

RESEARCH ARTICLE

Effect of Ancestry on Behavioral Variation in Two Species of Howler Monkeys (*Alouatta pigra* and *A. palliata*) and Their HybridsLUCY HO^{1*}, LILIANA CORTÉS-ORTIZ², PEDRO AMÉRICO D. DIAS³, DOMINGO CANALES-ESPINOSA³, DAWN M. KITCHEN⁴, AND THORE J. BERGMAN^{1,2}¹Department of Psychology, University of Michigan, Ann Arbor, Michigan²Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan³Instituto de Neuroetología, Universidad Veracruzana, Xalapa, Mexico⁴Department of Anthropology, Ohio State University, Columbus, Ohio

Social differences between primate species may result from both flexible responses to current conditions or fixed differences across taxa, yet we know little about the relative importance of these factors. Here, we take advantage of a naturally occurring hybrid zone in Tabasco, Mexico to characterize the variation in social structure among two endangered howler monkey species, *Alouatta pigra* and *A. palliata*, and their hybrids. Work in pure populations has suggested that *A. pigra* females maintain closer proximity, exhibit higher rates of affiliation, and lower rates of agonism than *A. palliata* females, but we do not know what accounts for this difference. Using identical data collection and analysis methods across three populations, we first seek to confirm previously reported interspecific differences in social structure across all sexes. We next examine: (1) how female social relationships changed with ancestry (by comparing pure and hybrid individuals); (2) how female social relationships changed with group size (*A. pigra* have smaller groups than *A. palliata*); and (3) whether female social relationships differed between two taxonomic groups within a single forest fragment (thus controlling for ecological variation). We confirmed previously described species differences, including closer proximity among females than among males in all populations. We also found that smaller groups maintained closer proximity. However, even after accounting for variation in group size, *A. pigra* females had closer proximity and more affiliation than *A. palliata* females. Furthermore, differences between *pigra*-like and *palliata*-like hybrids paralleled differences between pure populations and persisted even after controlling for ecological variation. Together, our results suggest that flexibility cannot account for all of the social differences between *A. pigra* and *A. palliata* and indicate an important genetic component in primate social behavior. *Am. J. Primatol.* 76:855–867, 2014. © 2014 Wiley Periodicals, Inc.

Key words: hybridization; *Alouatta pigra*; *Alouatta palliata*; proximity; female social behavior

INTRODUCTION

Primates are noted for the diversity of their social interactions and resulting social structures [Kappeler & van Schaik, 2002]. Aspects of their social structure may vary in response to a complex and interconnected set of social, ecological, and genetic factors. Such variation can occur within generations as a flexible response to current conditions. Alternatively, fixed genetic differences between taxa can also cause variation. Thus, a particular species may have a certain social structure irrespective of fluctuations in the surrounding environment. The first idea, that primate behavior is flexible, is an implicit assumption of socioecological models, where the strength and nature of intragroup female social bonds alter according to factors such as resource distribution, dispersal patterns, and infanticide risk. The resulting variation in levels of within-group female competition and cooperation in turn affect male

social relationships [Isbell & van Vuren, 1996; Sterck et al., 1997; Wrangham, 1980]. This view has been challenged recently by calls to incorporate phylogenetic information into studies of primate social systems [Clutton-Brock & Janson, 2012; Di Fiore & Rendall, 1994; Thierry, 2013]. Indeed, there is

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evidence for strong phylogenetic signal in the social systems of at least some primate taxa [Balasubramaniam et al., 2012; Shultz et al., 2011], and previous research in macaques has linked ancestry with variation in female affiliation and aggression [Maestripieri, 2003]. Thus, while flexibility and genetic differences both contribute to behavioral variation, the extent to which interspecific variation in social relationships can be attributed to these two factors remains largely unknown.

It is possible to tease apart the effects of genetics, social setting, and ecological variables in hybrid zones, where genetically distinct animals can be found in overlapping ecological and social settings [Hewitt, 1988]. To date, much of the research on behavior in primate hybrid zones has been concentrated in baboons (*Papio* spp.) [Bergman & Beehner, 2004; Bergman et al., 2008; Charpentier et al., 2012; Tung et al., 2012]. Evidence from these two different baboon hybrid zones suggests that some interspecific behavioral differences are inflexible: ancestry has an effect on mating strategies [Bergman & Beehner, 2003; Tung et al., 2012], and hybridization results in an admixture of species-typical patterns of intra- and intersexual relationships [Bergman et al., 2008]. However, no behavioral comparisons similar to the baboon studies exist from New World primate hybrid zones. Furthermore, comparisons across cercopithecine social systems suggest strong phylogenetic constraint, with a suite of traits that pertain to female social relationships found almost uniformly across extant taxa [Di Fiore & Rendall, 1994]. But in contrast, a study of New World primates from Izar et al. [2012] suggests a lack of phylogenetic constraint when comparing within-group social interactions in two closely related species of capuchins. Thus, at this point, we do not know whether the social inflexibility (e.g., genetically influenced social interactions) indicated by baboon hybrid zones is unique to that taxon, or whether it also applies to other, non-cercopithecine primates.

Here, we examine the effect of genetic ancestry on variation in the social structure [sensu Kappeler & van Schaik, 2002] of two species of howler monkeys and their hybrids. We use a naturally occurring hybrid zone in Tabasco, Mexico [Cortés-Ortiz et al., 2007] to characterize differences in proximity patterns, affiliation, and agonism among *Alouatta pigra*, *A. palliata*, and their hybrids. *Alouatta pigra* and *A. palliata* are sister taxa that diverged approximately 3 Ma [Cortés-Ortiz et al., 2003]. The two species are genetically and morphologically distinct [Cortés-Ortiz et al., 2003; Kelaita et al., 2011], with a parapatric distribution that includes known contact/hybrid zones in Mexico and possibly Guatemala [Baumgarten & Williamson, 2007; Smith, 1970]. Like other howler monkeys, *A. pigra* and *A. palliata* are folivore-frugivores that use an energy-minimization strategy [Strier, 1992] to digest their primarily

high-fiber diets [Di Fiore et al., 2011]. This similarity implies that, under the same ecological conditions, any behavioral differences between the two species should *not* be a result of species-typical feeding strategies but rather due to some other factor [Silver et al., 1998].

Despite being sister taxa, the two species reportedly have differences in many aspects of their social structure, particularly group cohesion and female-female social relationships (Table I). Notably, while *A. pigra* females engage mostly in affiliative behavior [Van Belle et al., 2011], studies in *A. palliata* report higher rates of dominance-related agonistic behavior among females, compared to *A. pigra* [Jones, 1980; Zucker & Clarke, 1998]. This is likely a reflection of differing female group entry strategies between the two species and the fact that, unlike *A. pigra* females, *A. palliata* females apparently have a discernible dominance hierarchy (Table I). Differences in male social relationships are less obvious; in both species, males rarely have affiliative interactions with one another and instead tend to associate with females [Van Belle et al., 2008; Wang & Milton, 2003]. However, although data on dispersal and group entry are limited (Table I), current knowledge implies that if there is more than one male in an *A. pigra* group, they are more likely to be related than males in *A. palliata* groups, possibly also affecting interspecific differences in proximity patterns.

In this study, we first make a descriptive analysis of our study populations, wherein we seek to confirm previously reported differences between *A. pigra* and *A. palliata*. Importantly, we are the first to study these two species' behavior using identical data collection methods. Although we examined both affiliative and agonistic interactions, *Alouatta* is notable for its relatively low rates of social behaviors. Thus, we also use proximity, which is considered an appropriate "first reading" of social structure in primates [Kummer, 1970b] and is a standard approximation of social relationships in *Alouatta* [e.g., Bezanson et al., 2008; Corewyn & Pavelka, 2007; Dias et al., 2008; Van Belle et al., 2008; Zucker & Clarke, 1998].

We compare proximity in multiple groups from populations in three separate Mexican states (Fig. 1): *A. pigra* outside the hybrid zone (from Campeche), *A. palliata* outside the hybrid zone (from Veracruz), and hybrid zone groups (from Tabasco). We expect to find that pure *A. pigra* individuals will be in closer proximity with other group members than *A. palliata* individuals [Crockett & Eisenberg, 1987]. Based on previous primate hybrid zone studies [e.g., Bergman & Beehner, 2004; Bergman et al., 2008; Charpentier et al., 2012; Tung et al., 2012], we additionally expect to find that this difference is genetically-based. In other words, we predict that individuals from the hybrid zone (mainly hybrid and backcrossed animals)

TABLE I. Summary of Social System Differences Between *Alouatta pigra* and *A. palliata*

	<i>Alouatta pigra</i>	<i>Alouatta palliata</i>
Group size	4–8 individuals, range: 2–16, with 1–5 adult males and 1–4 adult females [Di Fiore et al., 2011]	8–23 individuals, range: 2–45, with 1–8 adult males and 2–19 adult females [Di Fiore et al., 2011]
Group cohesion	Individuals tend to remain in close proximity [Corewyn & Pavelka, 2007]	Commonly split into sub-groups [Altmann, 1959; Bezanson et al., 2008; Dias & Rodríguez-Luna, 2006]
Sex ratio	1.2–2.1 females/male [Crockett & Eisenberg, 1987; Neville et al., 1988; Treves et al., 2001]	1.4–4.1 females/male [Crockett & Eisenberg, 1987; Neville et al., 1988]
Dispersal	Juveniles and adults of both sexes disperse [Brockett et al., 2000]	Juveniles of both sexes evicted from natal group by unrelated adults [Clarke et al., 1998; Clarke & Glander, 2008]
Mating system	Polygynous [Bolin, 1981], with reports of polygynandry [Horwich et al., 2000; Van Belle et al., 2008, 2009]	Polygynandrous [Ryan et al., 2008; Wang & Milton, 2003]
Male takeover	Resident males can be usurped and are often ousted from group [Brockett et al., 2000; Van Belle et al., 2008], often by coalitions [Horwich et al., 2000] of related males [Van Belle et al., 2012]	New males do not oust resident males but gradually join group, although takeovers by coalitions have been reported [Dias et al., 2010; Glander, 1980]
Infanticide	Documented [Knopff et al., 2004; Van Belle et al., 2010]	Rare, but documented [Clarke, 1983; Clarke et al., 1994]
Female entry	Rare due to high levels of harassment from resident females [Brockett et al., 2000; Kitchen, 2006]	Common; join with relative ease and rapidly increase rank [Glander, 1980, 1992]
Group formation	Reportedly common due to low ability to join groups—dispersing individuals form new groups with each other [Brockett et al., 2000]	Reportedly rare as dispersing individuals can join existing groups [Glander, 1992]
Female dominance hierarchy	None discernible; egalitarian with mostly affiliative interactions [Van Belle et al., 2011]	Reverse age-ordered (youngest female dominant) [Jones, 1980; Zucker & Clarke, 1998]
Female agonism	0.007 acts/hr [Van Belle et al., 2011]	0.38 acts/hr [Zucker & Clarke, 1998]; reports of female-female agonism [Larose, 1996]

will, on average, show intermediate proximity patterns given the inclusion of a broad distribution of genotypes, but *A. pigra*-like and *A. palliata*-like hybrids will have proximity differences between them that mirror observed differences between the pure species (see Methods for the definitions of these classifications).

We next consider female behavior specifically, as they are reported to have clearer interspecific social differences than males, and examine female-female affiliative and agonistic interactions. Again, we predict that within their groups, *A. pigra* females will be more affiliative and less agonistic than *A. palliata* females. We also predict that *A. pigra*-like and *A. palliata*-like hybrid females will differ behaviorally in the same direction as the purebreds (e.g., *pigra*-like females will exhibit higher affiliation and lower agonism than *palliata*-like females).

However, differences among these three populations (*A. pigra*, hybrids, and *A. palliata*) may be caused by social or ecological factors, rather than genetics. For example, variation in group size could

affect the level of within-group cohesion; larger groups may spread farther apart to forage, as they would otherwise deplete resources too rapidly. Thus, we include group size as a predictor variable in multivariate analyses and also control for group size effects with comparisons restricted to *A. pigra* and *A. palliata* groups matched in size. If group size is a stronger driving force than ancestry, we predict that similarly-sized groups of *A. pigra* and *A. palliata* will not differ in proximity.

Finally, because the three sites vary in their degree of anthropogenic habitat disturbance, we consider the possibility that this may affect patterns of social variation. Because we do not have detailed ecological data to examine the effects of resource variation, we chose to control for habitat disturbance by comparing the social structure of *pigra*-like and *palliata*-like groups that reside in the same patch within the hybrid zone. If ecological factors play a stronger role than ancestry in affecting social variation, then we predict that *pigra*-like and *palliata*-like hybrid groups within the same patch will not differ in their social structure.

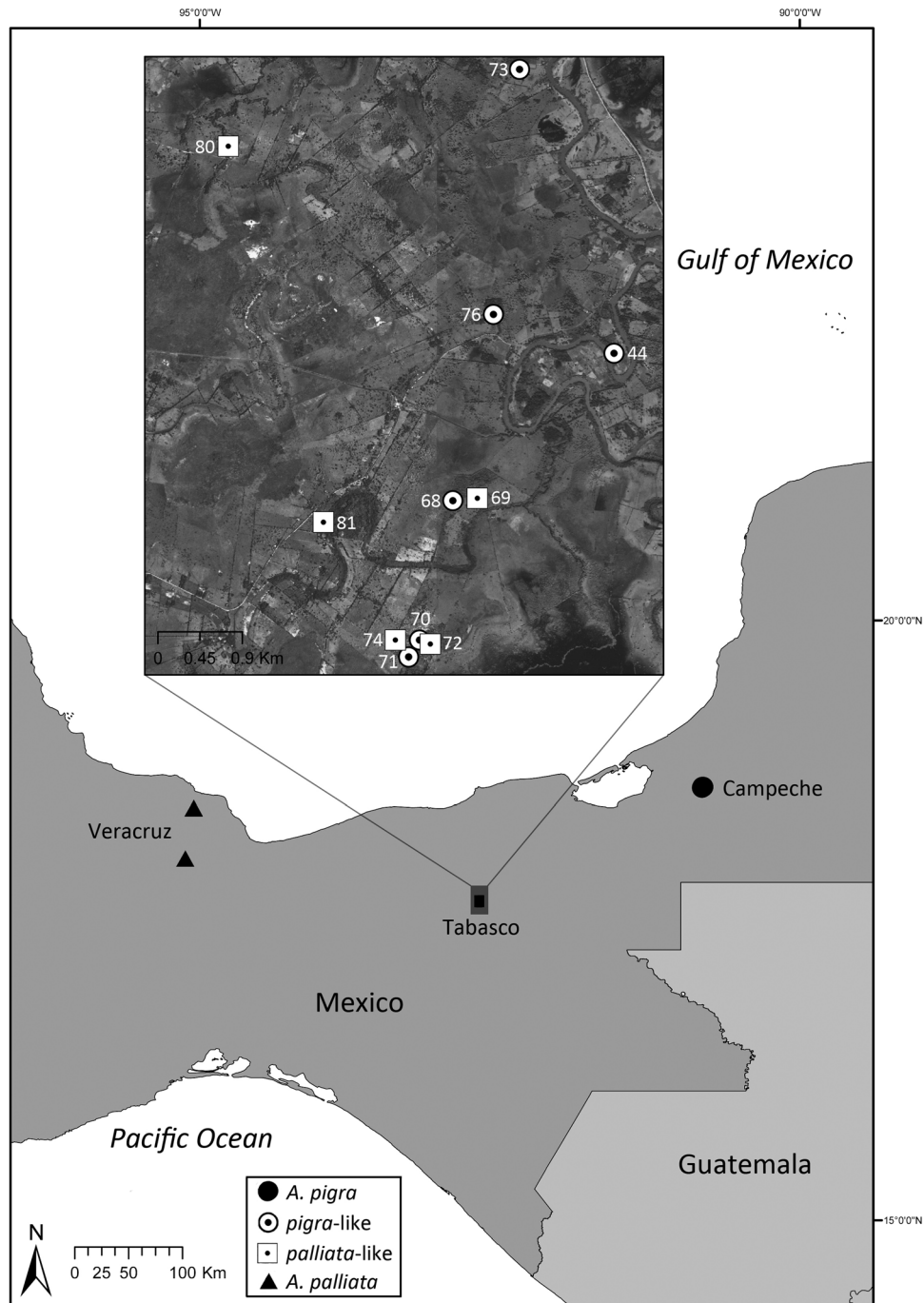


Fig. 1. Map of the study sites.

METHODS

Study Sites

We conducted data collection for this study in three separate populations (Fig. 1). We sampled within the *A. pigra* and *A. palliata* contact zone, where hybridization is confirmed to occur [Cortés-Ortiz et al., 2007], as well as in two areas with only

purebred animals. These purebred sites are well outside of the contact area (approximately >260 km away) and it is unlikely that the individuals there have had contact with the other species or with their genes (i.e., hybrid or back-crossed individuals).

The purebred *A. pigra* site near Escarcega, Campeche, is El Tormento Forest Reserve, a protected, relatively large area of primary tropical forest

of about 1,400 ha [Van Belle & Estrada, 2008]. The three purebred *A. pigra* groups studied at this site are in different locations within the reserve and their ranges were not observed to overlap (although they likely overlap with other groups that were not part of our study). The two purebred *A. palliata* sites are located in La Flor, Catemaco (~120 ha) and in Rancho Jalapilla, Acayucan (~30 ha), both in Veracruz (Fig. 1). La Flor is an ornamental palm plantation consisting of primary and secondary vegetation. The canopy is composed of arboreal species typical of undisturbed primary rainforest and the arboreal howler monkeys can move freely through the trees. Therefore, La Flor constitutes a practically undisturbed site, despite the daily harvesting of ornamental palms in the understory, and the two purebred *A. palliata* groups here were not observed to have overlapping home ranges. The remaining purebred *A. palliata* group is in Rancho Jalapilla, a narrow but long riparian strip of secondary forest surrounded by pastureland. This is part of a large private property with very restricted access to people, and thus the monkeys do not often interact with human settlements or dogs. Several groups occupy this stretch of forest, but again, they do not seem to have overlapping ranges. The hybrid site is located south of Macuspana, Tabasco, in the midst of the approximately 20 km wide contact zone [Kelaita & Cortés-Ortiz, 2013]. Of all the sites, it is the most affected by habitat disturbance, as individual howler monkey groups there reside in small, discontinuous patches of mainly secondary forest (~3 ha) separated by ranches

and farmland [Dias et al., 2013]. A single patch in Tabasco may be occupied by one or several howler monkey groups (up to four in the current study; see Table II). Additionally, the hybrid zone exhibits the following anthropogenic activity to a greater degree than the other two sites: (1) predation by domestic dogs associated with inter-patch movements for diet supplementation, which is more likely to occur in the smaller patches characteristic of the hybrid zone [Rangel-Negrin et al., 2011]; (2) logging, which currently occurs only in the hybrid zone among the study sites; and (3) visuo-acoustic contact with humans who work in the surroundings (e.g., cattle grazing and farming) and inside the patches (e.g., gathering firewood), which are far more frequent in the hybrid zone, given that monkeys there live in an embedded matrix of pastureland, human settlements and forest patches.

Subjects

We collected data simultaneously on three groups of purebred *A. pigra* and six groups of hybrids from February to August 2011, then simultaneously on three groups of purebred *A. palliata* and five new groups of hybrids from January to June 2012 (see Table II for more details on group composition and data collection). All adults in the study were individually recognizable by researchers via ankle bracelets or natural markings such as scars and, in the case of *A. palliata*, differences in characteristic patches of skin/fur coloration on their feet and tails.

TABLE II. Summary of groups sampled during study period (2011–2012)

Site	Group	No. of adult females (total focal hours)	No. of adult males (total focal hours)	Taxonomic category	Total hours per taxa	Total scans per taxa
Campeche	65	2 (52)	2 (62)	<i>A. pigra</i>	336	2,016
	66	3 (60)	2 (51)			
	67	2 (74)	1 (37)			
Tabasco	68 ^a	2 (19)	2 (18)	<i>pigra</i> -like	546	3,270
	70 ^a	3 (54)	1 (20)			
	71 ^a	2 (52)	1 (26)			
	44	3 (71)	2 (47)			
	73	3 (70)	2 (49)			
	76	2 (73)	1 (47)			
Tabasco	69 ^a	2 (45)	1 (26)	<i>palliata</i> -like	455	2,728
	72 ^{a,b}	10 (52)	3 (22)			
	74 ^a	12 (48)	5 (23)			
	80	8 (86)	2 (34)			
	81	4 (87)	1 (32)			
Veracruz	77B	3 (71)	2 (49)	<i>A. palliata</i>	360	2,153
	78	2 (47)	3 (73)			
	79	9 (63)	5 (57)			
Total		72 (1,024)	36 (673)		1,697	10,167 ^c

^aGroups 70, 71, 72, and 74 shared a patch in the hybrid site, as did 68 and 69. None of the other hybrid groups had ranges that overlapped.

^bOne *pigra*-like female, HSP72, was in this group, apparently integrated with the other, *palliata*-like individuals.

^cSix 10-min scans were performed for each 1 hr focal; however, a few scans were missing from the *A. palliata* and *pigra*-like groups, resulting in the discrepancy between the total focal hours and the total scans.

Despite most individuals in the hybrid zone resembling either *A. pigra* or *A. palliata* in terms of pelage coloration and size, our sample likely consists of highly backcrossed animals that are phenotypically similar to (and impossible to distinguish from) the parental species, and thus we consider all animals in the hybrid zone to be hybrids [see Kelaita & Cortés-Ortiz, 2013] for a genetic characterization of the admixture of individuals within the same population). Because we lack genetic data for the individuals included in this study, hybrids are broadly classified based on morphology and vocalizations (LH & LCO personal observation). We consider this method appropriate for our initial examination of hybrid variation because previous genetic analyses showed that most animals in the hybrid zone, and specifically in our field site, are highly backcrossed, multigenerational hybrids. These hybrids share most of their genome with one of the parental species, to which they are also morphologically similar (i.e., hybrids resemble the parental species with which they share most of their alleles [Kelaita & Cortés-Ortiz, 2013]). Though genetically intermediate hybrids cannot be so reliably categorized based on their morphology, the incidence of such animals in our study site is minimal [Kelaita & Cortés-Ortiz, 2013]. Therefore, the likelihood that we have an intermediate hybrid in our sample is very small, and the impact on our results should be negligible.

For this study, we classified subjects from the hybrid zone into two categories: *pigra*-like individuals had the discrete morphological features of *A. pigra*, most notably larger size, entirely black pelage, and a larger ruff of fur around the face, while *palliata*-like individuals were slighter, had golden flank fur, smaller faces, and a less prominent ruff of fur typical of *A. palliata* [Kelaita et al., 2011; Lawrence, 1933; Smith, 1970]. All subjects within each of our study groups possessed the same phenotype with one exception; group #72 (Table II) had a female whose phenotype was at odds with the phenotype of the other group members. This female was removed from all analyses, although we provide an account of her behavior (see Discussion).

Data Collection

All adults in a group were randomly chosen as subjects for hour-long focal sampling [Altmann, 1974], with no animals sampled twice until all were sampled once. Juveniles and subadults were not sampled. Observers rotated to another group after 1 week (approximately 40 focal hours) and attempted to follow all groups for 2 weeks in 2011 and for 3 weeks in 2012 (Table II). Groups were followed usually starting from ~7 AM to ~5 PM, with each day in the field lasting 8–10 hours; thus, each “week” of data consisted of about 4–5 days of fieldwork.

During each focal sampling, proximity data among adults were collected using instantaneous scan samples of all visible group members every 10 min (Table II). Each adult group member was placed into one of four categories based on their proximity to the subject (1: contact, 2: <1 m, 3: 1–5 m, 4: >5 m). The proximity scores were then dichotomized into “number of times a dyad was <5 m” and “number of times a dyad was >5 m.”

To examine female affiliation and agonism, we also recorded social interactions between female focal subjects and other adults in the group during focal samples. Affiliative behaviors included touching, grooming, and play. Due to the naturally low levels of social behavior exhibited by howler monkeys, all types of affiliative behaviors were combined and a rate was calculated for each individual female based on the total number of focal hours she was observed. This rate was then corrected for group size (dividing by the number of females in the subject’s group, not including the subject).

Agonistic behaviors included displacements, threats, chases, and fights. Rates of agonism were even lower in our study, and this made analyzing agonism on an individual female level unfeasible. Thus, counts of female-female aggression were tallied for each group and then combined according to their taxonomic categories: *A. pigra*, *pigra*-like, *palliata*-like, and *A. palliata*. Finally, a rate per hour of observation was calculated for each taxonomic group.

Statistical Analyses of Differences Across Purebreds and Hybrids

All analyses were run in Stata 12.1 (StataCorp). In addition to standard packages, we also used the package *gllamm* to run generalized linear mixed models (GLMM) [Rabe-Hesketh et al., 2005]. Tests are two-tailed and the initial alpha was set at 0.05. Multiple comparisons were corrected using false discovery rates (henceforth FDRs) as originally described in Benjamini and Hochberg [1995] and as applied to behavioral data [Verhoeven et al., 2005].

Proximity

We ran a GLMM on the dichotomized proximity scores of every possible dyad within each group ($N = 438$ dyads). Taxonomic categories (*A. pigra*, hybrids, and *A. palliata*), sex (analyzed by dyad; female-female, female-male, male-male), an interaction term between taxon and sex, and group size were entered as fixed effects. Dyad identity and group identity were entered as random effects. None of the predictors were significantly multicollinear (all variance inflation factors <2). Odds-ratios (OR) are reported for the effects of each predictor on proximity.

After the initial GLMM, we ran two post-hoc pairwise comparisons. First, we split the hybrids, including both sexes, into *pigra*-like and *palliata*-like groups to examine whether ancestry effects existed within the hybrid zone ($N = 303$ dyads). Second, we focused on female *pigra*-like and *palliata*-like individuals only, to see whether ancestry effects persisted among females ($N = 150$ dyads). We assumed that hybrid individuals resembling a particular parent species also share most of their genome with that species [Kelaita & Cortés-Ortiz, 2013]. For these comparisons, we used a simple binomial test to examine whether the proportion of time individuals in *pigra*-like groups spent in <5 m is greater than that of individuals in *palliata*-like groups.

Social Behavior

We next focused on female-female affiliative and agonistic social interactions. Because data residuals were non-normal, we analyzed affiliative social behavior using a Kruskal–Wallis non-parametric ANOVA, with the corrected rate of affiliation per female (number of behavioral acts/hour/group size) as the dependent variable, and taxonomic categories (*A. pigra*, *pigra*-like, *palliata*-like, and *A. palliata*) as the grouping variable ($N = 71$ females). After the Kruskal–Wallis test, we performed post-hoc pairwise comparisons using the Mann–Whitney U test.

We then used a Poisson regression to model the counts of female-to-female agonism (the dependent variable), with taxon (*A. pigra*, *pigra*-like, *palliata*-like, and *A. palliata*) as the predictor variable. Incidence rate ratios (IRR) between the taxonomic groups are reported.

Statistical Analyses of Potential Confounding Factors

Group size

In addition to including group size as a variable in the main GLMM analysis, we also took advantage of the fact that we had two relatively small *A. palliata* groups in our sample as an additional test of group size effects. We compared the dichotomized proximity scores in *A. pigra* groups (ranging in size from three to five adults) to small *A. palliata* groups (77B & 78; group size = five adults) by performing a second GLMM analysis restricting the dataset to only these animals ($N = 44$ dyads). Taxon and sex were included as fixed effects, while dyad identity nested in group identity were random effects. Additionally, we performed a post-hoc binomial test of the female-female dyads in these four groups to see if ancestry effects persisted among females ($N = 9$ dyads). Note that because we had already taken into account differences in group size when calculating affiliation rates, we did not perform any further analyses on that data here. Agonism data were too scarce for statistical analysis in this subset.

Ecological variation

As ecological conditions could affect patterns of social interaction, we controlled for this by using four hybrid groups—two *pigra*-like and two *palliata*-like—that resided in the same patch within the hybrid zone, thus having home ranges that overlapped (see Table II). Because the two *palliata*-like groups had a substantial number of dyads that were never within <5 m, a GLMM was not practical [Menard, 2002]. We therefore performed a binomial test to compare the proportion of time spent in <5 m between the *pigra*-like animals and *palliata*-like animals of this subset ($N = 216$ dyads). We then did the same test on the female-female dyads only ($N = 107$ dyads). Lastly, we examined female-female affiliation within these four groups using a non-parametric Kruskal–Wallis test, and excluded the agonism data due to its scarcity.

Protocol Statement

This research complies with the University of Michigan Committee on Use and Care of Animals, the Ohio State University Institutional Animal Care and Use Committee, and adhered to American Society of Primatologists' Principles for the Ethical Treatment of Non-Human Primates. All field methods described here complied with Mexican legal requirements.

RESULTS

Differences Across Purebreds and Hybrids

Proximity

The full model of proximity was significant (GLMM: $\chi^2_9 = 79.75$, $P < 0.00005$). Overall, individuals were further apart (a greater proportion of time spent >5 m) as group size increased (OR = 1.16, $P < 0.0001$).

The interaction of sex and taxon was not significant, indicating that we did not detect significant variation across sexes in the effect of taxon on proximity, nor was there variation across taxonomic categories in the effect of sex on proximity.

However, sex alone was a significant predictor of proximity in *A. pigra* and hybrids (Fig. 2). Within each of these two taxonomic groups, female-female dyads spent a greater proportion of time in <5 m than male-male dyads (*A. pigra*: OR = 3.73, $P < 0.03$; hybrids: OR = 3.67, $P < 0.0001$), but no significant difference was observed between female–female dyads and female–male dyads (*A. pigra*: OR = 1.64, $P = 0.27$; hybrids: OR = 0.91, $P = 0.50$). Female-male dyads spent a significantly greater proportion of time in <5 m than male-male dyads among hybrids only (OR = 4.00, $P < 0.0001$). Within *A. palliata*, no significant sex differences in proximity patterns were found.

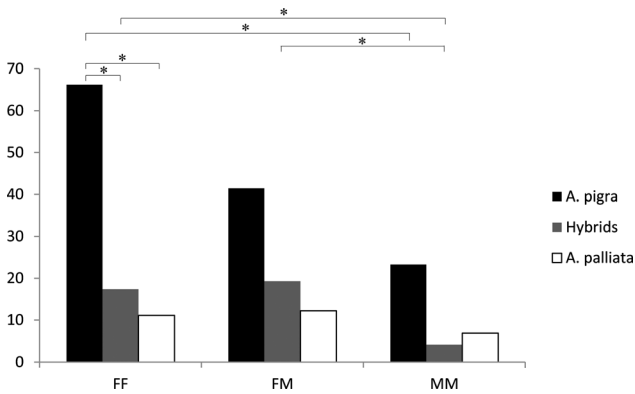


Fig. 2. Frequency (calculated as percentage) of being <5 m for each major taxonomic category (*A. pigra*, hybrids—*pigra*-like and *palliata*-like combined, and *A. palliata*), across the three sex categories: female–female (FF), female–male (FM), and male–male (MM). * marks significant differences ($P < 0.05$) on respective comparisons.

Taxon was also a significant predictor of proximity, but not across all sexes (Fig. 2). Among female–female dyads only, *A. pigra* were significantly closer together than *A. palliata* (OR = 2.76, $P < 0.05$) and hybrid dyads (OR = 2.48, $P < 0.05$), but *A. palliata* and hybrids did not significantly differ (OR = 0.92, $P = 0.81$). No significant differences were observed between female–male dyads or male–male dyads when comparing across the three taxa.

When hybrid groups were divided into *pigra*-like and *palliata*-like groups, *pigra*-like individuals spent 25% of their time <5 m, while *palliata*-like individuals spent 14% of their time <5 m. The proportion of time *pigra*-like animals spent close together was significantly higher than that of *palliata*-like individuals (binomial test: $P < 0.00005$). We observed the same pattern when restricting the analysis to female–female dyads; *pigra*-like females spent a significantly higher proportion of their time close together than *palliata*-like females (32–13%, binomial test: $P < 0.00005$).

Social behavior

Mean rates of affiliation among female–female dyads (adjusted for group size) were significantly different across the four taxonomic categories: *A. pigra*, *pigra*-like, *palliata*-like, and *A. palliata* (Kruskal–Wallis: $H_3 = 11.12$, $P < 0.02$; Fig. 3). We performed a post-hoc pairwise comparison based on our expectation that *A. pigra* should have higher rates of affiliation compared to *A. palliata* ($N = 21$); this prediction was supported (Mann–Whitney: $Z = 2.99$, $P < 0.005$; Fig. 3). Among hybrids, although *pigra*-like females seemed to have higher rates of affiliation than *palliata*-like females ($N = 50$), this result was not statistically significant (Mann–Whitney: $Z = 0.76$, $P = 0.45$; Fig. 3).

However, as predicted if behavioral patterns follow ancestry, *palliata*-like females had very simi-

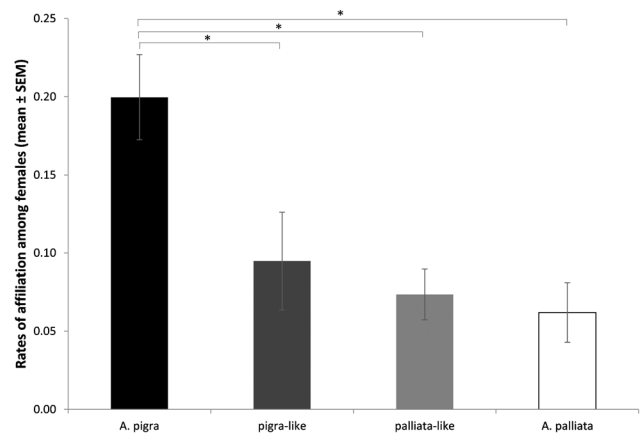


Fig. 3. Plot of the rates of female–female affiliation (acts/hr) corrected for group size (number of possible female dyads). * marks a significant difference ($P < 0.05$) between *A. pigra* and *A. palliata*, *A. pigra* and *palliata*-like hybrids, as well as *A. pigra* and *pigra*-like hybrids. *A. palliata* rates were not significantly different from *pigra*-like rates, and the rates of two hybrids, *pigra*-like and *palliata*-like, were also not significantly different.

lar rates of affiliation (0.074 acts/hour) to purebred *A. palliata* (0.062 acts/hr; $N = 49$; Mann–Whitney: $Z = 0.15$, $P = 0.88$). Also as expected, purebred *A. pigra* had higher rates of affiliation than *palliata*-like females ($N = 42$; Mann–Whitney: $Z = 3.12$, $P < 0.002$), similar to the difference between *A. pigra* and *A. palliata*. However, contrary to ancestry expectations, *pigra*-like females had significantly lower rates of affiliation (0.095 acts/hr) than purebred *A. pigra* (0.200 acts/hour; $N = 22$; Mann–Whitney: $Z = 2.43$, $P < 0.02$).

We observed only 35 instances of agonism by focal females toward other females across the full study period. Rates of agonism were 0 among *A. pigra* females (0 acts/186 hr), 0.021 among *pigra*-like females (7 acts/339 hr), 0.074 among *palliata*-like females (23 acts/310 hr), and 0.028 among *A. palliata* females (5 acts/181 hr). Results of the Poisson regression analysis revealed that the ratio of agonism rates between *palliata*-like and *pigra*-like females were significantly different from one, with the *palliata*-like female agonism rate being 3.59 times higher ($Z = 2.96$, IRR = 3.59, $P < 0.05$). However, the ratio of agonism rates between *A. pigra* females and *A. palliata* females did not significantly differ from one.

Potential Confounding Factors Affecting Social Structure

Effect of group size on proximity

The effect of taxon on proximity remained significant when we restricted our analysis to *A. pigra* and *A. palliata* groups matched for size, showing that although group size may have an overall effect on proximity, it is not enough to

override the effect of ancestry. We found that the proportion of time spent <5 m was still significantly higher in the three *A. pigra* groups with 3–5 adult members than in the two *A. palliata* groups with 5 adult members (GLMM: OR = 2.45, $P < 0.0001$). The effect of sex also remained significant, with female–female dyads spending a greater proportion of time <5 m than male–male dyads (OR = 2.98, $P < 0.0001$), and tending to spend more time <5 m than female–male dyads (OR = 1.37, $P = 0.059$). Finally, the post-hoc analysis within female–female dyads only revealed that female *A. pigra* spent a significantly higher proportion of time closer together than female *A. palliata* (66–19%, binomial test: $P < 0.00005$).

Effect of ecological variation on proximity and social behavior

To control ecological variation, we restricted our analysis to four groups (two *palliata*-like and two *pigra*-like) residing in a single fragment in the hybrid zone. We found that, in spite of home range overlap, hybrids in this fragment responded like individuals of the purebred species that they morphologically resembled. In other words, *pigra*-like groups spent a higher proportion of time in <5 m than *palliata*-like groups (40–7%, binomial test: $P < 0.00005$). Strikingly, a comparison of the proximity scores of the two *palliata*-like groups, revealed that 44% of dyads (24 out of 55) in group 72 and 52% of dyads (76 out of 146) in group 74 were never seen within <5 m. In contrast, all of the dyads among the two *pigra*-like groups spent at least 21% of their scans in <5 m. Finally, our post-hoc analysis examining only female–female dyads in this subset revealed that the ancestry effects still remained; females in the two *pigra*-like groups spent a significantly higher proportion of their time at <5 m than females in the two *palliata*-like groups (41–7%, binomial test: $P < 0.00005$). There were no significant differences in rates of affiliation.

DISCUSSION

Using identical data collection methods to compare proximity and social behavior across three populations of howler monkeys, we concluded that both ancestry and flexibility contribute to social variation among members of sister taxa *A. pigra* and *A. palliata*, and their hybrids.

We found differences in social structure (proximity and social interactions) between the pure populations that matched previous descriptions [e.g., *A. pigra*: Van Belle et al., 2011; *A. palliata*: Zucker & Clarke, 1998]. First, *A. pigra* female–female dyads spent a significantly greater proportion of time at <5 m than *A. palliata*, and in fact spent the most time close together out of all the taxon–sex categories. Second, *A. pigra* females engaged in significantly

higher levels of affiliative social interactions as compared to *A. palliata* females. We should point out, however, that rates of affiliation were quite low in this study, and so our results should be interpreted with caution.

We also found that hybrids had variable behavior that generally differed according to ancestry, as determined using phenotype. These differences mirrored the purebred patterns and, particularly with respect to proximity patterns, persisted when we examined four groups of hybrids occupying the same forest fragment (sharing the same ecological conditions). In this analysis, *pigra*-like hybrids were significantly closer together than *palliata*-like hybrids, implying an effect of ancestry rather than potential ecological factors. Taken together, this study is the first demonstration that ancestry drives differences in social behavior in New World monkeys, suggesting similarities to Old World monkeys [Bergman et al., 2003; Di Fiore & Rendall, 1994; Tung et al., 2012].

On the other hand, our analysis of group size effects suggested flexibility in some of the variation in social structure. Indeed, group size was a significant predictor of proximity in our model. Because groups are more cohesive when they are smaller, individuals may spend more time interacting with each other when in smaller groups [Lehmann et al., 2007; Sueur et al., 2011]. *Alouatta pigra* groups are smaller on average than *A. palliata* groups, creating the possibility that the smaller groups of *A. pigra* resulted in stronger female–female relationships. For example, in our analysis on the four hybrid groups residing the same fragment (mentioned above), we were unable to control for group size due to the nature of our data, and thus it remains possible that the *pigra*-like hybrids were simply closer together because their groups are smaller than the *palliata*-like hybrids. However, we continued to find an effect of taxon on proximity even when comparing similarly-sized purebred groups, suggesting that ancestry plays a role in addition to the role of group size.

In general, agonistic encounters between the adult females of our study were very infrequent, regardless of taxonomic categories (but in particular, agonism between *A. palliata* females seems lower than other reports, see Table I), and this again affects the interpretation of our results. That being said, we found that within the hybrids, *palliata*-like females had significantly higher rates of agonism than *pigra*-like females. While the difference between hybrid females could reflect actual species differences in agonism rates, the lack of significant differences between the purebred *A. pigra* and *A. palliata* seems to suggest otherwise. If the hybrid sites are indeed more impacted by human disturbance, and given that *A. palliata* are more affected by decreases in fragment size than *A. pigra* [Dias et al., 2013], this

could explain why the hybrid females—and *palliata*-like females in particular—engaged in more instances of agonism.

Overall, our results suggest a stronger influence of ancestry in the social structure of *Alouatta*, while the impact of ecological variation is less clear. For example, despite inhabiting the site with arguably the greatest degree of human disturbance, *pigra*-like and *palliata*-like animals residing in the same forest fragment still exhibited proximity patterns typical of the species they most resemble. Further, in our analysis controlling for the effect of group size on proximity (discussed above), we compared only the *A. palliata* groups at La Flor to the *A. pigra* groups in El Tormento (both sites with relatively less prominent human activity), and we still found differences in proximity patterns based on taxon. Howler monkeys have been documented to be resilient to environmental change, retaining fairly species-typical behavior while living in disturbed habitats [e.g., Biccamarques, 2003; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Martínez-Mota et al., 2007; Palma et al., 2011; Pavelka & Knopff, 2004], and such resilience may in fact have a genetic basis. Nonetheless, this study does not rule out the effect of major ecological factors that may be important in explaining behavioral differences across sites. These factors include density of preferred food trees or forest composition, aspects that need to be incorporated in future studies.

Another alternative explanation of our results is that individuals in a group simply adopt the behavioral strategies of the majority (i.e., *A. palliata* individuals behave like *A. palliata* because they are surrounded by other *A. palliata* individuals). For example, some studies report that an individual of one species may flexibly learn and adopt the social behavior patterns of another species if they are accepted into a heterospecific group [Fragaszy & Visalberghi, 2004; Verzijden et al., 2012]. Though these examples often stem from cross-fostering experiments where a critical period of learning appears to be crucial, the learning of social behavior from conspecifics has also been documented in adult primates [e.g., baboon transplant experiments: Kummer, 1970a].

In our study, it is difficult to rule out social learning because all individuals in a group were of the same taxonomic category (i.e., a “*pigra*-like” group consists of *A. pigra*/*pigra*-like individuals only). Thus, when individuals behave similarly in the same group, it is impossible to discriminate learning from genetic influences on behavior. However, one hybrid female in our study did reside with animals that were phenotypically different from her. This *pigra*-like female (HSP72) resided for an entire season in the *palliata*-like group 72. During that time, HSP72 was farther away from her female *palliata*-like group-mates than *pigra*-like females in

other groups were from each other, and the proportion of time she spent in <5 m was comparable to *palliata*-like females. Additionally, HSP72 engaged in few affiliative behaviors with her female group-mates during her focal hours, another pattern similar to many *palliata*-like females. However, we found that she initiated nearly all approaches to other females in her group, while very few of her group-mates approached her. This implies that HSP72 was attempting to behave in a *pigra*-like manner (i.e., more cohesively), but the *palliata*-like females in her group did not respond to these attempts. Similar reports of hybrid individuals behaving in a species-typical manner, rather than in the manner of their heterospecific group, also exist in the baboon hybrid zone in Awash [Bergman & Beehner, 2004; Bergman et al., 2008; Phillips-Conroy et al., 1991]. Thus, we argue that the patterns reported here are more likely to reflect the effect of ancestry rather than social learning.

Though we have demonstrated that ancestry does indeed affect social structure variation (on top of variation resulting from flexible responses to group size and possibly habitat disturbance), several unresolved issues remain to be addressed through the inclusion of genetic data. First, because our study used phenotype to assign individuals and groups as *pigra*-like or *palliata*-like, it is possible that we are misrepresenting the underlying genetic variation. For instance, hybrid affiliation patterns were closer to those of *A. palliata*: neither *pigra*-like nor *palliata*-like females differed significantly from *A. palliata* females, and *pigra*-like females actually had significantly lower affiliation than *A. pigra* females, the most affiliative category. This result may have two possible explanations: (1) the potential inclusion of genetically intermediate individuals within the *pigra*-like females that is not possible to distinguish based on morphology alone; or (2) the potential introgression of *A. palliata*-type genes associated with female-female affiliation. As we continue to gather genetic information of the individuals sampled for behavior, we will be able to better understand how proximity and social relationships relate to different degrees of genetic admixture in the hybrid population.

Additionally, kinship may impact the results presented here, because closely related individuals should spend more time closer together and be more affiliative than distantly related individuals. Our current knowledge suggests that *A. pigra* females are likely to be more closely related than *A. palliata* females due to their reported ability to keep out other, presumably unrelated, females (Table I). Thus, *A. pigra* females within a group should become more related over time, similar to red howler monkeys [Brockett et al., 2000; Pope, 2000]. In fact, recent research in *A. pigra* has demonstrated that in most groups, females, males, or both sexes lived with adult

same-sex kin [Van Belle et al., 2012]. On the other hand, within-group relatedness among *A. palliata* females should be low because juveniles are forced to disperse and are able to join new groups that do not have kin [Glander, 1992]. Interestingly, genetic studies on the *A. palliata* population in Barro Colorado Island [Milton et al., 2009] demonstrated that *A. palliata* have higher relatedness than expected; however, it is not clear whether these results also apply to *A. palliata* living under less insular conditions. A recent comparative genetic analysis on purebred *A. pigra* and *A. palliata* in Mexico and Guatemala provides further insight, showing that within-group relatedness of same sex dyads are actually high in both species [Baiz, 2013]. Thus, kinship does not seem to explain the differences in social behavior that we see. Still, more studies that incorporate genetic and behavioral data for the same set of individuals are necessary to better understand the kinship patterns of these two species in a comparative context, and thus reveal how kinship impacts social structure [Chapais & Berman, 2004].

The evidence of a genetic component in social behavior presented here raises the question of why we see this pattern in howler monkeys, a genus that exhibits dramatic group size and composition fluctuations in response to current environmental conditions [Fernandez-Duque et al., 2012]. The answer may come down to the fact that different aspects of social systems have different degrees of phylogenetic constraint. For instance, though broad dispersal patterns are fairly consistent within-taxa, fluctuations in environmental conditions that change food or territory availability are likely to result in corresponding changes to group size and composition within populations, as individuals may delay dispersal or are prevented from entering groups when they disperse. In contrast, the formation of social relationships has much to do with the motivation to seek out and interact with conspecifics. A lack of motivation should result in a lack of social interactions even if group size or composition alters, and how motivated animals are to affiliate with each other may be more influenced by genetic differences between species (e.g., differing levels of oxytocin [Campbell, 2008], involved in the formation of female social bonds [Massen et al., 2010]).

In sum, our study provides evidence of a genetic component as well as some flexibility to social structure, as defined by proximity patterns and social interactions. Detailed genetic analysis is the critical next step, which will bolster our abilities to categorize individuals to a more fine-tuned degree of admixture, allowing us to do with behavior what has recently been done for morphology [Kelaita & Cortés-Ortiz, 2013]. But even as it stands, our results add to the growing body of evidence that demonstrates the importance of incorporating phylogeny in any

systematic attempt to understand interspecific differences among primate social systems.

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