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Socially Situated Navigation: Social Rank and Sex Influence Spatial Navigation Strategies in Japanese Macaques

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Abstract

Primates' social interactions are grounded in temporal and spatial relationships, with physical proximity commonly used to assess affiliation, dominance, and tolerance. Yet proximity is often treated as a static, categorical measure rather than a dynamic, continuous process. Here, we combine computer vision and environmental markers to precisely quantify short-range social distances in two groups of Japanese macaques housed in large outdoor enclosures. Our social tolerance test results show that, when entering a food-baited circle, macaques positioned themselves at greater-than-chance distances from conspecifics, particularly to dominants. Furthermore, lower-ranking individuals tended to follow more indirect paths before approaching the food resource, suggesting they weigh social risks alongside physical positioning. By treating social proximity as a dynamic process, our study provides new insights into how primates navigate social and physical environments. This illustrates the potential of our method for more nuanced measures of group organization, tolerance, and decision-making.

Keywords: Japanese macaque, computer vision, social distance, social tolerance, proxemics, navigation

Introduction

Primates' social lives are grounded in temporal and spatial relationships. Researchers often rely on physical proximity as an indicator of social dynamics such as affiliation, dominance, and tolerance (Sailer & Gaulin, 1984). Social proximity is readily observable and is a prerequisite for many social behaviors—including social grooming, food sharing, cooperation, displays, and conflicts—that offer insights into kin, affiliation, dominance and mating strategies. Moreover, proximity mediates the hypothesized correlations between terrestriality, advanced social learning, tool use (Meulman et al., 2012), and the emergence of complex social systems in great apes and humans (Henrich, 2016).

While behaviors like grooming or aggression are often transient and require time-consuming sampling (e.g., focal observations or behavior sampling), proximity data can be more efficiently collected, for instance through scan sampling. Yet, proximity is generally treated as a static, categorical measure. Observers often estimate distances visually in real time or from video recordings using egocentric (e.g., within arm's reach; Chaffin, Friedlen, & De Waal 1995) or allocentric (e.g., within three meters; Shimada, & Sueur, 2018) categories. Therefore, dynamics of the subtle, context-dependent distances of real-world social interactions are not measured, limiting the precision, modeling, and interpretability of previous research. Although researchers employ GPS tracking (e.g., Nishikawa, Suzuki, & Sprague 2014; Sugiura, Shimooka, & Tsuji 2011), which can provide precise coordinates over large distances, its error margins (~5–15 meters) are too large to capture short-range interactions relevant for many social affordances (Wing, Eklund, & Kellogg, 2005). Further, existing high-resolution tracking systems are costly and limited to small laboratory enclosures with few individuals rather than naturalistic environments and large groups (e.g., Ballesta et al., 2014).

Peripersonal space (PPS)—the "space surrounding the body where physical interactions with elements of the environment take place" (Bogdanova et al., 2021, p.28)—is flexible and can be socially modulated under varying contexts, including threats and cooperation (Bogdanova et al., 2021; Fanghella, Era, & Candidi, 2021). Ecological theories of perception (Gibson, 1977) further suggest that animals navigate their environment by assessing *affordances*, i.e., the opportunities for action presented by both the environment and other individuals. Primates, including macaques, can predict the actions of conspecifics based on their visual perspective (Canteloup et al., 2016), affordances (Orban, Lanzilotto, & Bonini 2021), kin and rank relations (Schino, Tiddi, & Di Sorrentino, 2006), and past interactions (Roumazeilles et al., 2021). Different distances afford different kinds of social interactions. For example, social grooming is only afforded when primates are within each others' reach. Entering within the reach of a conspecific affords both affiliative (e.g., grooming, food sharing, cofeeding, mounting, huddling) and agonistic (e.g., hitting, biting, theft) interactions.

Social proximity serves as a primary metric for social tolerance, commonly defined as the probability that conspecifics are in close proximity around valuable resources without aggression (Cronin & Sanchez, 2012). Measuring tolerance can reveal how primates trade off competing demands of gregariousness, including the benefits of social affiliation (e.g., protection against predators, protecting resources, social learning, cooperation) versus its costs (e.g., resource competition, aggression, disease transmission). There are various conceptualizations and operationalizations of social tolerance (DeTroy, Haun,

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& van Leeuwen, 2022). For the purpose of this study, we will not focus on group-level social tolerance, but rather tolerance in dyadic interaction.

Within the genus *Macaca*, a wide spectrum of social styles—from despotic to egalitarian—has made macaques a common model for studying the evolution of primate social organization (Thierry, 2000; Thierry, Singh, & Kaumanns, 2004). Japanese macaques (*Macaca fuscata*), for instance, are often described as highly despotic, with dominance strongly influencing spatial arrangements and access to resources. Yet the degree of tolerance can vary across groups and contexts, and capturing these nuances can clarify how dominants and subordinates manage resource conflicts. Detailed, continuous social proximity measurements in semi-naturalistic conditions thus hold the potential to advance our understanding of primate social organization, behavior, and cognition.

To address the gap of accurate social distance measurements at close range, we present a novel, hybrid approach that integrates computer vision (CV) with environmental measurements and manual annotation to accurately map continuous social distances in Japanese macaques. Our method allows for precise quantification of moment-to-moment social distances, enabling more detailed examinations and modeling of how macaques dynamically navigate their physical environment in relation to socio-cognitive assessments of their social environment.

CV techniques are typically non-invasive and scalable, making them well-suited for monitoring group-level dynamics. However, many existing CV-based methods only provide pixel-based measures of proximity. Our approach calibrates video data with real-world markers using monocular camera footage, allowing us to derive absolute distances. While multi- and stereo-camera setups can provide higher depth accuracy and precision for tracking, we intentionally chose single, monocular camera footage to increase affordability, potential applicability in field settings, and backwards compatibility for historic footage. Our method is well-suited for analyzing short-range social proximity, interactions, and affordances in larger primate groups in naturalistic environments.

Here, we describe social tolerance tests involving two groups of Japanese macaques housed in large outdoor enclosures. By distributing valuable food in a predefined circle, we set up a co-feeding scenario to compel macaques to enter or share proximity with others. Using a bespoke computer vision algorithm (calibrated with environmental measurements and supplemented by manual annotations), we tracked each macaque's trajectory and computed a "normalized entry distance" to quantify fine-scale approach patterns. We first validated this method against manual coding. We then tested predictions regarding how proximity is influenced by factors such as sex, dominance rank, and the presence of higher-ranking individuals. Additionally, we examined whether lower-ranking macaques traversed more circuitous paths before entering the circle as a potential strategy to avoid conflicts. Our findings demonstrate how treating social proximity not as a static outcome, but rather as a dynamic process, shows how macaques navigate their physical—in relation to their social—environment, providing novel insights on spatial organization and tolerance within primate groups.

Methods

We conducted social tolerance tests (e.g., Cronin et al., 2014) with two groups of Japanese macaques housed in separate large fenced outdoor enclosures with natural vegetation at the Born Free USA Primate Sanctuary in Southern Texas, USA. Both groups (Northwest: 24 individuals; Kyoto: 46 individuals) descend from the Arashiyama West troop and live under nearly identical ecological conditions (Huffman, 1991). Data was collected between February 26th and March 14th in 2024 and we obtained IACUC approval for this study.

Procedure

In each session, a circle was marked on the ground in a central open area near the enclosure fence, with the circle's size scaled to the number of monkeys (Northwest: 8m²; Kyoto: 15.33m²) to achieve a ratio of 15 food pieces per square meter. We provided five pieces of high-value food per monkey in each group, using red grapes for the first half and shelled peanuts for the second half of sessions to control for individual preferences. Tests were conducted either in the morning or late afternoon to ensure food motivation. The experimenters first displayed the food inside the enclosure before distributing it in the circle and exiting the enclosure to minimize interference. Two cameras simultaneously (Fujifilm X-T4, GoPro Hero 11) recorded approximately 30 minutes of each session. The GoPro camera was attached to the top of the enclosure fence for a top-down view and was used for all analyses described below.

Behavioral Coding

Video data were annotated using ELAN (Version 6.9, 2024) with coding focusing on the first 10 minutes of each session. This duration was chosen based on pilot data from both groups, ensuring that food resources inside the circle were not depleted. We recorded the duration, identity, sex, and rank of each macaque within the circle. Absolute and categorical rank estimates (alpha/high/middle/low) were obtained from sanctuary caregiver ratings.

Computer vision tracking

We deployed a custom monocular camera-based tracking pipeline to estimate macaque spatial trajectories. This pipeline is composed of the following steps: (1) macaque detection, (2) tracking detections across video frames, (3) manually correcting tracking & identifying macaques, (4) calibrating cameras, (5) projecting trajectories from pixel coordinates to world coordinates, and (6) interpolating physically plausible trajectories (Figure 1). Although a

monocular camera limits the application of our method to environments where one can assume terrestrial movement

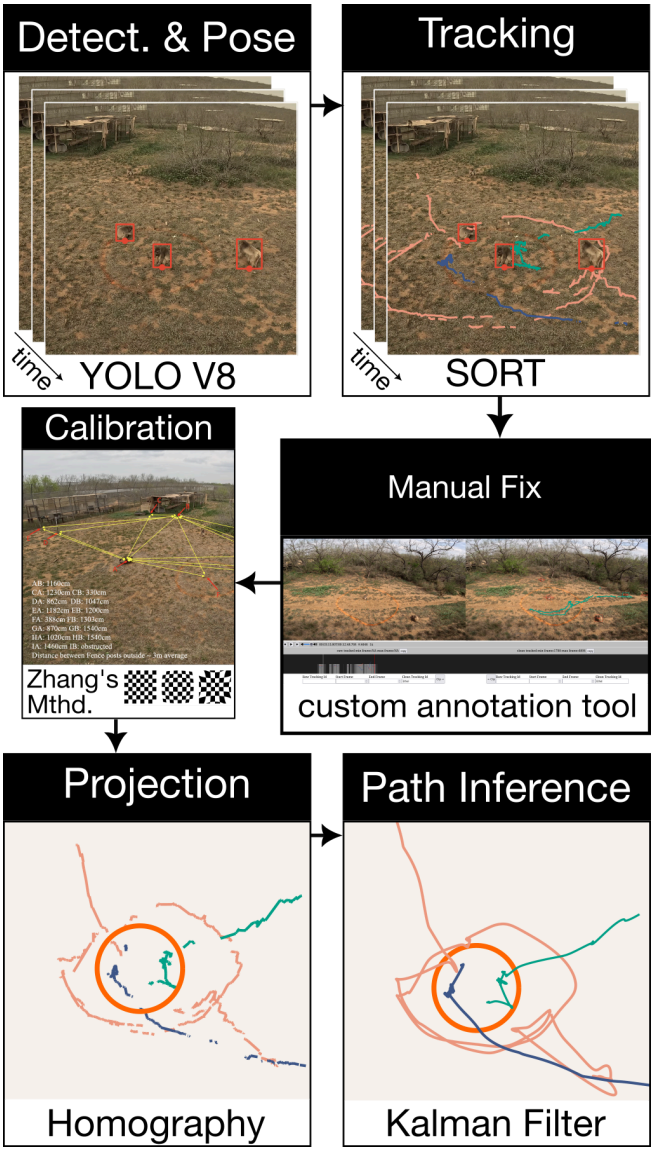

Figure 1: Visualization of our tracking method. (1) Macaque bounding boxes. (2) Tracking macaques across frames. (3) A screenshot of our bespoke annotation tool. (4) To calibrate our camera, we needed to know its intrinsic properties, i.e. how the lens distorts light (depicted with checkerboards), and where the camera was located in space. Landmarks from the Northwest are shown. (5) Raw world-coordinate trajectory data is shown with the food-baited circle marked in orange. (6) Inferred and interpolated data from Kalman filtering with RTS smoothing is shown.

on a flat ground plane, this choice allows one to analyze historical video recordings and to make cheap and low-tech field recordings 'in the wild'.

In order to detect macaques, we used YoloV8, a fast convolutional network architecture for object detection. We trained a new model using three publicly available datasets, namely MacaquePose (Labuguen et al., 2021), ChimpACT (Ma et al., 2023), and MSCOCO (Lin et al., 2014). The mid-point on the bottom of the bounding box was assumed as the point macaques contacted the ground. To track individuals across a video, we used the Simple Online Realtime Tracking (SORT) algorithm (Bewley et al., 2016), which works by estimating bounding box movement with a Kalman Filter (Kalman, 1960) and matching them between frames with the Hungarian Method (Kuhn, 1955).

Because SORT occasionally loses track of individuals, resulting in absent or errant detections, we manually corrected tracking errors[1] using a bespoke web-based annotation tool allowing direct manipulation (Hutchins, Hollan, & Norman, 1985; Dragicevic et al., 2008). Finally, we then manually identified each tracked macaque – these labels were then automatically propagated to all tracked detections of an individual within a video. Missing data was interpolated using a Kalman filter with Rauch–Tung–Striebel (RTS) smoothing (Bertozzi et al., 2004).

The GoPro cameras were calibrated using OpenCV's cameraCalibrate function in the fisheye module (Kannala & Brandt, 2006) with OpenCV's 9x7 corner checkerboard. Extrinsic camera calibration was performed by measuring 8 fixed landmarks (e.g., poles, fences, trees). After obtaining our camera's intrinsic parameters and pixel-landmark correspondences, we used OpenCV's findHomography function using the RANSAC method to solve for the linear mapping between pixel coordinates and enclosure coordinates. To fit a good homography, we selected inlier points by performing a gridsearch (0-25) over RANSAC's ransacReprojThreshold parameter.

We validated the accuracy of this automated tracking by assessing the Pearsons's correlation between the manual coding of each monkeys' time in the circle with the seconds in the circle inferred from the computer-vision generated trajectories.

Results

Descriptive statistics

We first provide the descriptive results of how macaques occupied the circle for both enclosures. Next, we show the results for comparing the manually coded time of individuals inside the circle with the results from our computer vision tracking.

Circle occupancy Across all sessions, the circle was occupied 91% of the time across both enclosures in the first ten minutes (Northwest: 88%; Kyoto: 94%). On average, 1.5 macaques were inside the circle at any given moment

[1] 1) False-positives and bounding-box errors were deleted, 2) cases where SORT split one individual's trajectory into multiple parts were consolidated, and 3) cases where SORT combined two individuals' trajectories into one part were separated.

(Northwest: 1.4; Kyoto: 1.7). For each session, around 6.9 separate individuals entered the circle (Northwest: 5.1; Kyoto: 8.6). Across all sessions, 43% (30/70) of monkeys inside the enclosures entered the circle at some point (Northwest: 42%, 10/24; Kyoto: 43%, 20/46). Figure 2 shows that the circle was predominantly occupied by higher-ranking macaques in both groups.

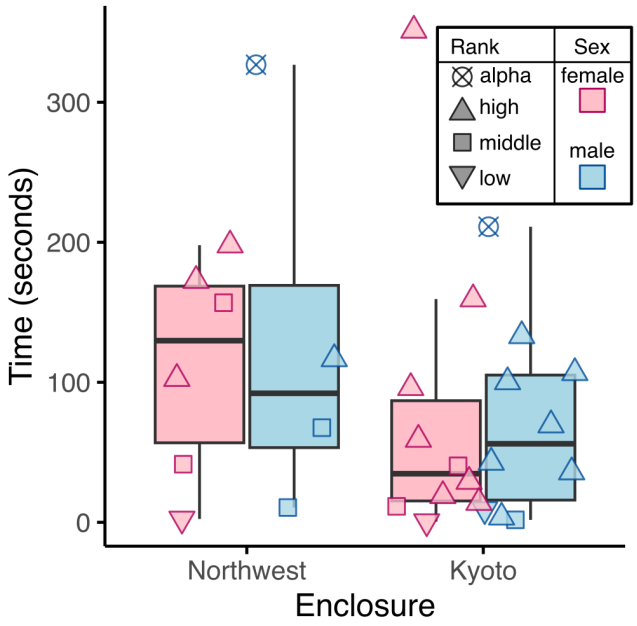

Figure 2: Box plots of mean time in seconds macaques spent inside the circle per session grouped by enclosure and sex. Individual mean times are plotted as points with shapes corresponding to rank categories and color to sex.

Computer vision tracking We found an almost perfect correlation between the manual annotation of the time specific individuals spent inside the circle and the results from our computer vision tracking (Pearson's $r = 0.995$, $p < 0.001$). Our mean hold-one-out reprojection error was 9.7cm±0.90.

Entry strategies take social rank & sex into account

To determine whether the process by which macaques become co-present in the resource circle depends on social rank, we first assess whether an entering macaque's point of entry depends on the social rank of an occupying macaque. Specifically, we were interested in whether entering macaques were more likely to put more distance between themselves and an occupying macaque when the occupier was higher-ranking. We operationalized this using what we call normalized entry distance (NED). NED is defined as the actual distance between an enterer and occupier normalized by the minimum possible distance and maximum possible entry distance so that it is on the [0,1] range, i.e. NED = (D-Dmin)/(Dmax-Dmin) (see Figure 3A). We excluded entry events in which an occupier was within 15cm of the circle center, since all points are equidistant from the circle center.

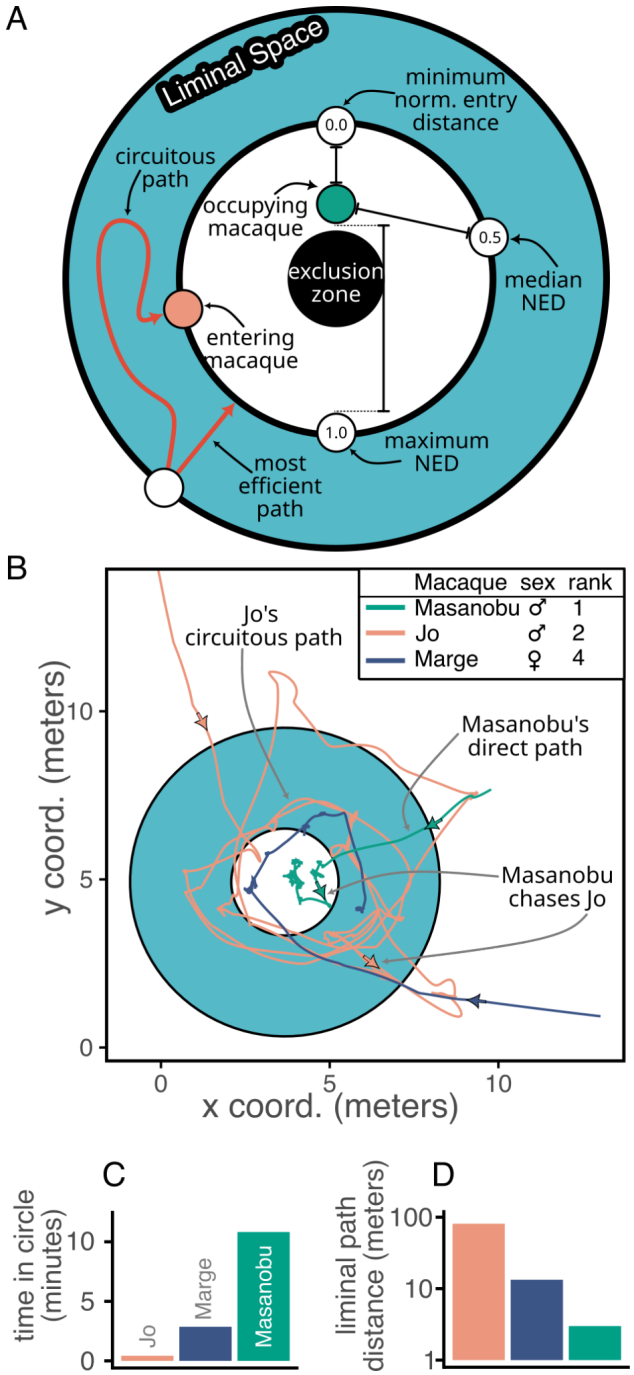

Figure 3: (A) A diagram of our normalized entry distance (NED) metric and liminal path distance (LPD). When analyzing NED, we remove all data where the occupier was near the exact center. (B) Estimated trajectories of Masanobu, Jo, and Marge from Session 3 in Northwest. The alpha, Masanobu, takes a direct path to the resource circle while Jo takes a circuitous path. Masanobu chases Jo away while tolerating Marge's proximity. (C) Time spent inside the circle in Session 3 in Northwest and (D) LPD from Session 3 in Northwest.

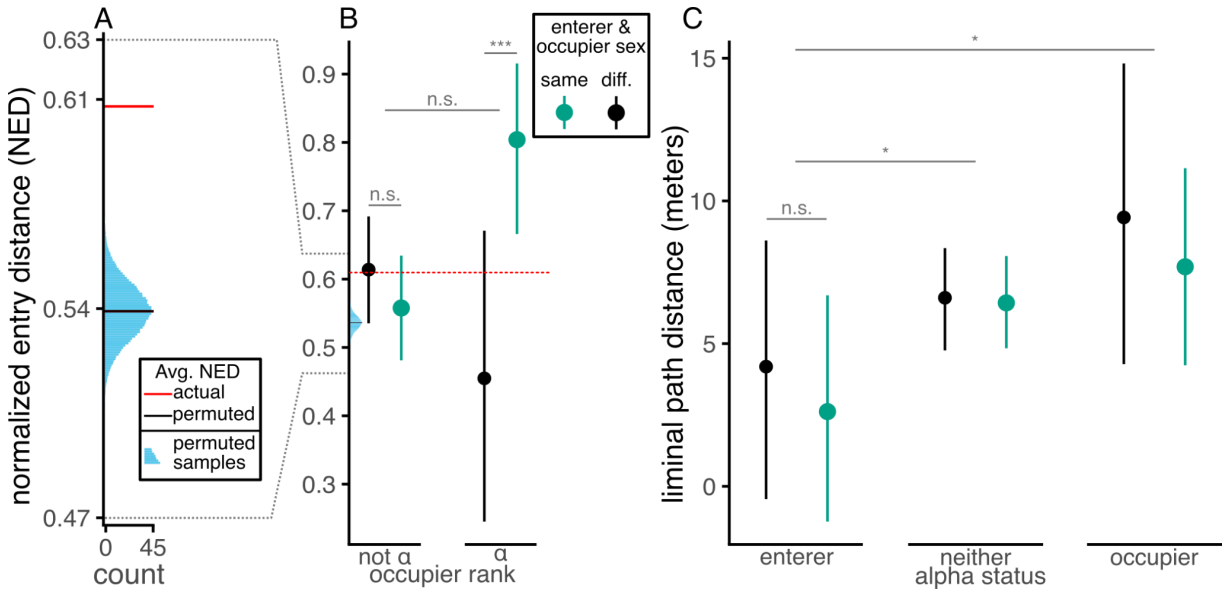

Figure 4: (A) A permutation test showing actual NED (red) is significantly greater than bootstrapped permutations of NED (black). (B) The estimated marginal mean NED by the social rank of the occupier (is group alpha or not) and whether the entering macaque and occupier are the same sex (green) or not (black). (C) Liminal path length by social rank of the enterer and occupier and whether the entering macaque and occupier are the same sex (green) or not (black).

First we tested whether macaques put more distance between themselves and others than would be expected by change by conducting a permutation test. With 100k bootstrapped samples, we found the distance between enterers and occupiers was significantly greater than would be expected by random chance ($p < .001$). NED was, on average, 6.85% greater than chance; macaques placed themselves 22.06 cm further away than chance.

Second, tested whether this distance varied based on rank. We modeled NEDs using the R package brms (Bürkner, 2017) to fit a generalized linear mixed effects model (gLMM) with a Beta link function, a distribution well suited to model a continuous variable in the [0,1] range. Fixed effects include (a) whether the occupier was a group's alpha, (b) whether the enterer & occupier were of the same sex, and (c) the enterer & occupier's rank distance. We controlled for food type and social group. Interactions include those between group, rank difference, occupier's alpha status, and enter & occupier sex. Our model accounts for three hierarchical structures of our data. First, it includes a by-group hierarchical structure. Nested within this structure, it includes by-occupying-macque random intercepts. Also nested within this structure, it includes a by-entering-macaque random intercept and random slope for the reward type. Together random intercepts for occupying & entering macaques approximates an Elo-rating or a Rasch model, where macaques are modeled on a continuous scale for each social group. Here these scales measure macaque-level effects for how likely they are to repel/encroach upon other macaques. This model was selected from a set of candidates with simpler or more complex fixed effects and random effect structures on the basis of its Bayes factor. We used 1-tailed tests to test whether effects were found in hypothesized directions.

We found no significant main effects of sex relation ($\beta = -0.01 \pm 0.12$, $p = .543$), whether occupier was alpha ($\beta = -0.91 \pm 0.65$, $p = .919$), or rank difference ($\beta = -0.02 \pm 0.01$, $p = 0.736$). However, we found significant interactions between sex and whether the occupier was the group alpha ($\beta = 2.12 \pm 0.55$, $p < .001$). By looking at the estimated marginal means of this interaction, we found that lower ranking males maximized entering further away from the alpha male (*EMM* = 0.80, 95% *CI* = [0.66, 0.91]) but females did not (*EMM* = 0.459, 95% *CI* = [0.263, 0.66]). We also found a marginally significant interaction between sex and rank differences ($\beta = 0.02 \pm 0.01$, $p = .054$), meaning a rank difference of 1 would increase NED by 2% and a rank difference of 10 would increase it by 20% between individuals of the same sex. Taken together, our results suggest that macaque monkeys adjust their entrance strategy depending on relations between rank and sex (Figure 4C), thereby integrating spatial cognition with social cognition to actively balance physical access to resources against potential social risks such as conflict or aggression.

Higher-ranking macaques take more direct and lower-ranking macaques more circuitous paths

From our observations, higher-ranking macaques would take more direct paths into the resource circle than lower-ranking macaques, ostensibly to find a strategic opening. To measure this, we considered a liminal space between the resource circle and an imaginary circle of 3m in radius greater than the resource circle (see Figure 3A). We operationalized path distance by what we call liminal path distance (LPD) and defined it as the length of a path in the liminal space before entering the resource circle.

To test the path length hypothesis, we fit an LMM that predicted LPD using the same fixed effects and hierarchical structure as the above NED model. We found that if the entering macaque was the alpha, they took significantly shorter, more direct paths through the liminal space compared to lower-ranking macaques ($\beta = -2.74 \pm 1.68$, $p = .050$). The alpha macaque took a path that was 2.74 meters shorter than lower-ranking macaques through a space where the shortest path was 3m. Conversely, we found a significant effect that when the occupier was the groups' alpha, entering macaques took longer paths ($\beta = 6.33 \pm 3.17$, $p = .024$). Subordinates took 6.3m longer paths when the alpha was inside the circle. We also found that the number of occupiers increased LPD ($\beta = 1.90 \pm 0.68$, $p = .003$). We found no effect of rank difference ($\beta = 0.08 \pm 0.10$, $p = .331$). Together, these results show that the process of navigating an environment with conspecifics takes social factors into account such as rank and sex (Figure 4C).

Discussion

Our results show that Japanese macaques approach food resources differently based on the sex and rank of others present. While high ranking individuals approach directly regardless of who is present, subordinate individuals take circuitous paths and maximize distance between themselves and others when higher ranking others of the same sex are present. This suggests that subordinate individuals balance the risks of getting too close to dominants with the benefits of gaining access to food. Such moment-by-moment navigation decisions show how primates' trajectories are shaped by social dynamics and resource conflict in real time.

In summary, we have shown that macaques' social structures considerably affect the physical trajectories macaques take through space. At the same time, these structures are latent. They cannot be directly observed by just any macaque or any primatologist. These structures are socially learned through longitudinally participating in and/or from observing a particular social environment, and they have to be continually relearned as the properties of groups change over time. At some point in the primate lineage, groups of individuals likely began to inhabit socially constructed umwelten of this sort (von Uexküll, 1934).

We argue that macaque navigation depends on a homolog of situated seeing (Hutchins, 1995; Goodwin & Goodwin, 1996). In order to navigate their environment, macaque monkeys appear to superimpose social knowledge and expectations onto their perception of the physical environment. As a macaque aims toward some resource, its decisions on how to approach, wait, or retreat are conditioned on where conspecifics are located within the enclosure and how social rank and affiliation relative to the macaque are distributed among these conspecifics. Under some circumstances, macaques' navigation appears more constrained by their social than their physical environment.

More broadly, tracking how individuals establish, maintain, and dissolve social proximity could reveal decision-making processes and consequences of social tolerance in other contexts. For example, being in close physical proximity to others is a prerequisite for social learning. Coussi-Korbel and Fragaszy (1995) discussed how social interaction predicts the likelihood of social learning and the type of information that can be transmitted. They propose several testable predictions for social learning likelihoods and outcomes in relation to social styles and coordination in space and time within primate groups. Here, we demonstrated that our tracking tool can provide high temporal and spatial resolution on the movements of macaques. Future studies could utilize this approach to quantify the association between tolerance, social learning, and cultural transmission. Our results support the view that navigation is not solely a response to physical constraints but also to socio-cognitive factors, reflecting an interplay between spatial reasoning, social knowledge, and anticipated consequences. Our current algorithm is tracking the location of individuals but does not track body or head orientation. Future iterations could overcome this limitation by integrating pose estimation to track body and head directions, potentially enabling us to assess the role of attention in social proximity and navigation (e.g., Chance, 1967).

Our methods and findings have broader implications for comparative and developmental research on social distance and spatial navigation beyond non-human primates. Similar methodological approaches can be extended to a wide variety of social primates, other mammals, and even humans. For instance, analogous tracking and modeling could be applied in developmental psychology to investigate preschoolers' social interactions during free play to study dynamics of peer relationships in everyday environments.

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