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Dispersal patterns in black howler monkeys (*Alouatta pigra*): Integrating multiyear demographic and molecular data

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Abstract

Dispersal is a fundamental process in the functioning of animal societies as it regulates the degree to which closely related individuals are spatially concentrated. A species' dispersal pattern can be complex as it emerges from individuals' decisions shaped by the cost–benefit tradeoffs associated with either remaining in the natal group or dispersing. Given the potential complexity, combining long-term demographic information with molecular data can provide important insights into dispersal patterns of a species. Based on a 15-year study that integrates multiyear demographic data on six groups with longitudinal and cross-sectional genetic sampling of 20 groups ($N = 169$ individuals, $N = 21$ polymorphic microsatellite loci), we describe the various dispersal strategies of male and female black howler monkeys (*Alouatta pigra*) inhabiting Palenque National Park, Mexico. Genetically confirmed dispersal events ($N = 21$ of 59 males; $N = 6$ of 65 females) together with spatial autocorrelation analyses revealed that the dispersal pattern of black howlers is bisexual with strong sex-biases in both dispersal rate (males disperse more often than females) and dispersal distance (females disperse farther than males). Observational and genetic data confirm that both males and females can successfully immigrate into established groups, as well as form new groups with other dispersing individuals. Additionally, both males and females may disperse singly, as well as in pairs, and both may also disperse secondarily. Overall, our findings suggest multiple dispersal trajectories for black howler males and females, and longer multiyear studies are needed to unravel which demographic, ecological and social factors underlie individuals' decisions about whether to disperse and which dispersal options to take.

KEYWORDS
bisexual dispersal, microsatellite marker, philopatry, population genetics, social mammals, spatial genetic structure

1 | INTRODUCTION

Dispersal plays a central role in the functioning of animal societies as it determines the degree to which relatives are spatially concentrated, and hence the potential for kin-biased social interactions and concomitant inclusive fitness (Hoezler et al., 2004; Lawson Handley & Perrin, 2007; Silk, 2007). Although dispersing from the natal group is hypothesized to have evolved to reduce inbreeding depression or competition with kin over limited resources (Clutton-Brock & Lukas, 2012; Greenwood, 1980; Lambin, 1994; Lawson Handley & Perrin, 2007; Perrin & Mazalov, 2000), dispersing individuals may bear the cost of higher mortality rates or reduced reproductive success due to either a delayed onset of reproduction or a lower survival rate of offspring in an unfamiliar ecological or social environment (Bonte

et al., 2012; Johnson et al., 2009; Maag et al., 2019; Martinig et al., 2020). Consequently, individuals' decisions about dispersal are expected to be sensitive to the relative costs and benefits associated with either remaining in or leaving their natal group (Lin & Batzli, 2004).

Among social animals, dispersal patterns vary from bisexual dispersal, in which both males and females disperse from their natal group at similar rates, to completely sex-biased dispersal, in which individuals of only one sex disperse while individuals of the other sex are philopatric (Clobert et al., 2009; Clutton-Brock & Lukas, 2012; Greenwood, 1980). However, between these extremes lies considerable variation. That is, even when dispersal is highly sex-biased, sometimes not all individuals of the "dispersing sex" leave their natal groups or ranges (Martins & Strier, 2004) and, conversely, individuals of the typically "philopatric sex" may sometimes emigrate and join new groups (Aureli et al., 2013). Even when both sexes regularly disperse, there might be a bias in dispersal rate (i.e., one sex disperses more often than the other) or in mean dispersal distance (i.e., one sex generally disperses farther than the other), with each sex thus contributing differentially to gene flow (van Hooft et al., 2018; Möller & Beheregaray, 2004; Roy et al., 2014). Additionally, the average age at which individuals of a particular sex disperse may vary considerably and can be as young as juveniles or subadults that may go through solitary stages while attaining adult body size or associate in groups with other same-sexed individuals prior to immigration into a new group (Arzamendia et al., 2018; Li et al., 2020; Woodroffe et al., 2020). In other species, individuals may only be able to disperse during encounters with neighbouring groups without any stage of solitary roaming (Furuichi, 2020; Manguette et al., 2020). Individuals may also disperse singly or in groups of two or more, may disperse with relatives or with nonkin, and may disperse into groups that already contain group mates from their natal group (i.e., parallel dispersal; Bradley et al., 2007; Monard & Duncan, 1996; Schoof et al., 2009). Successful immigration may entail joining an established group with or without much opposition from residents (Savage et al., 1996; Toda & Furuichi, 2020) or taking over a group and evicting same-sex residents (Fernandez-Duque & Huck, 2013; Mitchell, 1994; Sicotte et al., 2017). Dispersing individuals may also form new groups with other dispersing individuals of the opposite sex (Brockelman et al., 1998; Santos et al., 2016; Woodroffe et al., 2020). Lastly, individuals may disperse secondarily (or tertiarily) even after successfully reproducing in other non-natal groups (Clarke & Glander, 2010; Manguette et al., 2020).

Examining dispersal patterns in wild animal populations is a major challenge as it occurs infrequently in an individual's lifetime, and the fate (i.e., dispersal or death) of individuals that disappear from study groups, as well as the origin of immigrating individuals into study groups, are generally unknown. This is particularly true when dispersal distances are larger than the study area, or when unmarked individuals cannot easily be recognized outside of their original groups (Harris et al., 2009). However, given that dispersal contributes to gene flow and thus affects population genetic structure, genetic analyses can be used to detect nonrandom patterns of spatial genetic variation in a population and thus provide insight into dispersal patterns (Di Fiore, 2003; Harris et al., 2009; Huck et al., 2007; Lawson Handley & Perrin, 2007; Roy et al., 2014; Wang & Yao, 2017). For example, given that philopatric individuals remain close to same-sexed relatives, mean intragroup relatedness values and measures of genetic differentiation between groups (e.g., F_{ST} and related indices: Weir & Cockerham, 1984; Wright, 1943) are both expected to be higher for the more philopatric sex than for the dispersing or less philopatric sex (Di Fiore, 2003; Goudet et al., 2002; Lawson Handley & Perrin, 2007; Morin et al., 1994). Furthermore, spatial genetic autocorrelation analyses have proven useful by examining the fine-scale genetic population spatial structure to provide insights into dispersal distances (Huck et al., 2007; Lecompte et al., 2017; Li et al., 2020; Roy et al., 2014). That is, when dispersal is spatially restricted, we expect a positive correlation between pairwise genetic similarity measures and geographical distance because pairs of individuals that are geographically close should be genetically more similar than pairs of individuals that are more distant from one another (Peakall et al., 2003). As such, the extent of local positive genetic structure across a population can be assessed by comparing autocorrelation values across different distance classes (Peakall et al., 2003). Lastly, on the individual level, multilocus genotype data provide a reliable tool to corroborate the identity of individuals, and as such can be used to identify dispersal events if an individual was genetically sampled at different points in time when residing in different social groups.

Howler monkeys (*Alouatta* spp.)—large-bodied, arboreal, non-human primates that are broadly distributed throughout Central and South America—are characterized by a bisexual dispersal pattern in which both males and females may emigrate from their natal group and subsequently may immigrate into an established group, form a new group with other solitary individuals, or remain solitary (Crockett, 1984; Glander, 1992; Pope, 1992; Rumiz, 1990; Van Belle, Estrada, & Strier, 2008, 2011). Nevertheless, there is substantial variation among species and populations, with males and females dispersing at similar rates in mantled howlers (*Alouatta palliata*: Glander, 1992) and black-and-gold howlers (*Alouatta caraya*: Collevatti & Telles, 2013; Oklander et al., 2010; Rumiz, 1990), while females are more philopatric than males in ursine howlers (*Alouatta arctoidea*: Crockett, 1984; Pope, 1992) and Guianan red howlers (*Alouatta macconnelli*: Lecompte et al., 2017). Little is known about the dispersal pattern in black howlers (*Alouatta pigra*). This species lives in small, cohesive groups of one to four adult males, one to four adult females, and one to seven immatures (Van Belle & Estrada, 2006). Previous studies have reported both males and females immigrating and emigrating (Dias et al., 2015; Van Belle et al., 2008, 2011). However, genetic studies have revealed that groups may contain some male–male dyads and female–female dyads that are close kin (Van Belle et al., 2012, 2014).

In this study, we investigated the dispersal patterns of black howler monkeys at Palenque National Park, Mexico, based on demographic data from six groups followed for between 4 and 15 years combined with molecular data from these six groups plus

14 additional groups. We predict that if black howler males and females disperse at comparable rates, then (P1.1) both daughters and sons will disappear, and presumably emigrate, from their natal group at similar rates, (P1.2) both males and females will immigrate into groups at similar rates, and (P1.3) global F_{ST} values for both sexes will be comparable. Additionally, (P1.4a) if dispersal rates are comparable between the sexes, but low overall, we predict that mean relatedness values within groups will be higher than those between groups for both adult males and females; however (P1.4b), if dispersal rates are high, then mean relatedness within groups will be comparable to that between groups for both males and females. That is, irrespective of dispersal rate, the difference in average within-group and between-group relatedness values will be comparable for adult males and females if both sexes disperse at comparable rates. Alternatively, if dispersal in black howlers is biased towards males, we predict (P2.1) that sons will disappear, and presumably emigrate, from their natal group at a higher rate than daughters, and daughters will be more likely to remain in their natal group, (P2.2) males will immigrate into groups at higher rates than females, and (P2.3) global F_{ST} values for females will be higher than those for males. Furthermore, if dispersal rates are low overall, but males nonetheless disperse at higher rates than females, we predict that (P2.4a) both males and females will have mean relatedness values within groups that are higher than those between groups, yet within-group relatedness values for males will be lower than those for females. With increasing male dispersal rates relative to females, we predict that (P2.4b) the difference in within-group and between-group mean relatedness values will become less pronounced for males and will increasingly differ from that difference for females. However, (P2.4c) if parallel dispersal is common among males, then within-group mean relatedness values for males are expected to be higher and could be comparable to those for females. Lastly, we predict (P3) that there should be a pronounced correlation between measures of genetic similarity and geographical proximity for whichever sex (or both) whose dispersal is spatially limited across the scale of sampling.

2 | MATERIALS AND METHODS

2.1 | Study site and subjects

Palenque National Park (PNP), Mexico (17°28′N, 92°03′W) encompasses an area of 1771 ha, of which ~1000 ha contain undisturbed or regenerating evergreen tropical rainforest. The remaining land consists of human-induced pasture.

S.V.B. started a long-term study on black howlers at PNP in June 2006 when she observed two groups (Balam and Motiepa) for 14 months. Observations resumed in January 2010, and these two groups along with a third (Pakal) have been observed continuously until the closure of the park as a preventive measure against the COVID-19 pandemic (26 March 2020). In February 2012, two additional groups were added to the project (Bolas and Unites). One of these groups (Bolas) partially dissolved in October–November 2013

and the remaining group members were displaced to an adjacent, less accessible area by a neighbouring group. After that, it became increasingly difficult to locate this group, and we stopped following it in September 2016. In November 2015, we started observations on the group (Naha) that took over the former home range of the Bolas group.

During the study periods (June 2006–July 2007, January 2010–March 2020), study groups were observed every 2–4 weeks. Whenever we observed a study group, we recorded the identity of all group members, including newborns and new immigrants, as well as any group member missing. We could recognize individuals within their group by natural markings (e.g., genital pigmentation, permanent scars, body size and temporary botfly infections). We classified individuals as infants (0–12 months), juveniles (12.1–36 months), subadults (female: 36.1–48 months; male: 36.1–60 months) or adults (female: >48 months; male: >60 months) (Crockett & Pope, 1993; Rumiz, 1990). The group compositions throughout the study period of the six study groups are provided in Figure S1. In addition to demographic data, we also collected behavioural data and data on patterns of travel and range use by recording the geographical coordinates of the group's location with a GPS unit (Garmin eTrex Venture HC) at 15-min intervals throughout the observation day.

During two censuses, S.V.B. with assistants searched for additional groups in PNP. During the first census in July 2007, we located six groups (Figure 1). Three of these groups later became study groups (Pakal, Bolas and Unites), and the other three groups were located again during the second census. During the second census, from February to November 2012, we devoted 2 days every 2 weeks to search for 13 additional groups (Figure 1). One of these groups became a main study group (Naha) in 2015. Once a group was encountered, we followed it for the time necessary (1–10 h) to record the group's composition and collect faecal samples (see below). We recorded the geographical coordinates of the location upon first encounter with a GPS unit. We provide the compositions of the census groups in 2007 and 2012 in Table S1.

2.2 | Faecal sample collection

Over the course of the study periods, we collected faecal samples from all group members of the six main study groups, including individuals that temporarily joined these groups, and from most group members (apart from infants) in a total of 14 additional groups (Figure S1). Most samples were collected during regular behavioural follows of the main study groups between 2006 and 2020 and during the wider censuses of 2007 and 2012. Additionally, two new groups formed (Uxmal in August 2015 and Puras in March 2017) in areas adjacent to those of our main study groups, and we collected faecal samples from these groups in November 2015 and October 2017, respectively. In total, we collected samples from 101 individuals of the six study groups and from 68 individuals in the additional groups. We were unable to collect samples from one adult male (*ZZ* in Pakal), two adult females (*Mina* in Balam, *Mota* in Motiepa), and 31
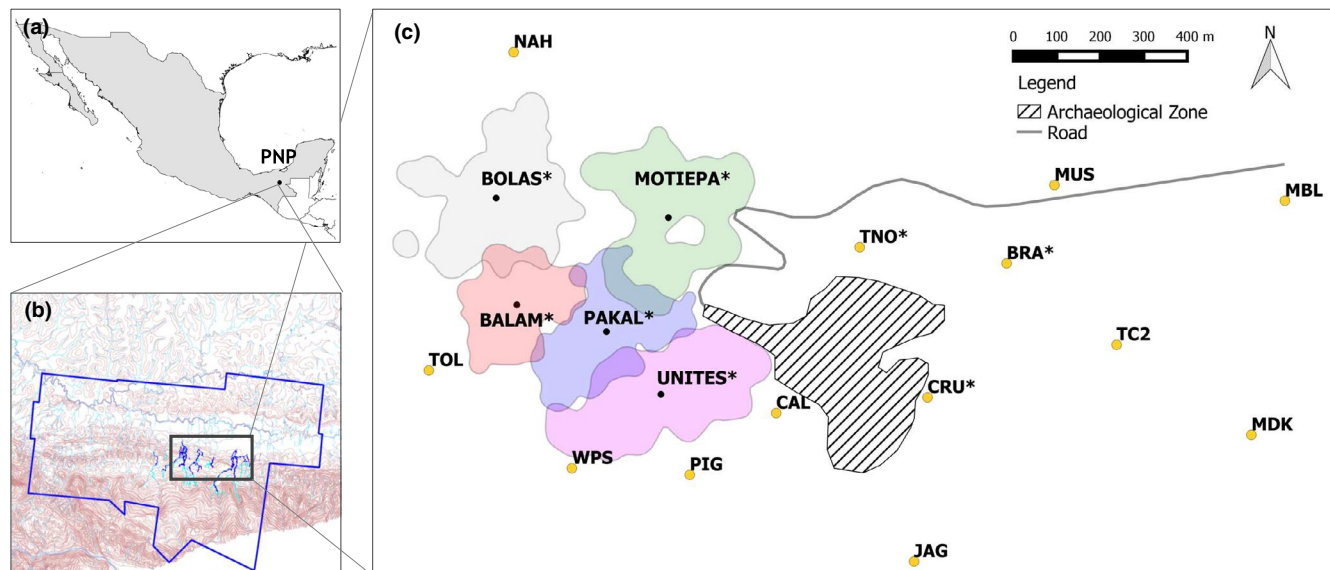
FIGURE 1 Location of the study site Palenque National Park (PNP) (a), the study area (b), and home ranges and their centroids (black dots) of five main study groups plus the contact locations of 13 additional groups (yellow dots) sampled in 2012 (c). Study group names (e.g., Bolas) are written out in full, while census groups are represented by three-letter abbreviations (e.g., TOL). The Naha group (shown as NAH here as it was first contacted as a census group in 2012) became a sixth study group in 2015 after it took over the home range of the Bolas group. Groups also sampled in an earlier census, in 2007, are indicated with an asterisk. The archaeological zone is an area of open grassland with excavated ruins unavailable for use by howler monkeys [Colour figure can be viewed at wileyonlinelibrary.com]

(of 69) infants born during the study period before they disappeared or died.

A small amount (~1 g) of fresh faecal material was collected whenever we could determine the defecator's identity and when the sample was not contaminated with other faecal matter. The faecal material was immediately stored in a 7-ml vial with 5.0 ml 90% alcohol for samples collected in 2006–2007 or 1.5 ml of RNAlater (Qiagen) for samples collected since 2010. We recorded the individual's ID, group and date of collection for each faecal sample. We stored the samples at −18°C until they could be transported to the Molecular Anthropology Laboratory at New York University for samples collected in 2006–2007 and to the Primate Molecular Ecology and Evolution Laboratory at The University of Texas at Austin for samples collected since 2010.

We were granted permissions to conduct this research at PNP by the Mexican government (SEMARNAT, CONANP and INAH). The research complied with protocols of the Animal Care Committee of Universidad Nacional Autónoma de México and adhered to the legal requirements of Mexico.

2.3 | DNA extraction and microsatellite analyses

The molecular analyses have been described in detail in previous studies that analysed 117 of the 169 individuals included in this study (Van Belle, Estrada, et al., 2014; Van Belle et al., 2012). Briefly, DNA was extracted using commercially-available QIAmp DNA Stool Mini Kits (Qiagen) following the manufacturer's instructions with slight modifications (Di Fiore et al., 2009; Strier et al., 2011). In a

series of uniplex and multiplex PCRs (polymerase chain reactions), we genotyped all individuals for a panel of 18 or 21 polymorphic microsatellite markers for the samples collected in 2006–2007 or since 2010, respectively. PCR products, along with a size standard (GeneScan 500 ROX), were separated and visualized on an ABI 3730 Automated DNA Analyzer. Allele sizes were scored in GENEMAPPER 4.0 (Applied Biosystems) and we visually confirmed all allele calls. We repeated homozygous genotype calls at least four times and heterozygous genotype calls at least twice (Morin et al., 2001; Taberlet et al., 1996). All 18 markers used in 2006–2007 were included in the 21 markers used since 2010. Individuals sampled in 2006–2007 were genotyped for a mean of 17.5 markers (SD =1.8; range =15–18, except for one male that was genotyped for only six markers) and individuals sampled since 2010 were genotyped for a mean of 20.9 markers (SD =1.8; range =20–21). Markers not genotyped for an individual were treated as missing data in the analyses below.

2.4 | Identifying dispersal events

Given the allele frequencies in the population, the chance that any two individuals or any two full siblings would have identical multilocus genotypes is vanishingly small (18-marker panel: $PI = 3.8 \times 10^{-12}$, $PI_{sib} = 9.1 \times 10^{-6}$; 21-marker panel: $PI = 6.0 \times 10^{-14}$, $PI_{sib} = 1.4 \times 10^{-6}$; twins have never been observed in our population). Hence, we presumed that sets of samples with matching genotypes across all loci were from the same individual. For 25 of these sets, the samples were collected at different times from animals residing in the same group, and the matching genotypes

confirmed the continued presence of the individual in the same group. This was particularly relevant for individuals sampled in 2006–2007 and then again since 2010. For 18 pairs of samples with matching multilocus genotypes, the same individual was sampled more than once, 2 months to 5 years apart, when living in different groups, and thus provide direct evidence of dispersal. All other individuals differed in genotype at least at three loci from any other individual.

To identify additional dispersal events, we conducted parentage analyses in CERVUS version 3.0.7 (Marshall et al., 1998) using adults as candidate offspring for the analysis ($N = 82$ possible adult "offspring"). In doing so, we aimed to identify the possible natal groups of those individuals that were considered adults when first observed (i.e., adults already present in a study group at the onset of observation, adults immigrating into the study groups and adults present in census groups). Candidate dams and sires for these parentage analyses included all sampled adult females ($N = 40$) and males ($N = 42$), respectively, across all groups and study years. For the analyses, we simulated 10,000 offspring with a genotyping error rate set at 1% and assuming that 20% of the candidate mothers or fathers were sampled. We assumed that we sampled ~20% of the candidate parents as our comprehensive census in 2012 covered ~18% of the total area of PNP (i.e., 180 of 1000 ha: Klass et al., 2020). We conducted these analyses in five steps: (1) maternity analyses without specifying a set of candidate sires, (2) paternity analyses without specifying a set of candidate dams, (3) maternity analyses including as candidate sires all males with positive LOD scores identified in step 2, (4) paternity analyses including as candidate dams all females with positive LOD scores identified in step 1, and (5) dual-parentage analyses in which both the most likely sire and most likely dam are assigned simultaneously using all sampled adult females and males as candidate dams and sires, respectively. In order for us to consider that we had confidently assigned the most likely sire and most likely dam for a particular adult offspring, the results of all these analyses had to be concordant, and the log likelihood ratios of both the most likely adult "offspring"–dam and adult "offspring"–sire pairs, as well as the most likely adult "offspring"–dam–sire trios, compared to the next-most-likely pairs or trio, had to be significant. Additionally, the adult "offspring"–sire–dam triad was allowed to have a trio mismatch at only one locus. We conservatively concluded that we successfully identified the likely natal group of an adult "offspring" if both likely parents resided in the same group. Although extragroup reproduction has been documented to occur in the study population (Van Belle, Estrada, et al., 2014; Van Belle et al., 2014), we cannot definitely address how common it is given incomplete sampling of possible dams and sires and a lack of information on group composition at the time of conception. We used additional information about the demographic history of the potential natal group, whenever available, to further evaluate these assignments (see Table S2). We considered those adults for which we could identify a likely natal group to have dispersed when their likely natal group was different from the group in which the adult "offspring" was residing during our study.

2.5 | Genetic structure analyses

To investigate sex-biased dispersal patterns, we estimated global F_{ST} for males and females separately in FSTAT version 2.9.4 (Goudet, 2001). For this, we used the genetic data only from the 18 groups sampled in 2012 (Figure 1). We only considered data from adults ($N = 29$ males, $N = 36$ females) to avoid biases caused by younger group members that have not yet dispersed from their natal group (see Section 3). To test for differences in these measures between males and females, we conducted randomization tests that randomly assigned a sex to a multilocus genotype while keeping the observed group size and sex ratio, as implemented in FSTAT. The p values were based on 10,000 randomizations.

To assess whether the dispersal patterns by males and females left a spatial genetic structure signal in the population, we conducted two sets of analyses using the same data set as above (i.e., only adults of 2012), the first a group-level examination of genetic vs. geographical distance and the second a spatial autocorrelation analysis based on individual genotypes. The group-level analysis calculates a correlation coefficient between the genetic distance between pairs of groups and the geographical distance between these pairs. Positive values indicate that groups geographically close to each other are genetically more similar compared to groups geographically further apart. We calculated genetic distance between groups (for males and females separately) as $F_{ST}/(1 − F_{ST})$ and examined the correlation between the genetic distance matrix and a matrix comprising the natural logarithm of the geographical distances between groups (Rousset, 1997). We calculated geographical distances between group ranges as the straight-line distances between coordinates of either the home range centroids for the five study groups or the first encounter location for the 13 additional census groups (Figure 1). Home ranges (95% fixed kernel density contour) of study groups were calculated based on the ranging behaviour collected throughout 2012, and the coordinates of the home range centroids were determined from these kernel density ranges using the Polygon Centroid function in QGIS 2.6.1. We ran these matrix correlation analyses in GENALEX 6.5 (Peakall & Smouse, 2012) using a Mantel test with 9999 permutations.

The individual-level spatial autocorrelation coefficient provides a measure of the genetic similarity for pairs of animals whose geographical separation falls within specified distance classes. We estimated pairwise relatedness values for adult males and females separately using the Queller and Goodnight (1989) estimator. We determined distance classes in two ways. First, we based them on the Euclidean distance among social groups, using home range centroids for study groups and first-encounter locations for census groups (Figure 1). Based on the frequency distribution of distances among neighbouring groups, we set the first distance class at 385 m (home range centroids were located between 161 and 385 m of each other for 70% of neighbouring groups). Subsequent distance classes were defined in increments of 385 m. Second, we determined distance classes based on the number of home range borders between pairs of individuals (i.e., 0 for individuals residing

in the same group, 1 for pairs residing in neighbouring groups, 2 for pairs residing two home ranges apart, etc.; Huck et al., 2007). Given that home ranges can differ in shape and size, this method might be more biologically meaningful than simple Euclidean distance between groups for explaining dispersal patterns as it represents the number of home ranges an emigrating individual needs to cross. We conducted these analyses in SPAGEDI version 1.5d (Hardy & Vekemans, 2002), which compares the observed spatial correlation with the one expected under the null hypothesis of no spatial correlation. The latter is achieved through permutations ($N = 19,999$) of the distance classes.

To characterize patterns of mean pairwise relatedness among males and among females within and between groups, we calculated, for each group, the mean relatedness among same-sex groupmates ($N = 10$ groups with at least one male–male dyad; $N = 14$ groups with at least one female–female dyad) as well as the mean relatedness between group residents and same-sex individuals residing in other groups. The latter, between-group values for each group were calculated as the grand mean of group means with each of the 17 other groups in the study population to account for unevenness in the number of between-group same-sex dyads in different pairs of groups. Confidence intervals (CIs) around each of these statistics were generated using a bootstrapping procedure that randomly sampled dyads from the observed relatedness matrix, with replacement, $N = 10,000$ times while maintaining the observed group structure and dyad types.

To examine whether mean pairwise relatedness values among adult male and adult female same-sex dyads was greater than expected within than between groups—and to evaluate whether the difference in mean within- and between-group pairwise relatedness among same-sex pairs differed for males vs. females—we constructed permutation distributions for these statistics via a randomization procedure that first shuffled ($N = 10,000$ times) the group assignment of each individual while maintaining the observed size and sex composition of each group in our study population. We then recalculated all pairwise relatedness value means based on these shuffled group assignments and compared observed values of the relevant statistics to the permutation distributions to obtain p values.

Similarly, to examine whether mean pairwise relatedness values within groups differed for males vs. females, we generated additional permutation distributions by randomizing ($N = 10,000$ times) sex assignments among group members while maintaining observed group compositions, sex ratios and individual genotypes within each group. For each permutation, we again recalculated all pairwise relatedness value means based on the shuffled sex assignments, and we compared the observed difference in mean pairwise within-group relatedness among males vs. females to the permutation distribution to assess significance. Custom R code used to generate bootstrapped confidence intervals and permutation distributions is provided in Dryad.

Finally, to further assess how "closely related" pairs of individuals were distributed within and between groups, we used ML-RELATE (Kalinowski et al., 2006), which uses simulations ($N = 10,000$) and maximum likelihood ratio tests, to evaluate whether a particular dyad could be considered as significantly more likely to be "closely related" (i.e., full siblings, half siblings or parent–offspring) than "unrelated." We then calculated the percentage of "closely related" pairs within each distance class based on the number of home range borders between pairs of individuals and compared that with what would be expected if closely related pairs were distributed evenly across the distance classes considering the total number of pairs for each distance class using χ^2 tests.

# 3 | RESULTS

3.1 | Confirmed dispersal events

3.1.1 | Males

Of the 21 males born in our study groups that survived their first year of life, 15 (71%) disappeared permanently from their natal groups at an age when dispersal is likely (mean $\pm$ SD = 4.7 $\pm$ 1.5 years, median = 5.1 years, range = 1.6—7.3 years). The six remaining males that still lived in their natal group at the end of the study were young (mean = 2.5 $\pm$ 0.7 years, median = 2.4 years; range = 1.7—3.5 years) and are considered to not have yet reached dispersal age. Of the 15 males that disappeared, eight (53%) were confirmed to have dispersed into another study group (Figure 2; for details see Table S2). In seven of these cases, the male dispersed into an established group adjacent to his natal group. The other male (*Uno*) formed a new group (Uxmal) with two dispersing females from another group (see below) adjacent to his natal group and that of the females (Figure 2). Additionally, one of these eight males (*Dos*) dispersed twice, once from his natal group to a neighbouring group (Pakal) and again a year later to another neighbouring group (Balam), two home ranges away from his natal group (Figure 2; Table S2).

From the parentage analyses of adults, we could assign both a most likely dam and a most likely sire from the same group for eight adult males sampled initially as adults (Table 1). Two of these males (*CAL-AM1* and *JAG-AM2*) were determined to still be living in their natal groups at the time of sampling as they resided with their most likely parents. The six other males for which we could assign both a dam and a sire immigrated into our study groups. Their natal group was either a neighbouring group ($N = 4$) or a group two home ranges away ($N = 2$; Figure 2). Two of these males (*Pedro* and *Louie*) were identified as full siblings and dispersed together into the Balam group (Van Belle et al., 2008). For four of these eight males, their natal group identity was corroborated because their genotypes matched with that of an individual sampled in that group during previous censuses (details in Table S2).

We found full multilocus genotype matches for five additional adult males (*Balam*, *Guz*, *Kriek*, *Momo* and *P-AM16*) that were sampled twice while living in different groups, thus reflecting at least five additional dispersal events involving males. For *Momo*, this probably

FIGURE 2 Overview of dispersal events of males (a) and females (b) across study years. Straight, black arrows and accompanying names represent confirmed dispersal between groups. Curvy, coloured arrows and names (males: blue, females: red) represent immigrations of individuals of unknown origin into our study groups. Approximate home ranges are shown for groups under study per year. The general locations of three nearby census groups (TOL, WPS, NAH) are shown by circles. Momo's original group (JAG) not shown (see Figure 1 for location). Dispersal events with asterisks shown in 2010 occurred during a period of no observations between July 2007 and December 2009 [Colour figure can be viewed at wileyonlinelibrary.com]
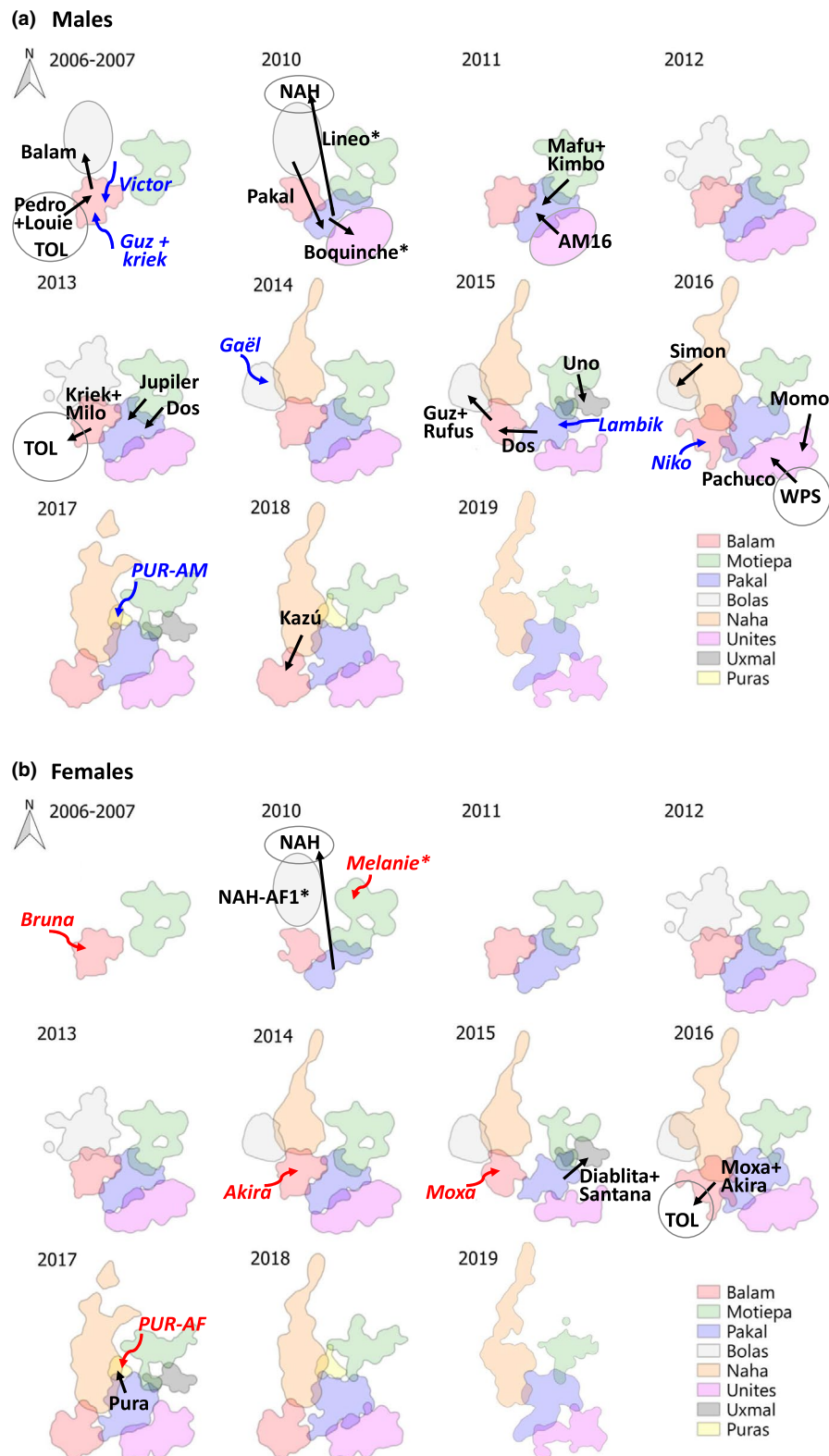
represents natal dispersal as he was first sampled as a juvenile in the JAG group. The other four cases are known to be instances of secondary dispersal, taking place after these males successfully reproduced in another group, as confirmed by genetic parentage results. In fact, *Kriek* and *Guz* immigrated together into the Balam group in 2006 (Van Belle et al., 2008). They then emigrated from Balam in

2013 and 2015, respectively, each having sired a male offspring in the Balam group during their tenures. Interestingly, they did not emigrate with their own son, but with each other's son (details in Table S2). Finally, we also confirmed (based on unique morphological features) the dispersal of an adult male (*Jupiler*) that had been present and reproducing in the Motiepa group since the onset of

TABLE 1 Parentage assignments for those adult males and females for which a most-likely dam and most-likely sire, both residing in the same group, could be assigned. LOD scores for the most-likely dam–offspring pair, most-likely sire–offspring pair and most-likely dam–sire-offspring trio are provided

Adult offspring	Adult offspring's current group	Candidate mother ID	Pair LOD score	Candidate father ID	Pair LOD score	Trio LOD score	Parents' group
Males							
Louie	Balam	TOL-AF1	8.85	TOL-AM	11.48	12.39/15.02/23.87	TOL
Pedro	Balam	TOL-AF1	5.85	TOL-AM	9.29	9.04/12.47/18.32	TOL
Lineo	Naha	Pura	8.82	Kin	10.66	7.28/9.12/17.94[b]	Pakal
Boquinche	Unites	Parcha	4.18	Kin	10.77	8.33/14.92/19.10	Pakal
Pakal	Pakal	Dinka	4.70	Rafiki	10.88	8.21/14.29/19.09	Bolas
Pachuco	Unites	WPS-AF	5.57	WPS-AM	12.66	10.87/17.96/23.53	WPS
CAL-AM1	CAL	CAL-AF1	8.43[a]	CAL-AM2	5.99	12.75/10.31/18.74	CAL
JAG-AM2	JAG	JAG-AF1	6.49	JAG-AM1	4.68	11.23/9.42/15.91	JAG
Females							
Anon	Bolas	Puma	7.84	Rafiki	2.53	11.26/5.59/13.79	Bolas
Kia	Naha	Zita	4.70	Lineo	7.7.87	8.84/12.00/16.70	Naha
PIG-AF1	PIG	PIG-AF2	6.76	PIG-AM1	11.13	8.59/14.72/21.48	PIG
NAH-AF1	Naha	Parcha	3.02[a]	Kin	9.21	8.16/14.36/17.38	Pakal
SolAF	—	NAH-AF1	7.35	NAH-AM1	7.79	10.89/11.34/18.69	Naha

Notes: The trio-LOD score column includes three LOD values separated by a "/". The first value is the score from a maternity analysis where a most-likely sire was assigned from among all males with positive LOD scores in an initial paternity analysis. The second value is the score from a paternity analysis where a most-likely dam was assigned from among all females with positive LOD scores in an initial maternity analysis. The third value is the score from a dual-parentage analyses that assigned a most-likely dam and most-likely sire simultaneously from among all candidate females and males, respectively. Also provided is the ID of the group of residence for each adult "offspring" and their identified parents.

[a]One locus mismatch for dam–offspring pair.

[b]One locus mismatch for the trio, but not for either the dam–offspring pair or the sire–offspring pair.

the study. In 2013, at an age of at least 17 years old, he dispersed to a neighbouring group, Pakal, and was residing there until the end of the current study (Figure 2).

In summary, for 59 males of dispersal age (i.e., those first observed as adults in study or census groups or as offspring in study groups that later reached adulthood) observed across 57 group years, we recorded 28 immigration events of adult males involving 24 unique individuals. Of these, eight immigration events involved four pairs of males; the males in three pairs were genetically closely related (*Pedro & Louie*: R = .492, *Kriek & Guz*: R = .262, *Mafu & Kimbo*: R = .301, Figure S1), while a fourth pair was not (*Guz & Rufus*: R = −.060). Two males immigrated singly into a group that already contained a genetically closely related male (*Jupiler* dispersed to Pakal where his son *Kimbo/Sibal* lived, R = .441; *Dos* dispersed to Pakal where his father *Jupiler* lived, R = .215). All other males immigrated singly into groups with no known closely related male residents. Ten of the immigrant males reproduced in their new group, where they resided for at least 5.1 ± 2.5 years (median = 5 years, range = 0.7—8.7 years) by the end of this study. The other males either resided in their new groups for shorter periods (mean = 3.2 ± 2.5 months, median = 2.7 months, range = 8 days to 9 months) or became noncentral males (*sensu* Van Belle et al., 2008; Van Belle, Garber, et al., 2014; *Jupiler*: 7 years, *Kimbo/Sibal*: 3.1 years both in the Pakal group, Figure S1).

During the study period, we also observed 43 permanent disappearances of adult or subadult resident males from our study groups (32 unique individuals; N = 13 sons sampled in their natal groups, N = 30 adult residents). We confirmed 21 dispersal events for which we knew the original and destination groups; 18 of these events occurred between adjacent groups and three occurred between groups two home ranges apart.

3.1.2 | Females

Of the 19 females born in our study groups that survived their first year of life, 10 (53%) disappeared permanently from their natal groups at an age when dispersal is probable (mean = 4.3 ± 2.2 years, median = 3.4 years, range = 3.1—9.5 years). Eight of these daughters disappeared prior to reproducing between the age of 3 and 4 years old (mean = 3.3 ± 0.3 years). Two daughters (*Zina* from the Unites group and *Saki* from the Motiepa group) that disappeared after reproducing two and three infants, respectively, in their natal groups did so at the age of 9.5 and 7.0 years, respectively. Of the 10 females that disappeared from their natal groups, two were confirmed to have dispersed as their genotypes matched with those of adult females sampled in the newly formed group Uxmal (see above). They

FIGURE 3 The linear correlation between genetic distance, measured as $F_{ST}/(1 − F_{ST})$, and the natural logarithm of the geographical distance between pairs of social groups ($N = 18$) of black howler monkeys (*Alouatta pigra*) at Palenque National Park, Mexico, sampled in 2012 for adult males (a) and adult females (b)
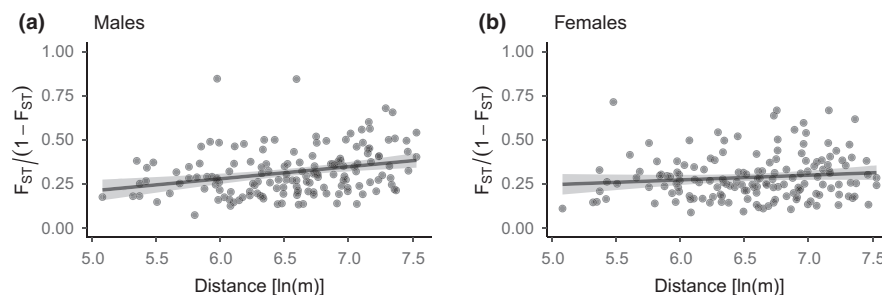
were two daughters born in the same group (Pakal) in 2011 and were identified as paternal half-sisters (Figure 2).

We recorded three additional dispersal events involving adult females. The two adult females, *Akira* and *Moxa*, that had immigrated into the Balam group in 2014 and 2015, respectively, dispersed and joined two males in a neighbouring group (TOL) in 2016 abandoning their resident adult male (*Niko*) (the resident female of the TOL group disappeared). The third dispersal event involved an adult female (*Pura*) that was present as an adult in the Pakal group in 2005 and was reproductively active ($N = 5$ offspring). At the age of at least 19 years, she disappeared from this group. Sixteen months later, she returned to the Pakal home range with a newborn. She was chased away by Pakal members during one of two observed encounters (details in Table S2). Seven months after her reappearance in the study area, she formed a new group (Puras) with a solitary male adjacent to the Pakal home range (Figure 2). Another solitary female joined them 6 months later.

Of the nine females that were still residing in their natal group by the end of the study, two were juveniles of ages 2.5 and 2.9 years when dispersal is rather unlikely. The remaining seven daughters became reproductively active in their natal groups and varied in age between 4.1 and 11.2 years by the end of the study (mean = 7.5 ± 2.4 years, median = 8.0 years). One of these nine daughters (*Luna*) disappeared temporarily from her natal group (Pakal) in February 2016 but returned 5 months later after another subadult female had disappeared from the group. Group members initially chased her, and she remained peripheral for 1.5 months. She then fully integrated back into her natal group and subsequently reproduced successfully.

From the parentage analyses of adults, we could assign a most likely dam and a most likely sire residing in the same group for five adult females (Table 1). Three of these females were determined to be residing in their natal groups along with their parents, and two of them (*Kia* and *Anon*) are known to be reproductively active in their natal group. The fourth female (*SolAF*) was sampled in March 2015 when she was moving together with the then-extragroup male *Uno* in the area where *Uno* and two other females later formed the new Uxmal group. This female was three home ranges away from her natal home range. The fifth female (*NAH-AF1*) dispersed from the then census group Pakal to the census group Naha, two home ranges away. Without records on the Naha group during the estimated time of dispersal, we do not know whether Naha was an existing group or was newly established. Interesting, a full brother of *NAH-AF1* (*Lineo*) was also present in the group when surveyed in 2012.

In summary, for 65 females of dispersal age (i.e., those first observed as adults in study or census groups or as offspring in study groups that later reached subadulthood) observed across 57 group years, we observed 11 immigration events of females into our study groups (nine unique individuals). Four of these immigration events involved two pairs of females, one of which were genetically closely related to each other (*Diablita* & *Santana*: $R = .410$), and the other were not (*Akira* & *Moxa*: $R = .028$). The first pair of females and a single female (*Pura*) formed new groups each with one solitary male (Uxmal and Puras, respectively), while the seven other females immigrated into established groups. Nine of the 11 females reproduced successfully in the groups to which they dispersed. *Pura* has not reproduced since establishing the Puras group in 2017. The other female (*Bruna*) joined the Balam group only temporarily (14 days) before disappearing, and presumably dispersing, again (details in Van Belle et al., 2011).

During the study period, 19 females permanently disappeared from the main study groups ($N = 13$ daughters from their natal group, $N = 6$ adult residents). We confirmed that six of these disappearances were dispersal events as we could discern the fates of these females: three involved females forming new groups adjacent to the home range of their natal group, and two involved females dissolving their own group to join males of a neighbouring group. We also recorded a dispersal event of a female between two census groups that were located two home ranges apart.

3.2 | Sex-biased dispersal

For both males and females, global F_{ST} values were positive and significant (males: 0.118, 95% CI: 0.072–0.156; females: 0.164, 95% CI: 0.137–0.213), but were not significantly different from each other ($p = .389$).

3.3 | Spatial autocorrelation

The isolation-by-distance model revealed a positive correlation between pairwise ratios of $F_{ST}/(1 − F_{ST})$ and ln(geographical distance) among groups for adult males ($r = .24$; $p = .024$; Figure 3a), but not for adult females ($r = .09$, $p = .237$, Figure 3b).

Compared to the null hypothesis of a panmictic distribution, spatial autocorrelation analyses indicated significant and positive

correlations for both adult males and adult females at the first distance class (i.e., within groups; $p < .0001$ for both; Figure 4). There was no discernible spatial genetic structure at larger distance classes for adult males. This was true when considering classes based on Euclidean distances (Figure 4a), as well as those based on the number of home ranges between pairs of males (Figure 4c). Spatial autocorrelation analyses for females using Euclidean distance classes indicated that adult females living 770–1155 m apart were more likely to be related than expected ($p = .032$) and those living 1155 to 1540 m apart were less likely to be related than expected ($p = .014$; Figure 4b). Repeating these autocorrelation analyses using home range distance classes rather than Euclidean distances found that pairs of adult females that live two and four home ranges apart are less likely to be related than expected ($p = .037$ and $p = .004$, respectively; Figure 4d).

3.4 | Relatedness patterns

For both males and females, the mean pairwise relatedness value among adults within groups was significantly higher than that between groups (males: within group: mean $r = .225$, $N = 10$ groups, 95% CI: 0.194–0.262; between groups: mean $r = −.010$, $N = 18$ groups, 95% CI: −0.021 to 0.001; $p < .0001$; females: within group: mean $r = .277$, $N = 14$ groups, 95% CI: 0.256–0.297; between groups: mean $r = .006$, $N = 18$ groups, 95% CI: −0.005-0.016; $p < 0.0001$). Within-group mean relatedness values did not differ significantly for

males vs. females ($p = .744$) nor did the difference in within-group vs. between-group mean pairwise relatedness values ($p = .837$).

Overall, individuals of both sexes tended to live as adults in groups with one or more closely related same-sex adult relatives: 78% ($N = 18$ of 23) of intragroup adult female–adult female dyads and 67% ($N = 8$ of 12) of intragroup adult male–adult male dyads were identified as closely related. A lower proportion of pairs of adult individuals that lived in separate groups (one to eight home ranges apart) were identified as closely related (females: 14%; $N = 89$ of 607; males: 20%, $N = 77$ of 394; Figure 5). The distribution of closely related adult pairs across the different distance classes (i.e., number of home range borders between dyads) was largely skewed towards intragroup pairs for both males ($\chi^2 = 19.5$, $p = .013$) and females ($\chi^2 = 70.0$, $p < .0001$, Figure 5). When only considering intergroup distance classes, the distribution of closely related adult pairs living one to eight home ranges apart was not statistically different from what would be expected by chance for either males ($\chi^2 = 3.2$, $p = .868$) or females ($\chi^2 = 9.6$, $p = .214$).

4 | DISCUSSION

This 15-year study that combined multiyear demographic data of six social groups with longitudinal and cross-sectional genetic sampling of a larger number of groups largely supported the hypothesis of bisexual dispersal with a bias towards males in black howler monkeys. As in other howler species (Clarke & Glander, 2008, 2010; Collevatti
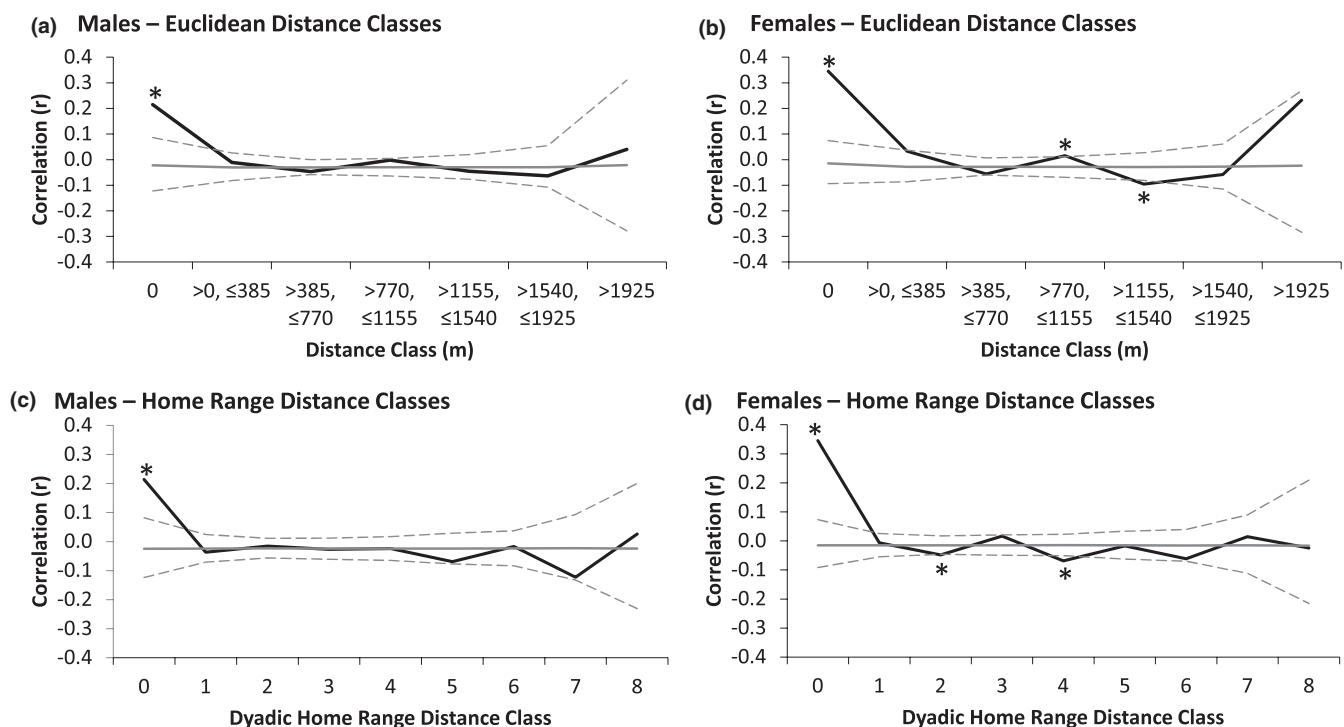

(a) Males – Euclidean Distance Classes

(b) Females – Euclidean Distance Classes

(c) Males – Home Range Distance Classes

(d) Females – Home Range Distance Classes

FIGURE 4 Correlogram plots of the correlation between genetic similarity (relatedness values) and distance between pairs of individuals (black line) across Euclidean distance classes (a, b) or home range distance classes (c, d). The null hypothesis (grey line) and 95% confidence interval (dashed grey lines) of a random distribution of genotypes are shown . Asterisks indicate statistical significance at α = .05
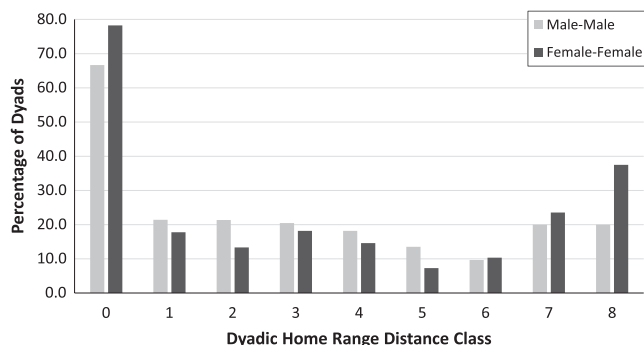
FIGURE 5 Percentages of dyads within each distance class that were considered to be closely related (i.e., parent–offspring, full siblings and half siblings). Distance classes represent the number of home range borders between pairs of individuals (e.g., 0: same group; 1: neighbouring groups; 2: two home ranges away, etc.). We considered adult male dyads and adult female dyads separately

& Telles, 2013; Crockett & Pope, 1993; Glander, 1992; Lecompte et al., 2017; Oklander et al., 2010; Pope, 1992; Rumiz, 1990), both black howler males and females disperse from their natal groups and either immigrate into an already-existing group or form a new group with other dispersing individuals. Yet, there is a high skew toward male dispersal as virtually all sons disappeared or emigrated from their natal group while over half of the daughters stayed and reproduced in theirs. Similarly, more males than females ($N = 28$ vs. 11) immigrated into groups. It is not yet clear to what extent this is because more males than females dispersed or because males were more successful than females at immigrating, as immigration events are rarely observed directly. The few events that have been observed ($N = 7$ males and $N = 1$ female; Van Belle et al., 2008; Van Belle et al., 2011; Table S2) generally involved agonistic reactions from resident group members, as was also the case during encounters between social groups and solitary individuals of either sex (S.V.B., pers. obs.). A higher dispersal rate for males compared to females also has been observed in ursine howlers (*Alouatta arctoidea*; Pope, 1992), Guianan red howlers (*A. macconnelli*; Lecompte et al., 2017), and black-and-gold howlers (*A. caraya*) in fragmented forest (Oklander et al., 2010), but not in a black-and-gold howler population living in continuous forest (Oklander et al., 2010) nor in mantled howlers (*A. palliata*, Clarke & Glander, 2008). Male-biased dispersal within a bisexual dispersal pattern has also been reported in ursine colobus monkeys (*Colobus vellerosus*; Teichroeb et al., 2011) and lions (*Panthera leo*; Pusey & Packer, 1987), but contrasts with the female-biased dispersal pattern observed in other atelid genera where males only rarely disperse (*Ateles*: Di Fiore et al., 2009; Shimooka et al., 2010; Symington, 1987; but see Aureli et al., 2013; *Brachyteles*: Strier et al., 2015) or disperse more commonly (*Lagothrix*: Di Fiore et al., 2009; Nishimura, 2003; Pain et al., 2021).

Male dispersal in black howlers seems to function mainly to avoid inbreeding rather than to avoid local resource competition. This is supported by our observations that sons generally remained in their natal group until being young adults (~5 years old) and that some sons ($N = 4$) returned to their natal group (Figure S1) in between

dispersal attempts without receiving overt agonism from natal group members upon returning. A similar pattern was observed in ursine howlers (Crockett, 1984; Crockett & Pope, 1993). In contrast, the main function of female dispersal seems to be related to avoiding competition for limited resources with female kin as females typically disappeared or dispersed from their natal groups as older juveniles or young subadults (~3.5 years old). The resource at stake appears to be a breeding position within the group, given that the number of adult females in black howler groups is limited to four (Van Belle & Estrada, 2006). This is also the case for ursine howler groups, and it has been hypothesized that ursine howler groups with three to four adult females are more susceptible to male takeover attempts than groups with one or two females (Crockett & Janson, 2009). Given that infanticide may occur during or after takeover events, females may attempt to limit the number of other adult females residing in their groups by preventing female immigration and by evicting natal maturing females (Crockett, 1984; Crockett & Janson, 2009; Crockett & Pope, 1993; Pope, 2000). While increased takeover risks according to female group size have not been corroborated in black howlers, infanticide has been observed after male takeovers (Van Belle et al., 2010), and some daughters have been evicted from their natal group (Van Belle, Estrada, et al., 2014; Van Belle et al., 2011). On one occasion, a daughter that left her natal group was able to return after another subadult female disappeared from the group and thus perhaps freed up a space in the queue for future breeding positions. Nonetheless, she was chased on various occasions prior to successfully rejoining her natal group by a resident adult female that was not her mother, perhaps in an attempt to prevent her from immigrating back into the group.

Contrary to what we had predicted for bisexual dispersal with a bias towards males, and more in line with our prediction for a dispersal pattern with no sex bias, global F_{ST} values were comparable between the sexes. Similarly, mean pairwise relatedness values between pairs of individuals living in the same group were significantly higher than between pairs living in different groups for both sexes, and the difference in within-group and between-group mean pairwise relatedness values for males was comparable to that for females. These results suggest a certain level of philopatry for both males and females. For females, this is in accordance with a high level of philopatry within a male-biased dispersal pattern. For males, these findings probably reflect the inclusion of some father–son pairs in our analyses even though we only considered adult group members (i.e., probably post-dispersal individuals). Given that males tend to remain in their natal group until they are young adults, it is plausible that some intragroup male dyads were father–son pairs, particularly for census groups of which we do not have the demographic history. Indeed, our parentage analyses did identify some adult males coresiding with their most likely sire and dam, suggesting that these males had not yet dispersed from their natal group. Another possibility for the high intragroup relatedness among males and a male F_{ST} value comparable to that for females is parallel dispersal, whereby either pairs of males that are kin disperse together or a male disperses into a group that already contains a male relative that

had previously dispersed into that group (Schoof et al., 2009). Both of these patterns of parallel dispersal were observed in our black howler population.

We also recorded parallel dispersal for females in that pairs of females occasionally dispersed together from their natal group, a pattern also observed in female lions (Pusey & Packer, 1987). This is unlikely to occur frequently in black howlers as (1) social groups are small with a maximum of four breeding females, (2) reproduction is not strictly seasonal (S.V.B., unpublished data), (3) females give birth to singletons, and (4) natal females that disperse do so as older juveniles, making it unlikely for them to wait for younger females to reach dispersal age to disperse together. The two cases of female parallel dispersal we observed involved two daughters of a cohort of three females that differed in age by only 15–30 days and two adult females abandoning their resident male to join the males of a neighbouring group.

The large number of male dispersal events recorded in this study suggests that males frequently disperse to neighbouring rather than more distant groups. Some males succeeded in obtaining a breeding position in their new group while others dispersed or disappeared again. Our direct observations of short male dispersal distances are consistent with the overall results of our isolation by distance model for males, which suggest that within the 2-km spatial scale considered in this study, male dispersal seems to be spatially restricted. Surprisingly, the autocorrelation models, considering either Euclidean distance or the number of home range borders between pairs of individuals, did not reveal a positive effect on pairwise genetic relatedness in the second distance class (representing neighbouring groups), and dyads of males living one and two home ranges apart were not more likely to be closely related than would be expected by chance. This suggests that males can and do disperse farther than neighbouring groups. Indeed, several adult males immigrated into our study groups; their groups of origin were unknown and thus they must have come from outside the study area. Short dispersal distances for males have also been suggested for Guianan red howlers, where autocorrelation values were significantly positive within the first distance class (i.e., 500 m; Lecompte et al., 2017), and for ursine howlers, where the mean male dispersal distance is estimated to be 275 m (i.e., one home range diameter) even though one ursine howler male was known to disperse as far as 3 km from his natal group (Crockett & Pope, 1993).

Despite some confirmed female dispersal events to areas adjacent to their original group (e.g., by establishing a new group), females appear to generally disperse farther than males given that we found no correlation of genetic and geographical distance in the isolation by distance model for adult females. Additionally, the autocorrelation model based on Euclidean distance classes suggested that pairs of females living 770–1155 m apart—equivalent to a separation of three to five home ranges—were more likely than expected by chance to be genetically related and thus suggests that females tend to more frequently disperse such distances. However, the autocorrelation model based on the number of home range borders separating female dyads suggested that dyads living two or four

home ranges apart were actually less likely to be genetically related than would be expected by chance. Similarly, the distribution of closely related female dyads across the different distance classes up to eight home ranges apart also did not reveal a common dispersal distance for females. It is possible that females tend to disperse even greater distances and that a study considering a larger study area would reveal more clearly the average dispersal distance for females. In Guianan red howlers, no positive autocorrelations were found across the different distance classes within a 2-km spatial scale for females (Lecompte et al., 2017). In ursine howlers, mean dispersal distance for females was estimated at 1.4 km, equivalent to five home ranges away, but one female was known to disperse at least 6 km away from her natal group (Crockett & Pope, 1993). The same pattern where males disperse closer to their natal groups than females do was observed in moustached tamarins (*Saguinus mystax*; Huck et al., 2007). However, in mountain gorillas (*Gorilla beringei*) and lions, the pattern is reversed with females generally dispersing to neighbouring groups while males disperse farther away (Pusey & Packer, 1987; Roy et al., 2014).

Given the difficulty of studying dispersal based on observational data alone, molecular methods—including genetic mark–recapture and spatial autocorrelation studies—have become increasingly powerful and popular tools for inferring dispersal patterns (Cayuela et al., 2018). However, often neither direct nor indirect methods alone adequately capture the complexity of the dispersal patterns of a species, and the combination of observational studies, demographic censuses and repeated genetic sampling might be required to obtain a fuller understanding of a species' dispersal patterns (Di Fiore et al., 2009; Griesser et al., 2014; Harris et al., 2009; Rollins et al., 2012). Indeed, the results of our 15-year demographic study of six groups with longitudinal and two cross-sectional genetic surveys of a larger number of groups revealed important insights into the dispersal patterns of black howlers that would not have been possible if we had relied on either component alone. For example, our multiyear demographic study provided important insights into immigration patterns, but without the ability to recognize most of our study subjects outside their original groups our insights into emigration patterns were limited as we failed to relocate and/or recognize some of these individuals after they moved into other groups. Consequently, many dispersal events went unnoticed during the observational study. Only through genotyping all group members of our study groups over the course of 15 years, as well as those in neighbouring groups during two genetic surveys 5 years apart, were we able to reconstruct the multiple dispersal events that had taken place. Similarly, our spatial autocorrelation analyses based on a cross-sectional genetic study of 18 groups during one census year (2012) suggested some spatial restriction in male dispersal, but such an approach alone did not reveal the many cases of male dispersal to neighbouring groups that we were able to detect using the combination of longitudinal observation and repeated genetic sampling. Nevertheless, the spatial autocorrelation analyses were crucial to understand that females generally disperse to farther distances than males. Additionally, we could only correctly

contextualize our measures of genetic population structure for males (e.g., global F_{ST} values, within- and between-group mean pairwise relatedness values) when we considered the mean age at dispersal for males—life history data which can only be obtained through a long-term study of known individuals—and, likewise, take into account cases of parallel dispersal by related males, which were confirmed using genetic data. Other studies have also demonstrated the productive integration of demographic and molecular methods for studying animal dispersal (e.g., lesser kestrel, *Falco naumanni*: Alcaide et al., 2009; guereza monkey, *Colobus guereza*: Harris et al., 2009; chestnut-crowned babbler, *Pomatostomus ruficeps*: Rollins et al., 2012). Still, it is important to note that even when both direct and indirect approaches provide similar results, direct observations are crucial in understanding the proximate mechanisms underlying dispersal decisions and the ultimate consequences of those decisions (e.g., Siberian jay, *Perisoreus infaustus*: Griesser et al., 2014).

In conclusion, the dispersal pattern of black howlers is bisexual but with a strong sex bias in both dispersal rate (males dispersed more than females) and dispersal distance (females dispersed farther than males). Both dispersing males and females are successful in immigrating into established groups: males can join social groups without evicting resident males or can take over a group, evicting some or all resident males (Van Belle et al., 2008), while females seem to join groups with only one resident female present. Dispersing individuals can also form new groups and carve out a home range among those of established groups. The rate and success with which new groups form will depend on the population density, as was observed across different ursine howler populations (Crockett & Pope, 1993; Pope, 2000). Both males and females were observed to occasionally disperse secondarily after they had attained a breeding position in a group. We also confirmed parallel dispersal for both sexes, but it appears to be more prevalent in males, as others have suggested would be expected (Schoof et al., 2009). Our results are in line with demographic data obtained in a long-term study of another black howler population (Dias et al., 2015). Overall, the dispersal pattern of black howlers is complex, and this complexity was revealed by combining a multiyear demographic study with a longitudinal and cross-sectional genetic study. Longer multiyear studies are needed to unravel which demographic, ecological and social factors may play a role in individuals' decisions to disperse or which dispersal option to take (Behr et al., 2020; VanderWaal et al., 2009).

AUTHOR CONTRIBUTION

S.V.B. conceived and designed the research, S.V.B. collected data, S.V.B. conducted genetic and statistical analyses with guidance from A.D. A.D. contributed laboratory space, materials and reagents. S.V.B. and A.D. wrote the manuscript.

DATA AVAILABILITY STATEMENT

Genotype data of all sampled individuals, geographical data of 18 sampled groups, as well a customized R script to calculate within-group and between-group mean pairwise relatedness values for same-sex adult dyads and corresponding EXCEL files used in this study are available via Dryad: https://doi.org/10.5061/dryad.3ffbg79j4

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