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Whole group tracking reveals that relatedness drives consistent subgrouping patterns in white-nosed coatis



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Keywords: biologging cohesion collective movement fission-fusion relatedness social behaviour subgrouping white-nosed coati The formation of subgroups can allow group-living animals flexibility to balance the costs and benefits of sociality over time. Subgrouping dynamics emerge from individual decisions about whether and with whom to maintain cohesion, with these decisions potentially influenced by ecological, physiological and social factors. We GPS-tracked the movements of nearly all members of three wild white-nosed coati, *Nasua narica*, social groups that differed in their demographic profiles to better understand how these highly social, frugivorous carnivores weight the relative importance of these different factors in their grouping decisions. Quantifying group movements and subgrouping patterns, we found that two of the three groups we tracked exhibited fission—fusion behaviours, with groups splitting into subgroups that persisted over varying time spans from minutes to days. In contrast, the third group remained together across the entire observation period. When groups split, they did not do so randomly; instead, in-dividuals tended to form subgroups with the same individuals consistently over time. Assessing the drivers of subgrouping patterns revealed that subgroup membership was associated with genetic relatedness, but not physiological similarity as quantified by age and sex homophily. Our results demonstrate great variation in subgrouping patterns within a single species, while also highlighting a consistent role of relatedness in driving social preferences when subgroups form.

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Social animals are strongly influenced by their neighbours; thus, the size, structure and demography of their groups are important drivers of individual behaviour and fitness (Krause et al., 2002). When groups forage together, individuals must balance resource competition, which can drive individuals apart, with predation avoidance, which generally brings animals together (Hirsch, 2007). To balance the costs and benefits of grouping, some animals flexibly adjust their patterns of spatial association, breaking into smaller subgroups or fusing into larger aggregations in response to local conditions. The spatiotemporal scale and social boundaries of these

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fission—fusion dynamics vary substantially among species, from bird flocks and fish schools where individuals join and leave frequently and freely to the more constrained splitting and merging within defined social communities seen in chimpanzees, *Pan troglodytes*, vulturine guineafowl, *Acryllium vulturinum*, and spotted hyaenas, *Crocuta crocuta* (Holekamp et al., 1997; Kelley et al., 2011; Mcfarland Symington, 1990; Papageorgiou et al., 2019; Silk et al., 2014). Because fission—fusion dynamics emerge from sets of individual decisions about the relative costs and benefits of association, they provide insight into the social and environmental conditions that favour the formation, maintenance and, ultimately, the evolution of animal societies.

Ecological, social, and physiological factors are all known to influence the formation and composition of subgroups in species that show fission–fusion dynamics (Aguilar-Melo et al., 2020;

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Aureli et al., 2008; Grueter et al., 2023). While ecological factors typically drive overall subgrouping tendencies (Aureli et al., 2008; Sueur et al., 2011; van Schaik & Brockman, 2009), the composition of the resulting subgroups is often influenced by the characteristics and relationships among group members (Sueur et al., 2011). Social factors, such as the strength of social bonds, position in a dominance hierarchy and kinship, can shape subgroup composition. with group splits allowing individuals to avoid group members from whom they receive aggression, while remaining with those who tolerate them or from whom they receive benefits (Carter et al., 2013; Silk et al., 2014; Sueur et al., 2011). Variation in physiological traits, such as differences in age, sex and reproductive status, can influence subgroup membership when individuals have different needs or physical constraints that cause them to split apart (Conradt & Roper, 2000; Hartwell et al., 2014; Krause et al., 2002; Matthews et al., 2021). In such cases the resulting subgroups are expected to be composed of individuals with similar physiological traits (Clutton-Brock et al., 1977; Ruckstuhl, 1998). While both social and physiological factors can be important for driving subgrouping patterns, these factors may act in opposition. When kinship drives association, differences between related individuals in age or sex may lead to the emergence of substantial physiological heterogeneity within subgroups (Archie et al., 2006; Konrad et al., 2018; Wittemyer et al., 2009). Conversely, individuals with similar preferences and constraints may not be related (Metheny et al., 2008). Patterns of fission-fusion behaviour can thus shed light on the main drivers of social cohesion in a species.

Fission-fusion dynamics can provide insights into the costs and benefits of grouping and the evolution of social behaviour (Aureli et al., 2008; Holekamp et al., 2007). However, quantifying how groups split and merge to understand the decision-making processes that drive these patterns presents a methodological challenge. It is infeasible for human observers to simultaneously record the location and behaviour of all members of social groups, especially when they have split into multiple subgroups. Field studies that employ direct observation typically locate or track one subgroup at a time, leaving the movement patterns of other group members unrecorded (Grueter et al., 2023; Hartwell et al., 2021). Given that the frequency of fission-fusion events and the composition of subgroups may vary across the landscape, traditional methods may lead to biases in which subgroups and events are observed. Tracking technologies such as GPS tags offer the potential to monitor the movements of multiple individuals simultaneously (Della Libera et al., 2023; Kays et al., 2015; Strandburg-Peshkin et al., 2015). This approach can give us greater insights into the decision-making processes of group members by allowing us to determine which subgroups individuals choose to join as well as those they reject.

White-nosed coatis, Nasua narica, live in heterogeneous social groups where group membership is relatively stable; however, these groups can break up into smaller foraging parties during the day (Gilbert, 1973; Gompper, 1997; Kaufmann, 1962; Romero & Aureli, 2007). They are generalist, opportunistic foragers that predominantly feed on fruit and leaf litter invertebrates (Gompper, 1994; Hirsch, 2009; Valenzuela, 1998). In response to reduced fruit availability coatis forage in smaller subgroups (Gompper, 1996, 1997). Their social and ecological flexibilities enable them to thrive across a broad spectrum of forested habitats spanning Central, South and North America (Frey et al., 2013; Nigenda-Morales et al., 2019; Valenzuela & Ceballos, 2000). Groups range in size from four to over 30 individuals and typically consist of multiple adult females and their dependent offspring (Gompper, 1996; Hirsch & Gompper, 2018; Kaufmann, 1962). These groups are primarily composed of highly related individuals; however, they may contain unrelated females which often receive a disproportionate amount of aggression from other group members (Gompper et al., 1997). Group composition changes seasonally (Kaufmann, 1962). Adult males are predominantly solitary, except during the breeding season when they temporarily join female groups (but see Gompper & Krinsley, 1992). Adult females, which form the core of the group for most of the year, leave a few days before giving birth and only return to the group 1–2 months later with their new offspring (Hirsch & Gompper, 2018). Predation risk can play an important role in the spatial structure of coati groups, with juveniles, which are at the highest risk of predation due to their smaller body size, positioning themselves close to one another (Hirsch & Gompper, 2018; Russell, 1979). Despite our understanding of the spatial structure of coati social groups, little is known about how groups dynamically change composition.

Here, we used simultaneous tracking of entire groups to quantify coati fission—fusion dynamics, including the frequency of splits and merges, the temporal aspects of splits, the distribution of subgroup sizes and the patterns of subgroup membership. Using data from three groups with different demographic and relatedness structures, we tested whether individuals show consistent subgrouping patterns across time, and the extent to which group splits are driven by social versus physiological factors. If social bond strength drives subgrouping patterns, we predicted that group fissions will take place along kinship lines (Gompper et al., 1997). If physiological factors drive fission—fusion dynamics, we expected subgroups to divide according to age/sex class (Harel et al., 2021).

METHODS

Study Site and Data Collection

Fieldwork was conducted in Soberania National Park (SNP; 9°12'N, -79°70'W) and on Barro Colorado Island (BCI; 9°16'N, -79°83'W), Panama. Both study sites consist of semideciduous lowland tropical forest. Although the sites are only 5 km apart, they have been isolated from one another since 1914 when the Chagres River was dammed to create Lake Gatun and the Panama Canal. We equipped three groups of wild white-nosed coatis with custom-built collars that recorded group members' positions using GPS sensors (e-Obs Digital Telemetry, Gruenwald, Germany, https://e-obs.de/). Coatis were caught using Tomahawk traps and chemically immobilized using Telazol (50 mg/ml tiletamine and 50 mg/ml zolazepam; 5.4 ± 0.5 mg/kg). The breeding season typically occurs during the early dry season in Panama (January to February), but the start of the breeding season varied between the study sites. The first group (Galaxy) was tracked during the breeding season which is when adult males temporarily join groups; therefore, we also collared the adult male associating with the group during this time. All members except one adult female were tracked in this group (10/ 11 or 92% of group members). The second group (Trago) was collared when the adult females had left the group to give birth solitarily; therefore, the group was composed of mostly juveniles. The third group (Presidente) was collared before the breeding season, when the group was composed of adult females, subadults and juveniles (see Table 1 for details on group composition and tracking times). Owing to the high battery consumption of the collars, collar deployments lasted between 15 and 21 days.

GPS data were recorded at a rate of one fix per s from 0600 to 0900 each day. From 0900 to 1800, a burst of six GPS points was recorded every 10 min. During the night (1800–0600) a burst of six GPS points was recorded every hour. The mean GPS fix success rate was 96.5%, 96.1% and 96.9% for the Galaxy, Trago and Presidente groups, respectively. The average relative GPS error (measured under dense canopy typical of the coatis' habitat as the relative error between two collars at known distances apart) was

Table 1
Tracking periods and age/sex class compositions for the three coati study groups

Group	Tracking period	Location	Adult		Subad	Subadult		ile	Group collared/group size
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Galaxy	24 Dec 2021–13 Jan 2022	SNP	7	1	1	2	1	0	10/11
Trago	24 Mar 2022–10 Apr 2022	SNP	0	0	0	1	5	1	7/7
Presidente	19 Jan 2023–02 Feb 2023	BCI	3	0	5	2	2	4	16/16

Study groups were collared in Soberania National Park (SNP) and on Barro Colorado Island (BCI), Panama. Adult males are generally solitary and therefore were excluded from the group collared and group size values.

 3.86 ± 1.06 m. For collar recovery, automated drop-off devices (Micro-TRD, Lotek, www.lotek.com) were incorporated into the collars, and programmed to activate on day 18 of collar deployment. A technical problem meant that all drop-offs from the first group (Galaxy) failed to activate. For the two subsequent groups, this issue was resolved, resulting in 78% and 100% drop-off success rates for the Trago and Presidente groups, respectively. For cases where drop-offs failed, coatis were recaptured, and all collars were successfully removed within 4 weeks of the drop-off activation date.

SNP Genotyping and Relatedness Estimates

We used SNP genotyping of tissue samples collected during captures to calculate relatedness between members of the coati groups. While collaring individuals, we collected tissue samples from all study individuals and stored them in 95% ethanol for genetic analysis. We submitted the tissue samples to the University of Minnesota Genomics Center (UMGC) for genotyping-by sequencing (GBS). High-quality genomic DNA was extracted from samples using a QIAGEN DNeasy Blood and Tissue Kit (QIAGEN, Hilden, Germany) following manufacturer's protocols, and a double digest restriction-site associated DNA method (ddRAD) was followed, using the BamHI and Nsil restriction enzymes for digestion. Illumina primers and individual barcodes were ligated to DNA fragments and amplified using PCR. Sequencing was performed using the Illumina NextSeq 2000 platform with a 100-cycle run configuration, resulting in approximately 6.5 million reads per sample.

We used FastQC v0.11.9 software (Andrews, 2010) to assess and analyse the quality of the raw sequence reads. We trimmed adapter and padding sequences using a custom UMGC perl script gbstrim.pl (Garbe, 2023), and aligned to a white-nosed coati reference genome using the Burrows–Wheeler Aligner tool in BWA v0.7.17 (Li & Durbin, 2009). The aligned sequence files were sorted and indexed using SAMtools v1.6 (Li et al., 2009), and variants across all samples were called using FreeBayes v1.2.0 (Garrison & Marth, 2012) with the parameters: –use-best-n-alleles 4 –min-coverage 102 –limit-coverage 500. We removed low-quality variants using the vcffilter tool in vcflib v1.0.1 (Garrison et al., 2022), specifying the option: -f QUAL >20. We removed any samples containing more than 50% missing genotypes, and any variants with genotype calls in less than 95% of samples, as well as variants with a minor allele frequency of less than 1%.

We converted the filtered variant file containing 37 samples and 10 972 single nucleotide polymorphisms (SNPs) into a compatible file for input into COANCESTRY v.1.0.1.10 (Wang, 2011) using the dartR v2.9.7 package (Mijangos et al., 2022) in R (R Core Team, 2017). Although a variety of relatedness estimators exist for analysing SNP data, we implemented the triadic maximum likelihood estimator (TrioML; Wang, 2007) to calculate relatedness coefficients among each unique coati pair. We made this decision as each of the seven estimators available in COANCESTRY software were highly correlated for the coati data set (r > 0.93 for each comparison between relatedness estimators), and hence the

TrioML estimator was selected as the most suitable option as it is also considered robust to inbreeding, small sampling sizes and genotyping error (Hauser et al., 2022; Wang, 2007).

Ethical Note

Methods followed the ethical guidelines set by the American Society of Mammologists and were performed in accordance with the Institutional Animal Care and Use Committees guidelines (Smithsonian ACUC clearance number: 2017-0815-2020). Biological samples were exported under permit number: PA-01-ARG-160-2022. Following a three Rs approach, we refined our capture and collaring methodology to minimize stress and risk of injury to study animals (Russell & Burch, 1959). To reduce stress during the capture, traps were checked at least three times per day. All animal handling procedures were carried out by trained personnel with expertise in animal handling. Coatis were processed separately to minimize distress. We covered their eves to reduce their stress and we continuously monitored their heart rate and temperature to ensure their safety. If there were open wounds, we applied antiseptic cream. When each animal was anaesthetized, we attached the collars around their neck (<5% body weight); these collars were custom built to minimize discomfort. Small tissue samples were obtained from the coatis' ears, as a by-product of the ear-tagging process (34 samples; 1–2 mm² in size). After processing, we returned each animal to its cage to allow it to fully recover from the anaesthetic in the shade before being released. Members of each group were released at the same time to minimize the distress of losing one another. Once the coatis were released, we monitored their movements and found all coatis recovered from the anaesthetic safely. It took on average 1 day for collared animals to return to their normal movement behaviours. Although we could not reduce the number of study animals, we reduced the collar duration. The collars had an inbuilt drop-off device to avoid recapture; however, in cases where drop-off devices failed, we conducted the same capture protocol that we did for the collar fitting. We observed no signs of injury from the collars and all animals recovered quickly and safely.

Analyses

GPS data processing

We used RStudio (R Core Team, 2017) for all analyses. To examine the overall dynamics of subgrouping, we downsampled the 1 Hz GPS data (recorded from 0600 to 0900) to one GPS point every 10 min, which resulted in a consistent sampling interval of 1 fix every 10 min across the entire active period (0600–1800). One of the Galaxy group members (Venus) remained stationary in a tree for 3 days after collaring before rejoining the group, which may have been a response to the capture. These data points were removed from the analysis. Two group members from Presidente group (Peron and Moscoso) wore collars that fell off before the scheduled drop-off date, and these individuals were refitted with

new collars. The data recorded from the fallen collars were removed from the analysis, and this resulted in a gap of 101 h for Peron and a gap of 5 h for Moscoso.

Identifying subgroups

We defined subgroup membership at each time step using density-based spatial clustering (DBSCAN: Ester et al., 1996). This algorithm is similar to the 'chain rule' employed in previous observational field studies to quantify group membership (Whitehead, 2008), where a group is defined as a set of individuals who are within a distance ε of the nearest group member. We set the noise parameter of the DBSCAN algorithm to 1, meaning that groups of all sizes were identified. We ran the DBSCAN analysis at a range of spatial scales and the results remained gualitatively similar but with more groups identified for shorter values of ε as expected (see Fig. A1 for results at different ε -neighbourhood distances). Previous studies have found that the group spread of coatis is typically <30 m (Hirsch, 2011a). Based on our assessment that coatis, with their poor vision and quiet contact calls, are unlikely to be able to communicate or coordinate group activities at distances greater than 50 m in this dense tropical forest habitat, we used this threshold as a conservative *e*-neighbourhood distance for all analyses presented here. To check for robustness, we also repeated all our analyses with ε values of 30 m and 70 m and found qualitatively similar results (Figs A2–A7).

For every 10 min time step, we recorded the number and identities of individuals in each subgroup. Note that a subgroup by this definition may contain a single individual (if it is not within ε distance of any other group member). One potential downside of this clustering method is that it can result in a likely-spurious 'group merge' if two subgroups are between ε and $2x \varepsilon$ distance from one another and one individual moves between the two subgroups, momentarily joining them together. However, in our downsampled data, we did not observe any instances of this edge case.

Characterizing subgrouping patterns

To determine the proportion of time groups were split into subgroups, we calculated the frequency distribution of the number of subgroups across the entire collaring period for each study group. To determine how subgroups were divided, we filtered these data to periods when the group was split into two and three subgroups, which accounted for 96.5% and 99.4% of splitting events in the Galaxy group and Presidente group, respectively. We then calculated the frequency distribution of the number of members in each subgroup.

We defined group splits as instances in which a group, at time t, split into two or more subgroups in the next time step t + 1 (10 min later; Fig. 1). We excluded instances where a single individual (often the adult male) left or entered the group, as our goal was to investigate the social correlates of subgroup membership (see Fig. A8 for the percentage of time each group member was not in a group). For cases when individuals had missing data (due to poor satellite connection) before or after a split event, their data for that event were excluded from analyses (i.e. that individual was not considered part of any groups; see Fig. A9 for details on missing data). We calculated the duration of splits as the time between the last split event to the next merge event, excluding single individuals. This was because there was the possibility of further splits occurring in a group that had previously split off from the full group.

Quantifying consistency of subgroup membership

To quantify subgrouping preferences, we first calculated the overall proportion of time each dyad was in the same subgroup for all days tracked. To account for missing data, we only incorporated times when both individuals' locations were known into this calculation.

To determine whether subgrouping patterns were driven by one long fission event or from repeatedly splitting with the same individuals over time, we assessed whether subgroup membership across repeated group splits showed consistent patterns, that is, whether certain pairs of individuals tended to be in the same subgroup at a rate greater than that expected by chance. Across all group splits (see above definition), we first computed the probability, p_{ij} , that each pair of individuals *i* and *j* split into the same subgroup, given that both were present in the original group before the split occurred. We then defined the consistency of the subgrouping patterns across the entire group as

$$C = 1 - \frac{2}{n_{ij}} \sum_{i,j} f\left(p_{ij}\right)$$

where n_{ij} is the total number of dyads and $f(p_{ij})$ is a function whose value equals p_{ij} if $p_{ij} < 0.5$ and $1 - p_{ij}$ otherwise. The value of *C* ranges from 0 to 1, with the theoretical minimum of 0 occurring if all dyads have a probability of 50% of joining the same subgroup, and the theoretical maximum of 1 occurring if each dyad is either always ($p_{ij} = 0$) or never ($p_{ij} = 1$) in the same subgroup.

After computing the consistency *C* for the real data from each study group, we compared these values to permuted data assuming that individuals joined subgroups at random during each group split. To construct this null model, we maintained the same number of real splits as occurred in the data as well as the same subgroup sizes and individuals involved in each split, but randomly allocated individuals to the different subgroups for each split. We repeated this procedure 1000 times, computing the value of *C* for each artificially randomized data set and generated a distribution of these expected *C* values under the assumption of random subgroup assignment. Finally, we compared this null distribution to the value of *C* observed in the real data to determine how likely the real or a greater level of consistency would be to occur based on the random null model (i.e. to compute a *P* value).

Quantifying the role of social and physiological factors with subgroup membership

We used a multiple regression quadratic assignment procedure (MRQAP) with the double semipartialling (DSP) method to determine whether age homophily (i.e. individuals of the same age), sex homophily or relatedness were associated with subgroup membership (Dekker et al., 2007). The dependent matrix was the proportion of time each dyad was in the same subgroup when the group had split and the independent matrices were age-based homophily, sex-based homophily and genetic relatedness. When dyads in the homophily matrices were the same, they were given a value of 1, while dissimilar dyads were given a value of 0. All networks were undirected.

RESULTS

The three study groups differed in their fission—fusion dynamics: the Galaxy and Presidente groups often split into multiple subgroups, whereas the Trago group remained cohesive and did not exhibit fission—fusion dynamics (Fig. A10). The Trago group was therefore excluded from further analyses of subgrouping dynamics. The frequency of fission events and the duration of time that groups remained split into subgroups differed between the two remaining groups. Over the tracking period, the Galaxy group split 29 times whereas the Presidente group split 43 times, with median split durations of 10.5 h (interquartile range 2.7–15.3) and 2 h



-79.704

(e)

•

-79.702





0600 0900 1200 1500 Figure 1. Whole group tracking and quantifying fission-fusion dynamics. (a) Example of movement trajectories of coati group members on 1 day (0900-1800). Data are shown

from the Galaxy group on 28 December 2021, excluding the single adult male. Points are coloured by the resultant subgroup, and arrows denote the direction of travel. (b, c) Illustration of how subgroups and group splits were defined from GPS data. (b) An initial moment in time (t) when the full group was together and (c) a moment 10 min later (t + 1)when the group had split into two subgroups. Outlined white circles represent the 50 m e-neighbourhood for each group member; overlapping groups of circles are considered distinct subgroups. (d) Photo of an adult female coati wearing a tracking collar and ear tags used for identification. (e) Visualization of subgrouping patterns of a coati group over a 9 h period. Coloured points represent individuals, and outlined groups of points represent subgroups identified at each moment in time.

(interquartile range 1.3-4.3), respectively. We found no consistent pattern in the time of day when fissions occurred for either group (Fig. A11). The two groups also varied in the size of subgroups formed during fission events. The Galaxy group was either cohesive or split into either two or three subgroups, with the most common number of subgroups being two (Fig. 2a). When there were two subgroups, the group split either evenly or the majority of the group was together and one individual was alone (Fig. 2b). A similar pattern was observed when there were three subgroups, which typically occurred when one individual was alone and the rest of the group was evenly split (Fig. 2c). The Presidente group exhibited similar subgrouping patterns (Fig. 2d), but subgroup sizes were often unevenly divided into a larger group of about 12 individuals and a smaller group of about four individuals (Fig. 2e). When divided into three groups, subgroups of a range of sizes were observed (Fig. 2f).



Figure 2. Number of subgroups and subgroup sizes across two coati groups. (a, d) Probability of observing different numbers of subgroups at any moment in time for two different coati groups. (b-f) Histograms of the number of individuals in each subgroup when the group was split into (b, e) two or (c, f) three subgroups. (a-c) Data from the Galaxy group. (d-f) Data from the Presidente group. The Trago group remained together throughout the tracking period (i.e. one subgroup), so their data are not shown here.

Coatis showed high consistency in subgroup membership across splitting events (P < 0.001 for both groups based on permutation tests; Fig. A12). When not together, both groups were most often split into two specific subgroups (Fig. 3a, c, yellow blocks). In the Galaxy group, one of the subgroups was composed of four adult females and one juvenile, while the other subgroup consisted of all three subadults and two adult females. The single adult male was more often alone compared to group members. When he was with one of the subgroups, however, he tended to associate with the adult females. The Presidente group tended to split unevenly, with the smaller subgroup composed of two subadults and one adult female and the larger subgroup composed of eight juveniles, three subadults and two adult females.

In both study groups, relatedness was a significant predictor of subgroup membership (Table 2, Fig. 3b, d, Fig. A13). In contrast, age and sex homophily showed no significant effect on subgroup membership in either group.

DISCUSSION

Whole group GPS tracking revealed substantial variation in the extent and nature of fission—fusion dynamics of coatis, while also demonstrating common drivers of subgroup membership. In alignment with findings from captive populations (Romero & Aureli, 2007), we found that coatis repeatedly formed subgroups with the same set of individuals and that these subgroups tended to consist of related individuals rather than individuals of the same age or sex. Genetic relatedness has been shown to influence patterns of association in a variety of species that show fission—fusion dynamics, including spotted hyaenas (Holekamp et al., 1997; 2012; Van Horn et al., 2004), African elephants, *Loxodonta africana* (Archie et al., 2006), and Bornean orang-utans, *Pongo pygmaeus wurmbii* (van Noordwijk et al., 2012). A common feature across many of these animal societies is the integration of individuals with

varying levels of relatedness (e.g. multiple matrilines) into the same social group or community, as well as the maintenance of longterm, differentiated social relationships among group members that are often correlated with relatedness (Archie et al., 2006; Carter et al., 2013; Sueur et al., 2010). Within such complex social landscapes, consistent subgrouping patterns may result from a preference to maintain cohesion with specific group members that provide social benefits, by avoiding individuals that are costly to be near, or a combination of both mechanisms (Romero & Aureli, 2007, 2008). In coatis, individuals tend to have stronger affiliative relationships with their close relatives, which is often exhibited by grooming and coalitionary support during aggressive encounters (Hirsch et al., 2012). Such close relationships have been shown to provide major fitness benefits in other species (Silk, 2007); hence, maintaining cohesion with related individuals is likely to come with fitness benefits in coatis. On the other hand, forming subgroups with related individuals might be a strategy to avoid unrelated group members. Previous studies have shown that coatis not related to other group members receive far more aggression (Gompper et al., 1997). Distancing themselves from unrelated individuals could be an adaptive strategy for individuals to minimize their risk of receiving aggression during foraging. Further work investigating the behavioural context and social interactions that occur before, during and after group splits could help differentiate between these possible underlying mechanisms.

Our results do not support physiological drivers as being the primary determinant of subgrouping patterns in coatis. These results contrast with patterns seen in several other fission—fusion species, where physiological differences play a role in subgrouping patterns (Bond et al., 2019; Galezo et al., 2018; Hunt et al., 2019; Surbeck et al., 2017). In spider monkeys, *Ateles geoffroyi*, social, ecological and physiological factors influence their fission—fusion dynamics (Aguilar-Melo et al., 2018; Hartwell et al., 2021), and previous studies have found that group members often split with



Figure 3. Subgroups observed in the coati groups that exhibited fission—fusion dynamics. (a, c) Association matrices representing the proportion of time each dyad was in the same subgroup across the full data set for the (a) Galaxy and (c) Presidente groups. Rows and columns of each matrix represent individuals, with coloured points representing the age/sex class of each individual. Coloured squares in each matrix indicate the proportion of time each dyad was found in the same subgroup, across all times when both individuals in the dyad were tracked. (b, d) Relatedness matrices for the (b) Galaxy and (d) Presidente groups, using the triadic maximum likelihood method. This estimator has coefficients of relatedness ranging from 0 to 1 (full siblings and offspring are approximately 0.5, half siblings are 0.25, and aunts and uncles are 0.125).

individuals of similar nutritional requirements, which correlates with sex homophily (Hartwell et al., 2014; Rodrigues, 2014). The lack of support for physiological drivers of group splits could reflect a lack of strong differences in preferred foraging patches or travel speed in this species. Alternatively, such differences may exist but are not strong enough to outweigh social drivers, leading individuals to compromise their own physiological needs to remain associated with related individuals. Even though we did not find any effect of age and sex homophily on subgrouping patterns, other physiological factors which are not associated with these broad categories, such as variation in nutritional requirements and reproductive status, could still play a role in driving subgroup composition.

Although we focused our investigation on the drivers of group splits, one of the groups we tracked did not split at all. The Trago group, unlike the Galaxy and Presidente groups, was smaller and

Table 2

Results of MRQAP regression predicting subgroup membership based on relatedness, age homophily and sex homophily between dyads for both g	groups
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Dependent matrix	Independent matrices	Galaxy group			Presidente group		
		Coefficient	Р	Adjusted R ²	Coefficient	Р	Adjusted R ²
Subgroup membership	Age Sex Relatedness	-0.041 0.059 0.710	0.399 0.247 0.001	0.169	-0.030 -0.025 0.363	0.235 0.207 0.003	0.085

The dependent matrix is subgroup membership, defined as the proportion of time each dyad was found in the same subgroup across the full data set. Independent matrices are age and sex homophily (1 if dyad was in the same class, 0 if dyad was in a different class). Significant effects are shown in bold.

composed of six juveniles and one subadult male that was visibly limping at the start of the collar period (Table 1). Although the injured subadult male had reached the age when he was expected to leave the group permanently, it is likely that he remained in the group to minimize his risk of predation. Although his condition improved, the group's level of cohesion remained the same, suggesting this had little influence on the likelihood of the group splitting. The other adult females and subadults had left the group to give birth or disperse before or shortly after collaring. Juveniles are expected to have a greater predation risk because they are significantly smaller than adults (Hass & Valenzuela, 2002). The increased group cohesion observed here, particularly in this small group composed mostly of juveniles, supports the hypothesis that subgrouping patterns are influenced by predation risk. An alternative explanation for the lack of fission-fusion behaviour observed in this group is that juvenile cohesiveness could have been driven by social attraction, as juvenile coatis often spend a considerable amount of time playing and closely associate with one another within groups (Hirsch, 2011a, 2011b; Kaufmann, 1962). Furthermore, the members of this group were mostly closely related (Fig. A10b), so the tendency to associate together might also reflect cohesion based on social relationships as seen in the other two groups.

Even though we identified some shared features in the subgrouping behaviour of coatis, our results also highlight the substantial variation in fission—fusion dynamics that can occur within a species. The tendency to split, the durations of splits and the relative subgroup sizes all varied across the three groups we studied. Differences in group size, demographic composition and the relatedness of group members (Lehmann & Boesch, 2004) may all have contributed to this variation, highlighting the importance of studying multiple groups. The drivers of fission—fusion dynamics are likely to reflect a complex balance of factors that may fundamentally change depending on both the social and ecological context. Such variation can have important consequences for group members' foraging efficiency and predation risk, ultimately impacting reproductive success and survival (Rubenstein, 1978).

Relatedness-driven subgrouping may also have important implications for the processes of collective decision making regarding movement in social groups. Consensus costs based on differing preferences are commonly invoked to explain patterns of group cohesion and decision making across species, since splitting into subgroups can provide an alternative to achieving consensus when group members disagree about where and when to move (Conradt & Roper, 2005). However, if individuals split with related group members rather than those with similar physiological needs, the resulting subgroups will likely not be more aligned in their preferences than the group as a whole. In groups with relatednessdriven subgrouping patterns, such as we observed here in coatis, conflicts of interest within subgroups may remain high. The distribution of preferences within subgroups can have important consequences for the mechanisms of decision making and the distribution of influence over collective decisions (Conradt & Roper, 2005), as well as on the ultimate costs and benefits of grouping. Investigating how collective movement decisions arise under different subgrouping patterns could provide further insights into the mechanisms of group decision making as well as the costs and benefits of social grouping in coatis and other social animals.

In conclusion, our study has highlighted a consistent role of relatedness in driving subgrouping patterns in wild white-nosed coatis, demonstrating the importance of kinship in their social behaviour and collective decision making. These results offer valuable insights into the mechanisms driving fission—fusion dynamics within this species. Although we have a detailed understanding of their subgrouping patterns in the dry season, to understand how groups respond to seasonal fluctuations, future studies could track groups across seasons. Collecting data on a larger sample of social groups under different ecological conditions could also shed further light on the drivers of this variation. Expanding our approach to other study systems could yield comparable data across a range of species, enabling a broader investigation of the ecological, social and physiological underpinnings of fission—fusion dynamics in animal societies.

Author Contributions

Emily M. Grout: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Josué Ortega:** Project administration, Data curation. **Pranav Minasandra:** Writing – review & editing, Validation. **Matthew J. Quin:** Writing – review & editing, Formal analysis. **Margaret C. Crofoot:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Ariana Strandburg-Peshkin:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Ben T. Hirsch:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Ben T. Hirsch:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Data Availability

Data and code are available on Zenodo: https://doi.org/10.5281/ zenodo.11204635 (Grout et al., 2024).

Declaration of Interest

The authors declare no financial or nonfinancial conflicts of interest.

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Appendix

Alternative parameterizations

To test the robustness of our results to the distance threshold chosen for determining subgroups ($\varepsilon = 50$ m), we re-ran the analyses in the main text with alternative thresholds of $\varepsilon = 30$ m and $\varepsilon = 70$ m. The results are shown in Figs A2–A7 and Tables A1, A2, which are comparable to the main analyses represented by Figs 2 and 3, Fig. A12 and Table 1. Results did not differ qualitatively between these three different parameterizations.

Table A1

Results of MRQAP regression (for the parameterization $\varepsilon = 30$ m) predicting subgroup membership based on relatedness, age homophily and sex homophily between dyads for both groups

Dependent matrix	Independent matrices	Galaxy group			Presidente group			
		Coefficient	Р	Adjusted R ²	Coefficient	Р	Adjusted R ²	
Subgroup membership	Age Sex Relatedness	-0.040 0.058 0.715	0.409 0.262 0.002	0.168	-0.032 -0.022 0.345	0.161 0.230 0.003	0.086	

The dependent matrix is subgroup membership, defined as the proportion of time each dyad was found in the same subgroup across the total data set. Independent matrices are age and sex homophily (1 if dyad was in the same class, 0 if dyad was in a different class). Significant effects are shown in bold.

Table A2

Results of MRQAP regression (for the parameterization e = 70 m) predicting subgroup membership based on relatedness, age homophily and sex homophily between dyads for both groups

Group	Independent matrices	Galaxy group			Presidente group		
Dependent matrix		Coefficient	Р	Adjusted R ²	Coefficient	Р	Adjusted R ²
Subgroup membership	Age Sex Relatedness	-0.041 0.058 0.701	0.389 0.236 0.001	0.172	-0.032 -0.022 0.345	0.162 0.230 0.003	0.086

The dependent matrix is subgroup membership, defined as the proportion of time each dyad was found in the same subgroup across the total data set. Independent matrices are age and sex homophily (1 if dyad was in the same class, 0 if dyad was in a different class). Significant effects are shown in bold.



Figure A1. Number of subgroups for the Galaxy and Presidente groups when the e-neighbourhood distance is set to 10 m, 20 m, 30 m, 40 m, 50 m and 100 m.



Figure A2. Characterization of subgrouping patterns for the (a, b, c) Galaxy and (d, e, f) Presidente groups when the e-neighbourhood distance was set to 30 m (compare with Fig. 2). (a, d) Histogram of the probability of finding subgroups of different sizes in the tracking data. (b, e) Histograms of the number of individuals in each subgroup when the group was split into two subgroups. (c, f) Histograms of the number of individuals in each subgroup when the group was split into three subgroups.



Figure A3. Subgroups observed in the coati groups that exhibited fission—fusion dynamics when the *e*-neighbourhood distance was set to 30 m (compare with Fig. 3). Subgrouping patterns in the (a, b) Galaxy and (c, d) Presidente groups. (a, c) Association matrices representing the proportion of time each dyad was in the same subgroup across the full data set for the (a) Galaxy and (c) Presidente (c) groups. Row and columns of each matrix represent individuals, with coloured points representing the age/sex class of each individual. Coloured squares in each matrix indicate the proportion of time each dyad was found in the same subgroup, across all times when both individuals in the dyad were tracked. (b, d) The proportion of time individuals in each dyad joined the same subgroup during events when the full group split into subgroups, for the (b) Galaxy and (d) Presidente groups.



Figure A4. Consistent subgroup membership across group splits when the *e*-neighbourhood distance was set to 30 m (compare with Fig. A5). Histograms show the distribution of the subgroup consistency metric under a null model assuming random allocations of group members to subgroups during group splits (1000 permutations) for the (a) Galaxy and (b) Presidente groups. Orange line shows the consistency value for the real split data.



Figure A5. Characterization of subgrouping patterns for the (a, b, c) Galaxy and (d, e, f) Presidente groups when the *e*-neighbourhood distance was 70 m (compare with Fig. 2). (a, d) Histogram of the probability of finding subgroups of different sizes in the tracking data. (b, e) Histograms of the number of individuals in each subgroup when the group was split into two subgroups. (c, f) Histograms of the number of individuals in each subgroup when the group was split into three subgroups.



Figure A6. Subgroups observed in the coati groups that exhibited fission-fusion dynamics when the e-neighbourhood distance was 70 m (compare with Fig. 3). Subgrouping patterns in the (a, b) Galaxy and (c, d) Presidente groups. (a, c) Association matrices representing the proportion of time each dyad was in the same subgroup across the full data set for the 9a) Galaxy and (b) Presidente groups. Row and columns of each matrix represent individuals, with coloured points representing the age/sex class of each individual. Coloured squares in each matrix indicate the proportion of time each dyad was found in the same subgroup, across all times when both individuals in the dyad were tracked. (b, d) The proportion of time individuals in each dyad joined the same subgroup during events when the full group split into subgroups, for the (b) Galaxy and (d) Presidente groups.



Figure A7. Consistent subgroup membership across group splits when the *e*-neighbourhood distance was 70 m (compare with Fig. A12). Histograms show the distribution of the subgroup consistency metric under a null model assuming random allocations of group members to subgroups during group splits (1000 permutations) for the (a) Galaxy and (b) Presidente groups. Orange line shows the consistency value for the real split data.



Percentage of time alone

Figure A8. Percentage of time each group member was alone in the (a) Galaxy and (b) Presidente groups across all data where group members had a GPS fix.



Figure A9. (a, c) Histograms for number of individuals tracked via GPS during daytime hours for the (a) Galaxy and (c) Presidente groups. (b, d) Bar plots for number of total GPS points from each individual used in this study's analysis for the (b) Galaxy and (d) Presidente groups.



• Subadult male • Juvenile

Figure A10. (a) Proportion of time each individual was in the same subgroup for the Trago group (measured using dbscan with 50 m e-neighbourhood distance), across all data where all group members had a GPS fix. Coloured squares indicate the proportion of time each dyad was found in the same subgroup, across all times when both individuals in the dyad were tracked. (b) Relatedness matrix for the Trago group using the triadic maximum likelihood method. This estimator has coefficients of relatedness ranging from 0 to 1 (full siblings and offspring are approximately 0.5, half siblings are 0.25, and aunts and uncles are 0.125). Rows and columns of each matrix represent individuals, with coloured points representing the age/sex class of each individual.



Figure A11. Number of subgroups for each hour of the day for the Galaxy and Presidente groups. The size of the point is proportional to the frequency of data points for each time of day across the total collar period for both groups.



Figure A12. Consistent subgroup membership across group splits when the *e*-neighbourhood distance was 50 m. Histograms show the distribution of the subgroup consistency metric under a null model assuming random allocations of group members to subgroups during group splits (1000 permutations) for the (a) Galaxy and (b) Presidente groups. Orange line shows the consistency value for the real split data.



Figure A13. Correlation between relatedness and proportion of time together (subgroup membership matrices) for the (a) Galaxy and (b) Presidente groups. Black line is the linear regression and the r^2 value is denoted.