# Habitual tool use on monopolizable resources alters group cohesion

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## Abstract

Tool-aided extractive foraging expands access to novel foods, but its effects on social dynamics are less understood. When tool-use resources are monopolizable, tool use may increase intragroup competition. While intragroup competition encourages reduced cohesion, this comes at the cost of increased vulnerability to predation and intergroup conflict. We examined how use of spatially fixed, monopolizable resources, anvils, influences cohesion by comparing groups of tool-using and non-tool-using white-faced capuchins (*Cebus capucinus imitator*) on Jicarón Island in Coiba National Park, Panama. Jicarón lacks terrestrial mammalian predators and stone tool use is locally restricted to a ∼2 km stretch of coast. We deployed two grids of camera traps to compare daily activity patterns, and temporal variation in party size, party composition, and spatial cohesion. We compared observed patterns with simulations of groups exhibiting different cohesion regimes. We found that tool-using capuchins showed smaller, less variable party sizes than non-tool-using capuchins. Adult females and adult males were less likely to co-occur in a sequence. Tool-using and non-tool-using capuchins differed in their patterns of spatiotemporal cohesion. Simulations support that these patterns are consistent with the tool-using group engaging in fission-fusion subgrouping. Although only male capuchins use tools, the entire tool-using group shows reduced cohesion, suggesting that increased competition for one sex can have cascading effects within the group. Our findings suggest that habitual tool use relying on monopolizable resources incentivizes lower group cohesion. This creates differences in the social environment of tool-using and non-tool-using animals sharing a habitat, and reveals culture as a potential driver of social organization.

**Keywords**: culture; primates; behavioral ecology; social structure; intragroup competition

# Introduction

Across human societies, culture (i.e., socially-learned behaviors transmitted across and within generations) is intertwined with social structure. An individual's learned behavioral repertoire is shaped by their close associations [1, 2] and culture influences how and with whom they associate [3–5]. Culture is also widespread in non-human animals [6–8]. The roles of social tolerance and social demography in the spread of cultural behavior have been considered theoretically [9–11] and experimentally [12–14]. However, the reverse influence, how culture shapes social structure, remains understudied [15]. Most research on this topic has focused on cetaceans [15, 16] with limited empirical evidence for culture affecting social structure. One example is the finding that dolphins who adopted a cultural behavior (a foraging technique of following trawling boats) became temporarily socially segregated from group members who did not adopt [17]. Understanding the bi-directional relationship between culture and social bonds is key as both can affect fitness [7, 18–21]. Further, expanding this research to other animal taxa can help identify general mechanisms linking culture and social structure, also informing hypotheses about the role of these processes in hominin evolution. One way to examine the effect of culture on social structure in wild animals is by contrasting comparable groups of the same species with and without a particular cultural trait.

## Tool use and intragroup competition

Percussive tool use is a tradition uniquely suited to this approach, because there is great within- and between-population variation in its expression. Hammerstone and anvil tool use is known to exist in at least four primate taxa chimpanzees (*Pan troglodytes*) [22], macaques (*Macaca fascicularis* spp.) [23, 24], robust capuchins (*Sapajus* spp. [25]), and gracile capuchins (*Cebus capucinus imitator*) [26, 27]). While there is variation among taxa in which populations of the same or related species perform percussive tool use [25, 28, 29], only gracile capuchins in Coiba National park show this variation at the species level in neighboring groups living on the same islands [26, 27].

The presence of hammerstone and anvil tool use may affect social dynamics. A habitual reliance on tool use at fixed anvils creates repeated access to spatially fixed and monopolizable resources. In group-living species, such conditions are predicted to increase intragroup contest competition (i.e., direct competition over monopolizable resources), yet this has rarely been tested empirically. Evidence from bearded capuchin monkeys (*Sapajus libidinosus*) suggests increased competition in tool-using females, as they showed higher aggression rates at anvil sites, but the social structure of the study population was comparable to non-tool-using populations [30]. This hypothesis has not yet been evaluated in other species, perhaps due to the difficulty of ruling out ecological factors that might explain the lack of tool use and thus identifying appropriate comparisons. If tool use on monopolizable resources can indeed increase intragroup competition, how could this competition be mitigated, and what effect would it have on social dynamics?

## Group cohesion and fission-fusion dynamics

Living in a social group is beneficial in myriad ways, including decreased predation risk, higher discovery rates of novel habitats and resources, and increased mating opportunities [31, 32]. However, living in groups also comes with drawbacks, such as more resource competition within the group, and higher risks of disease [31]. One way to reduce contest competition is by reducing spatial-temporal overlap among group members, thereby decreasing opportunities for direct competition over resources. This is consistent with findings from feral horse populations, where monopolizable resources (e.g., water) increased within-group contest competition and led to reduced social cohesion [33]. However, this reduced cohesion comes at the cost of increased predation vulnerability and intergroup competition. Social groups may balance these tradeoffs of group size via flexible spatiotemporal associations with group-members.

The extent of variation in spatiotemporal cohesion of group members are called fission-fusion dynamics—a multi-dimensional, flexible concept reflecting temporal variation in i) spatial cohesion among group members, ii) party size and, iii) party composition [34]. Fission-fusion behavior is characterized by fission (a group splitting into smaller subgroups) and fusion (subgroups merging into a larger group) events [35]. It is flexible and occasionally inconsistent within species [34]. A higher degree of fission-fusion behavior can occur

in response to environment, such as reduced predation risk, or more scarce or dispersed food resources. One study comparing two species of *Sapajus* capuchins found that the species experiencing less predation and more dispersed, low-quality resources foraged in subgroups more frequently (i.e., showed a higher degree of fission-fusion behavior) than the species with more predation and clumped, high-quality resources [36]. In various primate species, fissioning was found to occur more frequently when food resources were scarce [37–39]. Comparable fission–fusion dynamics are observed across non-primate taxa, where variation in predation risk and resource distribution shapes grouping decisions in ways consistent with ecological constraints models [31, 32, 40].

## A natural experiment in tool use and social dynamics

Disentangling the effects of cultural behavior from ecological variation on social structure is challenging, because both often covary across populations and environments. One system where this can be addressed is white-faced capuchins (*Cebus capucinus imitator*) living on Jicarón island, Coiba National Park, Panama. This island and the neighboring island of Coiba are the only two sites in the world where natural populations of gracile capuchins habitually perform percussive hammerstone and anvil tool use [26, 27]. On Jicarón, tool use is further localized to an approximately 2 km stretch of coast, occupied by a maximum of three capuchin groups [41]. Despite there being no physical boundaries, differences in material availability, or other clear ecological differences, habitual hammerstone and anvil tool use does not occur in capuchin groups living in other parts of the island [26]. It is therefore possible to directly compare tool-using and non-tool-using groups of the same species in the same habitat.

Both tool-using and non-tool-using groups have minimal predation risk due to an absence of terrestrial predators [42] and show decreased vigilance and neophobia. Capuchins also live at high density [26, 43], which may lead to more relaxed intergroup interactions [44] — though on Barro Colorado Island, capuchins occur at high density yet have more intense intergroup encounters [45]. Predation pressure and intergroup competition are two major factors driving group cohesion [32, 46], and relaxation of these pressures on Jicarón means we expect the capuchins to be overall less socially cohesive than mainland capuchins. In long-term study sites on the mainland, white-faced capuchins are generally described to forage as a cohesive group and resting together (e.g. grooming, playing) at the hottest part of the day [47]. Capuchins might scatter widely while foraging [48, 49], but individuals do not generally travel independently of other group members and remain in contact via frequent vocalizations [49]. As such, they are not described as a species with a high degree of fission-fusion grouping.

Due to the variation in tool use behavior within Jicarón island, we can directly assess whether presence of tool use is linked to differences in social dynamics. Because terrestrial predators are absent on Jicarón and both groups experience similar environmental conditions, this system offers a rare opportunity to isolate the potential effects of competition over monopolizable resources. Comparable to findings by [30], there might be increased competition over spatially fixed, usurpable anvil sites, favoring solo foraging or less cohesive grouping to mitigate this competition. The stone tool use on Jicarón appears to be a largely solitary activity [50], and during in-person observations the tool-using group appears very spread out, providing some support for this hypothesis. Furthermore, since tool-use is an exclusively male activity on Jicarón [51], only males would be predicted to experience increased intragroup competition, which could have cascading effects on both within- and between-sex social interactions.

## Aim

Here, we systematically assess this question by comparing one group of tool-using and one group of non-tool-using white-faced capuchins of similar size and composition living on Jicarón island in Coiba National Park, Panama. Both groups border the coast, where similar resources are available (e.g., coastal species like sea almonds, as well as intertidal resources). Using two grids of camera traps, we compare daily activity patterns and fission-fusion dynamics between tool-using and non-tool-using capuchins. Following [34], we quantify the degree of fission-fusion dynamics through temporal variation in three dimensions: 1) party size, 2) party composition, and 3) spatial cohesion. We developed an agent-based group movement model to test specific, quantitative predictions based on our hypotheses. Agents could either move (a)

'together' as one group; (b) as two non-interacting 'subgroups'; or (c) as entirely 'separate' entities not influencing each others' movements. A grid of simulated camera traps then recorded observations of these animals when the animals approached within a threshold distance (specific to each camera trap). We compared metrics computed from real observations with metrics obtained from these simulated camera trap observations. We expect that—if tool use increases intragroup competition—the tool-using group will be less cohesive and/or show more fission-fusion behavior than the non-tool-using group (Fig. 1).

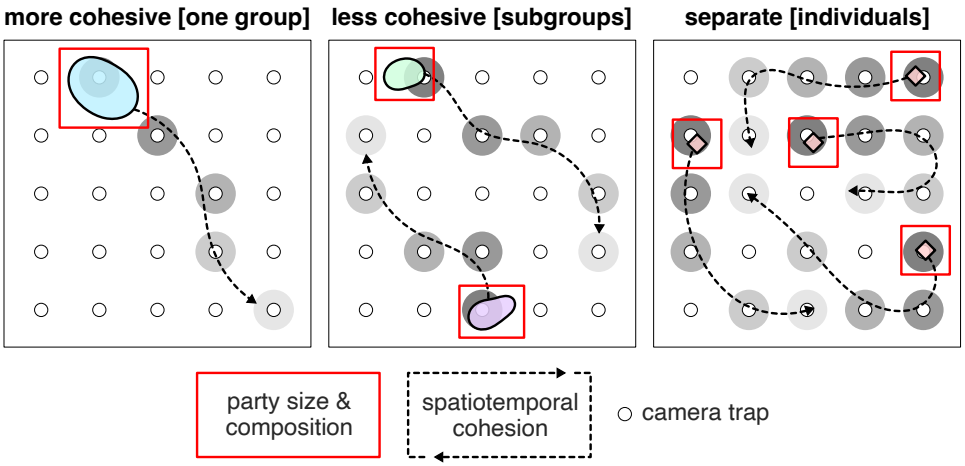


Figure 1: Overview of measurements of cohesion from camera trap data, with as an example a cohesive group moving together (left), a less cohesive group moving in subgroups (middle), and every individual moving separately (right). Party size and composition are measured within detections of capuchins by camera traps, while spatiotemporal cohesion is assessed by considering the relationship between capuchin detections.

# Results

## Daily activity patterns

The daily activity of tool-using and non-tool-using groups overlapped considerably (coefficient of overlap = 0.857, 95 % CI [0.854-0.860]) (Fig. 2). The non-tool-using group showed slightly more activity in the morning, and the tool-using group considerable more activity in the afternoon. A striking difference is the presence of nocturnal terrestrial (after sunset and before sunrise) activity by the tool-using group, which was absent in the non-tool-using group. Six sequences (a sequence is all images from a camera trap triggered within 30 seconds of one another) show capuchins from the tool-using group traveling on the ground between 19:00 and 05:00, when it is dark. For the tool-using group, there was also one camera location where capuchin sightings were two times higher in the morning ($<$ 7:00) and evening ($>$ 17:00) than at other cameras, which might be located near a likely sleep-site. For the non-tool-using group there was no single camera location with much greater capuchin activity in the early morning and late evening.

## (Social) party size

Based on identifiable individuals and maximum observed co-occurrence across age–sex classes, we inferred that the two capuchin groups were comparable in size and composition (Table 1). Despite this similarity in group size, we never observed more than 10 individuals together in a sequence in the tool-using group, while in the non-tool-using group the largest party size was 16. Importantly, these values reflect partial detections of parties, as camera traps might capture only a subset of individuals present and under-represent true party size [52]. Since 69% of sequences contained only a single capuchin, we focused on comparing 'social party

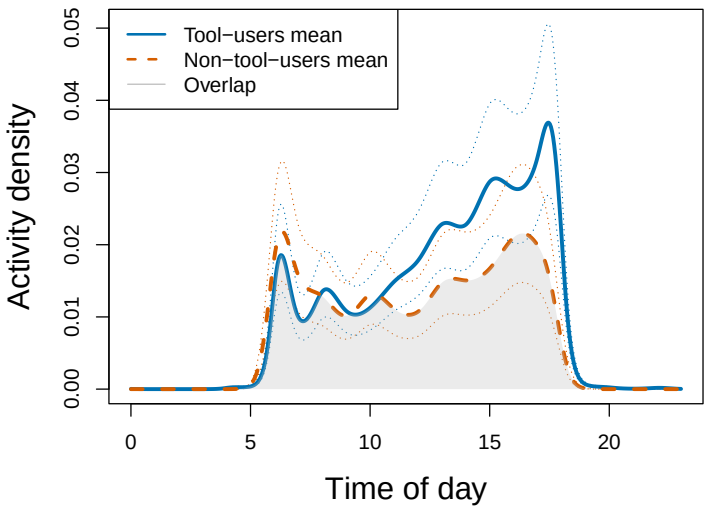


Figure 2: Density plots of daily activity of tool-using group (in orange) and non-tool-using group (in green). The thick line reflects the model estimates, the shaded gray the area of overlap, and the dotted lines the 95% confidence intervals. Circles are used to represent the observations of capuchins during the night.

size', where parties of 1 are reflected as a 0, and each number above 0 reflects the number of other partners available, to account for this skew through hurdle-modeling. When comparing the social party size, we found different results for the zero and non-zero component of the model (Fig. 3A & D, for model estimates see Table S1). Singletons were slightly more common in the tool-using group than the non-tool-using group, although there was weak evidence for this effect (i.e., less than 80% of the posterior distribution of the contrast was on one side of 0). The model estimated a 1.8% increase (PP $>$ 0: 0.69, Fig. 3B) in the probability of observing single parties in the tool-using group (estimated probability of 0 = 0.73, 95% CI [0.68, 0.78]) compared to the non-tool-using group (estimate = 0.71, 95% CI [0.66, 0.76]). However, when parties larger than a single individual were observed, they were likely to be larger in the non-tool-using group than the tool-using group. We have strong evidence (PP $>$ 0: 0.96, Fig. 3E) that there are larger social parties in the non-tool-using group (estimate = 1.36, 95% CI [1.09, 1.63]) than in the tool-using group (estimate = 1.05, 95% CI [0.82, 1.28]).

To interpret these patterns, we compared the empirical results to the most comparable simulation condition (20 capuchins, 25 cameras). These simulations showed that varying cohesion produces distinct social party size patterns (Fig. 3C & F, for model estimates see Table S2 and for simulation details see Methods). Simulated capuchins moving in two subgroups were considerably more likely to have singleton detections by camera traps than capuchins moving together (PP $>$ 0: $\approx$ 1) . Capuchins moving together were estimated to have higher average social party sizes in detections than those moving in two subgroups (PP $>$ 0: $\approx$ 1). A broader exploration of simulations varying capuchin number (10–50) and camera coverage (4–81 cameras) produced qualitatively similar trends (Figs. S2-S5).

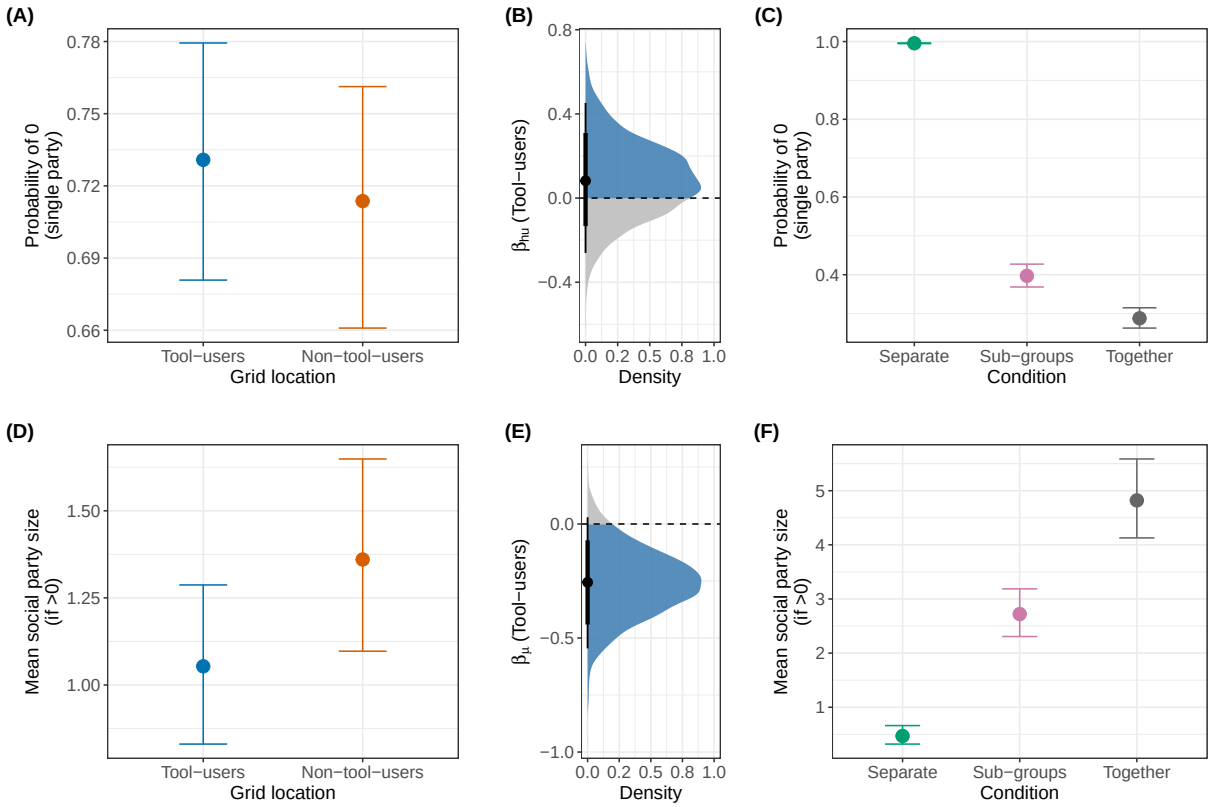


Figure 3: Model estimates from hurdle-Poisson models comparing mean social party size between the tool-using and non-tool-using group in the real data (panels A and D) and between varying levels of cohesiveness in simulated data (panels C and F). The top (panels A-C) show model estimates of the zero (hu) component of the models, and the bottom (panels D-F) the non-zero (mu) component. Points reflect averages estimated by the model, and the whiskers the 95% credible interval. Panels B and E show the posterior distributions of the MCMC-estimated contrasts for the hu and mu components corresponding to panels A and D, with 80% and 95% credible intervals.

## Party composition

Due to camera traps' limited view and the quick passage of many individuals, reliable aging and sexing of individual capuchins was not feasible in all sequences. Adult sex was most reliably classified (sex assigned to 93% of observed adults), and as such we focused on presence of adult males and adult females to compare party composition. Adult females were more likely to be seen together in the non-tool-using group than in the tool-using group (for model estimates see Table S3). Our model estimated a higher mean number of adult females present in a sequence in the non-tool-using group (0.36, 95% CI [0.31, 0.42]) than in the tool-using group (0.27, 95% CI [0.22, 0.31]), and evidence for this effect was strong (PP $>$ 0: 0.98). Adult males were also more likely to be seen together in the non-tool-using group than in the tool-using group (see Table 4 for model estimates). Our model comparing the number of adult males estimated strong evidence (PP $>$ 0: $\approx$ 1) for a higher mean number of adult males present in a sequence in the non-tool-using group (0.32, 95% CI [0.26, 0.38]) than in the tool-using group (0.18, 95% CI [0.15, 0.22]). Both models estimated a different relationship between the number of adult females and number of adult males present for the tool-using and non-tool-using group (see Fig. S6). In the non-tool-using group the models estimated a positive relationship: the more adult males were observed, the more adult females were observed. In the tool-using group, the relationship was negative: the more adult males observed, the fewer adult females.

## Spatial cohesion

### Co-occurrences

When the time between subsequent detections was high and the distance too great for a capuchin to have been able to cross it in that time, these "co-occurrences" likely do not reflect the same party being captured. We therefore used a threshold of detections >150 m apart within 1 minute, which would require movement speeds of ∼9 km/h, well above observed white-faced capuchin travel speeds of ∼0.3–2 km/h during active movement bouts [53]). When such co-occurrences occurred within a group's known range, we interpreted them as evidence of subgrouping events. Since we hypothesize the tool-using group is less cohesive to avoid competition over anvil sites, we considered whether anvils are actually used at the same time. We looked for such evidence of subgrouping in the tool-use group by taking a sample of camera traps on anvil sites in their known range and using a cut-off time of 60 seconds at 150 meters between sightings to identify co-occurrences. Over a 20-month period, we found 217 such co-occurrences (Fig. S7).

### Spatiotemporal cohesion

We assessed spatiotemporal cohesion by focusing on distance (in meters) and time (in seconds) between subsequent capuchin sightings within the same day, reflecting how capuchins trigger cameras as they move through the grid space. Different spatiotemporal patterns emerged for the tool-using and non-tool-using group (Fig. 4, see Table S5 for model estimates). If the distance between subsequent sightings was 0 meters, the next capuchin sighting was at the same camera. Non-tool-using capuchins were more likely to trigger the same camera again than tool-using capuchins (Fig. 4C). We found strong evidence (PP $>$ 0: $\approx$ 1, Fig. 4D) for the probability of a subsequent sighting at the same camera being higher in the non-tool-using group (estimated probability of 0 = 0.35, 95% CI [0.28, 0.43]) than the tool-using group (estimated probability of 0 = 0.29 95% CI [0.21, 0.35]). If the subsequent sighting was at a different camera (distance $>$ 0), the distance to the new camera was slightly higher in the tool-using group (264 m, 95% CI [238 m, 294 m]) than the non-tool-using group (244 m, 95% CI [218 m, 269 m]), though evidence for this effect was moderate (PP >0: 0.82, Fig. 4F & G). For both tool-users and non-tool-users, increased time between subsequent sightings was associated with greater distances between the cameras being triggered. However, tool-users showed more sightings short in time but further in space than the non-tool-users, resulting in different patterns in the link between distance and time (Fig. 4A).

To interpret these patterns, we again compared to the most similar condition in agent-based simulations (20 capuchins, 25 cameras). Here too, we found that varying levels of cohesion result in distinguishable variation in the relationship between distance and time between subsequent sightings (Fig. 4B, see Table S6 for model estimates). Simulated capuchins moving together had a higher probability of subsequent detections at the same camera than capuchins moving in two subgroups (PP $>$ 0: $\approx$ 1), Fig. 4E), while capuchins moving in subgroups had higher distances between subsequent detections not at the same camera (PP $>$ 0: $\approx$ 1), Fig. 4H). Varying capuchin number (10–50) and camera coverage (4–81 cameras) led to qualitatively similar trends (Figs. S8 & S9). The different spatiotemporal patterns of the tool-using and non-tool-using capuchins are also visible in our animation of capuchin sightings (online supplement).

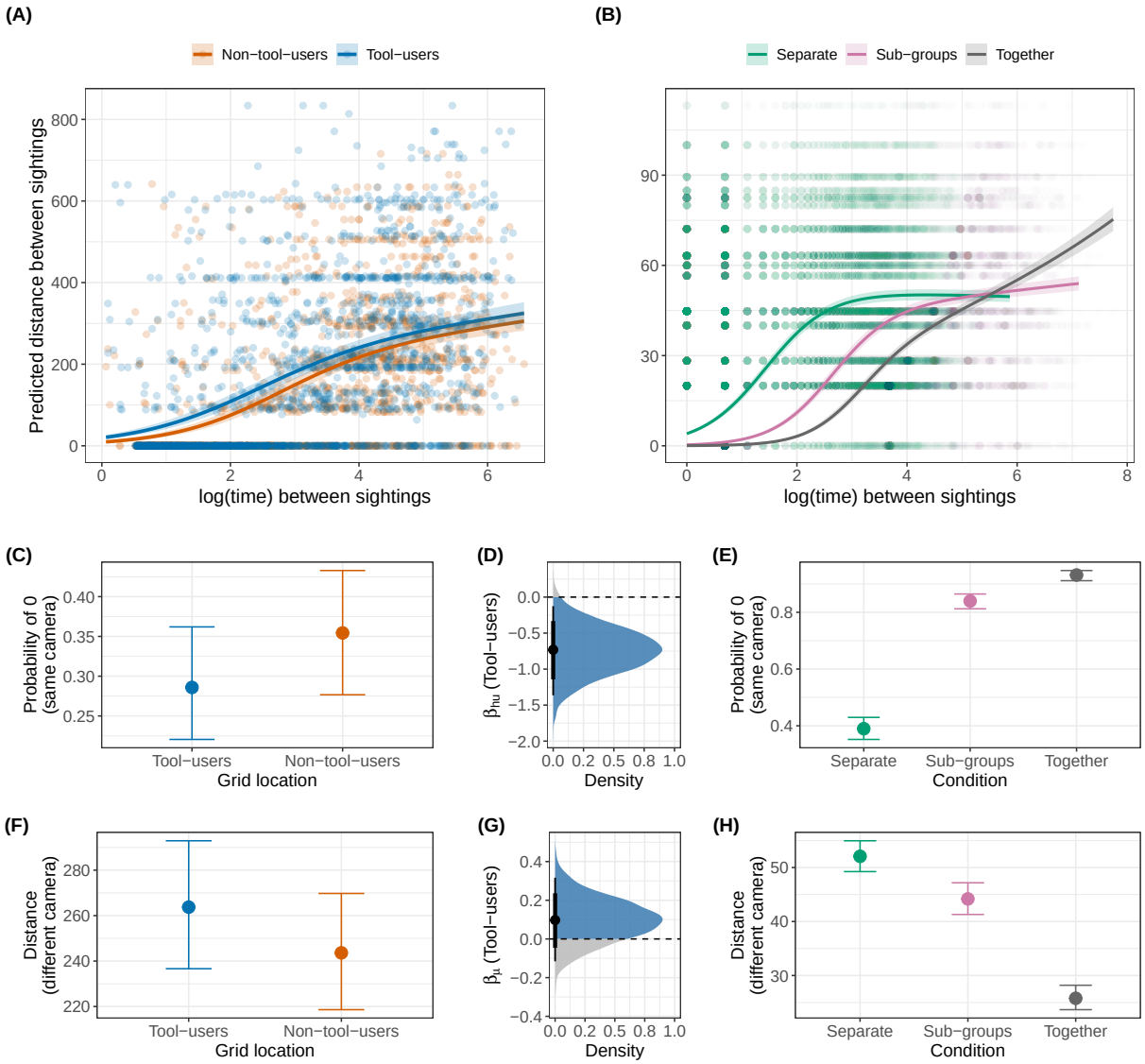


Figure 4: Model estimates from hurdle-gamma models comparing the interaction of distance and time between subsequent capuchin sightings for the tool-using and non-tool-using group in the real data and for varying levels of cohesiveness in simulated data. Panels A and B show the interaction between distance and time, where lines reflect the model estimates, the shaded area the 95% credible interval, and points raw data. Panels C-E show model estimates of the zero (hu) component of the models, and the panels F-H the non-zero (mu) component. Here points reflect averages estimated by the model, and the whiskers the 95% confidence interval. Panels D and G show the posterior distributions of the MCMC-estimated contrasts for the hu and mu components corresponding to panels C and F, with 80% and 95% credible intervals.

# Discussion

We investigated whether increased intragroup competition from habitual tool use in white-faced capuchins is linked to reduced group cohesion. Using two grids of camera traps, we compared the social cohesion of one group of tool-using and one group of non-tool-using white-faced capuchins sharing the same habitat and located 3 km apart on the same island. We found that, despite large overlap in daily activity patterns and only 3 kilometers of distance between them, there are marked differences in group cohesion between the tool-using and non-tool-using groups.

We measured cohesion following [34] as temporal variation in i) party size, ii) party composition and iii) spatial cohesion. The tool-using group had a higher probability of singleton detections, and smaller observed party sizes than the non-tool-using capuchins. Simulations show that these patterns emerge with reduced cohesion (subgrouping), and these relationships were robust across a wide range of group sizes and camera configuration. The differences in party composition between the two groups—despite comparable group composition—also supported the hypothesis of a more cohesive non-tool-using group and a tool-using group which is less cohesive. In any one observation, capuchin parties in the tool-using group had fewer adult males, fewer adult females, and fewer adult males and females together than parties in the non-tool-using group. Patterns of spatiotemporal cohesion further supported this interpretation. For the non-tool-users, capuchin detections often occurred at cameras neighboring the camera of the previous sighting, in line with cameras being triggered by a group traveling in a specific direction. In contrast, for the tool-using group, we see that subsequent detections are not usually at a neighboring camera, but rather somewhere else on the grid entirely, as expected when capturing several subgroups rather than one big group, as supported by our simulations.

An advantage of using two comparable grids of camera traps is that they allow direct comparison of cohesion between the tool-using and non-tool-using groups under similar sampling conditions. However, because these grid cameras do not capture tool use itself, they do not directly link reduced cohesion to its hypothesized driver: competition over tool-use sites. The numerous simultaneous sightings at different anvils within the tool use group's range provide direct behavioral evidence of spatially separated subgroups and are consistent with the interpretation that competition over tool-use sites promotes fission–fusion dynamics in the tool-using group. While the non-tool-using group shows social cohesion comparable to that described for the species, the tool-using group exhibits a more fission–fusion-like structure than is typically described for white-faced capuchins in long-term field studies. Importantly, reduced cohesion was not limited to the males that perform tool use. Differences in party composition and female co-occurrence suggest that altered grouping patterns extend across the group, indicating that the effects of this behavioral tradition may cascade beyond the individuals directly engaging in tool use.

## Tool use linked to reduced group cohesion

Our findings provide evidence for a potential link between habitual tool use at fixed, monopolizable resources and reduced group cohesion. The tool-using group and non-tool-using groups inhabit the same habitat with comparable resource availability. Yet they differ behaviorally: the tool-using group has a habitual stone tool use tradition which has persisted over two decades [26]. Here, we show that the social cohesion of these two groups also differs. On Jicarón, where predators are absent and capuchins are more terrestrial [42], the selective pressure to maintain tight social cohesion may be relaxed. However, because both groups share this environment, predation cannot explain the observed between-group differences. Instead, these differences are consistent with a role of habitual tool use on monopolizable resources in shifting social organization towards being less cohesive and more fission-fusion-like. In the tool-using group's range, at least 10 heavily used anvil sites near sea almond or coconut trees are fixed and monopolizable, previously hypothesized to generate intragroup contest competition [26], as observed in bearded capuchins [30]. Such competition can be mitigated through agonistic displacement, as seen in mainland white-faced capuchins where higher ranking individuals secure greater energy intake than lower ranking individuals by displacing them from feeding patches [54]. However, on Jicarón, direct agonistic interactions at anvils are incredibly rare [50, 51]. The intensity of intragroup competition can also be mitigated via reduced group cohesion [55–57], which appears to be the case on Jicarón, where competition over anvils may be reduced through spatial separation. Comparative data from mainland and other island populations will be necessary to disentangle the relative

contributions of tool use, predation pressure, and island ecology to variation in capuchin group cohesion.

Differences in space use could influence camera detections and therefore represent an alternative explanation for some observed patterns. Mainland white-faced capuchins in neotropical dry forests in Costa Rica occupy home ranges with median estimates of 1.82 $km^2$ [58], with slightly lower estimates from the tropical moist forests of Barro Colorado Island, Panama [45, 59]. We lack precise data on the home range sizes of capuchin groups on Jicarón, but the minimum extent appears comparable to in other tropical moist forests (at least 1 $km^2$)[45, 59]. Nevertheless, differences in home range configuration and movement patterns, potentially associated with concentrated use of anvil sites and intertidal foraging by tool users [41], could influence detection patterns and mean that our grids sampled different portions of each group's range. This is supported by the presence of nocturnal detections in the tool-using grid, absent in the non-tool-using grid, indicating that we likely sampled sleep sites in the former, and/or that they have different nocturnal behavior. More generally, variation in space use, resource distribution, and social cohesion are likely interconnected, and future work integrating spatial ecology with behavioral observations will be needed to disentangle these effects.

Previous studies have shown that fission-fusion dynamics are highly flexible [34] and can vary seasonally, for instance in response to fluctuations in food availability [37–39]. Tool use on Jicarón also has a seasonal component [26]; we observe peaks in tool use frequencies in the transitions between wet and dry season (see [50]) The camera traps used in this study were deployed for 7 months, overlapping in time with at least one of the peaks in tool use activity. As such, the reduced cohesion we observed by the tool-using group may reflect their grouping dynamics only during this time period of increased competition. It is possible that cohesion increases when tool use frequency decreases. Further research is needed over larger timescales to shed light on seasonal components of grouping dynamics, also taking into account fluctuations in availability of other food resources which may affect intragroup competition and cohesion for tool-using and non-tool-using capuchins on Jicarón alike.

## Cascading effects of a sex-biased tool use tradition

Despite tool use on Jicarón being restricted to males [51]—and thus only males experiencing contest competition at anvils—our results suggest the whole tool-using group shows reduced group cohesion. This has several important implications for their social system and behavior. First, in well-studied populations of white-faced capuchins at mainland sites,females are typically philopatric while males typically disperse [47], leading to social bonds of females being having large impacts on coalition formation, foraging access, and survival [60] . While we did not measure detailed social behavior in this study, we do see that adult females are much less likely to co-occur in the tool-using group than in the non-tool-using group and thus seemingly have fewer opportunities for social contact. This would be a fruitful area for future research. Second, the male-exclusive nature of tool use in this population combined with reduced cohesion likely results in some degree of sexual segregation in space, at least at anvil sites, where females are observed less frequently than other age-sex classes [51]. This segregation, combined with the reduced group cohesion, affects social learning opportunities for immature individuals who are still dependent on their mothers, as it limits their observations of tool use and interactions with male group members. Our previous research found that social attention during tool use events is relatively rare [50], yet the persistence of the tool use tradition for at least 20 years suggests young individuals are capable of acquiring the behavior.

## Implications for intergroup dynamics

The reduced group cohesion in the tool-using capuchins may make them less competitive during intergroup conflicts. In mainland sites, white-faced capuchins are known to be xenophobic with hostile intergroup encounters [47, 53, 61]. On Jicarón, we know little about the nature of interactions between groups, personal observations suggest intergroup competition may be more relaxed, as on other islands [62, 63]. Due to the small size of the island and its genetic isolation, it is possible the capuchins have a high degree of inbreeding, and, as a result are less capable of differentiating in-group from out-group members, resulting in lower out-group aggression [64]. However, higher relatedness would account for differences in behavior between capuchins on Jicarón and mainland capuchins, not between tool-using and non-tool-using capuchins within

Jicarón island. More information is needed to assess whether intergroup conflicts on Jicarón is comparable to that observed in mainland populations, and to test if the tool-using group suffers a competitive disadvantage from reduced group cohesion. The observed difference in group cohesion within such a small geographic scale (a 20 $km^2$ island) also raises interesting questions regarding dispersal. While the details of the dispersal system on Jicarón are still unclear [26], dispersal between the tool-using and non-tool-using group is likely possible, as they are only 3 kilometers apart. As such, a non-tool-using capuchin migrating into the tool-using group would not only be faced with the novel behavior of tool use, but also a less cohesive social group than it was used to. Whether migrants would adapt to the cohesiveness of their new social group is a question that has not previously been explored, but could provide fascinating insights into the flexibility of social systems.

### Estimating cohesion using camera traps

Estimating group cohesion from camera trap data presents several challenges. Detection is constrained by camera-specific fields of view, and identification of individuals is often limited by image quality. This challenge is compounded in arboreal species such as capuchins, where a lack of detections by ground-level cameras does not necessarily indicate true absence. Arboreal camera traps on Jicarón indicate diel variation in arboreality in non-tool-using capuchins [42, 65], suggesting that patterns of vertical space use may further influence detection probabilities. Placing arboreal camera traps in the tool-using group's range would be necessary to assess whether such patterns differ between groups. Improved individual identification, for example using deep-learning approaches, could further enable reconstruction of social networks from camera trap data, as demonstrated in other primate systems [66, 67]. While we accounted for some of this variation statistically (e.g., by including camera identity as a random effect and focusing on numbers of individuals detected), camera trap data alone cannot definitively resolve whether observed patterns reflect true differences in cohesion or sampling artifacts.

To address these limitations of camera traps, we combined empirical data with agent-based simulations that explicitly model how groups with different levels of cohesion would be detected by a grid of camera traps. These simulations provide a mechanistic link between underlying social structure and observed spatiotemporal detection patterns, allowing us to interpret empirical differences in terms of variation in cohesion rather than sampling bias alone. Importantly, the simulations also revealed that the ability to distinguish a cohesive group from sub-groups depends on sampling intensity: under lower camera coverage, detection patterns increasingly overlap (Figs. S2, S3, & S8). More broadly, this approach demonstrates how integrating camera trap data with process-based simulations adds rigor, and can extend the inference space of camera trap studies, particularly for species where direct observation of group structure is difficult.

## Conclusion

Our results suggest that habitual tool use at fixed, monopolizable resources is associated with reduced social cohesion in wild white-faced capuchins. By comparing two groups of the same species sharing the same environment, but differing from one another in their tool-use behavior, we provide evidence that tool use itself could drive this difference in social cohesion. Given that group-living is a balancing act of advantages and disadvantages, this reduced group cohesion can likely only emerge in specific environments where the costs of fissioning are low, such as environments with few predators. On Jicarón, the absence of predators may allow the benefits of fissioning to use tools without competition to outweigh the costs of reduced cohesion. While tool use is restricted to males, its effects on social cohesion appear to extend beyond males, influencing group-wide dynamics, including adult social bonds and juvenile learning opportunities. Future research should aim to better contextualize the observed patterns by comparing island to mainland groups to assess the influence of island-living on group cohesion, and by conducting longer-term monitoring to capture potential seasonal variation in both tool use and cohesion. Studying these dynamics provides rare empirical insight into the bidirectional relationship between culture and social structure, highlighting how culturally mediated behaviors might reshape patterns of social association.

# Methods

## Site

Jicarón island (20 $km^2$) is located in Coiba National Park, an UNESCO World Heritage site 60 kilometers off the Pacific coast of Panama. It is uninhabited and only sees infrequent human activity in the form of scientific research and, rarely, ecotourism.

Capuchins on Jicarón use hammerstones and anvils to access a variety of resources, ranging from fruits like sea almonds (*Terminalia catappa*), coconuts (*Cocos nucifera*) and palm fruits (*Bactris major*) to invertebrates like Halloween crabs (*Gecarcinus quadratus*), hermit crabs (*Coenobita compressus*), and nerite snails (*Nerita sp.*)[26]. Habitual stone tool use is limited to a ∼2 km stretch of coast inhabited by an estimated 3 social groups [41]. Of these three groups, only one shows tool use at high accumulation sites (i.e., anvils). The other two neighboring groups have been observed to use tools in the intertidal zone and riparian banks primarily producing ephemeral sites (C. Monteza-Moreno, pers. comm., 2023; B. Barrett pers. observation).

The group of capuchins who use tools at anvil sites, referred to as the 'tool-using group', have been performing hammerstone and anvil tool use since at least 2004 [26]. They have been monitored using unbaited camera traps since 2017, with most sampling efforts focusing on 12 frequently used anvil sites.

## Grid deployment

To compare the cohesion of the tool-using group to a non-tool-using group, we placed two grids of 26 camera traps with 100 meter spacing in both the tool-using group's range and at a location on the other side of the island (approximately 3 kilometers away) between May 2022 and January 2023. We planned the grid placement by creating a 100-meter raster and overlaying this over satellite imagery of the field site (in `R` using the packages `sf` [68], `raster` [69] and `mapview` [70]). We had some information on the tool using group's home range, due to the high sampling since 2017, and placed the grid to fall within their expected range. For the non-tool-using group, we had very limited information on their movement patterns, and thus placed a grid in an area where we had previously captured photos of capuchins during camera trap surveys. After placement we evaluated whether we captured a single group or the boundary between several groups (see detailed methods below). We selected this area to be as far away from the tool-using group's range as possible, while still sharing similar features (bordering the coast near streams and sea almond trees), and oriented both grids to be parallel to the coast.

From the 100 meter raster, we generated coordinates of 40 possible camera locations using the center coordinates of each cell, of which 30 were preferred placement locations and 10 back up locations. Due to the steep topography on Jicarón, we aimed to have a range of randomly selected, equally spaced possible camera locations, and see how many were physically reachable. The placement went as followed: we navigated to a predesignated grid location stored on a handheld GPS (Garmin GPSMAP66i), and located a tree on which the camera could be mounted, ideally within 15 meters of the intended GPS coordinates. Each camera was placed on a tree at knee height (around 0.6 meters), facing a random direction (not facing into a hill or other obstacle). Cameras were tested using the Walktest function to see if it would trigger from movement on the ground. In the end, we successfully placed 26 cameras in the tool-using group's range, and 26 cameras in the non-tool-using group. Each grid camera was placed on average 10.63 meters (range 0.96-31.41) from the intended point, on a tree facing a random direction. All cameras were still cameras (Reconyx Hyperfire HF2X), and programmed to take to take 20 pictures per trigger with no delays between-triggers (approx. 1 s between images).

## Annotation

Following collection of all cameras, triggers within 30 seconds of one another were clustered together into a single sequence. Each sequence was coded on www.agouti.eu [71], coding how many animals were present and of which species. For each capuchin present, we determined their age and sex when possible, attempted to assign an individual ID, and coded their behavior following the ethogram standard to our project [72].

Three cameras had malfunctioned or were not placed correctly, resulting in 24 cameras in the tool-using group, amounting to 4508 trapping days, with a mean of 187.8 days per camera (range 44-256). In the non-tool-using group, we ended with 25 cameras, amounting to 5330 trapping days, with a mean of 213.2 days per camera (range 96-260). For all analyses presented here, we only considered sequences containing capuchins (n = 3807).

## Group size of tool-using and non-tool-using group

Before proceeding with analyses, we had to verify that the grids actually each captured a single social group. Due to the long-term monitoring of the tool-using group, we can reliably identify most group members, allowing us to be confident that nearly all of our cameras in their range only captured known individuals. Two grid cameras placed on what we expected was the edge of their range had some triggers of unfamiliar individuals not belonging to the tool-using group. We excluded all sequences with clearly unfamiliar individuals from analyses (3 sequences in the tool-user grid and 2 sequences in the non-tool-using grid), resulting in a total of 3802 sequences for analyses.

For the non-tool-using capuchins, we identified as many individuals as possible based on visual appearance (n =14). We then constructed a social network using the `sna` package [73] based on the co-occurrences of these identifiable individuals in the same sequence (Fig. S1). Since all identified and repeatedly sighted adult males and females were connected to one another in the resulting social network, we are confident that the non-tool-using grid captures a single social group of capuchins.

Our estimates of the size and composition of both capuchin groups are based on a) identifiable individuals, b) the maximum number of capuchins observed in a sequence, and c) the maximum number of individuals of a particular age-sex class observed together in a sequence. Due to the nature of data from camera traps and its inherent uncertainty from the limited visual field, plus the difficulty of identifying juvenile capuchins from images alone, we cannot provide exact estimates of the group size. However, based on this method, the tool-using group and non-tool-using group sampled with the grid appear to be of comparable size and group composition Table 1.

## Statistical analyses

We ran all analyses in R v. 4.3.1 [74]. All Bayesian models were fit via the `brm` function in the `brms` package v. 2.16.1 [75]. To evaluate the credibility of the difference between categories we used the `hypothesis` function in `brms` and estimated means on the response scale using the `emmeans` package [76]. We considered what proportion of the posterior probability (PP) of the contrast was greater than 0, using a cut-off of 0.95 and above to reflect strong evidence for an effect, 0.80 and above as moderate evidence, and below 0.80 as weak evidence. For each model, we performed a prior predictive simulation to compare our chosen priors to default priors, and to evaluate parameter identifiability. For the final models, we ran three chains of 3000 iterations each, with a 1500 iterations warm-up per chain. Our models were stable with Pareto k estimates below 0.7 and large effective sample sizes (Bulk_ESS and Tail_ESS over 1000 for all estimates [75] and Rhat values $\leq 1.01$ [77]. We visually assessed model fit and confirmed our choice of priors using the posterior predictive check function.

Table 1: Estimated average group size and composition of the tool-using group and non-tool-using group sampled by grid cameras.

| | Tool-using group | Non-tool-using group |
|---|---|---|
| Adult females | 5–6 | 5–6 |
| Adult males | 5–6 | 5–6 |
| Subadults | 3–5 | 2–3 |
| Juveniles | 7–10 | 7–9 |
| **Total** | 20–27 | 19–24 |

### Intra-diel activity

We quantified intra-diel activity of the tool-using and non-tool-using groups using Bayesian hierarchical generalized additive models (GAMs), following the method described by [78]. For each group, we modeled the probability of activity (detecting a capuchin on a camera trap) as a cyclic smooth function of time of day (0-23 h) using a binomial likelihood and a circular spline (bs = "cc"), with camera trap location included as a random intercept. We generated posterior predictions over a fine temporal grid while marginalizing over camera traps, and computed the coefficient of overlap [79] by applying the posterior-draw-wise minimum function to the two predicted activity curves. This created a posterior distribution of overlap values ranging from 0 (no overlap in activity) to 1 (complete overlap). Additionally, we considered the locations of the first and last sightings of the day, to examine if sleep sites of the capuchins were likely captured in our grid.

### Party size

With the term 'party size' we refer to the number of capuchins captured in a sequence together. Data was heavily 1-inflated — 69.02% of sequences only contained a single capuchin. Capturing larger parties of capuchins was rare at both sites. To account for this skew in analyses, we subtracted 1 from the party size to create a variable where 0's reflect captures of individuals alone (no social partners), and numbers above reflect the number of partners present. We refer to this variable as 'social party size' in order to differentiate it from the normally used 'party size' for the total number of individuals present. To compare mean social party size between the tool-using and non-tool-using group, we ran a hurdle Poisson GLMM (*model sps_ bm1a*). For the non-zero component of the model, the outcome was the number of partners in the sequence (total number of capuchins minus 1), and the predictor variables the grid location (tool-using or non-tool-using group, with non-tool-using as reference) as well as a random effect for each camera. For the zero-component of the model, we included the predictors of grid location and varying effects of camera location, under the assumption that both could affect single capuchin detection frequency.

### Party composition

We were unable to reliably estimate age or sex in 25.88% of the capuchins observed, mostly because only part of the capuchin was visible, or because it was not possible to determine if they were subadult or juvenile. Adults were easiest to identify — we reliably classified their sex in 93.22% of cases. Therefore, to compare party composition between the tool-using and non-tool-using group, we focused on adult males and adult females as these age-sex classes could be identified most reliably. As these variables contained many zeros (ranging from 70-74%), and these zeros could both reflect true absence as well as be a result of sampling, we used zero-inflated models, since these models assume the presence of both 'true' and 'sampling' zeros. To compare the number of adult females in a party between the tool-using and non-tool-using group, we ran a zero-inflated Poisson GLMM (*model pc_ bm1*). The outcome was the number of adult females in a sequence, and the predictors grid location and an interaction of grid location with the number of adult males in a sequence. Camera location was fit as a random effect. We ran another zero-inflated Poisson GLMM (*model pc_ bm2*) with the same structure except the number of adult males as the outcome, and the number of adult females as a predictor.

### Spatial cohesion

To compare covariance in time as well as space between the grid locations, we focused on subsequent capuchin sightings within the same day. Assuming both cohesive and less cohesive capuchin groups likely sleep together at night, we first separated all detections by day. Within a day, we assigned an increasing number to each observation of capuchins (so the first observation of the day a 1, the second a 2, and so on). The first sighting of a day served as the starting point. From this we calculated for each subsequent sighting i) how far away in space this observation was from the previous observation (0 meters for the same camera, and otherwise the distance between the cameras in meters) and ii) how far away in time this observation was from the previous (how many seconds passed). We then assessed the relationship between time and space between sightings for the tool-using and non-tool-using group separately, assuming that a cohesive group and

less cohesive group would show different patterns. In a cohesive group, subsequent sightings would be expected to mostly occur close in both time and space to the previous sighting. In contrast, a fission–fusion group would also show subsequent sightings that are close in time but far apart in space. To test this hypothesis, we ran a hurdle gamma GLMM (*model_spacetime*). The outcome was the distance between subsequent sightings (in meters) and the predictors an interaction of grid location and the time in seconds (on the log-scale) between sightings, as well as camera location as a random effect.

Furthermore, when individuals of the same group are detected close in time but far apart in space at cameras at a great distance, this can indicate that they have fissioned into sub-parties. Triggers of 150 meters apart within 1 minute would be very unlikely to originate from one cohesive group of capuchins, given that observed capuchins' travel speed (0.3-2 km/h; [53]) are far lower. We identified what we term as 'co-occurrences' by extrapolating this conservative rule (so 300 meters in 2 minutes, and so on) and flagging observations that occurred within these criteria. Given the importance of being certain that both triggers came from individuals from the social group, rather than two distinct groups being captured, we focused on camera traps placed inside the tool-using group's range, where we have never observed unknown individuals. Since we hypothesize that competition over anvil sites is driving the reduced cohesion in the tool-using group, we only included anvil sites. For this, we used our wider dataset (described here [41]), coded in Agouti in the same manner as the grid data. We focused on a sub-sample of the data, only including sequences that contained capuchins at anvil sites. We also filtered to a period when all camera traps were coded, and at least four camera traps at anvil sites were deployed at the same time, resulting in inclusion of 34 camera traps deployed at anvil sites in the tool-using group's range between July 2017 and March 2019. Lastly, we visualized capuchin sightings within 10 days at the two grids. We selected a period when both grids had multiple capuchin sightings within a day, and animated these sightings using the `gganimate` package [80].

## Simulations

To simulate camera trap observations of collectively moving groups with different levels of cohesion, first, we set up a $100 \times 100$ arena with a reflecting boundary. Agents were initialized at uniformly random locations in a $2 \times 2$ box around a randomly chosen location in the arena. The movement of agents followed the Vicsek model, a commonly used model of collective movement [81]. The agents moved at a speed of 0.03 units per iteration, and could interact with other individuals in a radius of 1 unit. We used a constant Vicsek $\eta$ noise parameter of 0.1. Group cohesion was controlled by using a pre-specified adjacency matrix $A$, wherein $A_{ij}$ was 1 if individuals $i$ and $j$ could interact, and 0 otherwise. We ran the models for 5,000 iterations. We performed 100 such repeats of each model.

8 different camera traps setups were chosen. These represented varying camera trap densities, populating the arena with $2^2$, $3^2$, $4^2 \cdots 9^2$ cameras respectively. Each camera was assigned a random sighting radius between 0.3 and 1.0 units. When any individual was present within a camera's sighting radius, a sighting was recorded at that camera for that timestep.

We explored three different group cohesion conditions. In the first batch of simulations, we set all elements of the adjacency matrix to 1 (i.e., all agents could interact with each other), resulting in one cohesively moving group. In the second batch of simulations, adjacency matrix values were 1 between all individuals in the first and second halves of the group respectively, but 0 across these two halves (i.e., there were two interacting subgroups, but interactions between members of these subgroups was not possible). In the third batch of simulations, all adjacency matrix values were set to 0 (i.e., individuals moved independently of each other). This was repeated for groups of sizes 10, 20, 30, 40 and 50 individuals.

As a result, a total of $3 \times 100 \times 5 = 1,500$ trajectories were generated. We then used the above mentioned eight camera trap setups to generate observations based on all these trajectories, resulting in $1,500 \times 8 = 12,000$ simulated camera trap datasets.

## Ethics statement

Data for this study were collected as minimally invasively as possible. We obtained permission for this study from the relevant authority Ministerio de Ambiente, Panama (scientific permit no. SE/A-37-17, SC/A-23-17, SE/A-98-19, SE/A-6-2020, ARB-158-2022, and corresponding renewals and addenda). As this was a camera trapping study without environmental modification or the use of lures, a STRI IACUC was not required.

## Data availability

Details of model output are available in supplementary material. All code and data necessary to replicate analyses can be found at
https://edmond.mpg.de/previewurl.xhtml?token=1346491d-540f-4f2d-bacf-0f0de26cec78.

## Author contributions

Conceptualization (ZG, MCC, BJB); Data curation (ZG, BJB); Formal Analysis (ZG, BJB, PM); Funding acquisition (ZG, MCC, BJB); Investigation (ZG, JL, PLC, EDR, BJB); Methodology (ZG, MCC, BJB, PM); Project administration (ZG, MCC, BJB); Resources (MCC, BJB); Supervision (MCC, BJB); Validation (ZG, BJB, PM); Visualization (ZG); Writing – original draft (ZG); Writing – review & editing (ZG, MCC, BJB, JL, PM).

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## Supporting Information

**Animation of capuchin sightings**: https://keeper.mpdl.mpg.de/d/ad41ce04639143589f79/
**Fig. S1**: Social network of the non-tool-using group.
**Table S1**: Posterior mean model estimates of model *sps_ bm1a*.
**Table S2**: Posterior mean model estimates of model *sps_ sim*.
**Fig. S2**: Variability in party size model estimates (hu-component) with varying number of camera traps in simulation.
**Fig. S3**: Variability in party size model estimates (mu-component) with varying number of camera traps in simulation.
**Fig. S4**: Variability in party size model estimates (hu-component) with varying number of capuchins in simulation.
**Fig. S5**: Variability in party size model estimates (mu-component) with varying number of capuchins in simulation.
**Table S3**: Posterior mean model estimates of model *pc_ bm1*.

**Table S4**: Posterior mean model estimates of model *pc_ bm2*.
**Fig. S6**: Model estimates from model *pc_ bm1* of relationship between number of adult females and number of adult males occurring together in a sequence.
**Fig. S7**: Co-occurrences of capuchin sightings at anvil sites in the tool-using group.
**Table S5**: Posterior mean model estimates of model *spacetime_ bm*.
**Table S6**: Posterior mean model estimates of model *spacetime_ sim*.
**Table S7**: Model estimates from hurdle-Gamma models comparing space and time between subsequent capuchin sightings from real data and simulation.
**Fig. S8**: Variability in spatiotemporal model estimates with varying number of cameras.
**Fig. S9**: Variability in spatiotemporal model estimates with varying number of capuchins.

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# Supporting Information

Goldsborough, Z, Crofoot, M. C., Minasandra, P., León, J., Castillo-Caballero, P. L., del Rosario-Vargas, E., and Barrett, B. J. Habitual tool use on monopolizable resources alters group cohesion. 2026.

**Animation of capuchin sightings**:
https://keeper.mpdl.mpg.de/d/ad41ce04639143589f79/

## 1 Supplemental methods

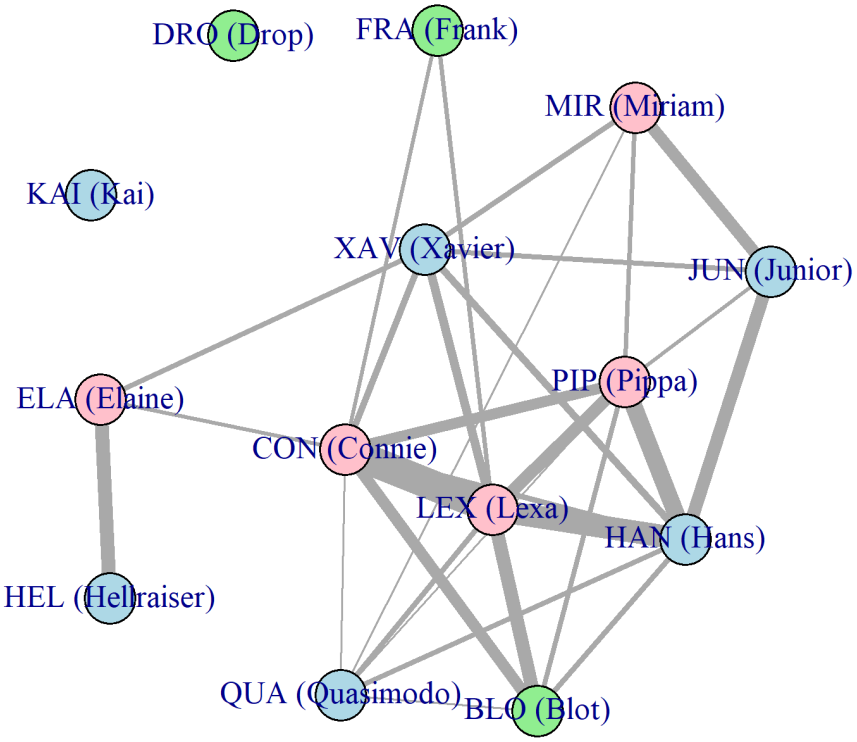


Figure S1: Social network of the non-tool-using group. Each node is an individual, and node color reflects the age-sex category (pink for adult females, blue for adult males, green for subadults and juveniles). If a line connects two individuals, they were observed in the same sequence, the thickness of the line reflects the frequency of individuals co-occurring.

## 2 Supplemental results

### 2.1 Models estimating party size

Table S1: Posterior mean model estimates of Model sps_bm1a, a hurdle Poisson GLMM (Bayes $R^2 = 0.06$) comparing mean social party size between the tool-using (TU) and non-tool-using group (NTU, the reference category). The link for the non-zero component of the model (mu) is log, and for the zero component (hu) logit.

| | *Estimate* | *Est. Error* | *CI_95_low* | *CI_95_high* |
|---|---|---|---|---|
| *Multilevel Hyperparameters* | | | | |
| locationfactor (levels: 49) | | | | |
| sd(mu_Intercept) | 0.39 | 0.07 | 0.28 | 0.54 |
| sd(hu_Intercept) | 0.51 | 0.08 | 0.38 | 0.69 |
| *Regression Coefficients* | | | | |
| mu_Intercept | 0.30 | 0.10 | 0.09 | 0.50 |
| hu_Intercept | 0.91 | 0.12 | 0.67 | 1.16 |
| mu_gridtypeTU | -0.26 | 0.15 | -0.55 | 0.03 |
| hu_gridtypeTU | 0.09 | 0.18 | -0.26 | 0.45 |

Table S2: Posterior mean model estimates of Model sps_sim, a hurdle Poisson GLMM (Bayes $R^2 = 0.40$) comparing mean social party size in simulated data of 20 capuchins moving through a grid of 25 camera traps in three conditions reflecting varying cohesiveness (moving separate, in two subgroups, or together, where separate is the reference category). The link for the non-zero component of the model (mu) is log, and for the zero component (hu) logit.

| | *Estimate* | *Est. Error* | *CI_95_low* | *CI_95_high* |
|---|---|---|---|---|
| *Multilevel Hyperparameters* | | | | |
| camera_id (levels: 75) | | | | |
| sd(mu_Intercept) | 0.39 | 0.05 | 0.31 | 0.50 |
| sd(hu_Intercept) | 0.28 | 0.04 | 0.21 | 0.36 |
| *Regression Coefficients* | | | | |
| mu_Intercept | -0.76 | 0.18 | -1.14 | -0.41 |
| hu_Intercept | 5.42 | 0.10 | 5.23 | 5.61 |
| mu_condition_subgroups | 1.76 | 0.20 | 1.38 | 2.16 |
| mu_condition_together | 2.34 | 0.20 | 1.96 | 2.75 |
| hu_condition_subgroups | -5.84 | 0.11 | -6.07 | -5.61 |
| hu_condition_together | -6.32 | 0.12 | -6.56 | -6.09 |

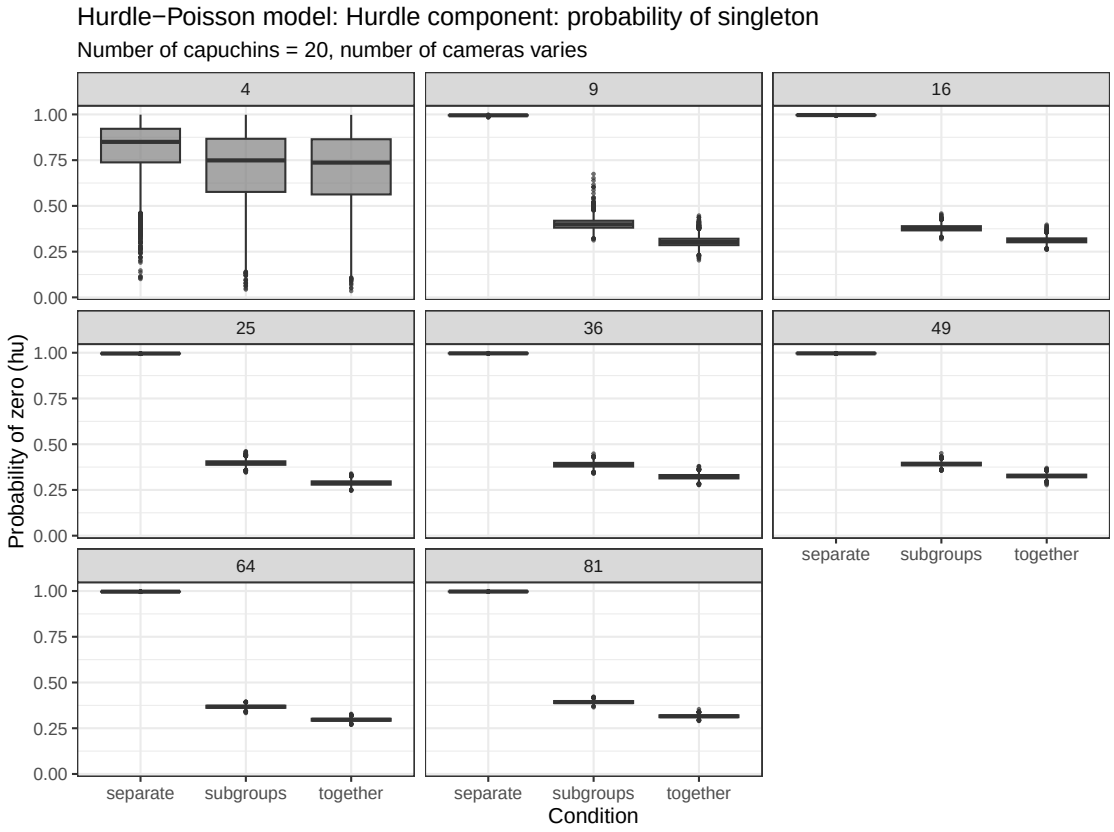


Figure S2: Variability in model estimates of probability of a social party size of 0 (singleton) in the simulated data with varying camera traps (4-81) but same number of capuchins (20).

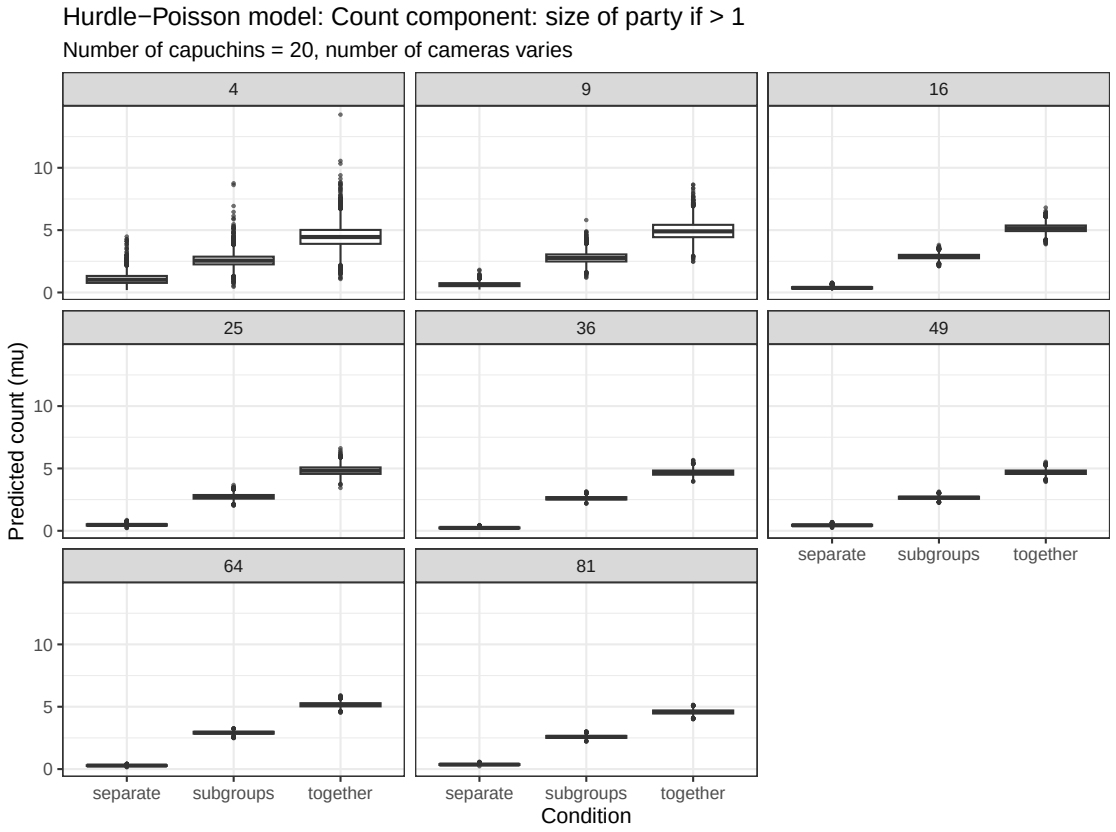


Figure S3: Variability in model estimates of social party size if >0 in the simulated data with varying camera traps (4-81) but same number of capuchins (20).

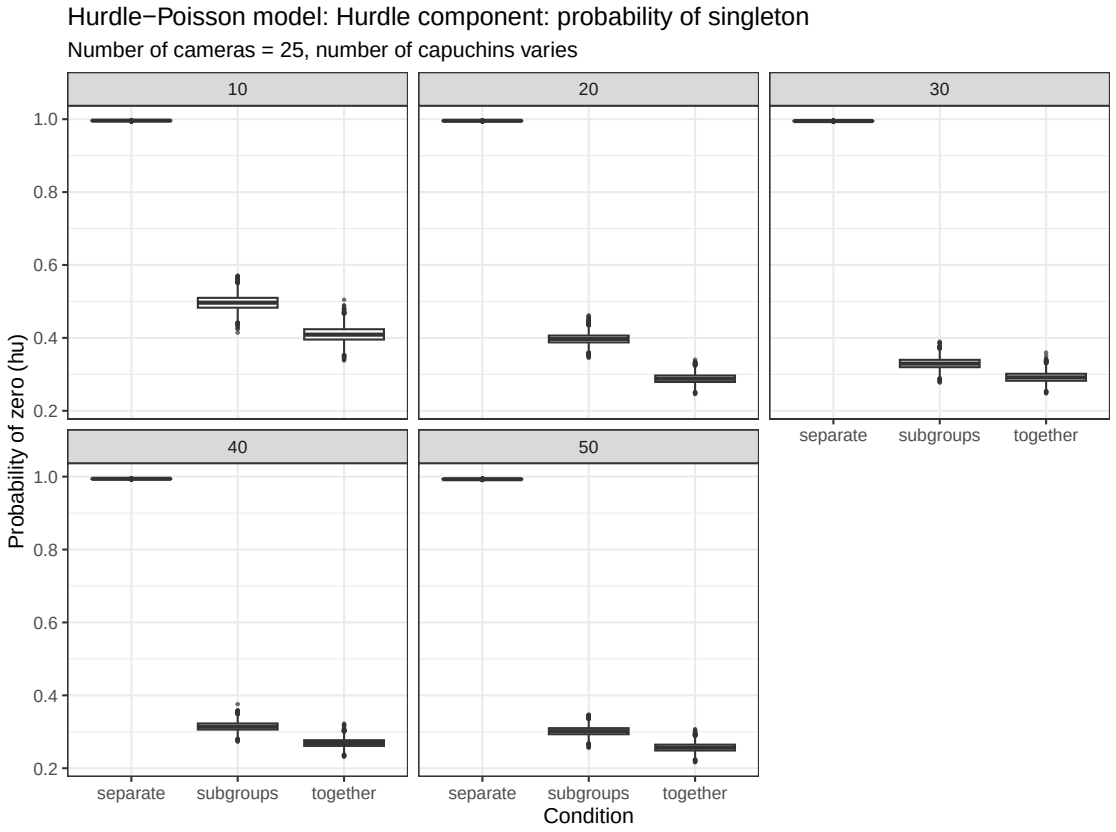


Figure S4: Variability in model estimates of probability of a social party size of 0 (singleton) in the simulated data with varying number of capuchins (10-50) but same number of cameras (25).

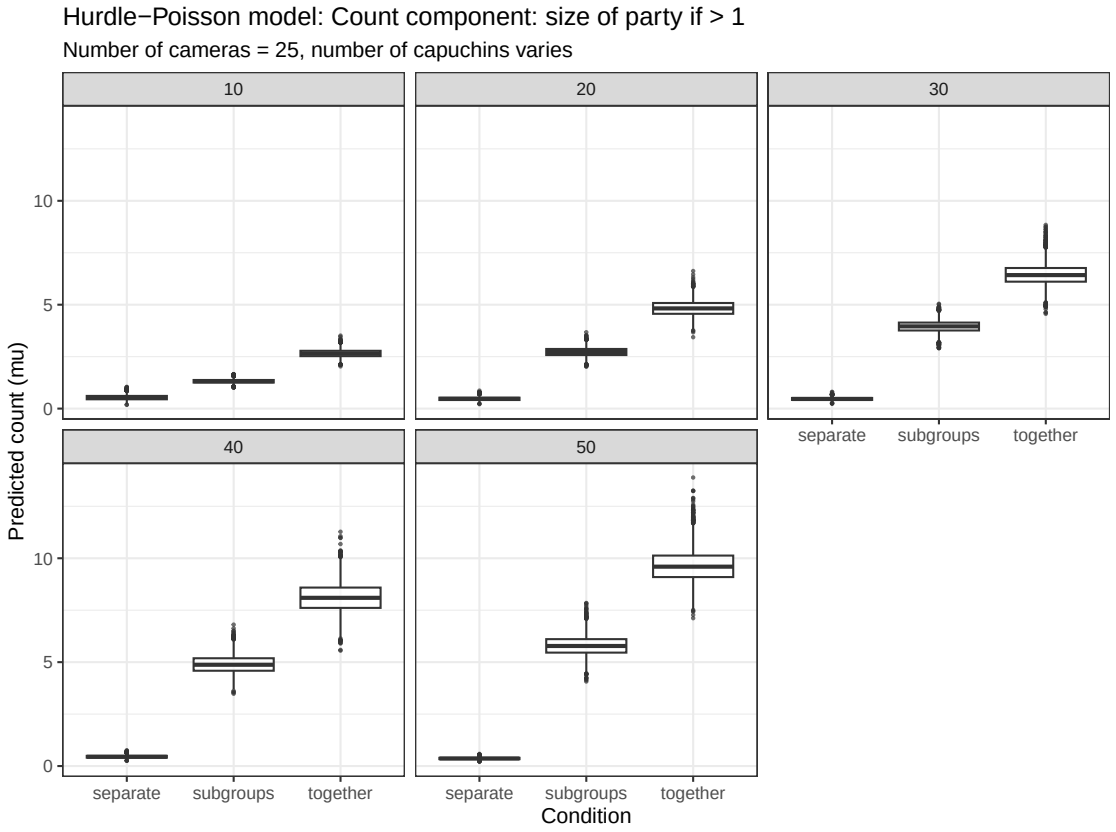


Figure S5: Variability in model estimates of social party size if >0 in the simulated data with varying number of capuchins (10-50) but same number of cameras (25).

## 2.2 Models estimating party composition

Table S3: Posterior mean model estimates of Model pc_bm1, a hurdle Poisson GLMM (Bayes $R^2 = 0.04$) comparing the number of adult females in a party between the tool-using (TU) and non-tool-using group (NTU, the reference category). All estimates are on the log scale.

| | *Estimate* | *Est. Error* | *CI_95_low* | *CI_95_high* |
|---|---|---|---|---|
| *Multilevel Hyperparameters* | | | | |
| locationfactor (levels: 49) | | | | |
| sd(Intercept) | 0.29 | 0.05 | 0.20 | 0.40 |
| *Regression Coefficients* | | | | |
| Intercept | -1.04 | 0.08 | -1.21 | -0.88 |
| gridtypeTU | -0.23 | 0.12 | -0.46 | -0.00 |
| nAM | 0.09 | 0.07 | -0.04 | 0.22 |
| gridtypeTU:nAM | -0.29 | 0.12 | -0.54 | -0.05 |
| *Further Parameters* | | | | |
| zi | 0.01 | 0.01 | 0.00 | 0.05 |

Table S4: Posterior mean model estimates of Model pc_bm2, a hurdle Poisson GLMM (Bayes $R^2 = 0.08$) comparing the number of adult males in a party between the tool-using (TU) and non-tool-using group (NTU, the reference category). All estimates are on the log scale.

| | *Estimate* | *Est. Error* | *CI_95_low* | *CI_95_high* |
|---|---|---|---|---|
| *Multilevel Hyperparameters* | | | | |
| locationfactor (levels: 49) | | | | |
| sd(Intercept) | 0.37 | 0.06 | 0.26 | 0.50 |
| *Regression Coefficients* | | | | |
| Intercept | -1.15 | 0.09 | -1.35 | -0.97 |
| gridtypeTU | -0.50 | 0.14 | -0.78 | -0.23 |
| nAF | 0.06 | 0.05 | -0.05 | 0.17 |
| gridtypeTU:nAF | -0.29 | 0.12 | -0.53 | -0.05 |
| *Further Parameters* | | | | |
| zi | 0.01 | 0.01 | 0.00 | 0.03 |

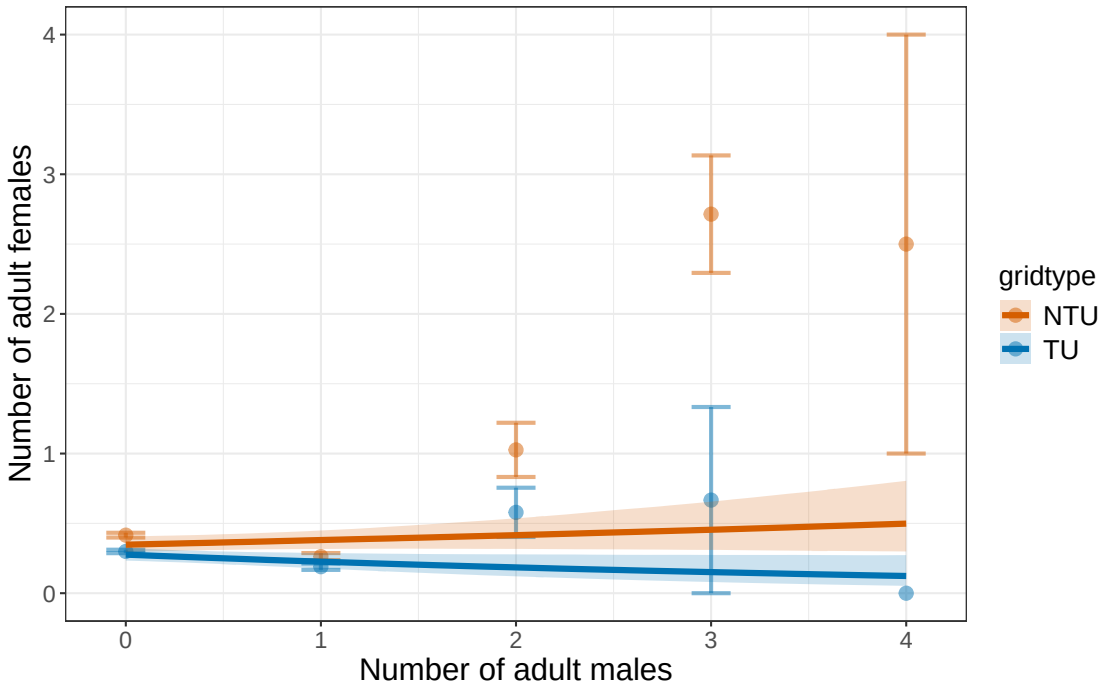


Figure S6: Model estimates from zero-inflated Poisson GLMM of relationship between number of adult females and number of adult males occurring together in a sequence for tool-using group (orange) and non-tool-using group (green). The bold line reflects the model estimates, with the shaded area representing the 95% confidence interval. Points reflects the means from the real data, with whiskers representing their 95% confidence intervals.

## 2.3 Models estimating spatial cohesion

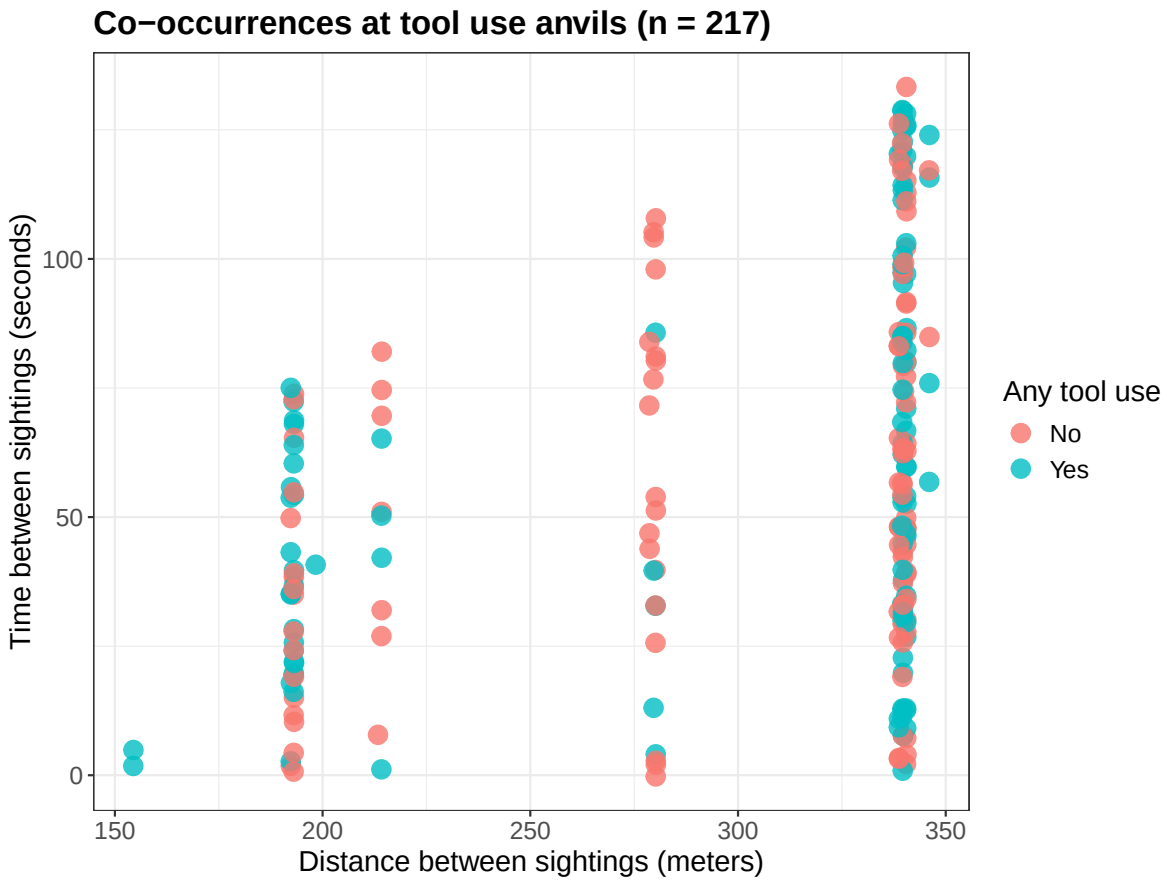


Figure S7: Co-occurrences at the anvil cameras in the tool-using group. Each dot represents the co-occurrence of two sightings. The x-axis reflects the distance in meters between the cameras where the co-occurring sightings were seen, the y-axis reflects the time in seconds between the co-occurring sightings. The color reflects whether tool use occurred in either of the sightings (blue for yes, red for no).

Table S5: Posterior mean model estimates of Model spacetime_bm, a hurdle Gamma GLMM (Bayes $R^2$ = 0.35) comparing the distance and time between subsequent capuchin sightings within the same day between tool-using (TU) and non-tool-using capuchins (NTU, the reference category). The link for the non-zero component of the model (mu) is log, and for the zero component (hu) logit.

| | *Estimate* | *Est. Error* | *CI_95_low* | *CI_95_high* |
|---|---|---|---|---|
| *Multilevel Hyperparameters* | | | | |
| locationfactor (levels: 49) | | | | |
| sd(mu_Intercept) | 0.23 | 0.03 | 0.18 | 0.30 |
| sd(hu_Intercept) | 0.72 | 0.11 | 0.54 | 0.96 |
| *Regression Coefficients* | | | | |
| mu_Intercept | 5.28 | 0.08 | 5.12 | 5.44 |
| hu_Intercept | 3.05 | 0.23 | 2.60 | 3.50 |
| time_log | 0.07 | 0.02 | 0.04 | 0.10 |
| mu_gridtypeTU | 0.10 | 0.11 | -0.12 | 0.32 |
| mu_time_log:gridtypeTU | -0.01 | 0.02 | -0.04 | 0.03 |
| hu_time_log | -1.18 | 0.06 | -1.29 | -1.07 |
| hu_gridtypeTU | -0.74 | 0.32 | -1.36 | -0.13 |
| hu_time_log:gridtypeTU | 0.14 | 0.07 | -0.01 | 0.29 |
| *Other parameters* | | | | |
| shape | 3.84 | 0.13 | 3.59 | 4.09 |

Table S6: Posterior mean model estimates of Model spacetime_sim, a hurdle Gamma GLMM (Bayes $R^2$ = 0.49) comparing the distance and time between subsequent capuchin sightings within the same day simulated data of 20 capuchins moving through a grid of 25 camera traps in three conditions reflecting varying cohesiveness (moving separate, in two subgroups, or together, where separate is the reference category). The link for the non-zero component of the model (mu) is log, and for the zero component (hu) logit.

| | *Estimate* | *Est. Error* | *CI_95_low* | *CI_95_high* |
|---|---|---|---|---|
| *Multilevel Hyperparameters* | | | | |
| camera_id (levels: 75) | | | | |
| sd(mu_Intercept) | 0.14 | 0.01 | 0.12 | 0.17 |
| sd(hu_Intercept) | 0.40 | 0.05 | 0.31 | 0.50 |
| *Regression Coefficients* | | | | |
| mu_Intercept | 3.97 | 0.03 | 3.92 | 4.03 |
| hu_Intercept | 2.50 | 0.09 | 2.33 | 2.67 |
| time_log | -0.01 | 0.00 | -0.02 | -0.01 |
| mu_condition_subgroups | -0.25 | 0.05 | -0.35 | -0.15 |
| mu_condition_together | -1.02 | 0.07 | -1.15 | -0.89 |
| mu_time_log:condition_subgroups | 0.05 | 0.01 | 0.03 | 0.06 |
| mu_time_log:condition_together | 0.19 | 0.01 | 0.03 | 0.06 |
| hu_time_log | -1.73 | 0.02 | -1.76 | -1.69 |
| hu_condition_subgroups | 2.30 | 0.15 | 2.01 | 2.59 |
| hu_condition_together | 3.48 | 0.22 | 3.06 | 3.93 |
| hu_time_log:condition_subgroups | -0.11 | 0.04 | -0.19 | -0.03 |
| hu_time_log:condition_together | -0.25 | 0.06 | -0.37 | -0.14 |
| *Other parameters* | | | | |
| shape | 5.16 | 0.05 | 5.06 | 5.25 |

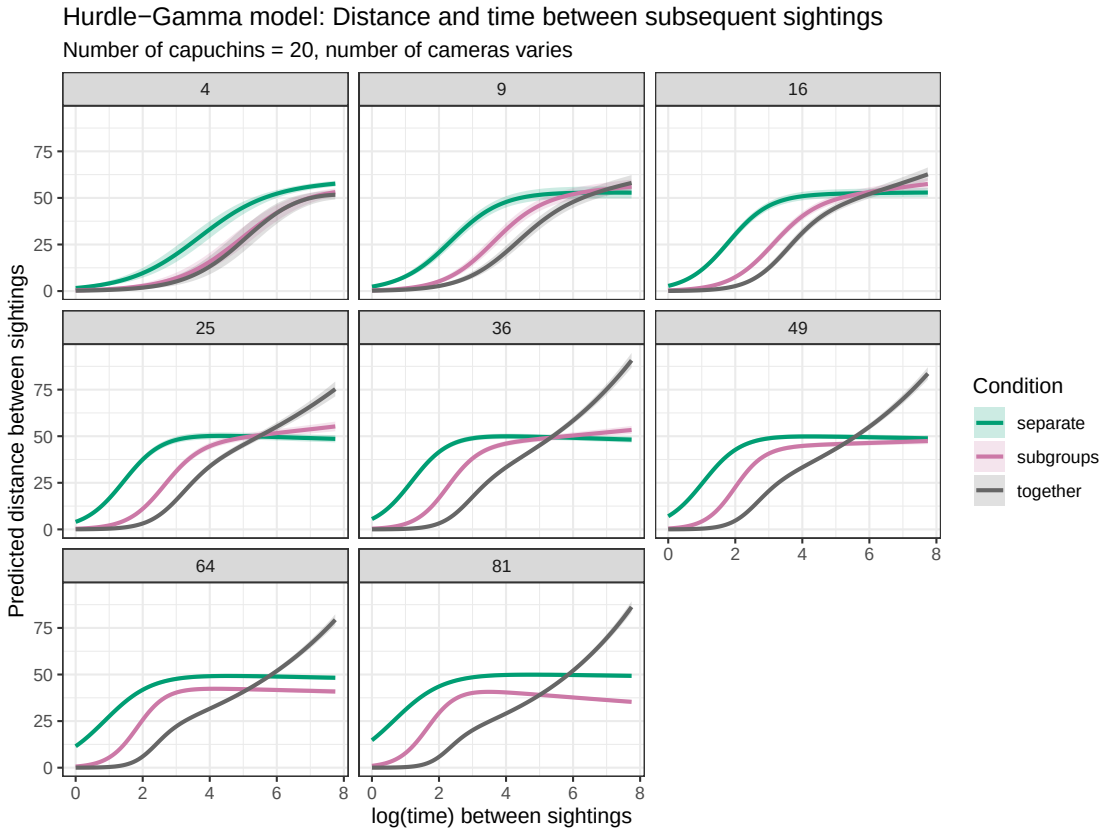


Figure S8: Variability in model estimates of interaction between distance and time between subsequent sightings in the simulated data with varying camera traps (4-81) but same number of capuchins (20).

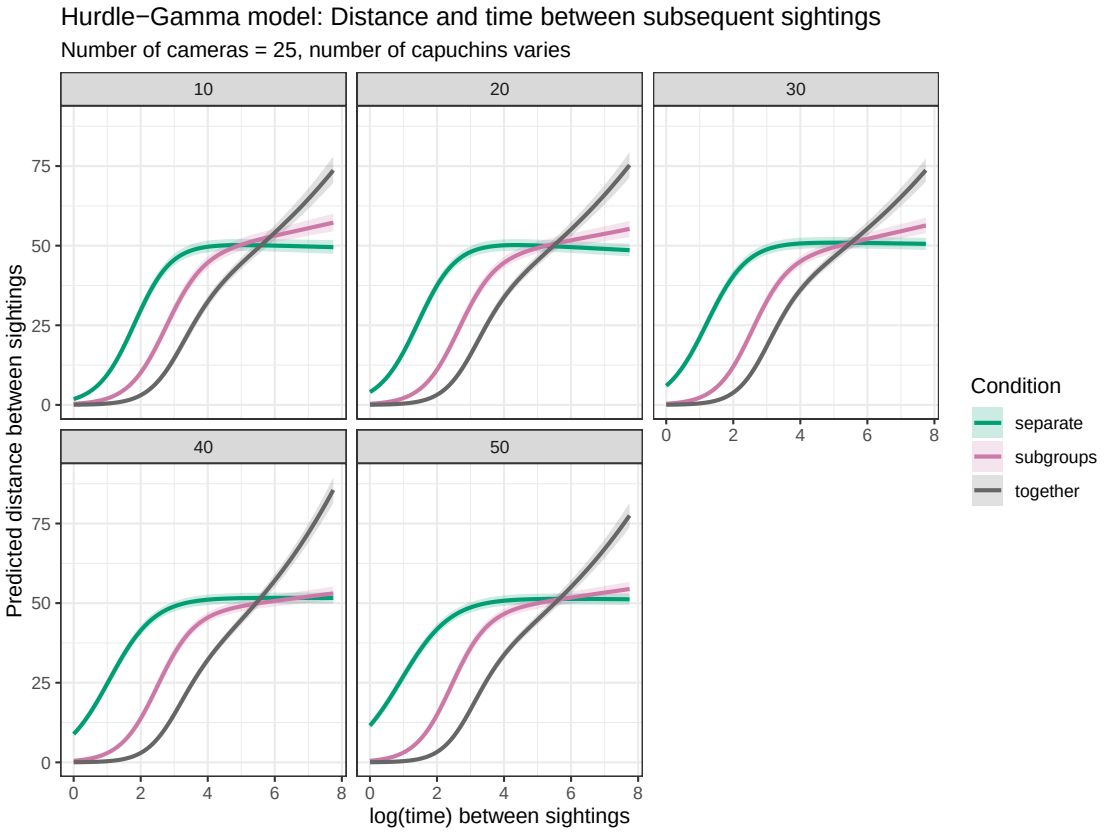


Figure S9: Variability in model estimates of interaction between distance and time between subsequent sightings in the simulated data with varying number of capuchins (10-50) but same number of cameras (25).