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Female social structure and sociosexual interactions in black and gold howler monkeys (*Alouatta caraya*)

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Abstract: Female social relationships play a central role in the organization of primate societies, yet it remains unclear whether an individual's position within affiliative social networks influences sociosexual interactions. We investigated the relationship between female reproductive condition, affiliative network position, and male sociosexual behavior in two wild groups of black-and-gold howler monkeys (*Alouatta caraya*) in northeastern Argentina. Behavioral observations were collected over 12 months using scan sampling and affiliative and sociosexual interactions were analyzed through Social Network Analysis (SNA) and Generalized Linear Mixed Models (GLMMs). Across reproductive states, one female in each group consistently occupied the most central position within affiliative networks, indicating stable differences in social connectivity. However, male sociosexual interactions were not significantly associated with female reproductive condition or female network position, suggesting that males did not preferentially direct sociosexual behavior toward either cycling or socially central females. In contrast, female–female association strength varied with reproductive condition, with lactating females exhibiting significantly fewer affiliative interactions than cycling females. Social position did not explain variation in female association strength. These findings indicate that affiliative network structure and sociosexual behavior represent partially independent dimensions of social organization. While some females consistently occupied structurally central positions, these did not confer detectable advantages in immediate sociosexual interactions. Instead, reproductive condition, particularly lactation, emerged as the principal factor influencing female affiliative relationships. Our results highlight the importance of integrating network-based and inferential approaches to better understand the mechanisms underlying social organization and reproductive behavior in group-living primates.

Significance Statement: Social relationships are fundamental to understand how animals live together, however, individuals do not necessarily benefit from being socially well connected in all aspects of their lives. We examined how female social relationships and reproductive condition relate to interactions with other group members in wild black and gold howler monkeys. Some females consistently occupied more socially connected positions within their groups, suggesting stable differences in how individuals participate in the social life of the group. However, these positions did not result in greater sociosexual interactions with males, indicating that being socially well connected does not necessarily translate into greater mating opportunities. In contrast, females interacted less with other females while nursing, suggesting that caring for dependent offspring can constrain social relationships. These findings show

that social connectedness and reproductive interactions can represent partly independent dimensions of animal social organization.

Introduction

Social organization is one of the most variable and complex aspects of mammalian behavioral ecology, reflecting the interplay between ecological conditions, life-history traits, and species-specific social strategies. Across mammals, social systems range from solitary individuals to stable family groups and highly complex multi-level societies, exhibiting remarkable variation in group size, dispersal patterns, dominance relationships, and mating systems (Clutton-Brock, 1989; Lukas & Clutton-Brock, 2018). For example, African elephants (*Loxodonta africana*) and killer whales (*Orcinus orca*) form long-term matrilineal societies in which older females play a central role in group cohesion, leadership, and offspring survival (McComb et al., 2001, 2011; Foster et al., 2012; Brent et al., 2015). In contrast, social carnivores such as spotted hyenas (*Crocuta crocuta*) and meerkats (*Suricata suricatta*) exhibit hierarchical societies in which dominance rank strongly influences access to reproductive opportunities and resources (Clutton-Brock et al., 2001; Smith et al., 2010). These examples illustrate that similar ecological pressures can generate markedly different forms of social organization, suggesting that social systems emerge through the interaction of ecological constraints with each species' evolutionary history.

Among mammals, primates display some of the greatest diversity in social organization, ranging from pair-living species to multi-male/female groups and fission–fusion societies (Kappeler & van Schaik, 2002; Strier et al., 2014). Their high levels of sociality make them an ideal model for examining the ecological and evolutionary mechanisms underlying social relationships, cooperation, and dominance (Snaith & Chapman, 2007; Huchard et al., 2025). Understanding how social relationships emerge and are maintained has therefore become a central objective of behavioral ecology. The socioecological model proposed by Sterck et al. (1997) has provided one of the principal theoretical frameworks for explaining variation in female social relationships. This model predicts that feeding competition determines female dominance structure and affiliative behavior, with species exploiting relatively homogeneous and abundant resources expected to exhibit egalitarian female relationships and weak dominance hierarchies. However, increasing evidence indicates that ecological factors alone cannot explain the diversity of primate social systems. Kinship, reproductive condition, familiarity, social preferences, and cooperative interactions have all been shown to influence female social organization, often overriding predictions based solely on feeding competition (Sussman et al., 2005; Thierry, 2008; Sussman & Garber, 2011; Clutton-Brock & Janson, 2012). More recent comparative studies further suggest that male–female dominance relationships depend on demographic and evolutionary factors, challenging traditional views of male-centered social systems and emphasizing the importance of female social strategies in shaping group organization (Smith et al., 2022; Huchard et al., 2025).

Social Network Analysis (SNA) has emerged as one of the principal approaches for quantifying social organization because it allows researchers to move beyond pairwise interactions and examine the structure of entire social groups (Brent et al., 2011; Sueur et al., 2011). By representing individuals as nodes and their interactions as social ties, SNA provides quantitative metrics describing cohesion, centrality, connectivity, and subgroup formation. Across mammals and other vertebrates, these approaches have demonstrated that social groups are not randomly organized but instead contain individuals occupying disproportionately important structural positions that contribute to information transfer,

cooperation, and group cohesion (Brent et al., 2011; Farine & Whitehead, 2015). In primates, network analyses have shown that central individuals can play a critical role in maintaining social cohesion, and experimental studies indicate that the removal of these individuals may substantially disrupt network connectivity (Flack et al., 2005, 2006; Kanngiesser et al., 2011). More recently, Asensio et al. (2026) showed that social networks in mantled howler monkeys (*Alouatta palliata*) contained individuals occupying differentially central positions, with immature individuals exhibiting particularly high centrality. These findings highlight that social connectivity may be unevenly distributed among group members and raise the question of whether individual social position also influences other dimensions of social behavior, including sociosexual interactions.

Among Platyrrhini primates, species of the genus *Alouatta* represent an excellent model for evaluating these ideas because they exhibit considerable ecological and social flexibility across species (Crockett & Eisenberg, 1987; Di Fiore et al., 2010; Cortés-Ortiz et al., 2014). Social groups generally contain multiple adult males and females, although unimale groups also occur, and mating systems range from harem-type polygyny to polygynandry and female promiscuity (Di Fiore & Campbell, 2007; Kowalewski & Garber, 2010). In black and gold howler monkeys (*Alouatta caraya*), behavioral and genetic evidence indicates that females frequently mate with multiple males and that reproductive success is not monopolized by a single dominant male (Kowalewski & Garber, 2010; Oklander et al., 2014). Females also actively participate in intergroup vocal displays and contribute to group defense and coordination (da Cunha & Byrne, 2006). Together, these findings suggest that female social relationships may play a central role in structuring mating opportunities and male–female interactions.

Despite the increasing application of SNA to studies of primate behavior, most research has focused on describing affiliative relationships, dominance structure, or group cohesion (Sueur et al., 2011; Roberts & Roberts, 2025). Much less attention has been paid to whether an individual's position within affiliative social networks influences interactions between the sexes. In particular, it remains unclear whether males preferentially direct sociosexual behavior toward females occupying central positions within the social network or whether these interactions are explained primarily by female reproductive condition. Understanding the relationship between female social organization and male sociosexual behavior is essential for evaluating how individual social position contributes to mating dynamics and reproductive strategies in group-living primates.

In this study, we examined intra and intersexual interactions in two wild groups of *Alouatta caraya* to evaluate whether male sociosexual behavior is associated with female reproductive condition, individual identity, and female social position within affiliative networks. We focused on sociosexual behaviors requiring close physical proximity (grooming, genital inspection, tongue-flicking, and copulation) and used SNA to characterize patterns of female social organization across reproductive states. We tested three hypotheses: H1) male sociosexual behavior varies according to female reproductive condition, with resident males directing higher rates of sociosexual interactions toward cycling than pregnant or lactating females, H2) resident males consistently direct sociosexual behavior toward particular females independent of reproductive condition, indicating individual mating preferences, H3) female reproductive condition and social position jointly influence female affiliative relationships, resulting in differences in female–female association strength within social networks. Together, these hypotheses allow us to evaluate the relative importance of reproductive condition, individual identity, and emergent social structure in shaping male–female and female–female

interactions in a wild primate. Understanding whether female social position influences male sociosexual behavior provides a direct test of whether emergent social structure shapes mating dynamics in group-living primates

Methods

Study area: This study was conducted in a semi-deciduous gallery forest surrounding the Corrientes Biological Station (EBCo) and Parque Provincial San Cayetano (PPSC) in northwestern Corrientes, Argentina (27°30′ S, 58°41′ W). The study area includes 24 forest fragments (mean size = 9.24 ha, SD = 7.26, range = 1.4–29.3 ha) separated by an average distance of 1,763 m (SD = 538.7). Mean annual temperature is 21.7 °C and average annual precipitation is approximately 1,400 mm (Contreras et al., 2020).

Study Groups: From August 2011 to August 2012, we followed two neighboring habituated groups of *Alouatta caraya* from sunrise to sunset, each for 87 days.

Group "Se" (Sena) included 1 adult male, 2 subadult males, 2 adult females, 1 juvenile male, 1 juvenile female, and 2 infants. Group "Ta" (Tacuaral) included 2 adult males, 2 adult females, 2 subadult females, 1 juvenile female, and 2 infants. Adults were defined as individuals aged 4–5 years, subadults as 3–4 years, juveniles as 1–3 years, and infants as 0–12 months.

Behavioral data were collected using 10-min scan sampling (Altmann, 1974). During each scan, we recorded the identity of individuals engaged in sociosexual interactions, including grooming, genital inspection, tongue-flicking, and copulation, as well as the direction of the interaction (initiator and recipient). These behaviors were selected because they require close physical proximity (≤1.5 m). Individuals were identified based on natural markings (e.g., scars, facial features) or previously applied tags. Analyses focused on adult and subadult individuals. In total, 10 individuals were included across both groups. One subadult male in the Tacuaral group was also included. One adult male died during the study period (Raño, 2016). To examine variation in social interactions across reproductive conditions, we divided the dataset by female reproductive state. For the Sena group, networks were constructed for lactating and pregnant periods. For the Tacuaral group, networks were constructed for cycling and pregnant periods.

Reproductive status: We divided adult females into three reproductive states: (1) Lactating: females nursing an offspring; (2) Gestating: females that had conceived and were pregnant; and (3) Cycling: females that had not yet conceived but were undergoing hormonal changes consistent with an estrous cycle. Hormonal analyses were performed on urine samples to confirm reproductive status (see Raño 2016; Raño et al. 2018). Urine samples were collected from all adult females every 2 days over a 12-month period. In the "Sena" group, adult females were either lactating or pregnant, as no resident female was observed cycling. In the "Tacuaral" group, adult females were either cycling or pregnant, as no female was lactating (see Table 1).

	Sena		**Tacuaral**		
Month/Female	**Violeta (adult)**	**Inés (adult)**	**Clara (adult)**	**Alma (adult)**	**Lori (adult)**

August-11	Lactating	Pregnant	Pregnant	Precycling	Cycling
September-11	Lactating	Pregnant	Pregnant	Precycling	Cycling
October-11	Lactating	Pregnant	Pregnant	Precycling	Cycling
November-11	Lactating	Pregnant	Pregnant	Precycling	Cycling
December-11	Lactating	Lactating	Pregnant	Precycling	Cycling
January-12	Lactating	Lactating	Lactating	Cycling	Cycling
February-12	Lactating	Lactating	Cycling	Cycling	Cycling
March-12	Cycling	Lactating	Cycling	Cycling	Cycling
April-12	Cycling	Lactating	Pregnant	Cycling	Cycling
may-12	Pregnant	Lactating	Pregnant	Pregnant	Cycling
June-12	Pregnant	Lactating	Pregnant	Pregnant	Cycling
July-12	Pregnant	Lactating	Pregnant	Pregnant	Cycling
August-12	Pregnant	Lactating	Pregnant	Pregnant	Cycling

Table 1: Data indicating the reproductive status of resident adult howler females. Raño, 2016 - unpublished data.

Social network analysis (SNA): SNA represents an analytical tool that provides a visual map and metrics of the strength and direction of social interactions and preferences between dyads, individuals that form subgroups, and all social group members (Cárdenas Ortega, 2019). We constructed an SNA using weighted, undirected proximity matrices based on interaction frequency, participant identity, and interaction direction (A + B) (Hanneman et al., 2005; Sueur et al., 2011). In addition, we constructed four interaction networks based on female reproductive status. To assess each adult male's and each adult female's positions within the social structure, we calculated two centrality metrics: degree centrality and eigenvector centrality. Degree centrality is a measure of the number and strength of an individual's dyadic interactions with other group members, reflecting the extent of its immediate social interactions within the network (Freeman, 1979; Sánchez-Arrieta et al., 2021). Eigenvector centrality is a measure of the extent to which an individual is connected to other well-connected individuals, thereby capturing not only dyadic interactions but also an individual's overall influence within the social structure (Bonacich, 1987; Sánchez-Arrieta et al., 2021). We then generated undirected social networks, whose graphical representations (network graphs) were obtained and visualized using the NetDraw module (Borgatti et al., 2002). In these networks, nodes represent individuals (shown as circles for females or triangles for males), and edges denote proximity interactions between two or more nodes. Line thickness denotes the number of interactions between individuals, defined as the direct count of how many times a pair of individuals was observed together engaging in one of four activities (tongue-flicking, grooming, copulation, and genital inspection). These behaviors were selected because they require close physical proximity and constitute core sociosexual and affiliative interactions that are directly relevant to mating dynamics, reproductive condition, and social bonding. Degree centrality was estimated as the sum of the weights of each individual's direct dyadic connections, where each connection represents a pairwise interaction and is weighted by the frequency of observed interactions between individuals. This represents the level of direct social interaction within the network. Eigenvector centrality was calculated as the eigenvector associated with the largest eigenvalue in the adjacency matrix, allowing us to identify

individuals connected to other well-connected group members and therefore occupying more influential positions within the network. Metrics obtained for each network were compared across individuals and across reproductive states. In addition, to test Hypothesis 1, we examined whether adult males differed in the frequency with which they directed sociosexual behaviors toward females in different reproductive states (cycling, pregnant, or lactating), using the same behavioral dataset used to construct the networks. Network metrics were interpreted descriptively, and no statistical tests of dyadic differences were performed due to the small number of individuals per group and the exploratory nature of the network analysis.

Statistical analysis

Behavioral data on howler monkey social interactions were collected using a scan-sampling method at 10-minute intervals (Raño, 2016). Although additional behavioral categories (e.g., feeding, resting, and locomotion) were recorded, the present analyses were restricted to four sociosexual behaviors (grooming, tongue-flicking, copulation, and genital inspection), as these require close physical proximity and are directly relevant to the study hypotheses. To test H1, we examined whether adult males differed in the frequency with which they directed sociosexual behaviors toward females in different reproductive states. Female–male association strength was calculated as the frequency of close-contact interactions between each adult female and adult males. To evaluate H2 and H3, we combined a network-based and statistical approach. Social network analyses were used to characterize patterns of association among individuals and to identify variation in female centrality across reproductive states. These descriptive metrics allowed us to assess whether males directed sociosexual behaviors disproportionately toward specific females independent of reproductive condition (H2), and whether female–female association patterns varied according to reproductive state and social position (H3). We then used Generalized Linear Mixed Models (GLMMs) to test whether female–male association strength (response variable) varied according to female reproductive state and male social position. Male social position was defined based on network centrality metrics rather than agonistic dominance rank, as overt male–male aggression is rare in this species. Adult males were classified as central or non-central based on degree and eigenvector centrality within each network. In periods with a single adult male, that individual was classified as central. Female identity nested within group was included as a random effect. Models were fitted using the *lmer* function in the lme4 package (Bates et al., 2015). Model fit was evaluated using likelihood ratio tests (LRTs) by comparing nested models (Bolker et al., 2009). Assumptions of normality and homoscedasticity were assessed graphically. All analyses were conducted in R (R Core Team, 2016), with statistical significance set at $\alpha = 0.05$.

Results

A single observer (MR) observed the two study groups for a total of 5,160 hours and recorded 2,598 interactions (993 in the Sena group and 1,605 in the Tacuaral group). On average, the activity budget of each adult and subadult howler included 4 ± 1.78% of grooming interactions (CV = 44.72%) and 2.67 ± 2.06% of sexual interactions (CV = 44.72%). Based on affiliative (grooming) and sociosexual interactions (tongue-flicking, copulation, and genital inspection), we constructed four weighted and undirected interaction networks. The total number of recorded interactions for each behavioral category differed between groups (Table 2), with grooming representing the most frequent interaction in both groups, particularly in Tacuaral.

Behavior	Sena (N)	Tacuaral (N)	Total (N)
Grooming	101	1582	1683
Tongue-flicking	0	40	40
Genital inspection	109	455	564
Copulation	33	98	131

Table 2: Total number of affiliative (grooming) and sociosexual (tongue-flicking, genital inspection, and copulation) interactions recorded in the Sena and Tacuaral groups.

Differences in the relative proportion of affiliative (social) and sociosexual interactions were observed across reproductive states and among females (Table 3). While the overall number of interactions did not vary markedly across reproductive conditions, the proportion of social versus sexual behaviors differed substantially among individuals and reproductive states.

	Violeta (Sena)		Ines (Sena)		Clara (Tacuaral)		Alma (Tacuaral)		Lori (Tacuaral)	
Reproductive status	**Social**	**Sexual**	**Social**	**Sexual**	**Social**	**Sexual**	**Social**	**Sexual**	**Social**	**Sexual**
Lactating	73,5%	26,5%	49,8%	50,2%	94,3%	5,7%	-	-	-	-
Pregnant	51,4%	48,6%	35,2%	64,8%	64,4%	35,6%	84,4%	15,6%	-	-
Cycling	31,2%	68,8%	-	-	77,9%	22,1%	72,8%	27,2%	50,6%	49,4%
Precycling	-	-	-	-	-	-	78,5%	21,5%	-	-

Table 3: Proportion (%) of affiliative (social) and sociosexual interactions for each adult female according to reproductive state. Values represent the percentage of total interactions classified as social (grooming) or sexual (tongue-flicking, genital inspection, and copulation). "-" indicates that no data were available for that individual in that reproductive state.

Sena Group - Reproductive State: Lactating.

During this period, Inés (Dec/11–Aug/12) and Violeta (Aug/11–Feb/12) were the only lactating females in the Sena group. Based on behavioral data, we constructed two types of interaction networks: an affiliative network based on grooming interactions and a sociosexual network based on tongue-flicking, genital inspection, and copulation.

The affiliative (grooming) network showed a density and clustering coefficient of 1, indicating that all individuals were directly connected through grooming interactions. The sociosexual network showed a similarly high level of connectivity, suggesting that sociosexual interactions were also widely distributed among group members.

Dyadic interaction strengths reflected the central role of the adult male Enzo, who exhibited the highest weighted degree (i.e., the sum of all interaction frequencies across partners) with a value of 1058. Both lactating females showed their strongest associations with Enzo (Inés: 707 interactions; Violeta: 579 interactions), whereas the

interaction strength between the two females was comparatively lower, consistent with the weaker connection observed in Figure 1.

The network centralization index was 46%, indicating that Inés occupied the most central position among females, followed by Violeta. No statistical tests were performed on these differences, and values are therefore interpreted descriptively based on network metrics, given the small sample size and the descriptive nature of the network approach.

The component ratio was 0, indicating that all individuals belonged to a single cohesive subgroup.

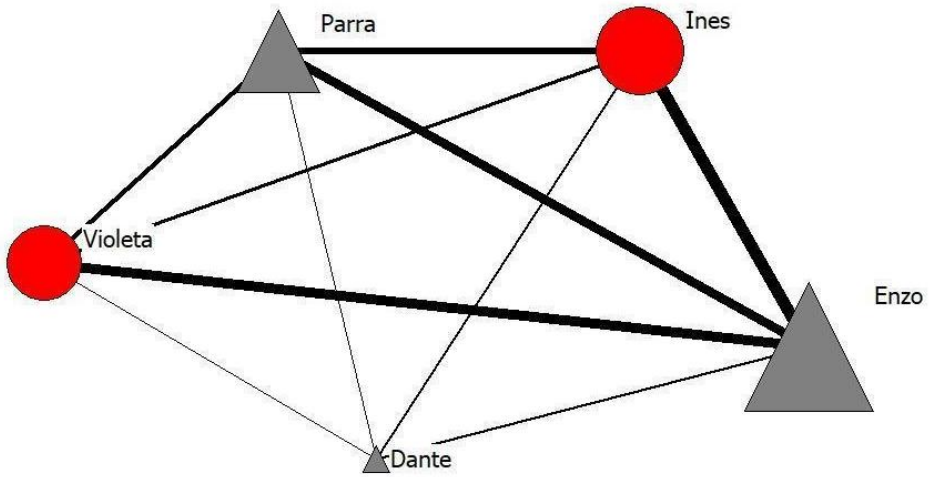


Fig 1: Spatial proximity of members of the Sena Group Reproductive State – Lactating: The triangles represent males, and the circles represent females; the thickness of the lines indicates the relative number of interactions between individuals. The thickness of the circles and triangles indicates the relative strength of each individual's connections, based on the total number of proximity interactions recorded. Statistically significant dyadic relationships are not shown because no statistical tests of dyadic association were performed. All individuals interacted with each other; however, the strongest relationships were Enzo-Inés, followed by Enzo-Violeta and Enzo-Parra (male-female relationships predominate).

Sena Group - Reproductive State: During the period from Aug/11 to Nov/11, Inés was pregnant, whereas Violeta was lactating. Based on all recorded close-contact behaviors (grooming, tongue-flicking, genital inspection, and copulation), we constructed a weighted interaction network including all adult members.

The network showed a density and clustering coefficient of 1, indicating that all individuals were directly connected, meaning that each dyad was observed interacting at least once during the sampling period. The network centralization index was 36%, indicating that interaction patterns were more strongly concentrated around Inés than around Violeta.

Variation in edge thickness reflected differences in the frequency of interactions between dyads, with thicker edges representing a higher number of observed interactions. These values represent weighted interaction frequencies and are interpreted descriptively rather than inferentially.

The component ratio was 0, indicating that all individuals were part of a single connected network. Consistent with the lactation period (Fig. 2), Inés occupied the most central position among females (degree = 420; eigenvector centrality = 0.511), suggesting that her social position remained stable across reproductive states.

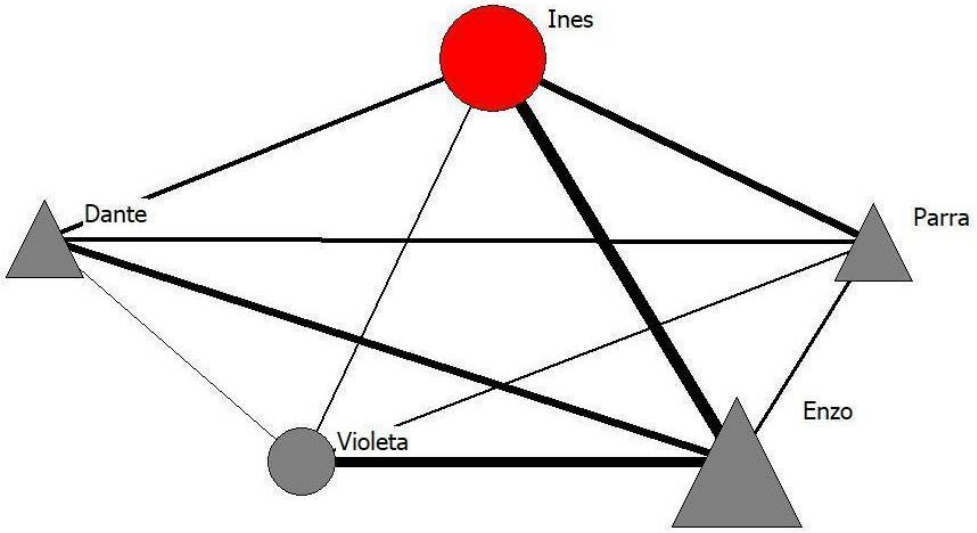


Fig. 2: Spatial proximity of members of the Sena Group Reproductive State - Pregnant: Triangles represent males and circles represent females. Line thickness indicates the relative frequency of <1.5 m proximity events. Node size reflects degree centrality. Node color indicates reproductive state (Inés = red; Violeta = gray). No statistically significant dyadic relationships were identified. All individuals interacted with each other; however, the main relationships were Enzo-Inés, followed by Enzo-Violeta and Inés-Parra, Dante-Enzo in equal proportion (male-female relationship preference).

Tacuaral Group Reproductive State: Cycling: This network represents the interaction patterns of the Tacuaral group during the months when the three adult females Alma (Jan/12–Apr/12), Lori (Aug/11–Aug/12), and Clara (Feb/12–Mar/12) were cycling. The network was constructed based on all recorded close-contact behaviors, including grooming, tongue-flicking, genital inspection, and copulation. The network had a density of 0.68, indicating that not all dyads were observed interacting during the sampling period, and a clustering coefficient of 1, suggesting that when interactions occurred, they tended to involve highly interconnected triads (Fig. 3). The network centralization index was 44%, indicating that interaction patterns were concentrated primarily around Lori (degree = 910; eigenvector centrality = 0.499), followed by Clara (degree = 794; eigenvector = 0.437) and Alma (degree = 789; eigenvector = 0.436). The component ratio was 0.20, indicating that although most individuals were part of a single connected network, some dyads showed weak or no interactions. This pattern was influenced by the limited participation of certain individuals, particularly Pacho, who died during the first days of sampling. This does not reflect the formation of distinct subgroups, but rather variation in interaction frequency among group members.

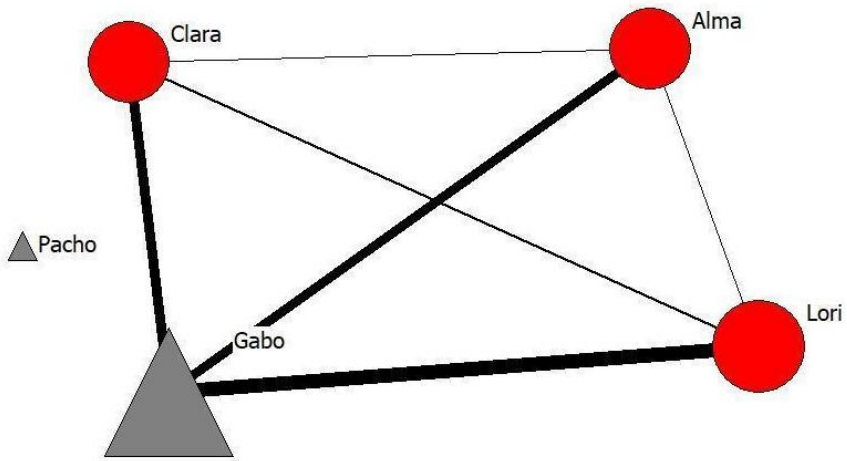


Fig. 3: Spatial proximity of members of the Tacuaral Group Reproductive State – Cycling: Triangles represent males and circles represent females. Line thickness indicates the relative frequency of proximity events <1.5 m, and node size reflects degree centrality. No statistically significant dyadic relationships were identified. All individuals were connected within the same component, although Pacho showed no proximity to any member of the group. The strongest proximity relationships were Gabo-Lori, Gabo-Alma, and Gabo-Clara.

Tacuaral Group Reproductive state: Pregnant: This network represents the interaction patterns of the Tacuaral group during the pregnancy period of adult females Alma (May/12–Aug/12) and Clara (Aug/11–Dec/11). The network was constructed based on all recorded close-contact behaviors, including grooming, tongue-flicking, genital inspection, and copulation. The network had a density and clustering coefficient of 1, indicating that all individuals were directly connected, meaning that each dyad was observed interacting at least once during the sampling period. Network centralization was 36%, indicating that interaction patterns were concentrated primarily around Clara, who showed the highest degree and eigenvector centrality among females (0.479). All individuals belonged to a single connected network (component ratio = 0), indicating that no structural subdivision of the group was detected during this reproductive period (Fig. 4). The strongest interaction patterns were observed between Gabo–Clara, followed by Gabo–Alma, suggesting that male–female interactions predominated during this period.

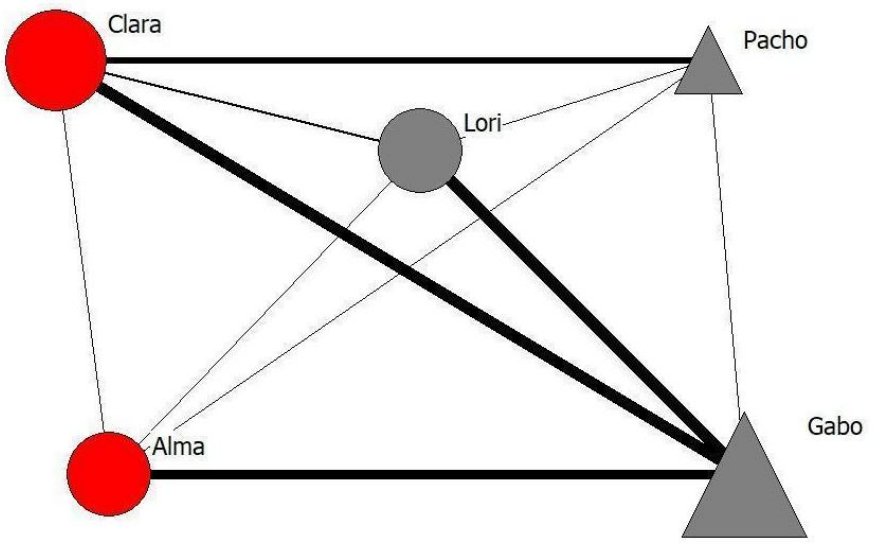


Fig. 4. Spatial proximity of members of the Tacuaral Group Reproductive State – Pregnant: Triangles represent males and circles represent females. Node color indicates reproductive state (red = pregnant female; grey = non-pregnant female). The thickness of the lines represents the relative number of proximity interactions (≤1.5 m) between dyads. All individuals interacted with each other; however, the strongest relationships were Gabo–Clara and Lori–Gabo, followed by Gabo–Alma (male–female relationships predominated).

Statistical Analyses of Female–Male Association Strength

Descriptive statistics indicated substantial individual variation across females from both groups (Table 2), but the GLMM analyses showed that neither predictor had a significant effect on association strength. Likelihood-ratio tests demonstrated that including male social position (central vs. non-central) did not improve model fit ($\chi^2 = 0.17$, $p = 0.678$), and female reproductive state was also non-significant ($\chi^2 = 3.68$, $p = 0.298$). Parameter estimates suggested lower association values during lactation, although these effects were not statistically significant ($|t| < 1.7$) (Fig. 5; Table 5). We selected the null model (no fixed effects) as the final model (Table 4). These results indicate that differences in female association strength were not explained by reproductive condition or by whether the male was central or non-central in the dominance hierarchy.

Table 4: Descriptive statistics for female association strength by reproductive state and male hierarchical rank.

Predictor	Mean	SD	N
Reproductive state			
Cycling	218.89	200.21	9
Lactating	140.83	120.66	12
Pregnant	194.50	107.48	8
Male social position			
Central male	171.58	116.74	12

Non-central male	158.29	149.40	28

Table 5: Fixed-effect estimates from the Generalized Linear Mixed Model testing the effect of female reproductive state and male social position (central vs. non-central) on the strength of association toward adult males. No fixed factors showed statistical significance.

Fixed effect	Estimate	SE	t-value	Significance
Intercept (Cycling)	236.49	64.6	3.66	----
Lactating (vs. Cycling)	–82.5	62.7	–1.32	n.s.
Pregnant (vs. Cycling)	–32.1	70.7	–0.45	n.s.
Male non-central (vs. central)	–19.5	50.3	–0.39	n.s.

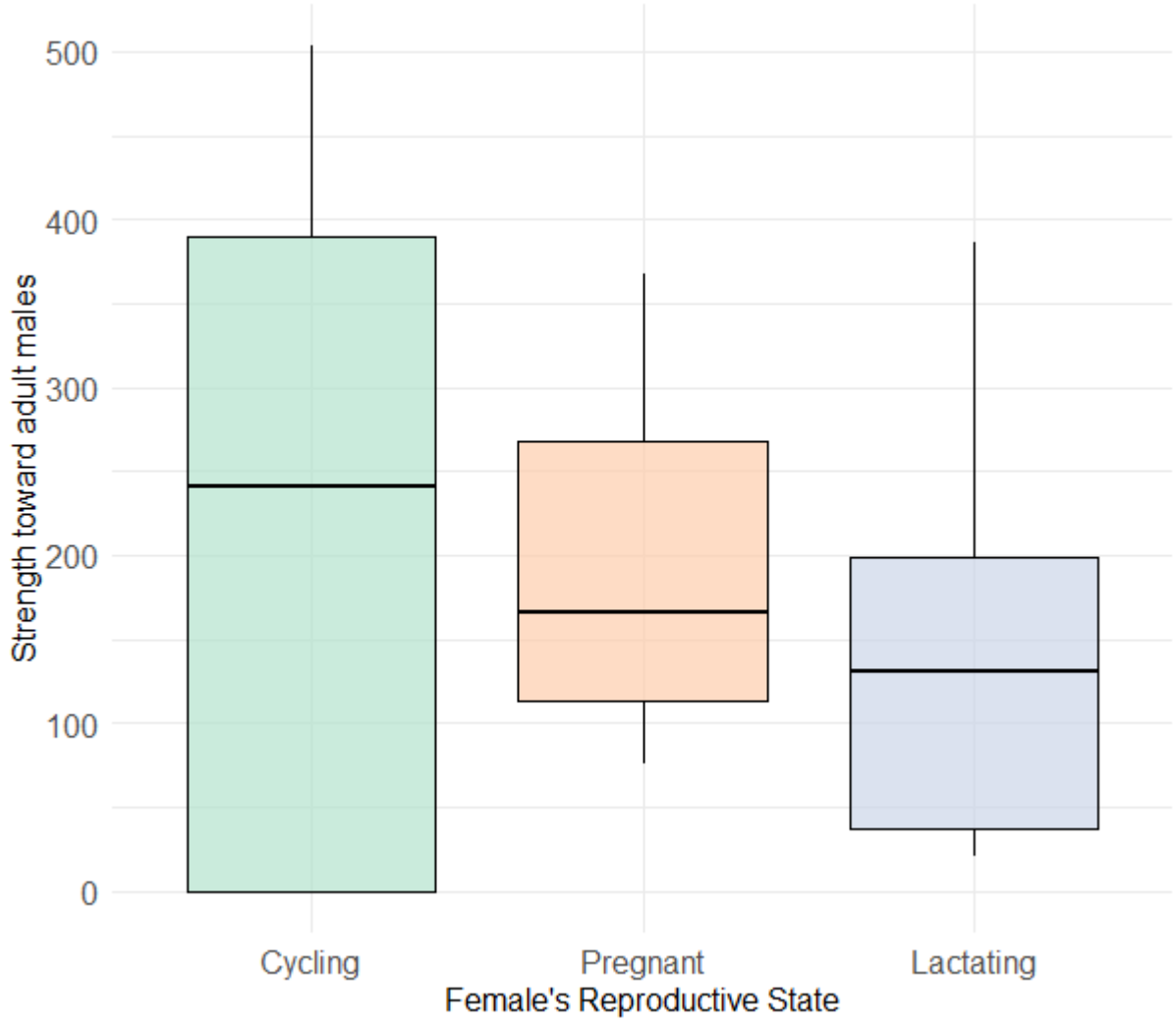


Fig. 5. Distribution of female association strength toward adult males according to their reproductive state. Although Cycling Females tended to show higher association strength, differences among states were not statistically supported.

Statistical Analyses of Female–Female Association Strength

Likelihood-ratio tests demonstrated that including female reproductive state significantly improved model fit compared to the null model ($\chi^2 = 6.64$, $p = 0.036$). The addition of social hierarchy (central vs. non-central) resulted in a marginal improvement in model fit ($\chi^2 = 3.08$, $p = 0.079$). Parameter estimates indicated that association strength was significantly lower during lactation, whereas no clear differences were detected for pregnant females. Non-central females also tended to show lower association values, although this effect was not statistically significant (Fig. 6).

We selected the model including reproductive state as the final model (Table 6). These results indicate that lactation had a significant negative effect on female–female association strength, whereas social position (central vs. non-central) did not have a statistically significant effect.

Table 6: Fixed-effect estimates from the Generalized Linear Mixed Model testing the effect of female reproductive state and female social position (central vs. non-central) on female–female association strength. Lactation had a significant negative effect, whereas other predictors were not statistically significant.

Fixed effect	Estimate	SE	t-value	Significance
Intercept (Cycling)	79.21	26.20	3.02	----
Lactating (vs. Cycling)	-67.90	25.55	-2.66	*
Pregnant (vs. Cycling)	-8.49	22.92	-0.37	n.s.
Female non-central (vs. central)	-44.53	28.07	-1.59	n.s.

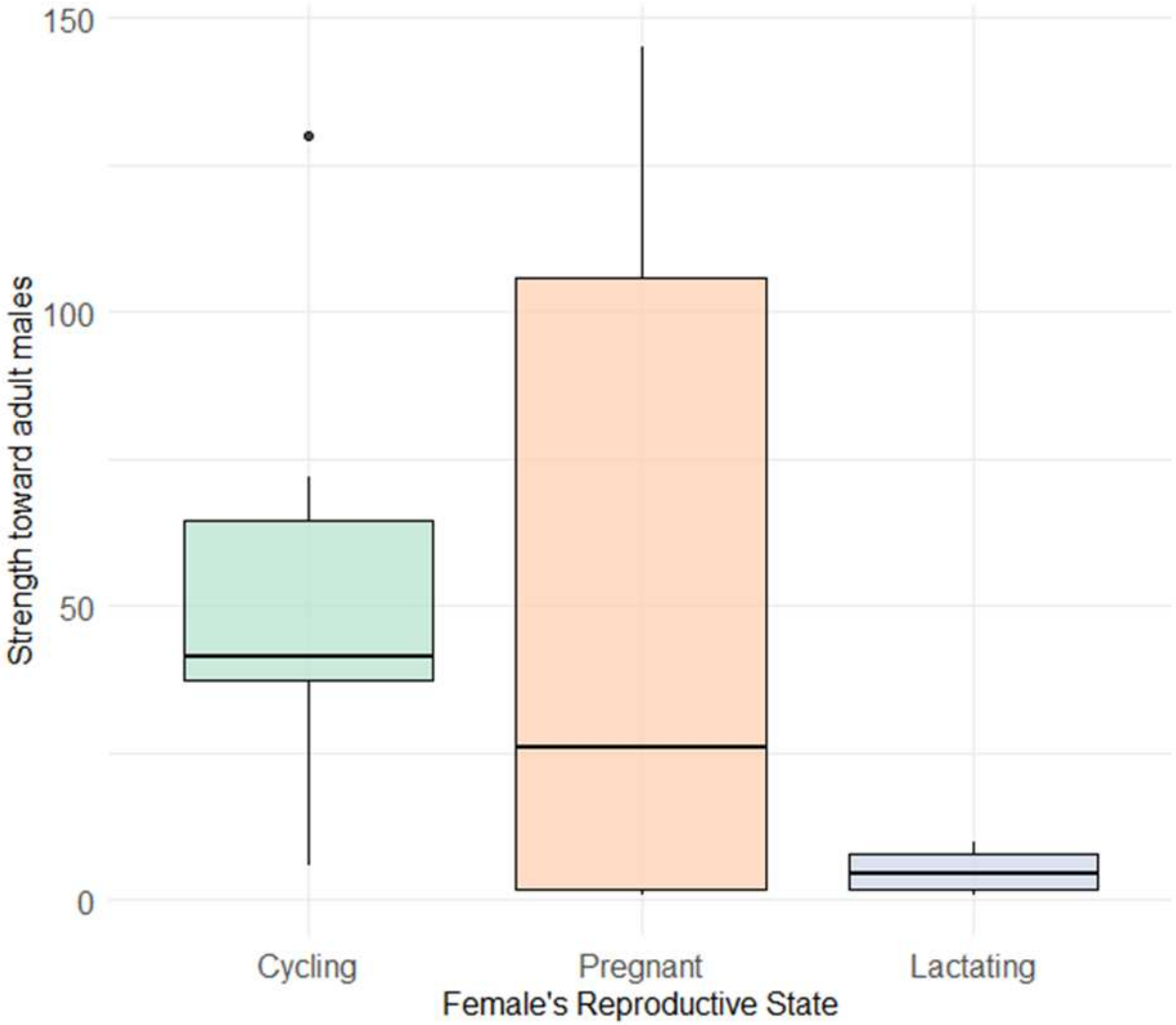


Fig. 6: Distribution of female association strength between adult females according to their reproductive state. Association strength was markedly lower in lactating females compared to cycling and pregnant individuals.

Discussion

Our results show that female social organization in *Alouatta caraya* is characterized by consistent differences in affiliative structure. Social network analyses revealed that one female in each group occupied a more central position across reproductive states, suggesting stable differences in patterns of social connectivity. In this study, centrality reflects the frequency and distribution of affiliative interactions, particularly grooming, rather than dominance expressed through overt aggression. These findings may indicate that some females maintain stronger and more frequent affiliative ties, potentially contributing to group cohesion (Silk, 2007; Koenig & Borries, 2012; Thompson, 2019; Beisner et al., 2026).

Regarding H1, we predicted that male sociosexual behavior would vary according to female reproductive status, with males directing higher rates of sociosexual interactions toward females in estrus. However, our statistical analyses did not support this prediction. Female reproductive status did not significantly influence the strength of the female-male

association, indicating that males did not preferentially direct sociosexual behaviors toward females in estrus over pregnant or lactating females. Although preferential male access to fertile females has been documented in several primate species, including some howler monkey populations, reproductive interactions in *Alouatta* appear to be more flexible. In *A. caraya*, females have been observed copulating with multiple resident and extragroup males, with no significant difference in the number of mating partners between potentially fertile and non-fertile periods (Kowalewski and Garber, 2010; Raño, 2016). Similarly, reviews of reproductive behavior in howler monkeys indicate substantial variation in the degree to which males monopolize or preferentially associate with fertile females, depending on social organization, male competition, and female mating strategies (Di Fiore et al., 2011; Van Belle & Bicca-Marques, 2015). Therefore, the absence of an effect of female reproductive status in our study may reflect the promiscuous mating system characteristic of *A. caraya*, in which female mating with multiple males may reduce the extent to which male sociosexual behavior is focused on females in estrus. The mating behavior of males may, therefore, be influenced by additional social factors, such as choice of female, male social status, the number and composition of resident males, or the opportunity to maintain mating relationships with females outside their fertile period.

For H2, we tested whether males consistently directed sociosexual behavior toward specific females independent of reproductive condition. Although descriptive patterns suggested that certain females were more frequently involved in interactions, these patterns were not supported statistically. The absence of significant effects indicates that males did not show strong or consistent preferences for particular females. This finding is consistent with previous genetic and behavioral evidence indicating that multiple males may sire offspring within the same group and that female promiscuity reduces the potential for reproductive monopolization (Kowalewski & Garber, 2010; Oklander et al., 2014). From a behavioral ecology perspective, our findings suggest that an individual's structural position within a social network does not necessarily determine patterns of sociosexual interactions. Although certain females consistently occupied more central positions within affiliative networks across reproductive states, this structural advantage was not associated with increased sociosexual interactions with resident males. These findings indicate that emergent social structure and mating behavior may be shaped by partially independent processes, suggesting that social cohesion and mate choice represent distinct dimensions of social organization. Future studies integrating social network analyses with genetic estimates of relatedness and reproductive success will be essential to determine whether network centrality provides indirect fitness benefits, such as enhanced social support, increased offspring survival, or long-term reproductive success, rather than influencing immediate sociosexual interactions.

For H3, we found that female–female association strength varied significantly with reproductive condition, with lactating females engaging in fewer affiliative interactions than cycling females. However, female social position (central vs. non-central) did not significantly explain variation in association strength. These results indicate that reproductive condition, rather than social position, is the primary factor structuring female–female interactions. The observed reduction in affiliative interactions during lactation is consistent with life-history constraints associated with infant care, as lactating females likely allocate more time to nursing and offspring protection, thereby limiting opportunities for social engagement (Silk et al., 2003; Karaskiewicz et al., 2021; Forero et al., 2024).

Together, these findings highlight an important distinction between structural and inferential approaches to social organization. While social network analyses captured consistent differences in female centrality and overall group cohesion, these structural patterns did not translate into statistically significant predictors of dyadic interaction strength

in the GLMMs. In small, cohesive primate groups such as those studied here, social structure may reflect multiple overlapping factors, including kinship, familiarity, and individual behavioral tendencies, that are not easily isolated in statistical models (Silk, 2007; Harrison, 2015). As a result, centrality may describe patterns of interaction without necessarily predicting them in an inferential sense (Farine & Whitehead, 2015). Contrary to expectations derived from the classical socioecological model, which predicts relatively egalitarian female relationships in folivorous primates (Sterck et al., 1997; Snaith & Chapman, 2007), our results indicate that some degree of social differentiation can emerge even in the absence of strong feeding competition or overt aggression. However, this differentiation appears subtle and is expressed through affiliative interactions rather than clear dominance hierarchies. Moreover, the lack of strong statistical effects suggests that these differences do not rigidly structure interaction patterns within groups.

Across all reproductive states, social networks were dense and cohesive, with most individuals belonging to a single connected component. This pattern indicates that group cohesion is maintained through widespread and flexible interactions rather than through stable subgroups or strongly differentiated roles. In this context, central females may function as hubs within an otherwise integrated network, facilitating connectivity without restricting access to social or reproductive partners.

The presence of consistently central females in our study also parallels patterns described in other socially complex mammals, in which particular individuals occupy disproportionate roles in maintaining group cohesion, information flow, or the coordination of social interactions. In African elephants (*Loxodonta africana*), for example, older females can function as important sources of ecological and social knowledge, influencing group coordination and responses to external threats (McComb et al., 2001, 2011). Similarly, post-reproductive female killer whales (*Orcinus orca*) can contribute to group decision-making and foraging success through their accumulated ecological knowledge (Foster et al., 2012; Brent et al., 2015). Among primates, social integration is also associated with important fitness-related benefits. Female baboons (*Papio cynocephalus*), for example, form stronger affiliative relationships with close kin, and females with stronger social bonds exhibit higher infant survival, suggesting that social integration may provide direct or indirect fitness benefits (Silk, Altmann & Alberts, 2006; Silk et al., 2009). However, the central females identified in our study should not necessarily be interpreted as leaders or as functionally equivalent to the older females described in elephants or killer whales. Rather, their consistently high centrality indicates that they occupy structurally prominent positions within the affiliative network. Whether these positions reflect kinship, age, social experience, individual social preferences, or accumulated social knowledge remains unknown. Importantly, their centrality was not associated with increased sociosexual interactions with males, suggesting that social importance within the affiliative network does not necessarily translate into greater access to reproductive opportunities. Thus, female centrality in *A. caraya* may represent a dimension of social organization that is more closely related to cohesion and social integration than to mating behavior.

In conclusion, our findings demonstrate that female *Alouatta caraya* exhibit consistent differences in affiliative network position, with certain individuals occupying more central roles across reproductive states. However, these structural differences did not translate into statistically detectable effects on male–female interaction patterns, indicating a decoupling between emergent social structure and dyadic-level predictors. This suggests that social organization in small, cohesive primate groups may be better understood as an emergent property of repeated affiliative interactions rather than as a direct outcome of individual attributes or short-term reproductive states. At the same time,

the significant reduction in female–female association strength during lactation highlights the role of life-history constraints in shaping patterns of social interaction. Together, these findings underscore the importance of integrating network-based and inferential approaches to better understand the complexity of primate social systems. Although our analyses were based on two well-habituated groups monitored intensively over an annual cycle, the relatively small number of groups limits the generality of our conclusions. Replication across additional populations will be important to determine whether these patterns are consistent throughout the species.

Authors' contributions: DRG analyzed the data and drafted the manuscript. MR collected the behavioral data. RBJ and SCO contributed to the social network and statistical analyses. MR, RBJ, and SCO contributed to the drafting and revision of the manuscript. MR and MMK coordinated the supervision and preparation of the final version of the manuscript.

All authors read and approved the final manuscript.

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