Habitual tool use on monopolizable resources affects group cohesion

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Abstract

Tool-aided extractive foraging changes animals' interactions with their environment by expanding access to novel and/or high-quality foods. If and how habitual reliance on tool use impacts animals' social dynamics is less understood. If materials for tool use are monopolizable, tool use might increase intragroup competition. While higher intragroup competition encourages greater group spread, this lower cohesion comes at the cost of increased vulnerability to predation and intergroup competition. We examined how use of spatially fixed, monopolizable resources (i.e., anvils) influences group cohesion by comparing groups of tool-using and non-tool-using white-faced capuchins (*Cebus capucinus imitator*) living on Jicarón island in Coiba National Park, Panama. Jicarón lacks terrestrial mammalian predators and habitual stone tool use at spatially fixed anvils is locally restricted to a ∼1.5 km coastal stretch. We deployed two grids of 24-25 camera traps to compare daily activity patterns, as well as temporal variation in party size, party composition, and spatial cohesion between tool-using and non-tool-using capuchins. We found that tool-using capuchins were more likely to exhibit smaller and less variable party sizes than non-tool-using capuchins, and that adult females and adult males were less likely to co-occur in a sequence. Tool-using and non-tool-using capuchins showed different spatiotemporal cohesion; consistent with a more cohesive non-tool-using group and fission-fusioning or less cohesive tool-using group. Although only male capuchins use tools, the entire tool-using group appears to show reduced cohesion, suggesting that increased competition experienced by one sex can have cascading effects on all group members. Our findings suggest that habitual tool use relying on spatially fixed, monopolizable resources incentivizes higher group spread, creating differences in the social environment of tool-using and non-tool-using animals sharing the same habitat.

Introduction

While hammerstone and anvil tool use has been observed in multiple primate species (chimpanzees [*Pan troglodytes* [1]], macaques [*Macaca fascicularis* spp. [2, 3]], tufted capuchins [*Sapajus* spp. [4]], and white-faced capuchins [*Cebus capucinus imitator* [5, 6]]), there is great behavioral variation. For example, hammerstone and anvil tool use for nut-cracking has only been observed in 22 of 144 studied wild chimpanzee communities [7]. In white-faced capuchins, another species that has been the subject of numerous studies across its distribution range, habitual stone tool use only occurs on two neighboring islands in the Pacific ocean [5, 6]. On one island, tool use is entirely male-biased [8]. Tool use can be valuable from an individual fitness perspective. It allows access to novel and/or high-quality food items [9, 10], and can spread between individuals via social learning [11–14]. Several hypotheses have been proposed to account for the observed variation in the emergence of tool use across populations [15]: i) *necessity*: tool use emerges as a response to decreased resource availability, ii) *opportunity*: tool use develops in environments with appropriate conditions for tool use (e.g., stones that can be used as a hammer, decreased predation), and iii) *limited invention*: tool use may only emerge rarely and relies on observational learning to spread. The last hypothesis was proposed by Fox and colleagues [15] to account for variation in the emergence of tool use between populations in the absence of any ecological explanation. Furthermore, the *relative profitability hypothesis* combines the opportunity and necessity hypothesis, stating that tool use will arise when it is more profitable than strategies without tools [16]. In later expansions of these hypotheses, it was proposed that the social and cognitive factors influencing (the transmission of) tool use are crucial to its emergence, with social tolerance mentioned as being most important [17].

Social tolerance and social demography play important roles in the spread of tool use behavior as they structure opportunities for social learning. The influences of social demography and tolerance on cultural transmission have been considered theoretically [18] and experimentally [19–21]. However, what is less well-understood is how the existence of a social tradition like tool use can affect the social dynamics of the group in which it occurs. Particularly in the case of hammerstone and anvil tool use, a habitual reliance on tool use at anvils might result in increased intragroup competition as anvils and many food resources are both *spatially fixed* and *monopolizable*,. One study in bearded capuchin monkeys (*Sapajus libidinosus*) found evidence for this hypothesis. For females of this species, using tools to crack nuts at fixed anvil sites was linked to an increase in intragroup contest competition, even though the social structure of the study population was comparable to that of non-tool-using populations [22]. The authors predicted that, in group-living species, tool use that results in usurpable food resources will increase contest competition.

This hypothesis has not yet been evaluated in other species, perhaps due to the difficulty of ruling out ecological factors driving the (non-)emergence of tool use and thus finding suitable comparisons. If tool use can indeed increase intragroup competition, how could this competition be mitigated, and what effect would it have on the social dynamics of a group? Living in a social group is beneficial in a myriad of ways, including better outcomes of intergroup competition, decreased predation risk, higher discovery rates of novel habitats and resources, and increased mating opportunities [23, 24]. However, living in groups also comes with drawbacks, which, in addition to more resource competition within the group, also includes higher risk of disease and infanticide [23].

A possible route to reduce intragroup competition is to be less socially cohesive. While higher intragroup competition encourages greater group spread, lower cohesion comes at the cost of increased vulnerability to predation and intergroup competition. One way to still enjoy the benefits of a smaller group, while also still profiting from those of a larger group, can be to be more flexible in spatiotemporal associations with group-members. The extent of variation in spatial and temporal cohesion of group members are called fission-fusion dynamics, which is a multi-dimensional, flexible concept reflecting *temporal variation* in i) spatial cohesion among group members, ii) party size and, iii) party composition [25]. Fission-fusion behavior is characterized by fission (a group splitting into smaller subgroups) and fusion (subgroups coming together into a larger group) events [26]. It is flexible and not necessarily consistent within species [25]. A higher degree of fission-fusion behavior can occur in response to environment, such as reduced predation risk, or more dispersed food resources. One study comparing two species of *Sapajus* capuchins found that the species living in an area with 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 [27]. In various primate species, fissioning was found to occur more frequently when food resources were scarce [28–30].

One study system where all these factors may be disentangled from one another is white-faced capuchins (*Cebus capucinus imitator*) living on Jicarón island, Coiba National Park, Panama. It and the neighboring island of Coiba are the only two sites in the world where white-faced capuchins are known to habitually show hammerstone and anvil tool use [5, 6]. On Jicarón, tool use is localized to an approximately 1.5 km stretch of coast, occupied by a maximum of three capuchin groups [31]. 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 [5]. It is therefore possible to directly compare tool-using and non-tool-using groups of the same species sharing the same habitat. Furthermore, since tool-use is entirely male-biased on Jicarón (though not on Coiba) [8], it means that only males would be expected to experience this increase in intragroup competition, which could have cascading effects on both within- and between-sex social interactions. The absence of terrestrial predators (i.e. large cats and mustelids) and large venomous snakes on this island reduce the constraint of group spread imposed by predation risk.

Several unusual features of the environment on Jicarón are expected to affect the social dynamics of the capuchins that live there. Terrestrial mammalian predators are entirely absent on Jicarón, and there is only one predatory snake species (*Boa constrictor*) which appears to occur at low densities. Perhaps as a result of this reduced predation risk, capuchins on Coiba and Jicarón are more terrestrial than mainland populations[32, 33]. Capuchins also live at high density [5, 32], something which may lead to more relaxed intergroup interactions [34] — though on Barro Colorado Island, capuchins occur at high density yet have more intense intergroup encounters (M. Crofoot, pers. comm.). Predation pressure and intergroup competition are two major factors driving group cohesion [24, 35]. Their absence may relax these pressures on Jicarón, leading to capuchins here having lower group cohesion than mainland capuchins. In long-term study sites on the mainland, white-faced capuchins are generally described to forage as a group, moving from food patch to food patch and resting together (e.g. grooming, playing) at the hottest part of the day [36]. White-faced capuchins are known to scatter widely while foraging [37, 38], but individuals do not travel independently of other group members and remain in contact via frequent vocalizations [38]. As such, they are not generally described as a species with a high degree of fission-fusion behavior. Similar to the comparison of two *Sapajus* species [27], reduced predation pressure on Jicarón may favor more frequent fission-fusion behavior and lower social cohesion. As such, we expect that capuchins on Jicarón might overall be less socially cohesive than mainland capuchins. However, there might also be differences within the island, namely between tool-using and non-tool-using groups. Comparable to findings by Verderane and colleagues in *Sapajus* [22], there might be increased competition over spatially fixed, usurpable anvil sites. Competition over fixed sites may favor foraging solo or in less cohesive groups, as it allows individuals to reduce competition over anvils with group mates. The stone tool use on Jicarón appears to be a largely solitary activity ([39]), which would support the hypothesis that individuals reduce competition over anvils by reducing social cohesion.

Hypotheses and predictions

Here we test the hypothesis that the use of spatially fixed, monopolizable resources (i.e., anvils) influences group cohesion by comparing one group of tool-using and one group of non-tool-using white-faced capuchins (*Cebus capucinus imitator*) living on Jicarón island in Coiba National Park, Panama. Using two grids of camera traps, we compare daily activity patterns and fission-fusion dynamics between tool-using and non-tool-using capuchins. Following Aureli and colleagues [25], we measure degree of fission-fusion dynamics through temporal variation in three dimensions: 1) party size, 2) party composition, and 3) spatial cohesion. 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. If competition is limited to the tool-using males, they might split off from the group to go use tools at specific times of day. However, changes in capuchin males' movement and motivation can also affect overall group cohesion. Thus it is also possible that the whole tool-using group will be less cohesive and/or splits into multiple subgroups throughout the day. In Table 1 we detail how these different possibilities translate to explicit predictions for each of the dimensions of fission-fusion dynamics.

Methods

Site

Jicarón island (2002 ha) 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.*)[5]. Tool use occurs at three types of sites, distinguished from one another through activity and intensity of tool use, and how debris accumulates at the site: 1) ephemeral sites, such as the intertidal zone, with low accumulation, 2) sites in streambeds with sporadic tool use resulting in low to medium accumulation, and 3) high accumulation sites, also known as 'anvils', away from streambeds where tool use activity is high and consistent, resulting in large amounts of debris accumulating over time [5]. Habitual stone tool use is limited to a ∼1.5 km stretch of coast inhabited by an estimated 3 social groups [31]. Of these three groups, only one shows tool use at high accumulation sites. The other two

Hypotheses	*Predictions*	
	TU males split off from cohesive main group	*TU overall less cohesive/splits into multiple subgroups*
H1 — **Party size**: More cohesive groups have larger party sizes on camera traps	**P1a_males**: TU more single party detections than NTU	**P1a_group**: TU more single party detections than NTU
	P1b_males: NTU larger average party size than TU	**P1b_group**: NTU larger average party size than TU
H2 — **Party size variability**: Variation in daily part size conditional on group cohesiveness	**P2a_males**: TU has higher standard deviation in party size per day than NTU (due to whole group vs single captures)	**P2a_group**: NTU has higher standard deviation in party size per day than TU (due to subgroups captures in TU)
H3 — **Party composition**: More cohesive group has more diverse party composition	**P3a_males**: TU parties fewer adult males and females together than NTU parties	**P3a_group**: TU parties fewer adult males and females together than NTU
	P3b_males: TU parties fewer adult males than NTU parties	**P3b_group**: TU parties fewer adult males than NTU parties
	P3c_males: No difference in number of adult females in TU and NTU party	**P3c_group**: TU parties fewer adult females than NTU parties
H4 — **Spatial cohesion**: Cohesive group higher correlation between close distance sightings, rapid decay at greater distances	**P4_males**: TU group has both a high correlation at close distances, and high correlation at distant cameras	**P4_group**: TU group has a slower decay of correlation between sightings with distance than NTU group
H5 — **Spatiotemporal cohesion**: Cohesive group has strong spatiotemporal correlation between sightings	**P5_males**: TU group has both high frequency of sightings close in space and time, as well as occurrence of sightings close in time but far apart in space	**P5_group**: TU group has fewer sightings close in space and time, and occurrence of sightings close in time but far apart in space

Table 1: Overview of hypotheses and predictions for dimensions of fission-fusion behavior, differentiating between expected patterns of the tool-using (TU) and non-tool-using (NTU) group in two scenarios. First, if males split off from a cohesive group to use tools, or second, if the whole tool use group is less cohesive and splits into smaller subgroups.

neighboring groups have recently been observed to use tools in the intertidal zone (C. Monteza-Moreno, pers. comm., 2023).

The group of capuchins who use tools at anvil sites, who from here on out will be referred to as the 'tool-using group', have been showing hammerstone and anvil tool use since at least 2004 [5]. They have been monitored using unbaited camera traps since 2017, with most sampling efforts focusing on 10 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 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` [40], `raster` [41] and `mapview` [42]). For the tool-using group, due to the high sampling since 2017, we had some information about their home range, 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 almendra trees), resulting in a location 3 kilometers away on the opposite shore of the island. We 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 very challenging and steep topography on Jicarón, we did not know which locations would be physically possible to reach, and as such we aimed to have a range of randomly selected, equally spaced camera locations to try, and see how many would be possible to place. The placement went as followed: we navigated to a pre-designated 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 the same 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 [43], 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 [44]. 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 individuals from their social group. 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. To be conservative, 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 [45] based on the co-occurrences of these identifiable individuals in the same sequence (Figure 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 2.

Estimated numbers	*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

Table 2: Estimated average group size and composition of the tool-using group and non-tool-using group sampled by grid cameras.

Statistical analyses

We ran all analyses in R v. 4.3.1 [46]. All Bayesian regression models were fit via the `brm` function in the `brms` package v. 2.16.1 [47]. 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[48]. We considered what proportion of the posterior probability (PP) of the contrast was greater than 0, using a cut-off of 0.89 to reflect a strong reliable effect. 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 [47] and Rhat values ≤ 1.01 [49]. We visually assessed model fit and confirmed our choice of priors using the posterior predictive check function.

Intra-diel activity

First, we compared intra-diel activity of tool-users and non-tool users using the `activity` package v. 1.3.4 in R [50]. We expressed capuchin activity relative to sunrise, and then fit an activity model for the tool-using and non-tool-using groups separately, with 1000 repetitions. We estimated the overlap between the two activity curves using the coefficient of overlap method [51], where 0 reflects no overlap and 1 complete overlap.

Party size

With the term ‘party size’ we refer to the number of capuchins captured in a sequence together. Data was heavily 1-inflated — 68.94% 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. From here on we will 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.

To consider temporal variation in party size, we examined party size variability within a single day as well as fluctuations in party size depending on the time of day. First, to examine variability in party size, we calculated the standard deviation in party size per day for each camera, as cameras differ in their likelihoods to capture large parties due to their varying detection distances. We excluded data when only one party was detected at a camera on a given day, and thus no standard deviation could be calculated. Due to the high occurrence of standard deviations of 0 (mostly resulting from two parties of the same size being observed at a camera in one day), we ran a hurdle-gamma GLMM (*model ps_ bm1b*), with the same predictors for the zero and non-zero component of the model. The outcome was the standard deviation in party size, and the predictors were the grid location (tool-using or non-tool-using group), a random effect of the camera location, and as an offset the log of the number of parties observed at the camera that day. Second, we considered how party size fluctuated depending on the time of day to test the hypothesis that the tool-using group was sleeping together (larger party sizes in the morning and evening) and splitting up during the day. To model this, we ran a hurdle-poisson GAM (*model sps_ gam1*), using the social party size (where 0 reflects a party of one) as the outcome. For the hurdle (zero) part, we used the grid location and a random effect of camera location as predictors. For the non-zero part, we included the same predictors as for the hurdle part, with the addition of a smooth of the hour of day, estimating a separate smooth for each grid location. Additionally, we considered the locations of the first and last sightings of the day, to examine if the sleep site of the capuchins was likely captured in our grid.

Party composition

Due to the limited view of the camera traps and quick passage of many individuals, reliable aging and sexing of individual capuchins was not feasible in all sequences. We were unable to reliably estimate age or sex in 23% 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 94% 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. We hypothesized that the number of adult females and number of adult males occurring together in a party would differ depending on the cohesion of the group. As these variables contained many 0s (ranging from 66-81%), and these 0s could both reflect true absence as well as be a result of sampling (i.e., an unknown capuchin is actually an adult female), we decided to use 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

We quantified temporal variation in spatial cohesion in several ways. Firstly, we ran two regressions where we modeled camera trap location as a Gaussian process for each grid location (*model gp_ tu* and *model gp_ ntu*). This permits us to estimate a unique intercept for camera trap location that models the spatial autocorrelation between traps. From this we can statistically compare how covariance of party sizes decays as a function of the distance between camera trap locations. We posited that in more cohesive groups we would see a higher covariance between camera traps at closer distances and a quick decay at greater distances, whereas with a fission-fusion or less cohesive group covariance would be lower at closer distances and decay slower. These models were fit in R using the `rethinking` package v. 2.13 [52, 53]). We created distance matrices per grid calculating the distance between each pair of cameras in hectometers. In our models, we estimated the party size (number of capuchins detected in a sequence) depending on the camera and distance between cameras. Each Gaussian process regression was run on 4 chains, with 5000 iterations per chain. We then compared posterior estimates of how covariance between cameras decayed depending on distance between the tool-using and non-tool-using group.

To compare covariance in time as well as space between the grid locations, we made several visualizations of 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 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.

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 are fissioned into sub-parties. For instance, triggers of 150 meters apart within 2 minutes would be very unlikely to originate from one cohesive group of capuchins, based on capuchins' travel speed [36]. We identified what we term as 'co-occurrences' by extrapolating this rule (so 300 meters in 4 minutes, and so on) and flagging observations that occurred within these criteria. For both the tool-using and non-tool-using group, we considered the frequency of co-occurrences, as well as how many individuals were present in each of the observed parties. 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 [54].

Data availability

Details of model output are available in supplementary material. All code and data necessary to replicate analyses can be found at https://github.com/ZoeGold/capuchingroupcohesion.

Results

Intra-diel activity

Tool-using and non-tool-using groups had a coefficient of overlap of 0.90 of their daily activity (Figure 1). The non-tool-using group showed more activity in the morning, and the tool-using group in the afternoon. A striking difference is the presence of night (after sunset and before sunrise) activity by the tool-using group, which was entirely absent in the non-tool-using group. We had a total of six sequences showing capuchins from the tool-using group traveling on the ground between 19:00 and 05:00.

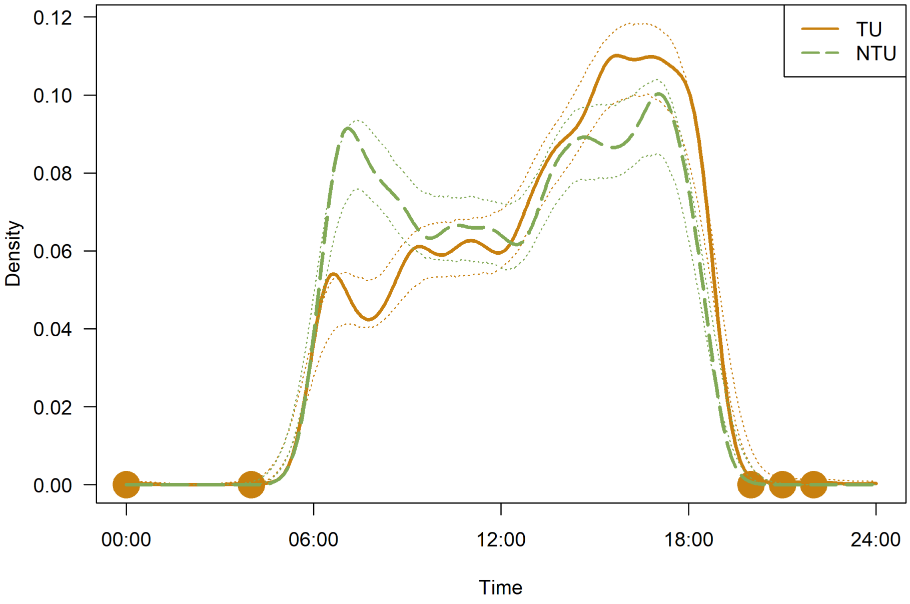

Figure 1: Density plots of daily activity of tool-using group (in orange) and non-tool-using group (in green). The thick line reflects the model estimates, and the dotted lines the 95% confidence intervals. Circles are used to represent the observations of capuchins during the night.

(Social) party size

In the tool-using group, we never observed a total party size larger than 10 individuals, while at the non-tool-using group the largest party size was 16. When comparing the social party size (where parties of 1 are reflected as a 0, and each number above 0 reflects the number of other partners available), we found different results for the zero and non-zero component of the model (Figure 2 and Figure S2, for model estimates see Table S1). Singletons were slightly more common in the tool-using group than the non-tool-using group, although this effect was not reliable (i.e., less than 89% of the posterior was on one side of 0). The model estimated a 1.8% increase (PP $> 0 = 0.69$) in the likelihood 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. The non-zero component of the model reliably estimated larger social parties (PP $> 0 = 0.96$) in the non-tool-using group (estimate $= 1.36$, 95% CI [1.10, 1.64]) than in the tool-using group (estimate $= 1.05$, 95% CI [0.83, 1.28]).

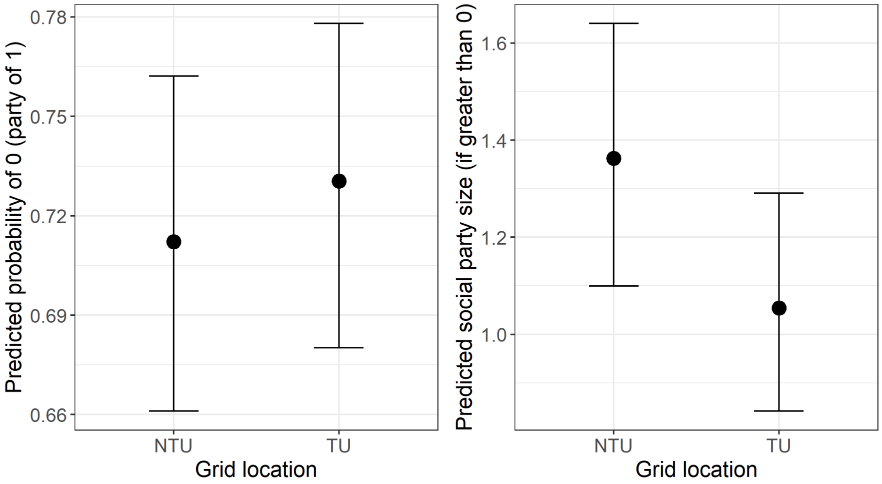

Figure 2: Model estimates from hurdle-Poisson model comparing mean social party size between the tool-using (TU) and non-tool-using group (NTU). On the left are model estimates of the zero (hu) component of the model, and on the right of the non-zero (mu) component. Points reflect averages estimated by the model, and the whiskers the 95% confidence interval.

The non-tool-using group showed more within-day variation in party size than the tool-using group (for estimates Table S2). Our model estimated a reliably (PP $> 0 =$ 0.95) larger standard deviation in party size in the non-tool-using group (estimate $=$ 1.50, 95% CI [1.29, 1.72]) than the tool-using group (1.27, 95% CI [1.08, 1.45]). Taking a closer look at how social party size fluctuated within a day, we found that the non-tool-using group had a slightly higher social party size during the day than in the mornings and evenings (Figure 3 for model estimates see Table S3). The tool-using group showed a slight increase in social party size as the day progressed, with highest estimated social party sizes in the evening. 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, suggesting that this is likely a sleep site captured within the grid. For the non-tool-using group there was no single camera location with much greater capuchin activity in the early morning and late evening.

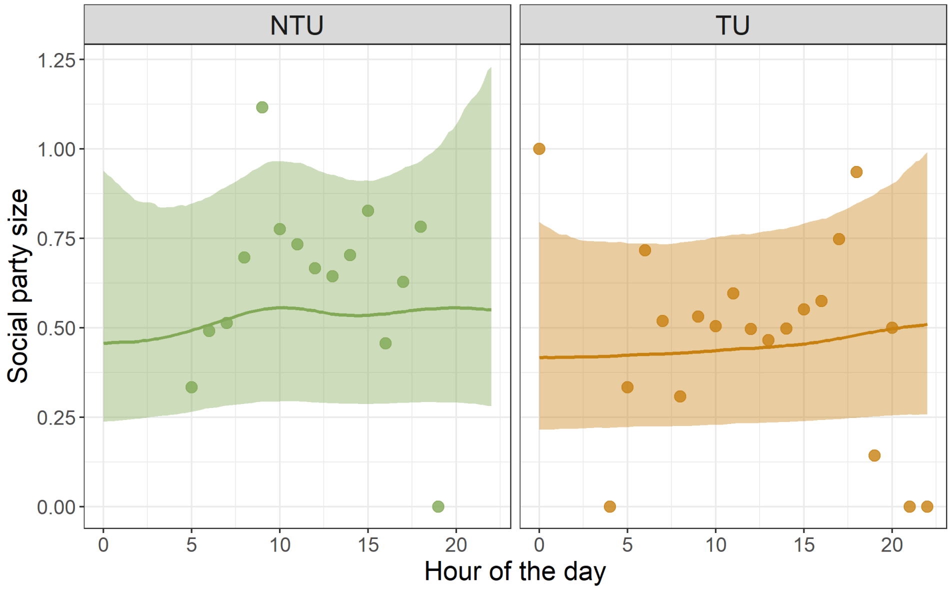

Figure 3: Daily fluctuation in social party size for the non-tool-using group (left in green) and tool-using group (right in orange). Lines reflect the social party size estimated by the hurdle-Poisson GAM, with the shaded area representing the 95% confidence interval. Points reflect the true means from the data.

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 S4). Our model estimated a higher mean number of adult females present in a sequence in the non-tool-using group (0.26 95% CI [0.31, 0.42]) than in the tool-using group (0.26, 95% CI [0.22, 0.31]), and this effect was reliable ($PP > 0 = 0.98$). Adult males were also more likely to be seen together in the non-tool-using group than in the tool-using group (for model estimates see Table S5). Our model comparing the number of adult males estimated 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 [0.14, 0.22]), and this effect was reliable ($PP > 0 = 1$). 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 Figure S3). 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

Covariance in space

Our Gaussian process regressions estimated greater covariance between party sizes at neighboring cameras for the tool-using group than the non-tool-using group (Figure 4 and Table S6 for model estimates). The covariance also decayed slower at the tool-using group than the non-tool-using group, the latter showed little covariance at cameras close together which quickly dropped to no covariance at cameras more than 200 meters apart. The tool-using group also showed greater posterior correlation between camera traps than the non-tool-using group (supplemental Figures S4 & S5)

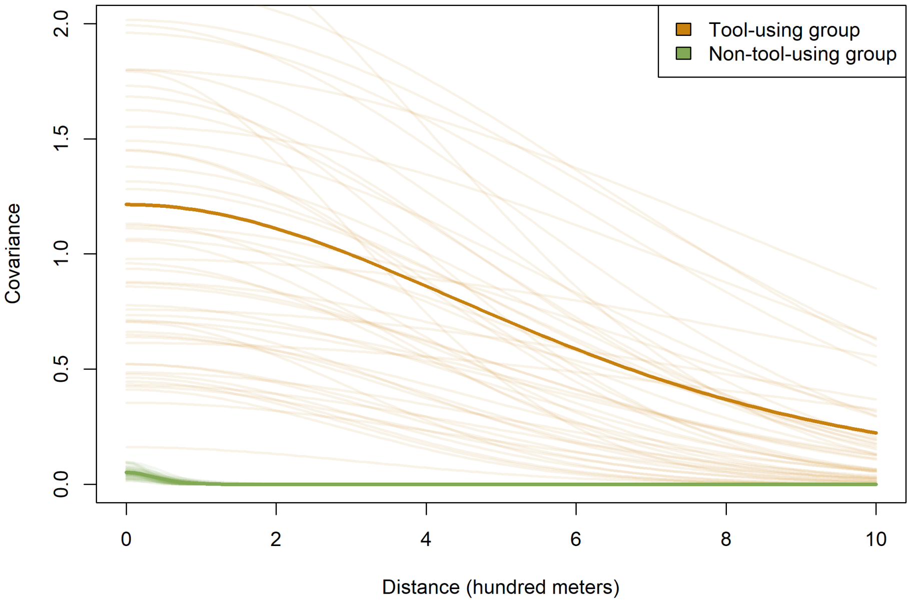

Figure 4: Posterior distribution of the spatial covariance for the tool-using group (in orange) and non-tool-using group (in green). The thick line represents the posterior mean covariance at each distance. The thin curves show 60 functions sampled from the posterior distribution.

Covariance in space and time

When examining the time and space between subsequent sightings of capuchins within the same day, a different pattern emerged for the tool-using and non-tool-using group (Figure 5). For both groups, if the subsequent sighting was at the same camera, in most cases only little time had passed. We observed slightly more occurrences of longer times at the non-tool-using group than tool-using group, but overall the distributions look very similar. However, we observed clear differences when considering when the subsequent sighting occurred at a different camera. For the non-tool-using groups, most subsequent sightings at a different camera were at cameras both close in space and in time, with subsequent sightings at great distances but close in time occurring less frequently. For the tool-using group, we see a greater frequency of detections that are far in space but close in time. These different patterns are also visible in our animation of capuchin sightings (online supplement). 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, more in line with capturing several subgroups rather than one big group. Using a cut-off time of 60 seconds at 150 meters, we found 26 co-occurrences in the tool-using group and 15 in the non-tool-using group (Figure S6)

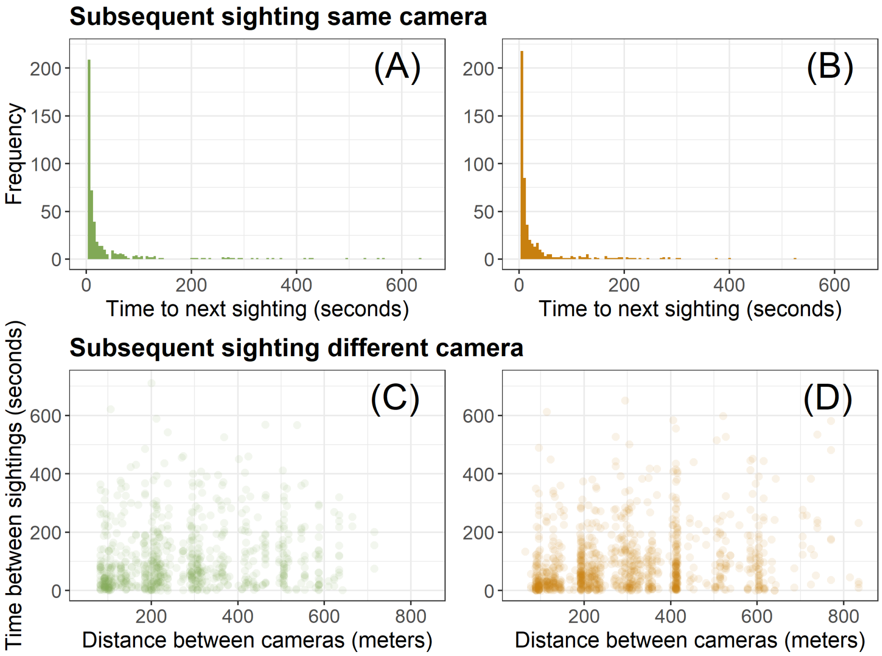

Figure 5: Subsequent capuchin sightings within a day for non-tool-using (green) and tool-using groups (orange). (A, B) show time to next sighting at the same camera; (C, D) show time and distance to next sighting at a different camera. Each dot represents one sighting.

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. Following our hypotheses (Table 1), we suggested two ways in which the tool-using group could be less cohesive to avoid competition over anvils: tool-using males could split off from a cohesive main group to use tools, or the entire tool-using group could be less cohesive and/or split into smaller groups. 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 group.

We measured cohesion following Aureli and colleagues [25] as temporal variation in i) party size, ii) party composition and iii) spatial cohesion. Our findings regarding party size all support the entire tool-using group being less cohesive and/or splitting into smaller subgroups. The tool-using group had a higher likelihood of party of one detections, and smaller and less variable party sizes than the non-tool-using capuchins. Our finding of the tool-using group showing higher party sizes in the evening suggests that they likely still sleep together. The differences in party composition between the two grids — despite comparable group composition — also supported the hypothesis of a cohesive non-tool-using group, and tool-using group which is less cohesive or splits. Capuchin parties in the tool-using group had fewer adult males, fewer adult females, and fewer adult males and females present together than parties in the non-tool-using group. Spatially, the tool-using group showed stronger covariance in party sizes between cameras at all distances, while the non-tool-users only showed little covariance at close cameras and none at distant cameras. The spatiotemporal patterns of detection and co-occurrences further qualitatively support a more cohesive non-tool-using group and a more fragmented tool-using group.

Tool use linked to reduced group cohesion

Our findings provide the first evidence for a potential link between habitual tool use at monopolizable anvils and reduced group cohesion. The tool-using group and non-tool-using groups sampled here are of comparable group size and composition, inhabit the same habitat with only 3 kilometers between them, and both border the coast, where similar resources are available (e.g., coastal species like sea almonds, as well as intertidal resources). Yet they differ behaviorally, since the tool-using group has a habitual stone tool use tradition which has persisted over two decades [5], and here we also show how the social cohesion of these two groups also differs. It seems plausible that, on Jicarón, similar to what has been observed in bearded capuchins [22], tool use on usurpable food resources has led to increased contest competition, which in turn was alleviated through reduced group cohesion. In the range of the tool-using group on Jicarón, there are at least 10 heavily used anvil sites close to sea almond or coconut trees, which can only be used by one individual at a time [5]. The fixed location of these anvils, combined with their potential to be monopolized suggests these areas are expected to be a source of intragroup contest competition. In a mainland study site, white-faced capuchins of higher rank had higher energy intake than lower ranking individuals due to their success at winning contest competition interactions and ability to displace others from feeding patches [55]. While we do observe individual capuchins displacing others from the anvil and/or hammerstone, displacements are rare in the Jicarón tool-using group [8, 39]). Thus, it appears as if the increased contest competition at anvil sites is either not present — which is unlikely given the high intensity of use — or is alleviated in some other way than through behavioral agonism.

Reduced group cohesion is one way to reduce the intensity of intragroup competition [56, 57]. However, reduced group cohesion can also result from a diminished need for social proximity when the benefits of group living are lower. On Jicarón, where predators are absent and capuchins are more terrestrial as a result [33], the selective pressure to maintain tight social cohesion may be relaxed. As both the tool-using group and non-tool-using group live in this predator-free environment, it is feasible that they are both less cohesive than mainland populations. However, predator absence alone cannot account for the *difference*s in cohesion between the tool-using and non-tool-using group described here, since they share the same ecological context. The most parsimonious explanation for this observed difference in behavior is the presence of habitual tool use at monopolizable anvils. To fully understand the relative contribution of tool use, predation pressure, and effects of island-living on capuchin group cohesion, comparative data from mainland populations and other islands are needed.

Cascading effects of a sex-biased tool use tradition

Despite tool use on Jicarón being restricted to males [8] — and thus only males experiencing contest competition at anvils — our results suggest the whole tool-using group shows reduced group cohesion. Rather than males splitting off from a cohesive group to use tools at an anvil and avoid competition, it appears as if either the entire tool-using group shows fission-fusion behavior and/or has greater group spread than the non-tool-using group. This has several important implications for the social system and behavior of the tool-using capuchins. First, in well-studied populations of white-faced capuchins at mainland sites, female-female social bonds are of great importance, and males are the dispersing sex [36, 58]. While we did not consider social behavior and grooming in this study, we do see that adult females are much less likely to be seen together in the tool-using group than in the non-tool-using group, thus seemingly having fewer opportunities for social contact. It is unclear how social bonds within- and between-sexes in the tool-using group differ from both non-tool-using capuchins on Jicarón, and from what we know from well-studied mainland populations, but this is a fruitful area for future research. Second, the male-exclusive nature of the tool use behavior combined with reduced cohesion likely results in some degree of sexual segregation, at least at anvil sites, where females are observed less frequently than other age-sex classes [8]. This 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 [39], yet the continued persistence of the tool use tradition suggests young individuals are capable of acquiring the behavior.

Implications for intergroup dynamics

One benefit of high group cohesion is more success during competitive encounters with other groups. The reduced group cohesion in the tool-using capuchins may make them less competitive in intergroup encounters. In mainland sites, white-faced capuchins are known to be xenophobic with hostile intergroup encounters [36, 59, 60]. On Jicarón, we know little about the nature of interactions between groups. We have observed (sub)adult males with injuries, but have no evidence whether these were caused by intra- or intergroup aggression, and personal observations suggest intergroup competition is likely more relaxed on Jicarón, as on other islands [61, 62]. 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 ingroup from outgroup members, resulting in lower outgroup aggression [63]. However, higher relatedness would again be able to 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 on intergroup encounters on Jicarón in order to assess whether they are comparable to those between mainland capuchin groups, and to see whether the tool-using group suffers a competitive disadvantage from reduced group cohesion. One possible way to obtain information on these rare events could be to use Passive Acoustic Monitoring (PAM) devices placed at several locations on the island to capture audio data of intergroup encounters, or playback experiments of calls from unknown individuals to see how the capuchins respond. The observed difference in group cohesion within such a small geographic scale (a 2002 ha island) also raises interesting questions regarding dispersal. While the details of the dispersal system on Jicarón are still unclear [5], 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 — potentially with more fission-fusion occurring — 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

There are several challenges to estimating group cohesion using camera traps, some of which can be addressed using statistical methods. Each camera trap has its own detection distance, where an animal passing by results in a trigger. Due to the limited view of camera traps, there is always the possibility of animals being present in the party captured but out of view from the camera trap. This bias is greater at camera traps with small detection distances, and to account for this we included the camera trap location as a random effect in all of our models. Nonetheless, while with our current methods we can show that there is a difference in the group cohesion of the tool-using and non-tool-using group, theoretical models will likely be needed to contextualize this difference. Ideally, one would have comparable data from a grid of camera traps placed in a mainland group of white-faced capuchins, but since capuchins are largely arboreal, such data does not exist. Capuchins' arboreality also means that a lack of detections at ground-level camera traps does not necessarily indicate their absence, since individuals may be present in the canopy. Arboreal camera traps placed on Jicarón — though only in areas with non-tool-using capuchins — found that capuchins were more arboreal during the morning [33, 64]. Placing arboreal camera traps in the tool-using group's range is necessary to assess whether patterns of terrestriality, both in timing and extent, differ between tool-using and non-tool-using groups. This information is also crucial for interpreting some of our results, such as the differing daily activity patterns between tool-using and non-tool-using group (Figure 1).

In the absence of comparable mainland data, modeling the movement of capuchin groups of different levels of cohesion (e.g., a group that fissions versus a cohesive group which stays together) over a grid of camera traps with varying detection probabilities would help contextualize the spatiotemporal patterns in capuchin detection that emerge. Additionally, identifying individual capuchins from camera trap images, especially from cameras with close detection ranges, is very challenging since images are often blurry with only parts of the animal in frame. If all individuals can reliably be identified, camera traps can be used to reliably assess demography and construct robust social networks, which has been demonstrated in chimpanzees [65, 66]. Our analyses would have greatly benefited from better identification of the individuals that were clearly captured, something which will potentially be possible in the future with the development of deep learning facial recognition algorithms. Given the large proportion of capuchins that we could not assign an age-sex to, it is also possible that some sightings were not of the group targeted with the grid, but one of their neighboring groups. This is especially likely in the non-tool-using grid, where we had to establish identities of capuchins during sampling for this study, rather than were able to rely on identification of individuals from years of prior data collection like in the tool-using group. It is important to keep this limitation in mind, since for instance the pattern observed in co-occurences in the non-tool-using group (Figure S6) could also reflect capture of two different social groups, rather than subgroups from the same group of capuchins.

Another important consideration given the nature of our data collection is the home range size of the capuchin groups which we studied. Mainland groups of white-faced capuchins tend to have home ranges of around 1 km^2 [67], and on another island, Barro Colorado Island — though here capuchins can swim to the mainland — home ranges are of comparable size [68, 69]. We lack precise data on the home range sizes of capuchin groups on Jicarón, but the camera trap grids offer some insight into their minimum extent, which appears to be broadly comparable to those reported elsewhere. One possible explanation for the detections at night in the tool-using site, while these were entirely absent in the non-tool-using site, could be that the grid covered more of the tool-using group's homerange. Thus, we may have captured their sleep sites with our grid, which is supported by the much higher frequency of capuchin sightings early in the morning and late in the evening at a specific camera in the tool-using grid. If the tool-using group is truly fissioning during the day, but sleep together, one may expect they have fewer sleep sites or switch them less frequently to allow the group to more easily come back together. Theoretically, the tool-using capuchins could also have a smaller home range as a consequence of their focus on the 10 heavily used anvil sites, as well as exploitation of the intertidal zone. The greater coupling of the tool-using group's coastal activity to the tidal cycles might also result in different spatiotemporal patterns of detections than the non-tool-using group [31]. Future research incorporating these many different drivers of movement is needed to be able to draw more concrete conclusions about the differences in group cohesion.

The motivation to fission

The advantage of using two similar grids of camera traps at the tool-using and non-tool-using group is that we have comparable data between these two groups. However, this design means that the grid cameras do not capture tool use—the hypothesized driver of the reduced cohesion in the tool-using group. To more directly test this hypothesis, data from camera traps placed at anvils—though not the focus of the present study—can offer additional insights into how competition over tool-use sites may influence group cohesion. By showing detections of individuals using tools at different anvils around the same time, we would have more concrete behavioral evidence of fission-fusion behavior in the tool-using group. Furthermore, previous studies have shown that fission-fusion dynamics are highly flexible [25] and can vary seasonally, for instance in response to fluctuations in food availability [28–30]. Tool use on Jicarón likely also has a seasonal component [5], where we see peaks in tool use frequencies in the transitions between wet and dry season (see [39]) The camera traps used in this study were only deployed for about 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 cohesion during this time period of increased competition, and cohesion may increase in times when tool use frequency decreases. Further research is needed over larger timescales to shed light on this, 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.

Conclusion

Our results suggest that habitual tool use can lead to reduced group cohesion as a strategy to reduce intragroup competition over monopolizable anvils. By comparing two groups of capuchins sharing the same environment, but differing from one another in their tool-use behavior, we provide evidence that tool use itself likely drives 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 minimized, such as environments with low predation pressure. On Jicarón, the absence of predators may allow the benefits of fissioning to use tools without competition to outweigh the costs of reduced cohesion like increased vulnerability to predation. While tool use is restricted to males, its effects 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 i) comparing island to mainland groups, either directly or through theoretical modeling, to assess the influence of island-living on group cohesion, ii) integrating data from cameras at anvil sites to directly examine the role of tool use, and iii) conducting longer-term monitoring to capture potential seasonal variation in both tool use and cohesion. Studying these dynamics will provide broader insights into the interplay between social structure and cultural behaviors in primates.

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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).

Supporting information

Animation of capuchin sightings:
https://keeper.mpdl.mpg.de/d/ad41ce04639143589f79/
Figure S1: Social network of the non-tool-using group.
Table S1: Posterior mean model estimates of model *sps_bm1a*.
Figure S2: Posterior distribution from model *sps_bm1a*.
Table S2: Posterior mean model estimates of model *sps_bm1b*.
Table S3: Posterior mean model estimates of model *sps_gam1*.
Table S4: Posterior mean model estimates of model *pc_bm1*.
Table S5: Posterior mean model estimates of model *pc_bm2*.
Figure S3: Model estimates from model *pc_bm1* of relationship between number of adult females and number of adult males occurring together in a sequence.
Table S6: Posterior mean model estimates of models *gp_tu* and *gp_ntu*,
Figure S4: Posterior correlations among cameras in geographic space for the tool-using group, estimated by model *gp_tu*.
Figure S5: Posterior correlations among cameras in geographic space for the non-tool-using group, estimated by model *gp_ntu*.
Figure S6: Co-occurrences of capuchin sightings in the non-tool-using and tool-using group.

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Supplementary information for ‘Habitual tool use on monopolizable resources affects group cohesion’

Zoë Goldsborough, Margaret C. Crofoot, Julián León, Pedro Luis Castillo-Caballero, Evelyn del Rosario-Vargas, and Brendan J. Barrett

Electronic Supplements

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

Supplemental methods

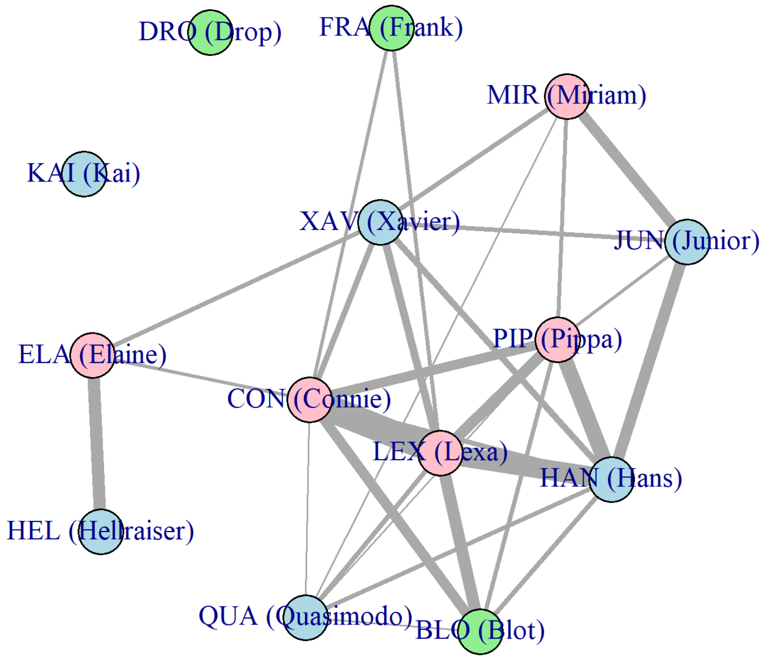

Figure S1: Social network of the non-tool-using group. Each node is an individual, and node color reflects the age-sex category (pink for adult females, blue for adult males, green for subadults and juveniles). If a line connects two individuals, they were observed in the same sequence, the thickness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

Supplemental results

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 party size between the tool-using and non-tool-using group. 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	0.06	0.28	0.53
sd(hu_Intercept)	0.51	0.08	0.37	0.68
Regression Coefficients				
mu_Intercept	0.31	0.10	0.09	0.49
hu_Intercept	0.91	0.13	0.67	1.16
mu_gridtypeTU	-0.26	0.15	-0.54	0.03
hu_gridtypeTU	0.09	0.17	-0.25	0.43

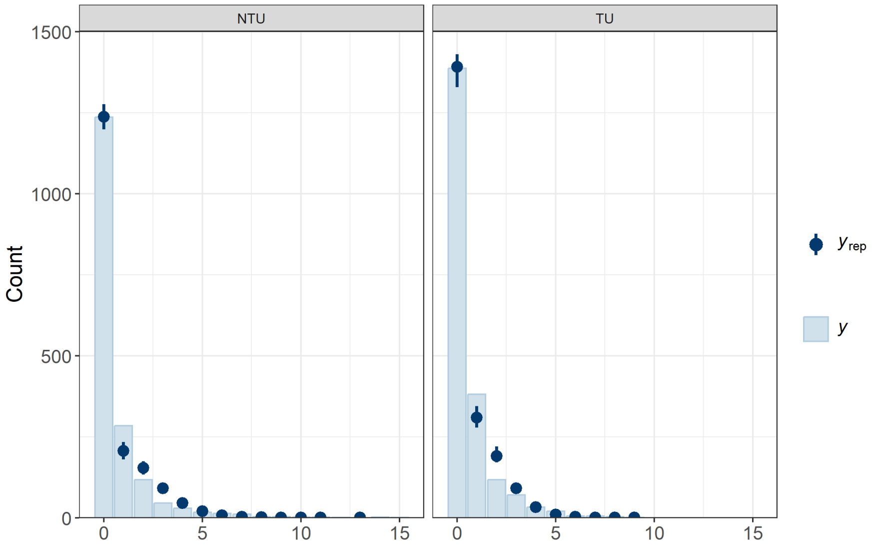

Figure S2: Posterior distribution from model sps_bm1a, comparing the mean social party size between the non-tool-using (NTU) and tool-using (TU) group. The light blue bars reflect the estimated frequencies of each social party size, with the dark blue error bars reflecting the variation in estimates of a 100 samples from the posterior.

Table S2: Posterior mean model estimates of Model ps_bm1b, a hurdle Gamma GLMM (Bayes R^2 = 0.24) comparing standard deviation in party size between the tool-using and non-tool-using group. The link for the non-zero component of the model (mu) is log, and for the shape and zero component (hu) identity.

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
locationfactor (levels: 48)				
sd(Intercept)	0.21	0.05	0.12	0.32
Regression Coefficients				
Intercept	-8.17	0.13	-8.43	-7.91
gridtypeTU	-0.17	0.10	-0.38	0.04
Further Distributional Parameters				
shape	1.86	0.11	1.65	2.09
hu	0.41	0.02	0.38	0.44

Table S3: Posterior mean model estimates of Model sps_gam1, a hurdle Poisson GAM (Bayes R^2 = 0.06) comparing the fluctuation in social party size depending on the hour of day between the tool-using and non-tool-using group. 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*
Smoothing Spline Hyperparameters				
sds(shourgridtypeNTU_1)	0.84	0.68	0.03	2.50
sds(shourgridtypeTU_1)	0.42	0.43	0.01	1.61
sds(slocationfactor_1)	0.39	0.06	0.28	0.53
sds(hu_slocationfactor_1)	0.51	0.08	0.37	0.67
Regression Coefficients				
Intercept	0.30	0.11	0.09	0.51
hu_Intercept	0.91	0.13	0.66	1.16
gridtypeTU	-0.27	0.15	-0.56	0.02
hu_gridtypeTU	0.10	0.17	-0.24	0.46
shour:gridtypeNTU_1	0.25	0.82	-1.42	1.93
shour:gridtypeTU_1	0.39	0.66	-1.09	1.64

Models estimating party composition

Table S4: 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 and non-tool-using group. 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	-1.20	-0.88
gridtypeTU	-0.24	0.12	-0.46	-0.01
nAM	0.09	0.06	-0.04	0.21
gridtypeTU:nAM	-0.29	0.12	-0.53	-0.06
Further Parameters				
zi	0.01	0.01	0.00	0.05

Table S5: 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 and non-tool-using group. All estimates are on the log scale.

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
locationfactor (levels: 49)				
sd(Intercept)	0.36	0.06	0.26	0.50
Regression Coefficients				
Intercept	-1.16	0.09	-1.35	-0.98
gridtypeTU	-0.49	0.14	-0.77	-0.23
nAF	0.06	0.06	-0.05	0.16
gridtypeTU:nAF	-0.28	0.12	-0.52	-0.05
Further Parameters				
zi	0.01	0.01	0.00	0.03

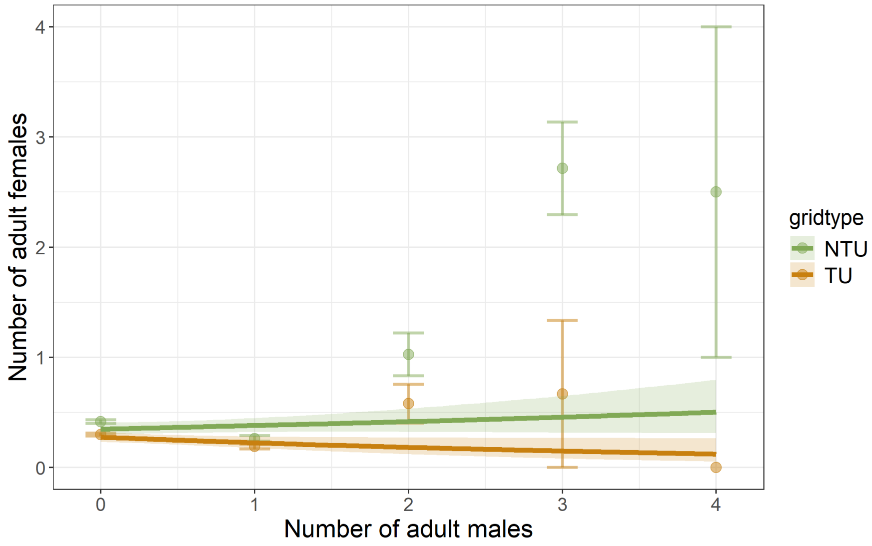

Figure S3: Model estimates from zero-inflated Poisson GLMM of relationship between number of adult females and number of adult males occurring together in a sequence for tool-using group (orange) and non-tool-using group (green). The bold line reflects the model estimates, with the shaded area representing the 95% confidence interval. Points reflects the means from the real data, with whiskers representing their 95% confidence intervals.

Models estimating spatial cohesion

Table S6: Posterior mean model estimates of models gp_tu and gp_ntu, Gaussian process regressions estimating the covariance of party size and distance between camera traps. All estimates are on the log scale.

Model gp_tu (tool-using group)					Model gp_ntu (non-tool-using group)				
	Mean	*Sd*	*5.5%*	*94.5%*		*Mean*	*Sd*	*5.5%*	*94.5%*
Camera locations (indexed)					*Camera locations (indexed)*				
cam[1]	-1.55	0.52	-2.34	-0.71	cam[1]	-0.04	0.16	-0.29	0.21
cam[2]	-1.73	0.52	-2.52	-0.89	cam[2]	-0.07	0.12	-0.27	0.13
cam[3]	-1.88	0.52	-2.67	-1.05	cam[3]	0.02	0.10	-0.14	0.17
cam[4]	-1.98	0.53	-2.77	-1.12	cam[4]	-0.12	0.15	-0.37	0.11
cam[5]	-1.92	0.53	-2.73	-1.06	cam[5]	-0.13	0.08	-0.26	-0.01
cam[6]	-1.82	0.53	-2.63	-0.98	cam[6]	0.62	0.08	0.49	0.74
cam[7]	-1.80	0.53	-2.60	-0.95	cam[7]	-0.16	0.17	-0.44	0.10
cam[8]	-1.92	0.53	-2.74	-1.06	cam[8]	-0.09	0.10	-0.26	0.07
cam[9]	-2.03	0.53	-2.84	-1.18	cam[9]	-0.18	0.11	-0.36	-0.01
cam[10]	-2.05	0.53	-2.86	-1.19	cam[10]	-0.15	0.12	-0.34	0.04
cam[11]	-1.91	0.54	-2.73	-1.05	cam[11]	-0.11	0.15	-0.35	0.12
cam[12]	-1.93	0.53	-2.73	-1.06	cam[12]	0.43	0.10	0.28	0.59
cam[13]	-1.90	0.53	-2.71	-1.05	cam[13]	0.04	0.09	-0.11	0.19
cam[14]	-1.88	0.53	-2.69	-1.03	cam[14]	-0.11	0.13	-0.31	0.10
cam[15]	-1.85	0.53	-2.66	-0.99	cam[15]	-0.24	0.17	-0.52	0.01
cam[16]	-1.99	0.53	-2.81	-1.12	cam[16]	0.11	0.07	0.00	0.23

cam[17]	-1.96	0.53	-2.78	-1.11	cam[17]	-0.11	0.21	-0.45	0.21
cam[18]	-2.05	0.53	-2.87	-1.20	cam[18]	0.01	0.12	-0.19	0.20
cam[19]	-2.01	0.52	-2.81	-1.16	cam[19]	-0.12	0.16	-0.39	0.13
cam[20]	-1.89	0.53	-2.70	-1.03	cam[20]	-0.01	0.12	-0.20	0.17
cam[21]	-1.80	0.53	-2.60	-0.95	cam[21]	0.06	0.15	-0.17	0.30
cam[22]	-1.72	0.52	-2.46	-0.89	cam[22]	-0.10	0.10	-0.26	0.06
cam[23]	-1.66	0.52	-2.46	-0.82	cam[23]	-0.16	0.11	-0.33	0.00
cam[24]	-1.97	0.53	-2.78	-1.11	cam[24]	-0.11	0.09	-0.26	0.04
					cam[25]	0.03	0.11	-0.15	0.22
Regression Coefficients					*Regression Coefficients*				
camera	2.26	0.52	1.42	3.05	camera	0.48	0.06	0.38	0.58
η^2	1.21	0.64	0.40	2.36	η^2	0.05	0.03	0.02	0.10
ρ^2	0.03	0.02	0.01	0.05	ρ^2	3.91	2.18	1.40	7.96

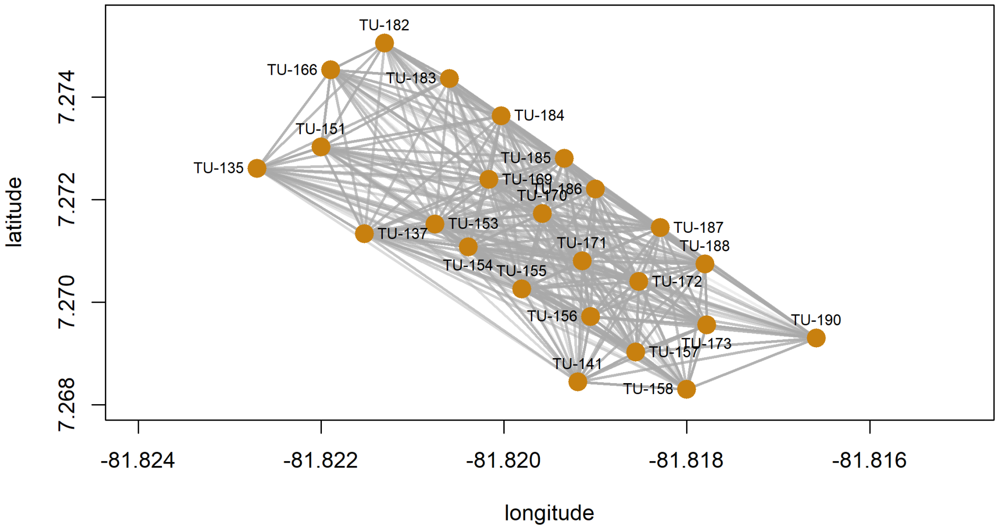

Figure S4: Posterior correlations among cameras in geographic space for the tool-using group, estimated by model gp_tu.

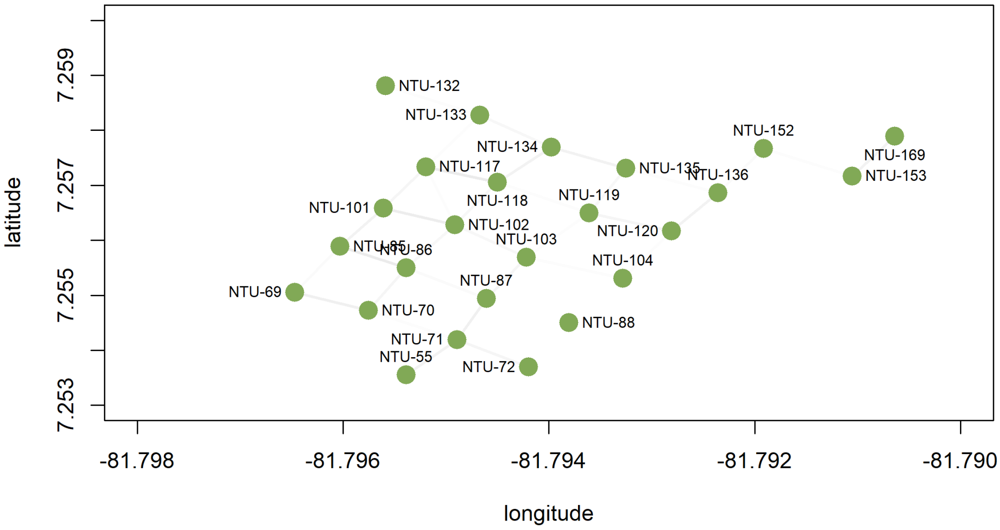

Figure S5: Posterior correlations among cameras in geographic space for the non-tool-using group, estimated by model gp_ntu.

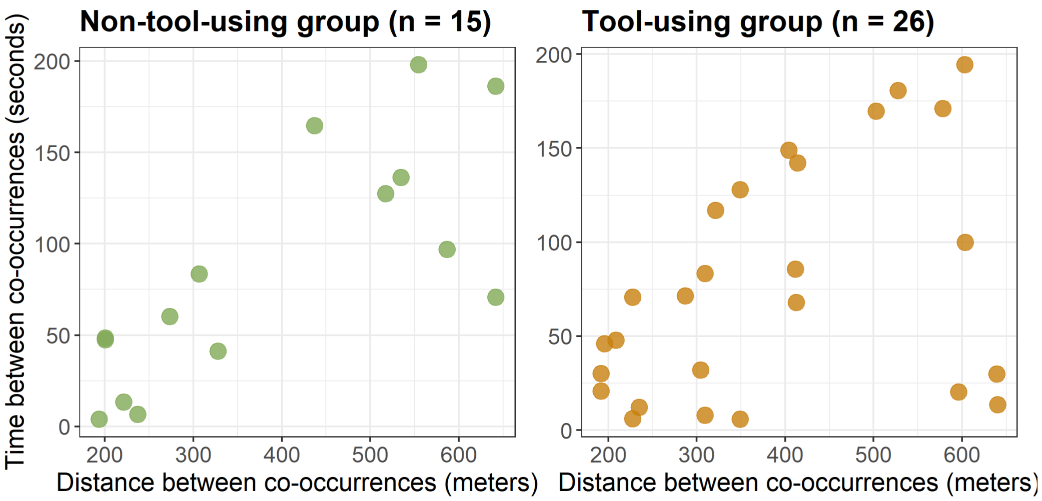

Figure S6: Co-occurrences in the non-tool-using (left in green) and tool-using group (right in orange). Each dot represents the co-occurrence of two sightings. The x-axis reflects the distance in meters between the cameras where the co-occurring sightings were seen, the y-axis reflects the time in seconds between the co-occurring sightings.