American Journal of Primatology

RESEARCH ARTICLE OPEN ACCESS

Roadside Dining: The Collective Movement Behavior of Sulawesi Moor Macaques in a Provisioning Context

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Received: 1 September 2024 | **Revised:** 14 December 2024 | **Accepted:** 22 December 2024

Funding: Funding for the research was provided by San Diego State University, specifically the College of Graduate Studies and the Division of Research and Innovation CORE Fellowship and the Graduate Student Travel Fund (awarded to Joshua Trinidad) and the U.S. National Science Foundation (Award #2222891, PIs: Erin P. Riley, Amanda Ellwanger, and Henry Scharf).

Keywords: anthropogenic | collective movement | decision-making | *Macaca* | provisioning | risk-reward

ABSTRACT

How group-living primates come to a consensus about navigating their environment is a result of their decision-making processes. Although decision-making has been examined in several primate taxa, it remains underexplored for primates living in anthropogenic landscapes. To shed light on consensus decision-making and flexibility in this process, we examined collective movement behavior in a group of wild moor macaques (*Macaca maura*) experiencing a risk-reward tradeoff as a result of roadside provisioning within Bantimurung Bulusaraung National Park in South Sulawesi, Indonesia. Our goal was to determine whether individual characteristics (e.g., sex, dominance rank, and/or social network centrality) predict the likelihood of initiating a collective movement and if the opportunity to receive food provisions along the road alters these patterns. Using the all-occurrences method, we recorded the location, time, and identity of initiators and followers of each collective movement observed from April to June 2023 ($N = 61$). We used conditional logistic regression models to examine which individual characteristics predicted initiation overall and based on two destination categories: forest- and road-directed collective movements. Initiation was distributed amongst most of the group, indicating a partially-shared decision-making style. Overall, adult males were more likely to initiate collective movements than adult females. However, for collective movements directed toward the risky roadside, dominance, rather than sex, was a better predictor of initiation, with higher ranked individuals being more likely to initiate collective movements. Examining the decision-making processes in this species through collective movements can provide insight into how primates come to a consensus and the extent to which anthropogenic factors shape these processes. By shedding light on how moor macaques navigate the risk-reward tradeoff at this site, our results can also inform the management of human-macaque interfaces.

1 | Introduction

In order for social organisms, such as primates, to enjoy the benefits of group living, they must be able make collective decisions, particularly with regard to movement. Collective movements are defined as a group of two or more animals that decide to move together, maintaining spatial proximity, direction, and cohesion until the group disassembles to pursue a new activity or stops moving, which results in the group changing locations (Petit and Bon 2010). At the same time, following others can result in interindividual conflict and consensus costs if followers forego their preferred destination (and potential

https://doi.org/10.1002/ajp.23727

Summary

- We found that *Macaca maura* exhibits partially-shared decision-making in collective movements.
- Who initiates depends on travel destination, with dominant individuals initiating more collective movements when going to the risky roadside habitat. In the forest, sex was the best predictor of initiation, with males initiating more than females.
- By shedding light on this risk-reward tradeoff, we provide insight into how primates come to a consensus and the extent to which anthropogenic factors shape these processes, both of which can inform the management of human-macaque interfaces.

foraging benefits) in favor of the group's decision (Conradt and Roper 2005). Reaching a consensus on when and where to travel can take three forms: a decision can be "equally shared" in that all group members contribute equally to the decision; "partially shared," whereby multiple members contribute to the decision; and, "unshared," meaning that one individual is responsible for the decision (Conradt and Roper 2005).

Primatology has witnessed a surge of interest in this area of research, focusing on understanding the ecological and social factors that structure collective movement in primates and advancing rigorous methodological tools to study it (Leca et al. 2003; Sueur, Petit, and Deneubourg 2009; Fichtel, Pyritz, and Kappeler 2011; Lee and Teichroeb 2016; Strandburg-Peshkin et al. 2017; Palacios-Romo, Castellanos, and Ramos-Fernandez 2019). Observed interspecific variation in decision making, in terms of who leads and the ordering of who follows, has been linked to social style (Sueur, Petit, and Deneubourg 2009; Seltmann et al. 2013) and individual characteristics. For example, dominance has been found to be an important variable, with higher-ranked individuals tending to control access to food (Boccia, Laudenslager, and Reite 1988) and initiating collective movements more often than lower-ranked individuals (Sueur and Petit 2008a; 2008b). An individual's sex has also been found to be a predictor of participation in collective movements. In adult female Tibetan macaques (Rowe et al. 2018) and vervet monkeys (Lee and Teichroeb 2016), dominant females and older females, respectively, were found to be the most successful in leading group movements. In contrast, dominant males led group foraging decisions in chacma baboons (King et al. 2008). Social network centrality can also influence individuals' participation in collective movements, often with more central individuals being initiators (Fratellone et al. 2019; Palacios-Romo, Castellanos, and Ramos-Fernandez 2019). The ecological context, such as the level of perceived predation risk and the availability of key food resources, has also been found to be important (Pyritz, Fichtel, and Kappeler 2010). And, while consensus decision making has been studied across the primate order (King and Sueur 2011), we still know very little about the extent of intraspecific variation in the patterning of decision making, particularly in the context of rapid human-induced environmental change (Anand and Radhakrishna 2022).

Here, we examined collective movements in a group of wild moor macaques (*Macaca maura*) in Bantimurung Bulusaraung National Park (BABULNP), South Sulawesi, Indonesia to characterize their decision-making processes and to examine the flexibility in these processes in human-altered landscapes. Our study group, "Group B," has been periodically studied since the 1980s (Okamoto, Matsumura, and Watanabe 2000; Watanabe and Matsumura 1996). In these early studies, moor macaques were provisioned with human foods, such as corn kernels, at set locations inside the forest. Since the 1990s, aside from occasional provisioning in the forest for tourism or media purposes by the park staff, researchers mostly discontinued deliberate provisioning, largely due to the negative impacts of provisioning wild primates (Maréchal et al. 2016; Morrow et al. 2019; Sengupta, McConkey, and Radhakrishna 2015). Beginning in 2015, a new provisioning context emerged in BABULNP when Group B began spending more time along the national two-lane road that bisects their home range where they consume human food that was tossed to them from passing vehicles.

Our study site represents a natural experimental context in which to examine flexibility in group coordination and decision making. When provisioning occurs along a major road, the risk of injury and/or death is high and the potential of being captured for the illegal pet trade and/or for bushmeat consumption rises due to increased habituation (Maibeche et al. 2015). Furthermore, while the potential nutritional and energetic benefits of provisioning are great (El Alami et al. 2012), previous research has found that not all individuals in a group equally benefit. In Barbary macaques and chacma baboons, for example, adult males tended to interact more with humans, and hence, gain a greater proportion of human foods compared to other age/sex classes (Maibeche et al. 2015; Kaplan et al. 2011). In three species of urban-dwelling macaques (long-tailed, bonnet, and pig-tailed), dominant individuals of both sexes consumed a significantly greater proportion of provisioned foods compared to lower ranking individuals (Marty et al. 2020). These studies indicate that foraging benefits in provisioning contexts may be highly skewed toward certain individuals, and hence, consensus costs for others may be high. Accordingly, it is possible that decision-making processes may shift in anthropogenic contexts as primates balance the risks and rewards present (Schweitzer et al. 2017; Bersacola, Hill, and Hockings 2021; Anand and Radhakrishna 2022; Bracken et al. 2022). Because moor macaques at our study site use both roadside habitat and interior forest, our study site provides an ideal context in which to assess anthropogenic impacts on behavior by quantifying macaque behavior in the forest (away from human impacts) and along the road (in the presence of humans and their activities).

We asked: (1) What do collective movements "look like" in *Macaca maura*? Our goal here was to determine what style of decision-making moor macaques use for collective movements (i.e., shared, partially-shared, or unshared). (2) What intrinsic factors influence an individual's role in collective movements (i.e., initiator or follower) in moor macaques? To address this question, we examined how an individual's role in collective movements is related to their dominance rank, social network centrality, and sex. (3) How does the risk-reward tradeoff present at our field site affect moor macaques' decision-making? In risky foraging contexts, such as the roadside habitat, conflicts of interest across individuals from different age/sex classes may emerge. In many primate species, males are more likely to engage in behaviors of higher risk (Santillán-Doherty et al. 2010), such as initiating crop foraging events (Schweitzer et al. 2017) and road crossing (Cibot et al. 2015), and hence, could be the impetus for groups moving closer to the road. In early observations conducted on moor macaques involving provisioning within the forest, Watanabe and Brotoisworo (1982) noted that adult males led group movements to the provisioning site. More recent research on moor macaques determined that while all age/sex classes were found along the road, subadult and adult males were disproportionately more likely to be present (Morrow et al. 2019). Given that macaques have been shown to flexibly adjust their social structure in response to altered ecological pressures, including those presented in anthropogenic settings (Ram, Venkatachalam, and Sinha 2003), and that provisioning contexts present a complex set of risks and rewards, we hypothesized that group decision-making in these settings differs from the decision-making process in non-anthropogenic contexts (cf. Schweitzer et al. 2017). Specifically, we predicted that when a collective movement's destination is the risky roadside habitat, males will initiate collective movements more often than females. Provisioning is often associated with heightened levels of competition, as provisioned food is often spatially clumped (e.g., at a single provisioning site; Saj, Sicotte, and Paterson 1999) and access to these resources can be determined by an individual's dominance status (Boccia, Laudenslager, and Reite 1988). However, at our field site, because provisioned food primarily comes from passing vehicles, it may be more evenly distributed (Riley et al. 2021), meaning that less dominant individuals may have greater access to provisioned foods than expected. We therefore predicted that an individual's dominance status would be a less important predictor of initiating travel to the roadside.

2 | Methods

2.1 | Ethics Statement

We adhered to the best practice standards following the laws/regulations stated in the United States Animal Welfare Act [7 U.S.C. 2131 et seq.] and the Indonesian Criminal Code [Article 302(1)]. The SDSU Institutional Animal Care and Use Committee approved this research as an animal observational study. This study received ethical clearance from the National Agency for Research and Innovation (BRIN) in Indonesia. We adhered to the ASP/IPS Code of Best Practices for Field Primatology and followed guidelines set by the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. We conducted this research with permits required by Indonesian law: BRIN research permit (SIP 339 A/SIP/IV/FR/2/2023) and permit to conduct research in a national park (SIMAKSI 51.27/T.46/TU/KSA/3/2023).

2.2 | Study Site

The field site is located in South Sulawesi, Indonesia in the Karaenta section of Bantimurung Bulusaraung National Park (BABULNP; 5°01′52.7″ S, 119°44′16.6″ E). The 43,750-hectare park was formed in 2004 to protect the area's karst (i.e., limestone formation) habitats, ecosystem, and biodiversity. Karaenta, which is dominated by primary and secondary karst forest, is characterized by seasonal differences (i.e., distinct dry and wet seasons) with anywhere from six to nine wet months (Whitmore 1984). A two-laned road (Figure 1a) traverses through 11 km of BABULNP and is important because it connects two provincial capitals: Makassar and Kendari. Due to the importance of the road, vehicular passage along it is consistent across days (work and weekend days) and seasons.

FIGURE 1 | (a) Group B along the road. (b) Nopi and her infant feeding from a food container that was provisioned. (c) One sub-adult male (left) and Gado, an adult male (right). (d) Adult females; Caca (left), Moka (middle), and Nopi (right).

2.3 | Study Species and Group

The moor macaque (*Macaca maura*) is one of the seven macaque species endemic to Sulawesi, Indonesia (Fooden 1969). Moor macaques live in multimale/multifemale, female-philopatric social groups. Moor macaques have previously been described as an egalitarian species (Thierry et al. 1994), exhibiting symmetrical aggression, high rates of affiliation and reconciliation, near-kin feeding tolerance, low influence of kinship on social interactions, and behaviors that reduce tension (Matsumura 1999; Riley et al. 2014). Moor macaques are primarily frugivorous, with figs (*Ficus* spp.) making up a large portion of their diet (Albani et al. 2020; Matsumura 1991; Sagnotti 2013). They are currently listed as Endangered by the International Union for the Conservation of Nature (IUCN) Red List and are threatened by habitat disturbance and fragmentation in addition to conflict with humans (Supriatna et al. 1992; Riley et al. 2020).

Group B is a well-habituated group that has been observed and intermittently studied since 1981. Group B's home range is estimated to be 36 ha (Riley et al. 2021), and includes both forest and roadside habitat. Along the road, the group forages in discarded trash piles and waits for food to be thrown to them by people in passing vehicles (Morrow et al. 2019; Figure 1a,b). During data collection, Group B consisted of seven adult males (Figure 1c) and nine adult females (Figure 1d), with adults being recognizable based on physical features. Non-adults consisted of five subadults, six juveniles, and four infants.

2.4 | Data Collection

We collected data on moor macaque behavior and movement over a 3-month period from April to June 2023 using focal animal sampling for grooming and proximity behaviors, all occurrence sampling for collective movement behavior, and *ad libitum* sampling for dominance behaviors (Altmann 1974). All data were collected by one observer across different observation periods. We followed Group B 5 days a week, Monday through Friday, between the hours of 0630 and 1500. We used a handheld device (Samsung Tablet or Smartphone) and the application CyberTracker, version 1.0.474 to collect the behavioral data. GPS waypoints were collected every 30 min while following the group using a handheld Garmin GPSMap 64s unit.

To establish a baseline for the collective movement attributes (cf. Pyritz, Fichtel, and Kappeler 2010; Seltmann et al. 2013), we began by spending 5 days conducting 10-min focal animal samples on each adult individual. Non-adults were not included in this study as previous research suggests that they do not initiate collective movements as often as adults (Anand and Radhakrishna 2022; Sueur and Petit 2008a, 2008b) and because the timeframe of the study did not allow for the accurate identification of non-adults. Randomized lists were created that established the focal order. Following Seltmann et al. (2013), we recorded any movements the focal individual took of more than a body length (estimated to the nearest meter). These observations established the "rules" that were applied for collecting data on collective movements during the main data collection period (Pyritz, Fichtel, and Kappeler 2010). These rules were as follows: ("A") the distance an individual must traverse in order for them to be considered an initiator; and, ("B") the amount of time the initiator must be stationary for the movement to be considered "terminated."

Once these rules were established, we began collecting data on collective movement behavior using the all-occurrence method. Additionally, before data collection the observer practiced measuring lengths of 10 meters from varying vantage points in preparation for estimating distances in the field. Once the group was stationary, we waited for 1.5 min (rule "B"). We then looked for any individuals who moved at least 10 meters (rule "A") without stopping for more than 2 s in a directed, linear manner, giving leeway for minor obstacles (cf. Seltmann et al. 2013). Once an individual achieved the above, this marked the start of a collective movement, and the individual was marked as the initiator. Each departing individual that moved at least five meters in the direction of the initiator (within an approximate 45 degrees) without stopping for more than 2 s was labeled as a "follower" (Jacobs, Maumy, and Petit 2008; Sueur 2011). Followers had up to 5 min to join, and others that joined after the 5-min cut-off were not included in the collective movement. Because one of the goals of this research was to determine what collective movements look like in moor macaques, the rules that were established favored the collection of successful collective movements. The termination of a collective movement was determined when the initiator was stationary for at least 1.5 min (rule "B") and had ceased the "directed manner" type of movement described above.

When the moor macaques were not engaging in collective movement behavior, we collected social network data by conducting 10-min focal animal samples, during which we recorded, at 1-min intervals, any individuals located within 1 meter of the focal animal, any grooming partners, and grooming direction. We recorded a total of 328 focal animal samples, with individuals being observed for a mean of 205 min (SD = 8.66). We recorded a total of 1298 dyadic interactions during the focal samples. Any data points involving multiple proximate individuals were recorded as multiple separate dyadic interactions with the focal individual, resulting in an overall network. The collection of all dyadic interactions can be represented by a network, with each individual as a vertex, and each edge weighted by the number of interactions featuring each pair of vertices. Separate networks were created for proximity- and affiliation-based dyadic interactions.

In between focal animal samples and all-occurrence sampling of collective movements, we used the *ad libitum* method to record dominance-related behaviors, which included displacement, avoidance, submission, retreat, and aggression (i.e., facial threat, lunges, chasing, slapping, grabbing, and/or biting). Dominance interactions in which there were multiple individuals involved at the same time or in which there was not a clear distinction between aggressor and the individual being aggressed against were not recorded. We recorded a total of 167 dyadic dominance interactions, with one individual considered the "winner" and the other considered the "loser."

2.5 | Data Analysis

2.5.1 | Dominance and Social Network Centrality

We assessed dominance status based on wins and losses observed during dyadic agonistic interactions. Of 167 dyadic dominance interactions observed, 59 were male-male interactions and 45 were female-female interactions, with the remaining 63 being male-female or female-male interactions. We only analyzed interactions between same-sex dyads. Accordingly, our sampling effort generated a ratio of interactions to individuals of 8.43 for adult males and a ratio of 5 for adult females. Sánchez-Tójar, Schroeder and Farine (2018) determined that a ratio of less than 10 interactions per individuals can still reasonably infer dominance hierarchies if the hierarchies are steep. To confirm hierarchy steepness, following Sánchez-Tójar, Schroeder and Farine (2018) we first plotted the hierarchy data and then used the package *aniDOM* and function "estimate_uncertainty_by_repeatability" to quantify the uncertainly of the hierarchy, which provides information about its steepness. This analysis generated values of 0.924 and 0.954 for the male and female dominance hierarchies, respectively, indicating relatively steep hierarchies, and therefore confirming that our estimates of the hierarchies are reasonably certain. We then used the *aniDOM* package (Farine and Sánchez-Tójar 2021) in R 4.3.1 (R Core Team 2023) to calculate the Elo rating (cf. Neumann et al. 2011, Sánchez-Tójar, Schroeder, and Farine 2018) for each individual within their sex class, with positive values representing a higher position in the dominance hierarchy.

We chose to use proximity, instead of affiliation, data to calculate the social network centrality of each adult individual (Castles et al. 2014), as more dyadic interactions were observed. We used the Eigenvector centrality metric to analyze the social network based on the dyadic interactions observed during focal animal samples because of its generality in estimating an individual's overall "importance" within a network (Bonacich 1987). Using R 4.3.1 (R Core Team 2023) and package *igraph*, we calculated the Eigenvector centrality score for each individual, which ranged from 0 to 1, with values closer to 1 representing more social connectedness. Both Eigenvector centrality and Elo ratings were standardized to have a sample mean of 0 and standard deviation of 1.

2.5.2 | Initiators

We used conditional logistic regression models to examine the relationship between initiators and individual characteristics, which included sex, social centrality, and dominance ranking. Originating in medical and public health research, conditional logistic regression models a binary response variable (e.g., success/failure or 1/0) for which the probability of "success" is a function of various predictor variables (Hosmer, Lemeshow, and Sturdivant 2013). It is distinct from conventional logistic regression in that it accounts for the stratification of observations into natural groups for which the total number of "successes" is fixed and known. In our study, conditional logistic regression was used to model the binary outcome of an individual either being an "initiator" or "follower" as a function of individual characteristics. The strata correspond to each collective movement for which individuals may be recorded as either an initiator or follower, with the total number of followers fixed at 1. We used the R 4.3.1 (R Core Team 2023) package *survival* (Therneau et al. 2024) to fit the conditional logistic regression with the response variable being whether or not an individual was an initiator (1) or follower (0) for a given movement. The predictor variables included individuals' sex, social centrality, dominance ranking, an interaction term between social centrality and sex, and an interaction term between dominance ranking and sex. We compared the predictor variables' p-values and coefficients from the conditional logistic regression to assess their effects. Results were considered significant at $p < 0.05$.

2.5.3 | Destination-Based Collective Movements

To assess the influence of anthropogenic effects on initiation, we split the collective movements into two categories, road and forest, based on the destination of each collective movement using the buffer tool in ArcGIS Pro (3.1.3., 2023). A 10-meter road buffer was created in ArcGIS Pro (3.1.3., 2023) using the polybuffer tool that spans from the center of the road to five meters on each side following previous studies (cf. Morrow et al. 2019). Collective movements for which the termination points fell within the 10-meter road buffer were considered to have the road as their destination, while those movements for which the termination points fell beyond the 10-meter road buffer were considered having the forest as their destination. We then fit separate conditional logistic regression models for each category. We then compared the predictor variables' coefficients and p values for corresponding t-tests from the conditional logistic regressions between and within the two categories (i.e., forest destinations vs road destinations). Results were considered significant at $p < 0.05$.

3 | Results

3.1 | Decision-Making Style

We recorded 61 successful collective movements. Successful collective movements were defined as those movements in which (a) an individual met the criteria presented in the methods section of being considered an initiator; (b) the initiation attempt did not result in the initiator returning to the group; and (c) included at least three other individuals who met the criteria of being considered a follower. The mean distance of successful collective movements (i.e., straight line distance between where the initiator started a movement to termination point that was collected via a handheld GPS unit) was 87.49 m (SD = 61.28). The mean number of followers in collective movements was 7.5 (SD = 3.2) individuals per collective movement. Of the 61 successful collective movements, 22 (36%) were initiated by females and 39 (64%) were initiated by males. Every adult in the group, except for two adult females (Erin and Korra), initiated at least one successful collective movement. Nonetheless, there was an unequal distribution of initiation in that some individuals initiated more collective movements than others. Two adult males, Daffa and Paman, initiated the most

TABLE 1 | Dominance (Elo score) and social centrality (Eigenvector centrality) scores for each adult in Group B. Individuals are separated by sex and ordered by rank.

Individual ID	Elo score (dominance rank)	Sex	Eigenvector centrality
Beti	1.5676311	F	1.2828458
Caca	1.2387039	F	0.3542098
Cri	0.3039152	F	0.5653761
Korra	0.2923702	F	0.1983940
Moka	−0.1864437	F	1.6135102
Erin	−0.7240093	F	−0.3568020
Nopi	−1.0344392	F	0.9320434
Lucia	−1.4247888	F	−0.3000086
Lavinia	−1.6804129	F	−0.9655171
Paman	0.9322320	M	−0.4484234
Hantu	0.8703837	M	0.2198441
Daffa	0.7186528	M	−0.4394311
Jaya	−0.3475084	M	−1.3661916
Mamoa	−0.8379693	M	−1.4463074
Gado	−1.0753887	M	−1.6948326
Hiu	−1.5417703	M	−1.6727140

TABLE 2 | Results of the conditional logistic regression models assessing how well individual characteristics predict initiation. The “female” classification is treated as the reference in the sex category. Significance levels: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Model	Factor	Coefficient	Exp (Coef.)	Std Err (Coef.)	*p* value
Overall	Dominance	0.34194	1.40767	0.20287	0.0919
	Centrality	0.03305	1.03361	0.27583	0.9046
	Sex (male)	1.14295	3.13602	0.45666	0.0123*
Forest	Dominance	0.08079	1.08414	0.23383	0.729713
	Centrality	0.41774	1.51852	0.31028	0.178202
	Sex (male)	2.08108	8.01311	0.56743	0.000245***
Road	Dominance	1.1505	3.1599	0.5373	0.0323*
	Centrality	−1.3110	0.2695	0.8213	0.1104
	Sex (male)	−1.9666	0.1399	1.1255	0.0806

collective movements at 10 each. Of the 61 successful collective movements, 11 (18%) of them had a termination point within the 10-meter road buffer, while 50 (82%) had a termination point in the forest (i.e., outside the road buffer).

3.2 | Role of Individual Characteristics

Individuals' dominance, centrality, and sex (Table 1) were included in the initial overall (i.e., all collective movements considered together) conditional regression model (Table 2). Pairwise interactions between dominance and sex, and centrality and sex were considered, but sequentially removed from the model based on large p values associated with t-tests for each effect. Sex was identified as a main predictor of initiation (coef = 1.14295, $p = 0.0123$), with males being over three times more likely to be initiators than females. There was also modest support of dominance rank as a predictor (coef = 0.342, $p = 0.0919$), with higher ranked individuals being more likely to initiate collective movements. Social centrality was not found to be a predictor of initiating collective movements in the overall model (coef = 0.0331, $p = 0.901$).

3.3 | Collective Movements in an Anthropogenic Context

Interactions between sex, dominance, and social centrality were investigated, but sequentially removed due to lack of evidence of meaningful effects. In the final forest-directed model (Table 2), sex was still the main predictor (coef = 2.08, $p = 0.000245$), with males being approximately eight times more likely to initiate collective movements than females. Neither dominance rank (coef = 0.0808, $p = 0.73$) nor centrality (coef = 0.418, $p = 0.178$) were identified as strong predictors of initiation.

Similar to the previous models, the interaction terms were removed in the final road-directed model, which only included the predictor variables of dominance, centrality, and sex. In this final road-directed model (Table 2), dominance rank was identified as a supported predictor of initiation (coef = 1.18, $p = 0.0323$), with more dominant individuals being more likely to initiate collective movements. Centrality and sex (coef = −1.31, $p = 0.1104$; coef = −1.97, $p = 0.0806$) were estimated to have weak, inverse relationships to initiation. In other words, in addition to higher ranked individuals being more likely to initiate collective movements to the road, there was weak evidence that less central individuals and females are more likely to initiate road-directed movements.

4 | Discussion

4.1 | Moor Macaques Show Partially-Shared Decision Making

This study was the first to examine the collective movement behavior of moor macaques, and to our knowledge, of any of the Sulawesi macaques in a wild setting. Accordingly, one of our research goals was to characterize what collective movements look like in this species. Collective movement distances in this study ($M = 87.49$ m, SD = 61.28 m) were longer than those reported in semi-captive populations of Tonkean ($M = 29$ m, SD = 1.29 m) and rhesus macaques ($M = 26.7$ m, SD = 0.73 m; Sueur and Petit 2008b). In wild Barbary macaques, Seltmann et al. (2013) reported a collective movement distance mean of 106 m (SD = 123 m), for adults, which is similar to what we reported here, suggesting that wild macaque populations may have similar thresholds for collective movement distances, but more research on other species of wild macaques is needed.

Within the collective movements themselves, most individuals initiated at least once, indicating that decision making may be shared. That being said, the majority of collective movements were initiated by only a few individuals. Therefore, it may be more appropriate to characterize the decision-making of moor macaques in Group B as partially shared. This finding aligns with what has been reported for other macaque species including Barbary (Seltmann et al. 2013), rhesus (Sueur and Petit 2008b), Japanese (Jacobs, Watanabe, and Petit 2011), and Tibetan macaques (Wang et al. 2016), but not the closely related Tonkean macaques that are reported to exhibit equally shared decision-making (Sueur and Petit 2008b). Because both Tonkean and moor macaques can be considered socially tolerant, compared to more despotic macaque species, the observed difference in decision-making style may be explained by the difference in research setting (i.e., semi-captive setting for Tonkean macaques). More data on wild populations of the various Sulawesi macaques are needed to confirm this.

4.2 | Adult Males are Most Likely to Lead Collective Movements Overall

Our findings show that one individual characteristic predicted initiation of collective movements: sex, with males being more likely than females. Sex has been previously linked to initiation in other macaque species, such as in Barbary macaques where males tried to initiate more group movements than females (Seltmann et al. 2013). However, in other macaque species, such as the closely related Tonkean macaques (Sueur and Petit 2008b), the Japanese macaques (Jacobs, Watanabe, and Petit 2011), and the Tibetan macaques (Fratellone et al. 2019) there was no observable relationship between initiation and sex. In other group-living mammals, males must often contend with the energetic demands of their sex-specific life history obligations of maintaining physical characteristics, such as larger bodies and other features pertaining to reproductive advantages (Clutton-Brock 2017). Individuals with the most need (i.e., lowest reserves of resources) can initiate collective movements more often than their satiated conspecifics (Sueur et al. 2010), which suggests that the potentially higher energetic requirements of males and the differences in body size between the sexes may be driving more male participation in initiations.

4.3 | Collective Movements Patterns Differ in Anthropogenic Environments

Our study group exhibited a partially-shared decision-making style for collective movements directed toward both the risky roadside habitat and the forest interior. In rhesus macaques, Anand and Radhakrishna (2022) found that the partially shared decision-making process shifts toward an equally shared process in anthropogenic landscapes. Given that their finding is in contrast to what we report here, there may be interspecies variation among macaques in how they adjust to anthropogenic habitats. It is also possible that specific factors about the environments in which these two studies took place, such as the type of human infrastructure/interaction, may influence which decision-making style is the most advantageous. In our case, previous research indicates that Indonesians who pass through the park desire to feed and interact with the macaques along the road (Morrow 2018).

Although we found the decision-making style to be similar across the two contexts, we did find differences in which individual characteristics best predict who will initiate collective movements. Sex was only a significant predictor in forest-directed collective movements, with males being more likely to be initiators to forest destinations. In contrast to our prediction, there was only weak support of sex as a predictor variable of initiating road-directed collective movements, with females emerging as moderately more likely than males. This result is surprising given that the road may represent a risky environment in which there are possible high costs (e.g., getting injured by vehicles). However, the road also presents high rewards in the form of calorically dense and easily digestible anthropogenic foods, thereby providing nutritional advantages that can lead to an increased rate of survival (Asquith 1989). The greater tendency for females to initiate collective movements to the roadside habitat may be explained by the caloric needs of females with infants, particularly given that females with infants require high caloric intake compared to their conspecifics to compensate for the energetic costs of producing milk and caring for infants (Key and Ross 1999). This explanation is supported by the finding that Caca and Cri, both of whom had infants at the time of the study, initiated more than half of the observed road-directed collective movements. Our results may be indicative of high level of desensitization to the road environment, whereby the perceived rewards of being along the road outweigh the risks (cf. Waterman et al. 2020).

While dominance was not a supported predictor of initiating collective movements to forest destinations, it was for road-directed movements, with higher-ranking individuals being more likely to initiate collective movements to the risky roadside habitat. This finding is also in contrast to our predictions. It may mean that individuals experience differing access to provisioned foods along the road, with provisioning being more clumped than expected. At other sites, dominant individuals have been found to consume more anthropogenic foods than lower-ranked ones (Kaplan et al. 2011; Marty et al. 2020), presumably due to their ability to monopolize access to these clumped food sources. Access to food resources in males can often determine their overall body size, which can be positively correlated with their rank (Marty et al. 2017). In females, high-ranking individuals often show faster growth and maturity rates as well as a shorter interbirth interval (Harcourt 1987; Shivani, Huchard, and Lukas 2022), partially due to their preferred access to food. A similar process regarding dominant individuals and provisioned food may be occurring with the individuals in our study group. Dominant individuals might be more inclined to initiate a collective movement to the road because they have the option to monopolize their access to provisioned and discarded foods. It is also possible that lower-ranked individuals may not be as interested as higher-ranked individuals to initiate road-directed collective movements because they may be aware of their own ranking (Mielke et al. 2018; Seyfarth and Cheney 2000), and therefore, their lower chances to obtain food.

Overall, to date, examining collective movements in the context of anthropogenic activity and/or provisioning has only been addressed by a few other studies (Bracken et al. 2022; Anand and Radhakrishna 2022). Here we observed the collective movement behavior of moor macaques in an heterogenous environment that included forest and roadside habitat. We found that the moor macaques of Group B displayed a partially-shared decision-making style, with males being more likely to initiate collective movements overall. We also found that differences existed when collective movements were directed toward the road, for which dominant individuals were more likely to initiate. Previous research on moor macaques has documented changes in social behavior (Morrow et al. 2019) and ranging behavior (Riley et al. 2021) depending on human-activity. Our results suggest that moor macaques also balance risks and rewards present in anthropogenic contexts when deciding when and where to forage and who will lead these movements, thereby further demonstrating their behavioral flexibility in human-modified environments.

One limitation of this study was that the data collection period was confined to only the rainy season. Weather conditions, in this case heavy rain, can affect primate behavior. In macaques specifically, heavy rain is associated with a decrease in activity, such as moving and socializing (Hanya et al. 2018). Anecdotally, we observed that our study group traveled less during periods of heavy rain. At the onset of heavy rain, the group would cease what they were doing and retreat to the canopy of large trees to huddle and take shelter from the rain. In a few cases we observed the group ceasing all roadside behavior during the onset of rainy weather. Future research would benefit from collecting data across the dry and wet seasons to account for possible changes and shifts in the group's behavior due to changes in weather. Doing so would also generate a larger sample of collective movements from the two contexts. Previous research with moor macaques indicates that they make use of anthropogenic food sources when fruit availability in the surrounding forest is low (Zak 2016), which is predicted to vary depending on the season. Expanding the research timeframe to cover both the dry and wet season and simultaneously collecting data on patterns of forest food availability would further contribute to our understanding of how ecological factors shape decision-making in moor macaques.

Future research could also benefit from examining the role of additional individual characteristics, such as personality. In the presence of predators, “bolder” personalities have been previously associated with riskier behaviors (Quinn and Cresswell 2005). Personality has previously been explored in the context of anthropogenic environments, in which more bold individuals are associated with increased use of urban mosaics (Honda et al. 2018); however, it not yet been addressed in the context of primate collective movements.

Ultimately, in addition to contributing to our understanding of primate behavioral flexibility in the face of human-induced environmental change, our findings can help inform conservation efforts for the Endangered moor macaque and the management of human-macaque interfaces more broadly. Because roadside provisioning of moor macaques in Bantimurung Bulusaraung National Park is what drew them to the road initially and is what likely reinforces their daily decision to come to the road, future efforts should focus on shifting the risk-reward tradeoff present at this site by curbing the rate of roadside provisioning. To date, the national park has tried using informational signage to discourage provisioning with little impact (Authors, personal observation), but regular and consistent monitoring of provisioning by park staff may be more effective. An interesting avenue that could be explored would be for park staff to selectively discourage provisioning around high-dominance (i.e., initiators, in the road context) individuals, which could ultimately reduce the amount of time the group spends near the road. However, monitoring could be difficult to sustain (park ranger, personal communication) and the roadside behavior, first seen in Group B, is now being observed in many other groups in the area.

This site is undergoing rapid environmental change as a result of on-going, large-scale road widening project, which has resulted in the destruction of several meters of forest on either side of the road. The Indonesian Ministry of Forestry's plans for future forest restoration could benefit from also considering the risk-reward tradeoff experienced by the moor macaques at this site. Namely, restoration efforts should avoid planting trees along the roadside that are known to be preferred moor macaque foods so as to reduce the attractiveness of human-modified areas (cf. Fehlmann et al. 2017).

Author Contributions

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Acknowledgments

Many thanks to the National Agency for Research and Innovation of Indonesia (BRIN), Balai Taman Nasional Bantimurung Bulusaraung (TNBABUL), and Hasanuddin University (UNHAS) for sponsoring and supporting this research. Funding for the research was provided by San Diego State University, specifically the College of Graduate Studies and the Division of Research and Innovation CORE Fellowship and the Graduate Student Travel Fund (awarded to Joshua Trinidad) and the U.S. National Science Foundation (Award #2222891, PIs: Erin P. Riley, Amanda Ellwanger, and Henry Scharf). We would also like to thank the following people: Pak Haro and Hendra for your knowledge and guidance; Mama Aco, Icang, and Anthi for your hospitality during our stay in Bengo.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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