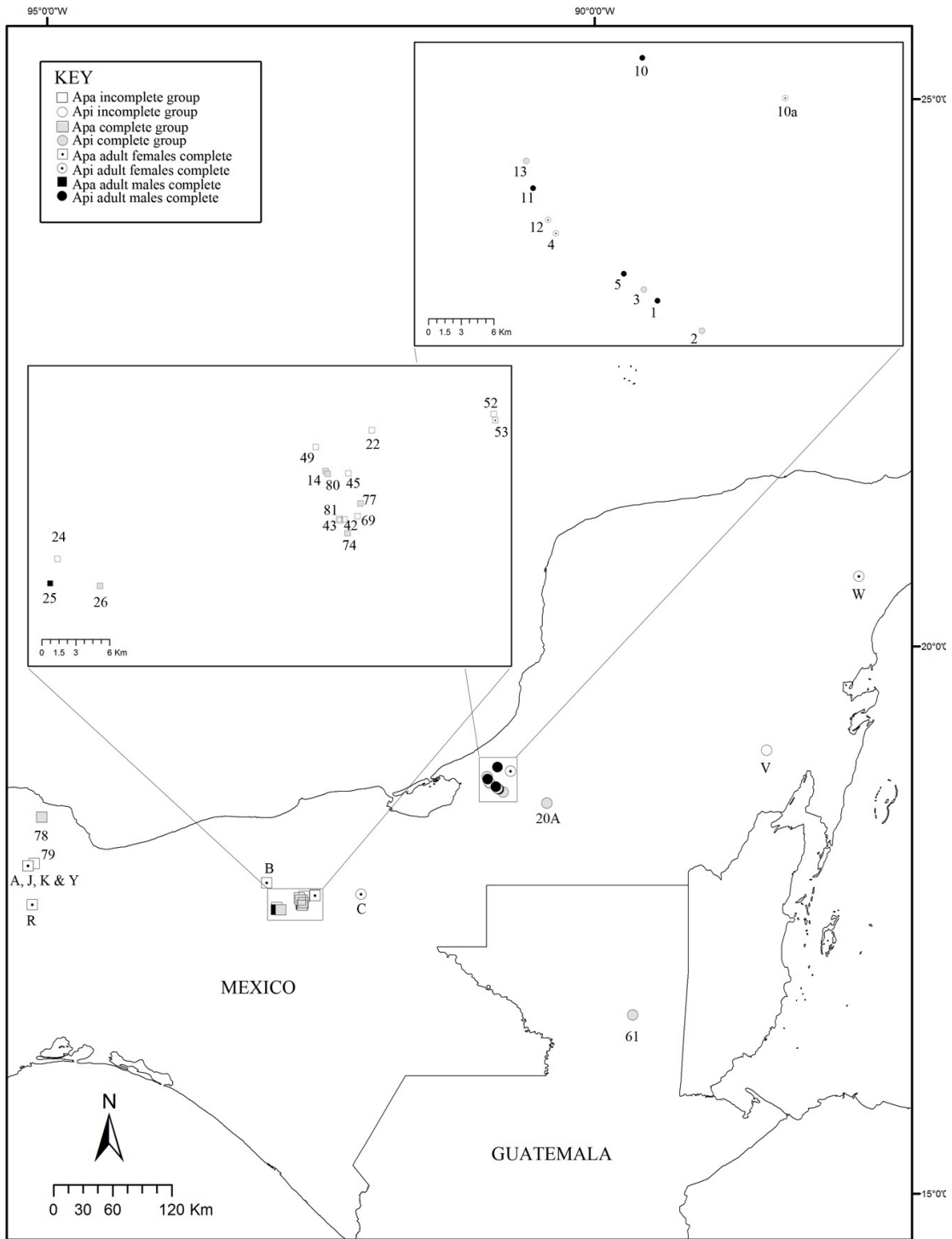
Figure 1. Map of sampling locations. Each symbol corresponds to a group of monkeys, see key for details. Incomplete groups are groups in which neither all adult males nor females were sampled and complete groups are groups in which all adults (males and females) were sampled. Females complete and males complete groups are those in which only all adult females and only all adult males, respectively, were sampled.
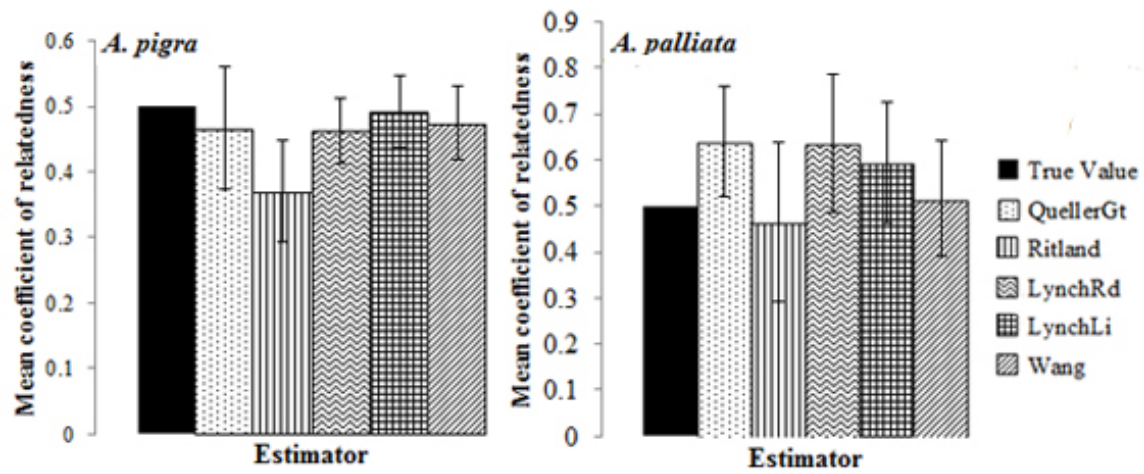
Figure 2. Mean estimates of genetic relatedness between known parent and offspring dyads of each species (*A. pigra* n = 4, *A. palliata*, n = 4) for several estimators in COANCESTRY compared to the true value (r = 0.50).
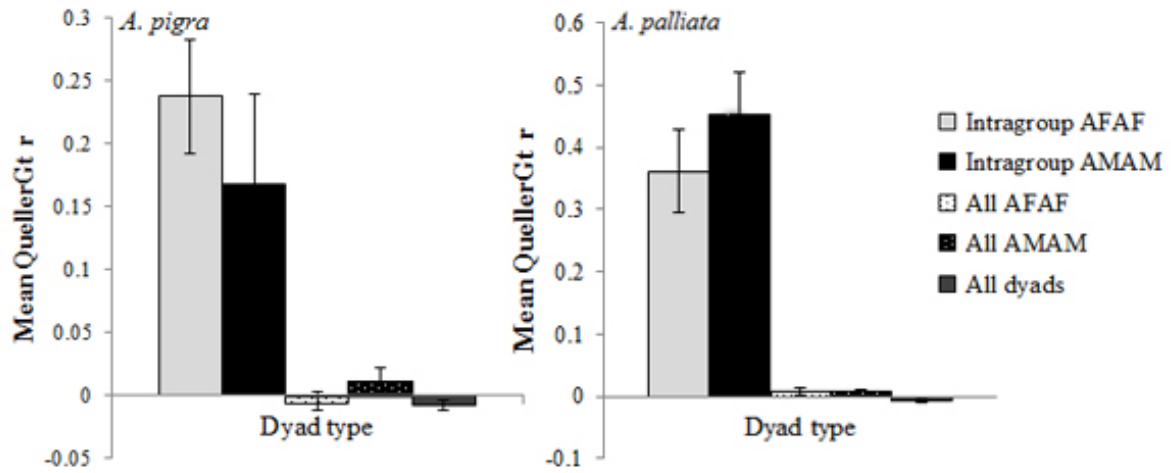
Figure 3. Mean Queller-Goodnight (QuellerGt) estimates of genetic relatedness for same-sex intragroup adults, all same-sex adult dyads, and all dyads in each species. AFAF = adult female-adult female dyads, AMAM = adult male-adult male dyads.

LITERATURE CITED

Altman, J., Alberts, S. C., Haines, S.A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D. J., Mututua, R. S., Saiyalel, S. N., Wayne, R. K., Lacy, R. C., and Bruford, M. W. 1996. Behavior predicts genetic structure in a wild primate group. Proceedings of the National Academy of Sciences of the United States of America 93: 5797-5801.

Arroyo-Rodríguez, V., Asensio, N., and Cristóbal-Azkarate, J. 2008. Demography, life history and migrations in a Mexican mantled howler group in a rainforest fragment. American Journal of Primatology 70:114-118.

Baker, A., and Dietz, J. 1996. Immigration in wild groups of golden lion tamarins (*Leontopithecus rosalia*). American Journal of Primatology 28:47–56.

Banks, S. C., Skerratt, L. F., and Taylor, A. C. 2002. Dispersal and relatedness structure in common wombats (*Vombatus ursinus*). Journal of Zoology 256: 389-399.

Blouin, M. S., Parsons, M., Lacaille, V., and Lotz, S. 1996. Use of microsatellite loci to classify individuals by relatedness. Molecular Ecology 5.3: 393-401.

Bradley, B. J., Robbins, M. M., Williamson, E. A., Steklis, H. D., Steklis, N. G., Eckhardt, N., Boesch, C, and Vigilant, L. 2005. Mountain gorilla tug-of-war: silverbacks have limited control over reproduction in multimale groups. Proceedings of the National Academy of Sciences of the United States of America, 102: 9418-9423.

Brockett, R.C., Horwich, R.H., and Jones, C.B. 2000. Female dispersal in the Belizean black howling monkey Alouatta pigra. Neotropical Primates 8: 32-34.

Carpenter, C. R. 1934. A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). Comparative Psychological Monographs 10: 1-168.

Chapman, C. A., and Balcomb, S. R. 1998. Population charachteristics of howlers: Ecological conditions or group history. International Journal of Primatology 19: 385-403.

Chapman, C. A., & Rothman, J. M. 2009. Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. Primates 50: 12-22.

Clarke, M. R. 1983. Infant-killing and infant disappearance following male takeovers in a groups of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. American Journal of Primatology 5: 241-247.

Clarke, M. R. 1990. Behavioral development and socialization of infants in a free-ranging group of howling monkeys (*Alouatta palliata*). Folia Primatologica 54: 1-15.

Clarke, M. R., and Glander, K. E. 1984. Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. *Female Primates: Studies by Women Primatologists, Alan R. Liss, New York*, 111-126.

Clarke, M. R., and Glander, K. E. 2004. Adult migration patterns of the mantled howlers of La Pacifica. American Journal of Primatology 62 (supplement 1), p. 87.

Clarke, M. R., and Glander, K. E. 2008. Natal emigration by both sexes in the la pacifica population of mantled howlers: When do some stay? American Journal Of Primatology: 70: 195-200.

Clarke, M. R., and Glander, K. E. 2010. Secondary transfer of adult mantled howlers (*Alouatta palliata*) on Hacienda La Pacifica, Costa Rica: 1975-2009. Primates 51: 241-249.

Clarke, M. R., and Zucker, E. L. 1989. Social correlates of timing of sexual maturity in free-ranging howling monkeys (*Alouatta palliata*). American Journal of Primatology 18: 140.

Clarke, M. R., and Zucker, E. L. 1994. Survey of the Howling Monkey Population at La Pacifica: A seven-year follow up. International Journal of Primatology 15: 61-73.

Clarke, M. R., Glander, K. E., Zucker, E. L. 1998. Infant-nonmother interactions of free-ranging mantled howlers (*Alouatta palliata*) in Costa Rica. International Journal of Primatology 19: 451-472.

Cortés-Ortiz, L., Bermingham, E., Rico, C., Rodrígues-Luna, E., Sampaio, I., and Ruiz-Garcia, M. 2003. Molecular systematics and biogeography of the Neotropical monkey genus, *Alouatta*. Molecular Phylogenetics and Evolution 26: 64-81.

Cortes-Ortiz, L., Mondragon, E., and Cabotage, J. 2010. Isolation and charachterization of microsatellite loci for the study of Mexican howler monkeys, their natural hybrids, and other Neotroptical primates. Conservation Genetics Resources 2: 21-26.

Cortés-Ortiz, L, Duda, T. F., Canales-Espinosa, D., García-Orduna, F., Rodrígues-Luna, E., and Bermingham, E. 2007. Hybridization in large-bodied New World primates. Genetics 176: 2421-2425.

Crockett, C. M. 1984. Emigration by female red howler monkeys and the case for female competition. Female Primates: Studies by Women Primatologists. M. F. Small, ed. New York, Alan R. Liss, p. 159-173.

Crockett, C. M., and J. F. Eisenberg, 1987 Howlers: variations in group size and demography, pp. 54–68 in Primate Societies, edited by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. Struhsaker. University of Chicago Press, Chicago.

Cuarón, A.D., Shedden, A., Rodríguez-Luna, E., de Grammont, P.C., Link, A., Palacios, E., Morales, A. & Cortés-Ortiz, L. 2008. Alouatta palliata. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. <www.iucnredlist.org>. Downloaded on 09 May 2013.

Di Fiore, A., and Fleischer, R. C. 2005. Social behavior, reproductive strategies, and population genetic structure of *Lagothrix poeppigii*. International Journal of Primatology 26: 1137-1173.

Di Fiore, A. 2009. Genetic approaches to the study of dispersal and kinship in New World primates. In *South American Primates* (pp. 211-250). Springer New York.

Dias, P. A. D., and Luna, E. R. 2006. Seasonal changes in male associative behavior and subgrouping of *Alouatta palliata* on an island. International journal of primatology 27: 1635-1651.

Dias, P. A. D., Rangel-Negrin, A., Veà, J. J., and Canales-Espinosa, D. 2010. Coalitions and male–male behavior in *Alouatta palliata*. Primates 51: 91-94.

Ellsworth, J. A. 2000. Molecular evolution, social structure and phylogeography of the mantled howler monkey (*Alouatta palliata*). Dissertation, University of Nevada.

Ellsworth, J. A., and Hoelzer, G. A. 1998. Charchterization of microsatellite loci in a New World primate, the mantled howler monkey (Alouatta palliata). Molecular Ecology 7: 657-666.

Eriksson, J., Siedel, H., Lukas, D., Kayser, M., Erler, A., Hashimoto, C., Hohmann, G., Boesch, C. and Vigilant, L. 2006. Y-chromosome analysis confirms highly sex-biased dispersal and suggests a low effective male population size in bonobos (Pan paniscus). Molecular Ecology 15:939–949.

Escobar-Paramo, P. 2000. Microsatellite primers for the wild brown capuchin monkey *Cebus apella*. Molecular Ecology 9: 107-118.

Estrada, A. 1982. Survey and census of howler monkeys (*Alouatta palliata*) in the rain forest of "Los Tuxtlas," Veracruz, Mexico. American Journal of Primatology 2: 363-372.

Excoffier, L. and Lischer, H. E. L. 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 10: 564-567.

Fernandez-Duque, E. and Huntington, C. 2002. Disappearances of individuals from social groups have implications for understanding natal dispersal in monogamous owl monkeys (*Aotus azarai*). American Journal of Primatology 57:219–225.

Glander, K. E. 1980. Reproduction and populations growth in free-ranging mantled howling monkeys. American Journal of Physical Anthropology 53: 25-36.

Glander, K.E. 1992. Dispersal patterns in Costa Rican mantled howling monkeys. International Journal of Primatology 13: 415-436.

Goncalves, E. C., Silva, A., Barbosa, M. S. R., and Schneider, P. C. 2004. Isolation and charachterization of microsatellite loci in Amazonian red-handed howlers Alouatta belzebul (Primates, Plathyrrini). Molecular Ecology Notes 4: 406-408.

Goossens, B., Graziani, L., Waits, L. P., Farand, E., Magnolon, S., Coulon, J., Bel, M., Taberlet, P., and Allainé, D. 1998. Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. Behavioral Ecology and Sociobiology 43: 281-288.

Goudet, J., Perrin, N., and Wasser, P. 2002. Tests for sex-biased dispersal using bi-parentally inherited genetic markers. Molecular Ecology 11: 1103-1114.

Hammond, R. L., Lawson Handley, L. J., Winney, B. J., Bruford, M. W. and Perrin, N. 2006. Genetic evidence for female-biased dispersal and gene flow in a polygynous primate. Proceedings of the Royal Society of London, B: Biological Sciences 273: 479–484.

Harris, T. R., Caillaud, D., Chapman, C. A., and Vigilant, L. 2009. Neither genetic nor observational data alone are sufficient for understanding sex-biased dispersal in a social-group-living species. Molecular Ecology 18: 1777-1790.

Henzi, S. P., Lycett, J. E., and Piper, S. E. 1997. Fission and troop size in a mountain baboon population. Animal Behaviour 53: 525-535.

Horwich, R. H., Brockett, R. C., and Jones, C. B. 2000. Alternative male reproductive behaviors in the Belizean black howler monkey (*Alouatta pigra*). Neotropical Primates 8: 95-98.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist 63: 152-161.

Jones, C. B. 1980. The functions of status in the mantled howler monkey, *Alouatta pallitata* GRAY: Intraspecific competition for group membership in a folivorous Neotropical primate. Primates 21: 389-405.

Jones, C. B. 1985. Reproductive patterns in mantled howler monkeys: Estrus, mate choice and copulation. Primates 26: 130-142.

Jones, C. B., and Cortés-Ortiz, L. 1998. Facultative polyandry in the howling monkey (*Alouatta palliata*): Carpenter was correct. Boletín Primatológico Latinoamericano 7: 1-7.

Kappeler, P. M., and van Schaik, C. P. 2002. Evolution of primate social systems. *International Journal of Primatology* 23: 707-740.

Kawai, M. 1958. On the system of social ranks in a natural group of Japanese monkeys. Primates 1: 11-48.

Kitchen, D. M., Horwich, R. H., and James, R. A. 2004. Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: Experimental evidence for the effects of intra-group male relationships and age. Behaviour 141: 703-723.

Knight, M. E., Van Oppen, M. J. H., Smith, H. L., Rico, C., Hewitt, G. M., and Turner, G. F. 1999. Evidence for male-biased dispersal in Lake Malawi cichlids from microsatellites. Molecular Ecology 8: 1521-1527.

Koenig, A., Beise, J., Chalise, M. K., & Ganzhorn, J. U. 1998. When females should contest for food–testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). Behavioral Ecology and Sociobiology, 42: 225-237.

Kurland, J. A. 1977. Kin Selection in the Japanese Monkey. Karger, Basel.

Langergraber, K. E., Mitani, J. C., and Vigilant, L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. Proceedings of the National Academy of Sciences, 104: 7786-7790.

Li, C.C., Weeks, D.E., and Chakravarti, A. 1993. Similarity of DNA fingerprints due to chance and relatedness. Human Heredity 43: 45–52.

Lynch, M. 1988. Estimation of relatedness by DNA fingerprinting. Molecular Biology and Evolution 5: 584-599.

Mandujano, S., Escobedo-Morales, L. A., and Palacios-Silva, R. 2004. Movements of Alouatta palliata among forest fragments in Los Tuxtlas, México. Neotropical Primates 12: 126-131.

Marsh, L.K., Cuarón, A.D., Cortés-Ortiz, L., Shedden, A., Rodríguez-Luna, E. & de Grammont, P.C, 2008. Alouatta pigra. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. <www.iucnredlist.org>. Downloaded on 09 May 2013.

Milton, K., Lozier, J, D., and Lacey, E. A. 2009. Genetic structure of an isolated population of mantled howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. Conservation Genetics 10: 347-358.

Möller, L. M. 2012. Sociogenetic structure, kin associations and bonding in delphinids. Molecular Ecology 21: 745-764.

Möller, L. M., and Beheregaray, L. B. 2004. Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). Molecular Ecology 13: 1607-1612.

Moore, J. A., Daugherty, C. H., Godfrey, S. S., and Nelson, N. J. 2009. Seasonal monogamy and multiple paternity in a wild population of a territorial reptile (tuatara). Biological Journal of the Linnean Society, 98: 161-170.

Oklander, L. I., Zunino, G. E., Di Fiore, A., and Corach, D. 2007. Isolation, charachterization, and evaluation of 11 autosomal STRs sutable for population studies in black and gold howler monkeys Alouatta caraya. Molecular Ecology Notes 7: 117-120.

Oklander, L. I., Kowalewski, M. M., and Corach, D. 2010. Genetic consequences of habitat fragmentation in black-and-gold howler (*Alouatta caraya*) populations from northern Argentina. International Journal of Primatology, 31: 813-832.

Peakall, R., and Smouse, P. E. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6: 288-295.

Pope, T. R. 1989. The Influence of Mating System and Dispersal Patterns on the Genetic Structure of Red Howler Monkey Populations. Unpublished Ph.D. thesis, Gainesville.

Pope, T. R. 1992. The influence of dispersal patterns and mating systems on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). Evolution 46: 1112-1128.

Pope, T. R. 1998. Effects of demographic change on group kin structure and gene dynamics of populations of red howling monkeys. Journal of Mammalogy 79: 692-712.

Pusey, A. E. 1980. Inbreeding avoidance in chimpanzees. Animal Behaviour 28: 543-552.

Queller, D. C., and Goodnight, K. F. 1989. Estimating relatedness using genetic markers. Evolution 43: 258-275.

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Ribeiro, A. M., Lloyd, P., Feldheim, K. A., and Bowie, R. C. 2012. Microgeographic socio-genetic structure of an African cooperative breeding passerine revealed: integrating behavioural and genetic data. Molecular ecology, 21: 662-672.

Ritland, K. 1996. Estimators for pairwise relatedness and inbreeding coefficients. Genetical Research 67: 175–186.

Robinson, J. G. 1988. Demography and group structure in wedgecapped capuchin monkeys, *Cebus olivaceus*. Behaviour 104: 202-232.

Rodríguez-Luna E, Cortés-Ortiz L. 1994. Translocacio´n y seguimiento de un grupo de monos Alouatta palliata liberado en una isla (1988–1994). Neotropical Primates 2:1–5.

Ryan, S. R., Starks, P. T., Milton, K., and Getz, W. M. 2008. Intersexual conflict and group size in *Alouatta palliata*: A 23-year evaluation. International Journal of Primatology 29: 405-420.

Sade, D. D., Cushing, K., Cushing, P., Dunaif, J., Figueroa, A., Kaplan, J. R., Lauer, C., Rhodes, D., and Schneider, J. 1976. Population dynamics in relation to social structure on Cayo Santiago. Yearbook of Physical Anthropology 20: 253-262.

Schradin, C., and Pillay, N. 2005. Intraspecific variation in the spatial and social organization of the African striped mouse. Journal of Mammalogy, 86: 99-107.

Sekulic, R. 2008. Behavior and ranging patterns of a solitary female red howler (*Alouatta seniculus*). Folia Primatologica, 38: 217-232.

Seutin, G., White, B.N., Boag, P.T., 1991. Preservation of avian blood and tissue samples for DNA analyses. Canadian Journal of Zoolology 69: 82–90.

Seyfarth, R. M., and Cheney, D. L. 1984. Grooming alliances and reciprocal altruism in vervet monkeys. Nature 308: 541-542.

Sinha, A., Mukhopadhyay, K., Datta-Roy, A., and Ram, S. 2005. Ecology proposes, behaviour disposes: Ecological variability in social organization and male behavioural strategies among wild bonnet macaques. Current Science, 89: 1166-1179.

Silk, J, B. Kin selection in primate groups. International Journal of Primatology 23: 849-875.

Stokes, E. J., Parnell, R., J., and Olejniczak, C.. 2003. Female dispersal and reproductive success in wild western lowland gorillas (Gorilla gorilla gorilla). Behavioral Ecology and Sociobiology 2003: 329-339.

Stow, A. J., Sunnucks, P., Briscoe, D. A., and Gardner, M. G. 2001. The impact of habitat fragmentation on dispersal of Cunningham's skink (*Egernia cunninghami*): evidence from allelic and genotypic analyses of microsatellites. Molecular Ecology 10: 867-878.

Streatfeild, C. A., Mabry, K. E., Keane, B., Crist, T. O., and Solomon, N. G. 2011. Intraspecific variability in the social and genetic mating systems of prairie voles, *Microtus ochrogaster*. Animal Behaviour, 82: 1387-1398.

Strier, K. B. 2011. Primate Behavioral Ecology. Pearson, 4th edition.
Strier, K. B., and Mendes, S. L. 2009. Long-term field studies of South American primates. In South American Primates (pp. 139-155). Springer New York.

Tomer, Y., Greenberg, D. A., Concepcion, E., Ban, Y., and Davies, T. F. 2002. Thyroglobulin is a thyroid specific gene for the familial autoimmune thyroid diseases. The Journal of Endocinology & Metabolism 87: 404-407.

Van Belle, S., and Estrada, A. 2006. Demographic features of *Alouatta pigra* populations in extensive and fragmented forests. New Perspectives in the Study of Mesoamerican Primates, Chapter Four: 121-142.

Van Belle, S., and Estrada, A. 2008. Group size and composition influence male and female reproductive success in black howler monkeys (*Alouatta pigra*). American Journal of Primatology, 70: 613-619.

Van Belle, S., Estrada, A., and Strier, K. B. 2008. Social relationships among male *Alouatta pigra*. International Journal of Primatology 29: 1481-1498.

Van Belle, S., Estrada, A., Ziegler, T. E., and Strier, K. B. 2009. Sexual behavior across ovarian cycles in wild black howler monkeys (*Alouatta pigra*): Male mate guarding and female mate choice. American Journal of Primatology 71: 153-164.

Van Belle, S., Estrada, A., and Strier, K. B. 2011. Insights into social relationships among female black howler monkeys *Alouatta pigra* at Palenque National Park, Mexico. Current Zoology 57: 1-7.

Van Belle, S., Estrada, A., Strier, K., B., and Di Fiore, A. 2012. Genetic structure and kinship patterns in a populations of black howler monkeys, *Alouatta pigra*, at Palenque National Park, Mexico. American Journal of Primatology 74: 948-957.

Van De Casteele, T., and Matthysen, E. 2006. Natal dispersal and parental escorting predict relatedness between mates in a passerine bird. Molecular Ecology 15: 2557-2565.

Van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., and Shipley, P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes 4: 535-538.

Vangestel, C., Mergeay, J., Dawson, D. A., Vandomme, V., and Lens, L. 2011. Spatial heterogeneity in genetic relatedness among house sparrows along an urban-rural gradient as revealed by individual-based analysis. Molecular Ecology 20: 4643-4653.

Vessey, S. H., and Meikle, D. B. 1988. Factors affecting social behavior and reproductive success of male rhesus monkeys. International Journal of Primatology 8: 281-292.

Wahlund, S. 1928. The combination of populations and the appearance of correlation examined from the standpoint of the study of heredity. *Hereditas* 11: 65-106.

Wang, J. 2011. COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. Molecular Ecology Resources 11: 141-145.

Wang, E., and Milton, K. 2003. Intragroup social relationships of male *Alouatta palliata* on Barro Colorado Island, Republic of Panama. International Journal of Primatology 24: 1227-1243.

Watts, H. E., Scribner, K. T., Garcia, H. A., and Holekamp, K. E. 2011. Genetic diversity and structure in two spotted hyena populations reflects social organization and male dispersal. Journal of Zoology 285: 281-291.

Wikberg, E. C., Sicotte, P., Campos, F. A., and Ting, N. 2012. Between-group variation in female dispersal, kin composition of groups, and proximity patterns in a black-and-white colobus monkey (*Colobus vellerosus*). PloS one 7.11: e48740.

Zucker, E. L., and Clarke, M. R. 1998. Agonistic and affiliative relationships of adult female howlers (*Alouatta palliata*) in Costa Rica over a 4-year period. International Journal of Primatology 19: 433-449.