Between-group competitive advantage offsets foraging costs for bigger groups in harsher seasons

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August 12, 2025

Keywords— home range, longitudinal data, movement ecology, group size, neighbor interactions, social relations model, feeding competition, *Cebus imitator*

Abstract

Larger animal groups are widely understood to require more space and travel farther to mitigate the foraging costs of within-group competition. Yet, between-group interactions and shifting resource distributions can confound the relationship between group size and behavior, making responses to demographic change difficult to predict— especially in highly seasonal environments. Leveraging 33 years of longitudinal data from 12 neighboring white-faced capuchin monkey (*Cebus imitator*) groups, combined with remotely-sensed environmental data, we show that within- and between-group competition jointly shape space-use patterns, with their relative importance shifting across environmental contexts. We found that: (1) larger groups compensated for reduced per-capita foraging efficiency by expanding into less-exploited areas over longer timescales rather than increasing daily travel; (2) range expansion by large groups was disproportionately directed toward smaller neighbors; (3) during the dry season, resource confinement to riparian zones reduced spatial overlap but increased intergroup encounters, especially in more productive areas; and (4) larger groups held higher-quality ranges in the dry season while maintaining consistent fruit intake across seasons, suggesting that benefits of between-group competitive ability offset within-group costs during resource-scarce conditions. Our findings show that environmental variation shifts the trade-offs of within- and between-group competition, shaping how group-living animals adjust to changing social and ecological conditions.

1 Main

Functional traits of animals (e.g., body size, life-history strategy, social structure) carry both costs and benefits that depend on specific ecological conditions [1, 2]. Understanding how environmental change alters the balance of these trade-offs is key to explaining their wide variation across and within species (and populations), as well as to forecasting evolutionary trajectories [3, 4]. Group size represents one such trade-off for group-living animals, as it affects both within- and between-group resource competition, but often in opposing ways [5–7].

Within-group competition imposes a cost by reducing individual foraging efficiency and thereby setting an upper limit on group size (i.e., the Ecological Constraints Model of Group Size; [8–10]). Consequently, larger groups face higher energetic costs from increased resource requirements and travel distances, driven by greater collective metabolic demands and faster resource depletion [11, 12]. They also often require larger home ranges (e.g., [13–16]; but see [17])—similar to how individual space use scales allometrically with body size [18].

While larger groups typically face greater costs from within-group competition, they often hold a competitive edge in between-group contests, leveraging their numerical advantage to exclude smaller neighbors from key resources [17, 19–22]. This advantage is especially pronounced when resources, such as fruiting trees, are distributed in defensible patches that vary in quality, allowing larger groups to monopolize the most valuable patches [6]. Larger groups also benefit indirectly, as smaller groups may avoid high-risk areas—granting larger groups access to a wider array of food patches with reduced opposition [23, 24]. With more (and better) foraging options available, larger groups can access richer and less-depleted patches, potentially mitigating the costs of within-group competition and contributing to higher survival and reproductive success [6, 25–27].

Ultimately, group size reflects a trade-off between the costs of within-group competition and the benefits of between-group competition [28]. Still, group sizes often vary widely within populations and fluctuate temporally, suggesting that this balance is mediated by additional ecological and social factors [29–31]. Demographic turnover reshapes the distribution of group sizes across the population, altering both ecological constraints and the balance of power among neighboring groups [22, 32]. Simultaneously, environmental conditions and the spatiotemporal distribution of resources influence both the intensity of within-group competition and the cost-effectiveness of resource defense [33–35]. For example, smaller groups may benefit when resources are abundant or widely distributed, making them less practical to defend— thereby reducing the importance of intergroup dominance [19]. In contrast, during resource-scarce periods, larger groups may gain an advantage by using their numerical superiority to outcompete smaller groups for remaining food patches [27, 36]. This advantage, however, could be offset if larger groups incur disproportionately high costs from within-group competition under the same conditions [37]. Nevertheless, whether small, large, or intermediate-sized groups are favored is likely context-dependent, shifting with dynamic demographic and environmental conditions over time [4, 28, 38].

The Ecological Constraints Model is widely accepted as a generalizable framework for understanding how within-group competition limits group size in social animals [8, 9, 11, 39–42]. As with any broad framework, however, real-world ecological complexity introduces important nuance: the interdependence of within- and

between-group competition, along with the dynamic nature of landscapes and competitive interactions, often obscures causal links between group size, resource availability, and behavioral outcomes. Thus, how the costs of within-group competition interact with the benefits of between-group competition at the population level— particularly as resource availability fluctuates— remains unresolved. Clarifying how this interaction unfolds over time is critical for understanding the evolution of sociality, the ecological conditions under which it is favored, and its trajectory in a rapidly changing world. Such insight requires requires long-term datasets from multiple, neighboring social groups that encompass meaningful demographic and ecological variation—data that are logistically difficult to obtain. Most previous research has therefore examined within- and between-group competition in isolation (often cross-sectionally), lacking either the temporal depth or number of social groups needed to explore their interaction.

Drawing upon 33 years of data on 12 white-faced capuchin monkey groups from the Lomas Barbudal Monkey Project in Costa Rica (10°29–32'N, 85°21–24'W), we examine how demographic and environmental variation structure population-level patterns of resource competition in a group-living animal [43]. Lomas Barbudal lies within one of the last remaining fragments of tropical dry forest [44]—a biome characterized by a highly seasonal climate with a distinct wet season (May–November) and a harsh dry season (December–April) (Figure 1b; [45]). Seasonal shifts dramatically alter resource distribution and availability. Most of the forest is deciduous, and during the dry season water, shade, and food become concentrated in evergreen riparian zones (subsection S1.3). This system offers a rare opportunity to study how long-term demographic and environmental fluctuations shape competition and space-use dynamics, due to both the exceptional breadth of the dataset and the pronounced environmental variation in the region. Capuchins in this population live in cohesive multi-male, multi-female groups of 5–40 individuals (mean = 18.8; [43]) that persist for years or decades, although occasionally split permanently into two independent units with distinct home ranges (nine events over the study period; Figure 1c). Capuchins are primarily frugivorous (∼50-55%), with invertebrates comprising most of the remaining percentage [46, 47]. Groups are range-resident for decades and their home ranges overlap extensively (Figure 1a). Inter-group contests occur frequently (∼1 per week per group) and are often aggressive [48, 49].

Here, we integrate conventional *group-level* predictions of the Ecological Constraints Model— linking group size to indicators of within-group competition— with *dyadic* comparisons of neighboring groups to test how relative group size influences between-group relationships. First, we evaluate annual and seasonal relationships between group size and (a) fruit foraging efficiency, (b) daily path length, (c) return rate to previously used areas, (d) home range area, and (e) home range quality. Next, we apply hierarchical social

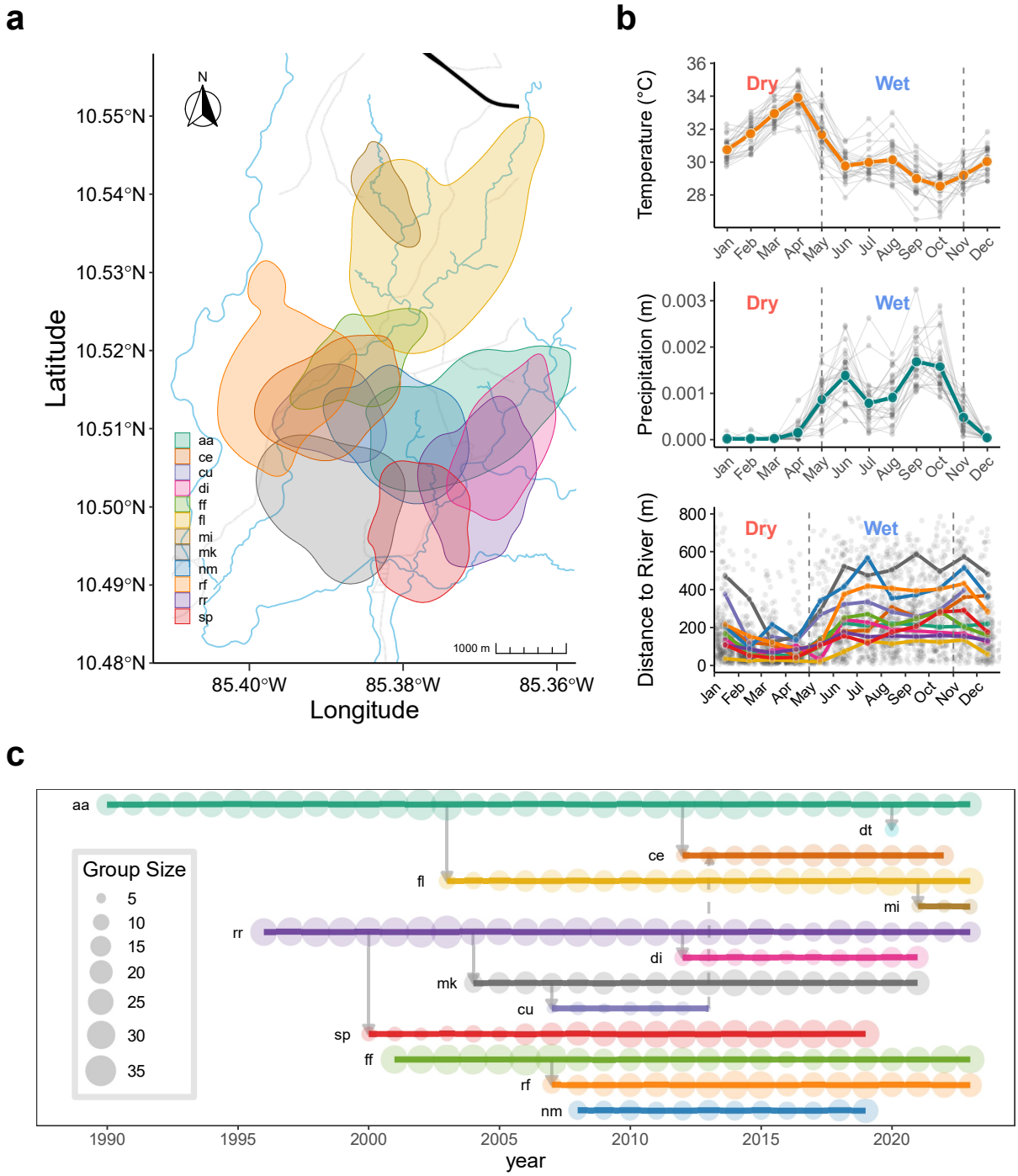

Figure 1: **Environmental and demographic context.** a: Annual home ranges of 12 white-faced capuchin study groups (95% auto-correlated kernel density contours) at the Lomas Barbudal Monkey Project, Costa Rica. Colors correspond to group identity. Estimates are derived from handheld GPS-tracking data collected in 2012, except for ce and di (formed after fissions in late 2012; shown using 2013 data) and mi (formed after a 2021 fission; shown using 2021 data). Group dt is not shown due to insufficient location data. b: Weather data near the Lomas Barbudal Biological Reserve from the ERA5 reanalysis dataset (1990–1993, 1997–1999, 2001–2020). Top panel shows temperature (°C); middle panel shows total precipitation (m); bottom panel shows each study group's mean distance to river. For temperature and precipitation, grey lines and points show monthly means per year; colored lines and points (orange for temperature, blue-green for precipitation) show the monthly mean across years. For distance to river, grey points represent mean daily distance to the river; colored points and lines show monthly means by group. Dashed vertical lines mark typical transitions between dry and wet seasons. c: Time series of data collection for all 13 study groups from 1990 to 2023. Group abbreviations indicate monitoring start dates or formation via permanent fission. Arrows denote fission events (solid) and a single fusion event (dashed).

relations models to evaluate how relative group sizes within group-dyads predict home range overlap and encounter rates, and how these relationships vary with seasonal shifts in vegetation productivity. Together, these analyses provide one of the first longitudinal tests of how group-living animals adjust both within- and between-group competition in response to demographic and environmental change. Our findings highlight the dynamic trade-offs of group living and show how ecological and social pressures jointly shape space-use strategies— factors that ultimately determine access to resources and individual fitness.

Table 1: **Summary of response variables.**

Response variable	**Abbreviation**	**Level**	**Competition type**	**Interpretation**
Per Capita Fruit Intake Rate	FIR	Individual	Within-group	Individual energy intake from fruit
Daily Path Length	DPL	Group	Within-group	Daily energy expenditure
Revisitation Rate	RR	Group	Within-group	Frequency of returns to previously used areas
Home Range Area	HRA	Group	Within-group	Long-term space requirement
Home Range NDVI	HRQ	Group	Between-group	Home range quality
Proportional Overlap	PO	Group-dyad (asymmetric)	Between-group	Encroachment by neighbor
Encounter Rate	ER	Group-dyad (symmetric)	Between-group	Frequency of intergroup encounters

2 Results

2.1 Larger groups face foraging costs but do not increase daily travel

To evaluate how group size influences resource competition, we combined long-term movement and observational data with continuous-time movement modeling (`ctmm`) and Bayesian generalized linear multilevel models (GLMMs) to estimate five response variables: (a) per capita daily fruit intake rate, (b) daily path length, (c) mean revisitation rate across the home range, (d) home range area, and (e) home range quality, assessed via normalized difference vegetation index (NDVI)— a satellite-derived measure of vegetation greenness. All GLMMs were run at both annual and seasonal scales.

We found strong evidence for a negative association between group size and per capita fruit intake

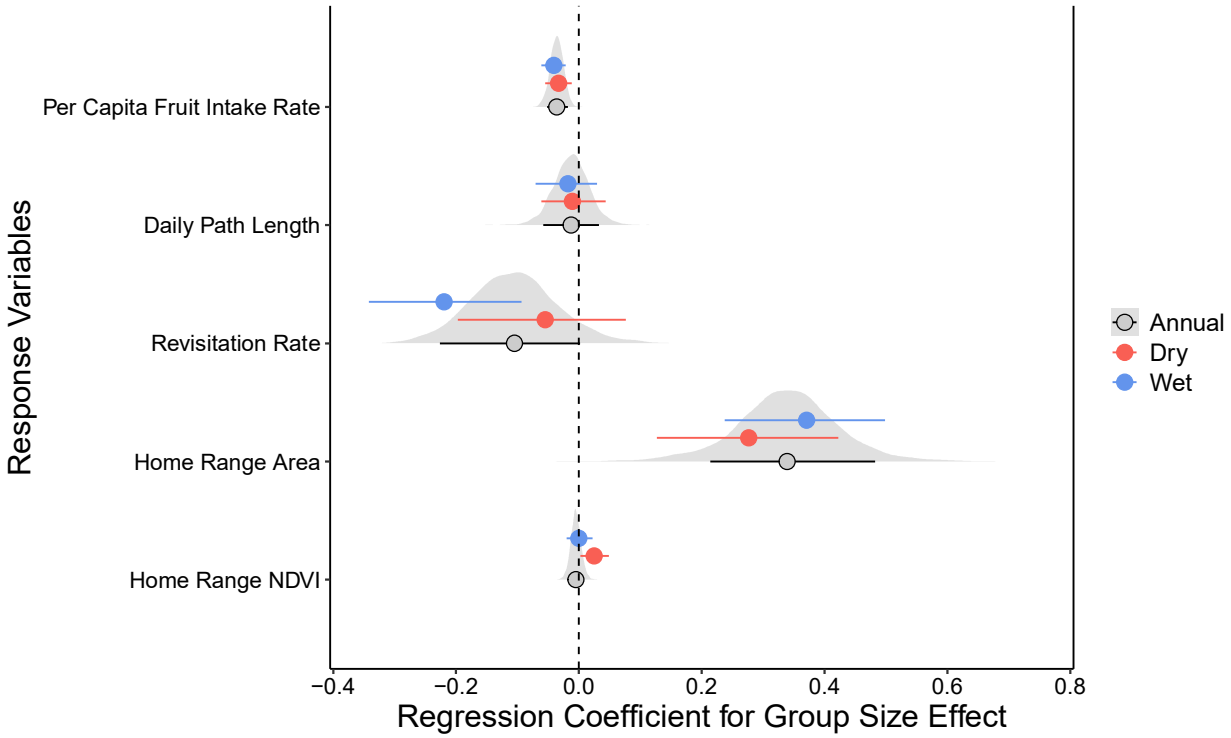

Figure 2: **Group size effects on resource and space use.** Posterior estimates of the effect of group size on five group-level response variables: per capita fruit intake rate, daily path length, revisitation rate, home range area, and home range normalized difference vegetation index (NDVI). Points indicate median posterior estimates, and solid lines represent 89% Highest Posterior Density Intervals (HPDIs). Blue and red point intervals correspond to wet and dry season effects, respectively, while black/grey intervals indicate annual (non-seasonal) effects. Grey density slabs show the full posterior distributions for the annual effects.

rate, with no clear seasonal difference (Figure 2). In contrast, group size showed little to no association with daily path length at either scale. Revisitation rates were lower in larger groups at the annual scale and during the wet season, but showed no relationship in the dry season ($\beta_{\text{annual}} = -0.11[-0.23, 0.00]$; $\beta_{\text{wet}} = -0.22[-0.34, -0.09]$; $\beta_{\text{dry}} = -0.06[-0.2, 0.08]$). Larger groups consistently occupied larger home ranges across both scales, with a stronger effect observed in the wet season ($\beta_{\text{wet}} = 0.36[0.24, 0.49]$; $\beta_{\text{dry}} = 0.27[0.13, 0.41]$). Larger groups occupied home ranges with higher NDVI in the dry season, but no relationship was observed in the wet season (Figure 2; $\beta_{\text{HRQdry}} = 0.02[0, 0.05]$; $PP > 0 = 0.94$; $\beta\text{HRQ}_{\text{wet}} = 0[-0.02, 0.02]$).

2.2 Larger neighbors encroach onto smaller focal groups

To evaluate how group size asymmetries shape intergroup spatial dynamics, we modeled proportional home range overlap between neighboring group-dyads using hierarchical Social Relations Models [50, 51] (SRMs)

within a causal inference framework [52]. This approach accounts for repeated measures within and across dyads by simultaneously estimating group-level tendencies (e.g., a group's general propensity to overlap with others) and dyad-specific effects (e.g., the unique overlap between a particular pair). We incorporated group-level predictors (focal and neighbor group size) and a dyad-level predictor (the interaction between focal and neighbor group size) to explain variation in asymmetric (i.e., directional) overlap (PO_{fn}), defined as the proportional home range overlap of a focal group f with a specific neighbor n. By adjusting for the home range area of f, PO_{fn} can be interpreted as the degree of encroachment by the neighboring group onto the focal group's range. While SRMs are typically applied to dyads of individuals, extending the framework to dyads of animal groups (a) is key to understanding how within-group and between-group competition jointly shape behavior, and (b) provides a new tool for assessing group-level social networks.

Using this approach, we found that an increase in neighbor group size tended to lead to an increase in PO_{fn} (Figure 3). However, this relationship was strongest when the focal group was small ($\sim$8 monkeys; $\beta_{PO} = 0.61[0.25, 0.98]$), moderate when the focal group was intermediate in size ($\sim$21 monkeys; $\beta_{PO} = 0.17[0.06, 0.28]$), and weakly negative when the focal group was also large ($\sim$35 monkeys; $\beta_{PO} = -0.26[-0.65, 0.11]$). This pattern held in the annual and wet season models but was not evident during the dry season, when PO_{fn} was generally reduced and neighbor group size had minimal impact.

To better understand which group (i.e., smaller or bigger group) in a dyad drove temporal increases in overlap (i.e., change in PO_{fn} at time t to any future timestep), we conducted a complementary analysis of dyads that showed both substantial increases in annual PO_{fn} (from $< 25\%$ to $> 45\%$) and shifts in relative group size (net change ≥ 5) (see section 4.4). In 84% of cases, the group that caused the increase in overlap was the one that became relatively larger over time (Figure 4), consistent with a competitive advantage of larger groups for space.

2.3 Dry conditions increase encounters despite reduced overlap

To investigate how seasonality affects intergroup encounter rates, we used the `ctmm` framework to estimate expected space-time overlap between group home ranges (i.e., encounter rate). We then fit dyadic Bayesian multiple-membership models to assess seasonal variation in encounter rates as a function of symmetrical (i.e., non-directional) dyadic predictors: absolute group size difference, overlap zone area, and vegetation greenness within the overlap zone (measured by mean NDVI). Predicted encounter rates were consistently higher in the dry season than in the wet season, despite reduced proportional overlap between dyads (Figure 5a). This pattern is consistent with a stronger effect of overlap zone size on encounter rate in the dry

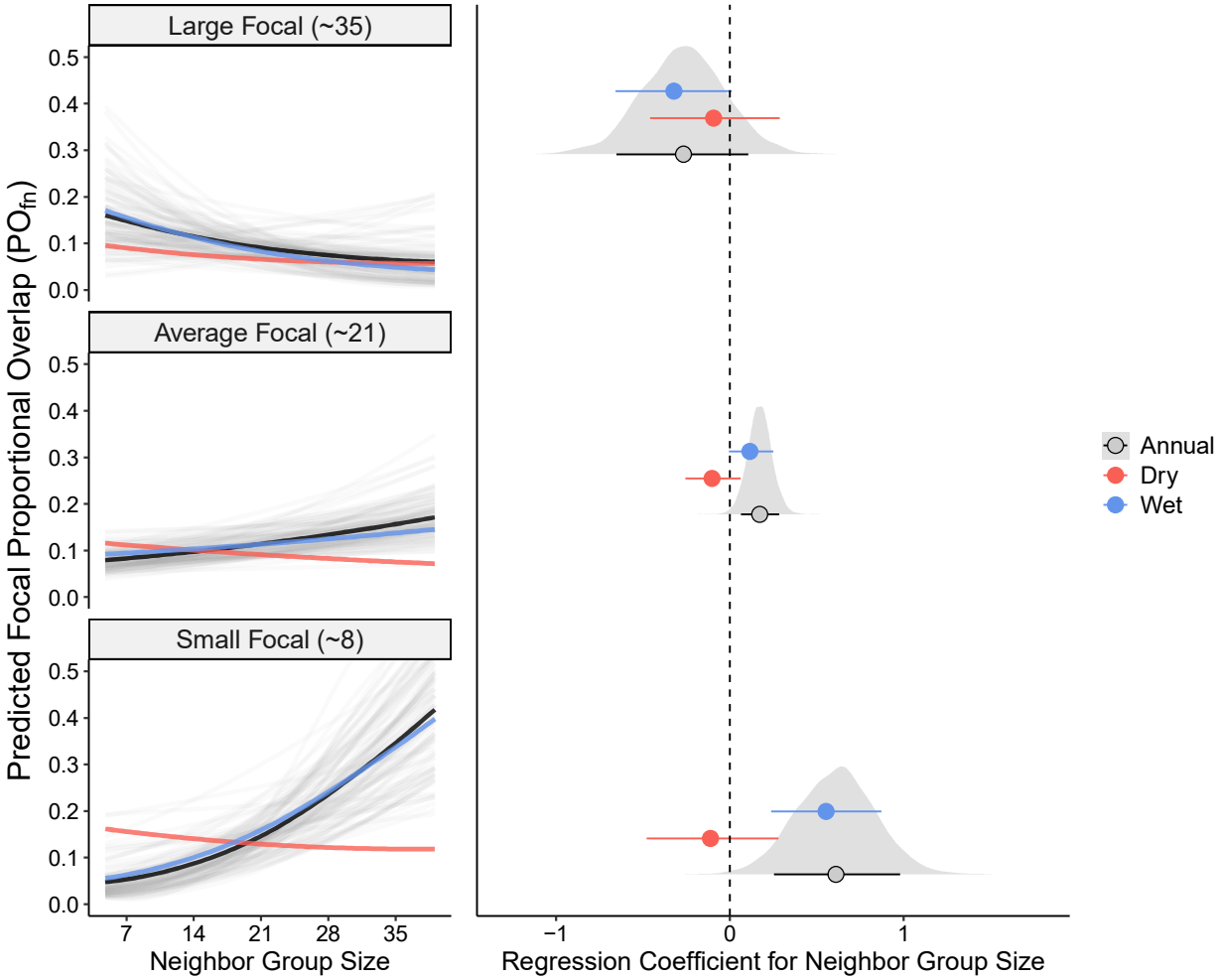

Figure 3: **Relative group size effects on neighbor encroachment.** Predicted effects of the interaction between focal and neighboring group sizes on proportional focal home range overlap (PO_{fn}). Left panels shows model predictions of (PO_{fn}) as a function of neighboring group size across representative focal group sizes. Light grey lines depict 100 randomly sampled posterior draws from the annual model; dark black lines show the median annual prediction; red and blue lines show median predictions for the dry and wet seasons, respectively. Right-hand plot displays median posterior effect sizes and 89% Highest Posterior Density Intervals (HPDIs) for both annual and seasonal models, corresponding to the predictions in the left panels. Grey density slabs are posterior distributions for the annual effects.

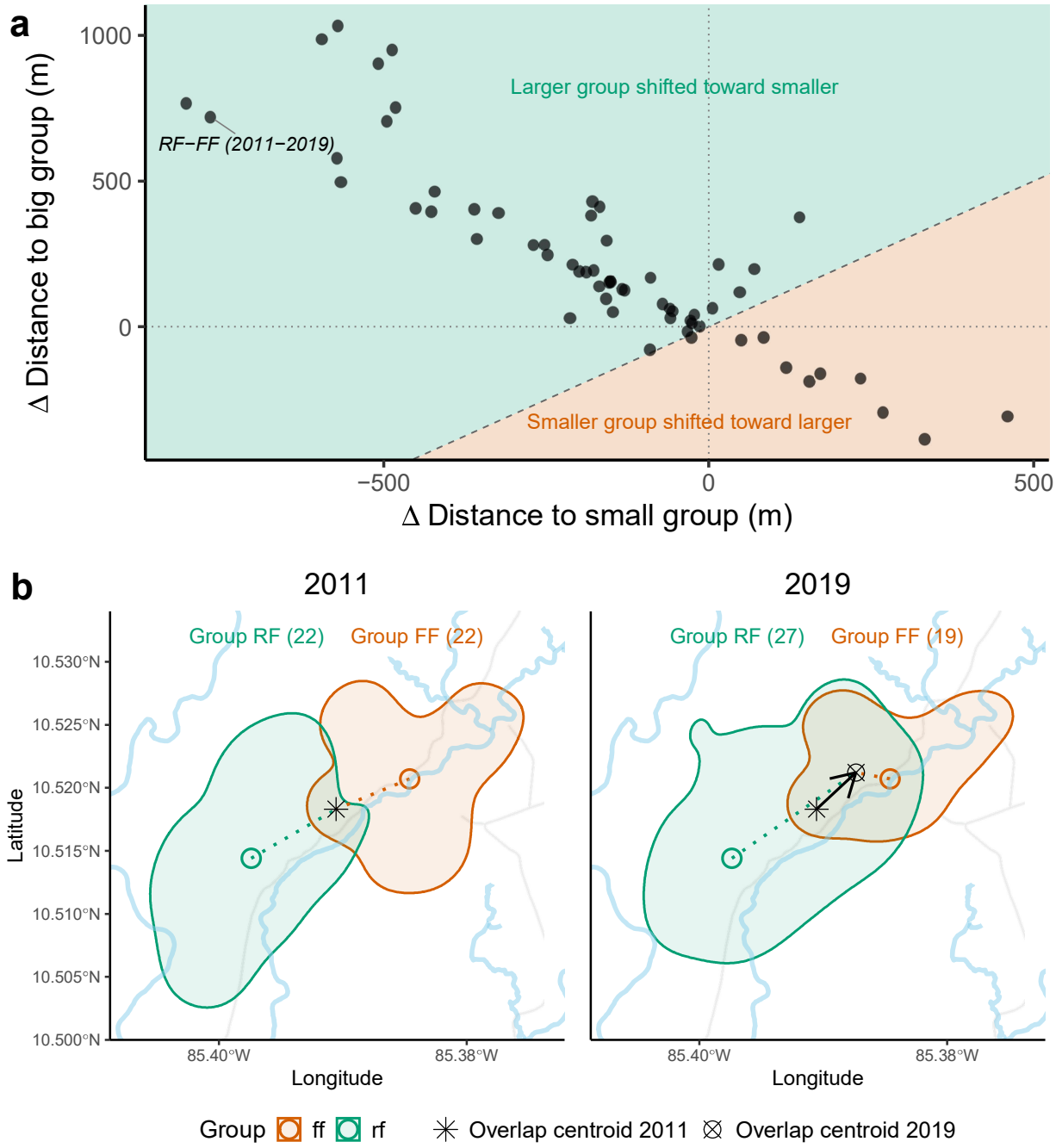

Figure 4: **Directional shifts in home range overlap.** (a) Each point represents a dyad-year pair with a marked increase in overlap and a substantial shift in relative group size. Axes show the change in distance ΔD from each group's home range centroid at time t to the overlap centroid at time $t+1$, relative to the original distance at t. The x-axis shows ΔD for the group that became relatively smaller; the y-axis for the group that became larger. Positive values indicate the overlap centroid moved away; negative values indicate it moved closer. Shaded colors indicate which group drove the shift. The dashed diagonal marks equal shifts. (b) Example of dyad RF–FF (2011–2019) showing the overlap centroid's shift. Polygons represent 95% home ranges; large circles show group centroids. Dotted lines connect group centroids to overlap centroids; the arrow shows directional change. Point shapes indicate overlap centroid locations; group sizes are in parentheses.

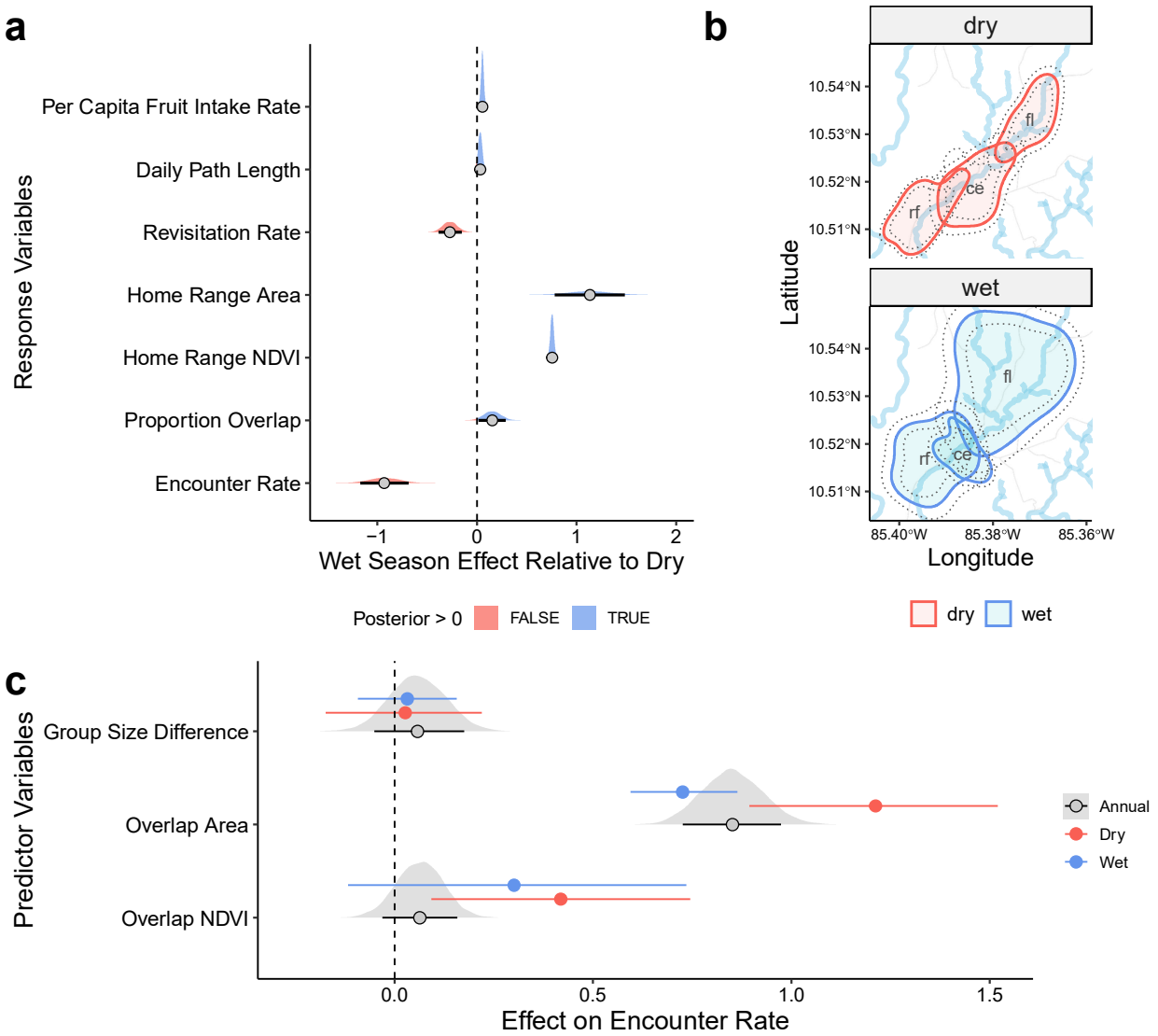

Figure 5: **Seasonal changes in fruit intake, ranging behavior, and encounter rates.** (a) Posterior densities, medians, and 89% Highest Posterior Density Intervals (HPDIs) for wet vs. dry season contrasts across all seven response variables: fruit intake, path length, revisitation rate, home range size, home range NDVI, proportional overlap (PO_{fn}), and encounter rate. Red shading indicates higher values in the dry season; blue shading indicates higher values in the wet season. (b) Seasonal comparison of home range overlap among three groups in 2018. (c) Posterior medians and 89% HPDIs for annual and seasonal effects of group size difference, overlap size, and overlap NDVI on encounter rate. Blue and red point intervals correspond to wet and dry season effects, respectively, while black/grey intervals indicate annual (non-seasonal) effects. Grey density slabs are posterior distributions for the annual effects. Note that seasonal and annual models are fit to different subsets of the data, which may contribute to discrepancies between seasonal and annual effect sizes.

season, indicating more frequent encounters per unit of shared space compared to the wet season (posterior contrast: $\beta_{\text{wet-dry}} = -0.49[-0.78, -0.16]$). Encounter probability was highest in overlap zones with greater vegetation productivity, particularly in the dry season ($\beta_{\text{HRQ}} = 0.42[0.09, 0.74]$). In contrast, absolute group size difference had no consistent effect on encounter rate, with substantial uncertainty across both scales (Figure 5c).

3 Discussion

Our findings show that trade-offs of group living are shaped by complex interactions between environmental conditions and group demography, which together mediate how within- and between-group competition influence the social and spatial structure of a population. Larger capuchin groups showed reduced per capita fruit intake efficiency, indicating stronger within-group competition over clumped resources— consistent with the Ecological Constraints Model [8]. However, this increased competition did not translate into higher daily travel costs for larger groups (contra common expectation; e.g., [11, 12]). Instead, they appear to mitigate foraging competition by leveraging their numerical advantage to outcompete smaller groups, gaining access to *less frequently visited* areas during the wet season (when food is abundant and dispersed) and to *higher-quality* patches during the dry season (when resources are concentrated in riparian zones).

The transition from wet to dry season may mark a shift from indirect to more direct between-group competition, as resources become limited and more economically defensible. Supporting this, we found that home range overlap declines in the dry season— suggesting increased territoriality [53]—while intergroup encounter rates rise, particularly in areas with higher vegetation productivity near permanent water sources. This pattern matches theoretical predictions from solitary species indicating that frequent encounters can drive longer-term spatial separation [54]. To our knowledge, our study provides the first empirical evidence of such a link in a group-living species, consistent with the mechanism proposed by Markham *et al.* [55] whereby repeated costly encounters drive subordinate groups to avoid contested areas, increasing spatial separation and reinforcing dominance relationships.

These findings parallel predictions from the resource dispersion hypothesis (RDH), originally developed to explain group formation in territorial social carnivores such as European badgers (*Meles meles*) and red foxes (*Vulpes vulpes*) [38, 56]. In these species, individuals that might otherwise occupy separate territories form groups when resources are sufficiently rich and dispersed to support multiple individuals within a single territory [17, 57]. This can promote sociality even in species with little cooperative behavior or predator-defense needs [33]. Although social primates like capuchins differ in many respects— including more rigid

social structures [58], additional drivers of sociality (e.g., alloparental care [43], social learning [59]), and generalist diets [60]— our findings suggest that similar ecological dynamics may still emerge. When the environment can support more individuals or groups, capuchins appear to reduce investment in active defense against neighbor intrusion.

While RDH alone cannot explain capuchin sociality— as groups remain hostile during intergroup encounters regardless of resource dispersion [48]— it may help explain how smaller groups persist on the landscape despite overlapping with multiple more powerful neighbors. For instance, our findings indicate that larger groups tend to avoid overlapping with other large groups, perhaps to reduce the risk and energetic cost of conflict with similarly powerful rivals, where outcomes are less predictable [61–63]. This pattern aligns with game-theoretic models of animal contests, which predict that when opponents are evenly matched, mutual assessment and conflict avoidance strategies evolve to reduce costly escalations [64, 65]. Such mutual avoidance may inadvertently benefit smaller groups by creating "buffer zones"— underused areas that smaller groups can exploit while remaining undetected [66]. Comparable patterns are seen with predator-prey dynamics: white-tailed deer (*Odocoileus virginianus*), for example, are more likely to occur in areas where wolf (*Canis lupus*) pack territories overlap [67, 68]. Similarly, during large-scale human conflicts, activity often declines near war zone buffer areas, leading to natural reforestation and surges in wildlife populations and biodiversity [69, 70]. Our results suggest that when resources are sufficiently abundant and dispersed to support multiple groups within a given area, spatial overlap increases— especially between groups with strongly asymmetric competitive abilities. Such conditions allow dominant groups to access new resources with minimal conflict while enabling smaller groups to persist in marginal or underused zones between the ranges of their more powerful neighbors.

Our results show that greater within-group competition with increasing group size does not necessarily lead to higher daily travel costs, even for species that primarily forage on clumped resources. While folivores are known to avoid this trade-off due to the relatively widespread and homogeneous nature of their food resources (the so-called folivore paradox) [39, 71], dietary generalists may achieve the same effect by shifting to more readily available resources like insects [72]. Beyond such fallback strategies, our findings suggest that larger groups can also alleviate foraging pressure by expanding their range, increasing the diversity of fruiting trees exploited, and lowering revisitation frequency. This strategy likely enables access to less-depleted, higher-quality patches, particularly along range peripheries where fruiting trees contain more ripe fruit [73]. Given capuchins' advanced cognitive capacity [74], such a pattern may reflect a planned ("thinking ahead") foraging strategy that draws on spatial memory to anticipate longer-term spatiotemporal patterns

of fruit availability [75], rather than a purely day-to-day, emergent response to feeding competition. Also, considering physiological constraints on daily energy expenditure [76, 77], rotating among foraging areas over longer timescales may be a more efficient strategy than increasing daily travel distance (see subsection S1.7).

We propose that between-group competition may have played a more significant role in the evolution of sociality than previously recognized [7, 78], particularly in fluctuating environments. Tropical dry forests like Lomas Barbudal are among the most seasonal ecosystems on Earth [44, 79]. During the dry season, capuchins face extreme heat and increased water stress [80], which, as we show, results in shorter daily travel distances, lower-quality habitat use, reduced foraging efficiency, and more frequent intergroup encounters. If within-group competition were especially costly under these conditions, larger groups should experience even lower fruit intake rates in the dry season compared to the wet season. Yet the negative effect of group size on per capita fruit intake remained stable across seasons, likely reflecting the ability of larger groups to secure access to higher-quality areas and offset within-group competition during periods of scarcity. This suggests that, during environmentally harsh periods, the benefits of between-group competition may outweigh the costs of within-group competition— a pattern consistent with broader evidence that ecological stress selects for enhanced cooperation and resource defense strategies [81–83]. Future work linking group size and climate to survival and reproductive success would clarify the ecological conditions that favor one form of competition over the other. Further insights into the evolution of social behavior could emerge from examining the trade-offs of within- and between-group competition— mediated through movement as a group-level trait— within a multilevel selection framework [84, 85].

We demonstrate that the benefits of between-group dominance and the costs of within-group competition vary predictably across changing environments. Such shifting trade-offs may help explain why group sizes vary widely within populations and over time. Small groups can persist by (a) having reduced within-group foraging pressure, (b) rooting themselves spatially to avoid conflict with neighbors, and (c) maintaining a competitive advantage within their core area regardless of opposing group size [36]. In contrast, large groups can endure by asserting spatial dominance and monopolizing the most valuable resources (particularly in range peripheries) which could act as a buffer against intensified within-group competition in the face of resource unpredictability. Nevertheless, this buffering capacity may have limits under particular ecological or social conditions, potentially explaining the rare occasions when large groups permanently fission [86]. Unlike 'facultative groupers' (i.e., fission–fusion species) that can flexibly adjust group size to local circumstances [30], 'obligate groupers' such as capuchins are bound by the long-term benefits of group living (e.g., cooperative breeding, protection from predators or infanticidal conspecifics [87]), which regularly outweigh the costs (e.g.,

within-group competition, disease transmission) [88]. For such species, permanent fission represents a last resort when groups approach the upper limit of viable size under prevailing conditions [89], with the potential to fundamentally alter the balance of power across the social landscape.

Understanding how group size influences resource competition is inherently complex. Many studies analyze within- and between-group dynamics in isolation, overlooking how they interact and vary with ecological context. Our study addresses this gap by integrating multi-group longitudinal data with a novel, spatially explicit extension of the social relations model. This framework quantifies how both focal and neighboring group traits shape ranging behavior, revealing whether competitive pressures are specific to certain group pairs or reflect broader, population-level patterns. A remaining obstacle, however, is accounting for unmonitored groups— a common limitation in long-term field studies [23]. Adopting a more holistic "neighborhood" perspective— akin to the distinction between local and global dispersal[90, 91]— could offer deeper insight by integrating the combined effects of multiple neighbors and inferring impact of unobserved groups. Our framework provides the foundation for such extensions, and for a more nuanced incorporation of group composition (e.g., age–sex structure) and the resource landscape.

Our study reveals that climate and demographic change shape the trade-offs between within- and between-group competition. While within-group competition imposes an upper limit on group size [9], and between-group competition and predation likely set a lower limit [10], these constraints are not fixed. Their relative influence shifts with climate and resource availability [37], allowing groups of different sizes to coexist, each benefiting from distinct ecological and social conditions. Yet, increasingly severe droughts driven by climate change, coupled with growing habitat fragmentation, are rapidly altering tropical landscapes [92–95], making resources more clumped and monopolizable. Our findings reveal that such changes could raise the upper limit on group size by enhancing the benefits of between-group competition, thereby shifting the balance in favor of larger, more dominant groups in the future.

4 Methods

4.1 Data Collection

The Lomas Barbudal Monkey Project dataset contains longitudinal records from 13 habituated groups of white-faced capuchins, spanning 1990 to 2025. These records include data on demographics, foraging, social interactions, and group movement. The 13 study groups have varying observation periods, reflecting differences in when each group was introduced into the study or formed through permanent fission from an existing

study group (Figure 1c). Here, we draw on data from 12 of the 13 study groups, as one group (DT) was excluded due to insufficient location data. Location data from 1991 to September 2009 (none available for 1990) consist of georeferenced sleep-site records digitized from field notes originally used to relocate groups each morning. From September 2009 to 2025, handheld GPS units (Garmin GPSmap 62s, 64, 64s, 66sr) were clipped to or placed in researchers' backpacks and used to record both sleep-site locations and daily movement trajectories as researchers followed the monkeys. GPS tracking data have been cleaned and processed through 2020, and GPS-derived sleep-site locations through 2023. Sleep-site data therefore span from the start of 1991 to the end of 2023, whereas GPS tracking data extend from September 2009 to April 2020 (Figure S1). Previous work has validated the reliability of both data types for estimating home ranges [42, 96].

Researchers positioned themselves near the group's center when not conducting focal follows. GPS units recorded locations at intervals of five minutes (2009-2012) or 30 seconds (2013-2020). We calculated median annual and seasonal group sizes from 1991 to 2023 using daily group censuses with at least six hours of observation to maximize the likelihood of detecting all individuals present. We summarized fruit foraging behavior from focal follows conducted from July 1, 2006 to June 30, 2021. These records included the number of bites of fruit observed to be ingested, the duration each individual was visible, and the age and sex of the focal individual. Further specifics on data collection and processing are provided in Jacobson *et al.* [96] and Perry *et al.* [97].

4.2 Environmental Data

The tropical dry forests in and around the Lomas Barbudal Biological Reserve experience strong annual and seasonal variation in vegetation phenology, affecting the availability of key resources such as food, water, and shade for capuchins. To quantify interannual and interseasonal variation in vegetation phenology across the study period, we extracted annual and seasonal Normalized Difference Vegetation Index (NDVI) values from 1991 to 2023 using satellite imagery extracted from Google Earth Engine [98]. Although NDVI can be an imperfect proxy for food availability in tropical forests [99], it has shown to measure long-term habitat variability well in this region [79], particularly in the dry season when resources such as water, fruit, and shade are concentrated in greener riparian zones. NDVI quantifies the "greenness" of each pixel in a given image, serving as a proxy for vegetation health and abundance. We defined a bounding box around the Lomas Barbudal Biological Reserve and surrounding forest as the spatial extent for all image processing. We used surface reflectance data from Landsat 5, Landsat 7, and Landsat 8 satellites to obtain red (`RED`) and

near-infrared (`NIR`) bands required for NDVI calculation. To remove cloud-contaminated pixels, we applied a mask using the quality assessment (`QA_PIXEL`) band. NDVI was calculated for each image as:

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{RED}}{\mathrm{NIR} + \mathrm{RED}} \tag{1}$$

For each year and season, we created pixel-wise maximum composites to reduce noise from residual cloud contamination and obtain the best quality pixel value. Seasonal windows were defined as February–April (peak dry season) and September–November (peak wet season). These seasonal and annual median NDVI images were clipped to the study area and exported at 30-meter resolution (see subsection S1.3 for details). In addition to NDVI, we extracted rasters of tree cover from the Hansen Global Forest Change dataset, [100], which were later used to refine home range estimates (see section 4.3). All processing of remote sensing data was conducted using Google Earth Engine's Python API, and rasters were exported as `.tif` files for further analysis in `R` [101].

4.3 Group-level Response Variables

For several of our questions of interest, our observation and response variables of interest were properties of individual groups (Table 1).

Quantifying fruit intake and daily path length

Per capita fruit intake rates were estimated from focal follow data collected between July 1, 2006, and June 30, 2021. This dataset includes 4,952 hours of usable observation time from 335 individually identified focal individuals. For each focal individual per day, we recorded the number of bites of fruit ingested, rather than whole fruits, as many fruits require multiple bites to consume. Intake data were restricted to periods when both the mouth and hands of the individual were visible, ensuring accurate detection of fine-scale foraging behavior.

To quantify daily energy expenditure, we used GPS-tracking data to generate 996 daily path lengths across 11 groups from September 2009 to April 2020, applying the continuous-time speed and distance (CTSD) method described by [102] using the `ctmm` `R` package [103]. This approach estimates daily path length by multiplying the estimated mean speed from a fitted daily continuous-time movement model by the total daily sampling duration. By separating the continuous-time movement process from the discrete-time sampling process, CTSD is less sensitive to sampling rate, path complexity, and location error than traditional methods based on totaling step lengths. We included only GPS tracks with at least 11 continuous

hours of data per day, corresponding to minimum daylight hours, as capuchins rarely move at night.

Quantifying home range area, greenness and revisitation rate

We used sleep-site data from 1991 to 2023 to estimate home range area (validated in [42]), enabling us to use the full 33-year dataset, including years pre-dating GPS, and capture the widest range of demographic changes and study groups over time. Our validation study demonstrated that 98% utilization distributions (UD) from sleep ranges accurately aligned with the conventional 95% UD from GPS-tracking data as capuchins typically refrain from sleeping in the far outskirts of their home range [42]. Based on this, we used 98% UDs to estimate home range area, representing the smallest area with a 95% probability of finding the group considering its total movements.

We calculated 156 annual and 224 seasonal sleep home ranges across 12 groups using auto-correlated kernel density estimation (AKDE) implemented using the `ctmm` `R` package [103]. AKDE estimates the UD by fitting a series of continuous-time movement models to the location data, selecting the best-fitting model based on the data's autocorrelation structure, which informs the kernel smoothing bandwidth and yields home range estimates that account for location error and irregular sampling [104, 105]. Seasonal ranges were segmented as January–April (dry) and May–December (wet), based on behavioral shifts in daily distance to rivers, rather than on climatic seasonality, which typically includes December in the dry season (Figure 1). Only data segments suitable for home range estimation, identified via visual inspection of variogram regression plots, were included in downstream analyses [106]. We also fit these home ranges using an integrated resource selection function (iRSF) of tree cover following [107]. This imposed "soft barriers" by down-weighting areas without trees, like pasture-lands, which home range estimates may expand into but capuchins rarely use. We measured home range greenness by extracting the mean NDVI value within each group's mean home range boundary for the corresponding year or season using the `terra` package [108].

We quantified revisitation rates using the `revisitation()` function from the `ctmm` package. This method estimates how frequently a capuchin group returns to previously used areas by calculating the mean revisitation rate per radial meter. Conceptually, it measures how often a group re-enters a small circular area, averaged across all locations within its home range. This is implemented by first estimating a group's UD using AKDE. A second kernel density surface— the revisitation range— is then computed by weighting the same movement data by the group's estimated speed, which reflects how frequently the group moves through each area. The revisitation rate is obtained by averaging the revisitation range over the original UD, yielding a single value representing the group's typical rate of return to areas within its range. We calculated revisi-

tation rates using both annual and seasonal UDs derived from our GPS-tracking dataset (September 2009 - April 2020). Although narrower in temporal scope than our sleep site records, the GPS-tracking data offer finer spatial and temporal resolution, yielding more accurate UDs and better capturing diurnal space-use patterns relevant to revisitation [42].

4.4 Dyad-level Response Variables

For other questions of interest, our observation and response variables of interest were properties of dyads of groups— a unique pairing of groups (Table 1). This distinction between group- and group-dyad-level outcomes is important for accurate statistical estimation.

Quantifying proportional overlap and range shifts

We measured home range overlap between group-dyads among known habituated groups throughout the study period. We calculated the proportion of a group's home range that overlaps with a specific neighbor (PO_{fn}). This approach allows us to assess the degree to which a neighbor can encroach into a focal group's range, and the potential loss of a group's available resources to that neighbor. PO_{fn}, was calculated by:

$$\mathrm{PO}_{fn} = \frac{\mathrm{IA}_{fn}}{\mathrm{HRA}_f} \tag{2}$$

Here, IA_{fn} represents the area of intersection between the focal and neighbor group's home ranges, and HRA_f is the home range area of the focal group. PO_{fn} measures an asymmetric group-dyad outcome. To demonstrate, imagine that group A and group B have home ranges with some intersection, IA_{ab}. While $\mathrm{IA}_{ab} = \mathrm{IA}_{ba}$, $\mathrm{PO}_{ab} \neq \mathrm{PO}_{ba}$ because $\mathrm{HRA}_a \neq \mathrm{HRA}_b$. Using this asymmetric variable, we focus on the proportional overlap from the focal group's perspective. For every observation, the neighboring group also has a PO_{fn} measurement but the groups are switched.

While PO_{fn} captures asymmetric space use and can suggest which group is being encroached upon at a given time, it does not track the directionality of range shifts *over time*. To assess whether larger or smaller groups drove increases in overlap, we conducted a complementary analysis on dyads that exhibited both a substantial increase in spatial overlap (from <25% to >45%) and a clear change in relative group size (absolute difference ≥5 individuals). These thresholds were chosen to isolate cases with meaningful shifts in both space use and relative group size, avoiding ambiguity in assigning which group is considered the "big" group (e.g., a group may remain larger overall but shrink more than its neighbor from time t to time $t+1$) and minimizing noise from minor fluctuations. For each of these dyads, we measured the distance from each

group's home range centroid at time t to the centroid of the overlap zone at both time t and time $t+1$, and calculated the change in distance (ΔD):

$$\Delta D = D_{t+1} - D_t \tag{3}$$

A positive ΔD indicates that the group shifted toward the other group in the dyad, while a negative value indicates the other group shifted toward them. The group with the larger magnitude of ΔD was considered the one that drove the increase in overlap.

Quantifying encounter rates

We computed encounter rates following [109] to quantify the expected space-time overlap between the home ranges of two groups, assuming stationary movement characterized by constant `ctmm` parameters (e.g., range crossing time and autocorrelation structure). As with revisitation rates, we used UDs derived from GPS-tracking data (2009–2020) to better capture fine-scale, diurnal space use. The encounter rate ER_{ij} between groups i and j represents the expected probability density of simultaneous co-occurrence in space and time. In this framework, ER_{ij} reflects the relative probability that, at any given moment, groups i and j are found within the same 1 m^2 area. These values are relative and only interpretable when compared across dyads. For example, if $\mathrm{ER}_{ab} = 0.4$ and $\mathrm{ER}_{ac} = 0.2$, then groups a and b are twice as likely to encounter each other as groups a and c, under the same modeling assumptions. Unlike PO_{fn}, ER_{ij} is symmetric, yielding the same value regardless of which group is labeled i or j, as group identity plays no directional role in this metric.

4.5 Statistical Analyses

4.5.1 Group-level models

We used a suite of GLMMs to examine the relationship between group size and several within-group outcomes: per capita fruit intake rate, daily path length, revisitation rate, home range area, mean home range NDVI. All models were fit in a Bayesian framework using the `brms` package [110]. We specified Gamma likelihoods for all models except the home range NDVI models, which used a Beta distribution. Group size was standardized, and additional covariates were included where appropriate based on causal assumptions outlined in our directed acyclic graphs (subsection S1.4). All models included varying effects by group, with additional varying effects by individual (for fruit intake) or by year (for home range NDVI), where appropriate. Models for home range area and daily path length also included error terms on the response to account

for measurement uncertainty. Because key resources regenerate annually [111] but also fluctuate between wet and dry seasons, each model was run in two versions: one including seasonality (via an interaction between group size and season), and one without. While only home range area and NDVI were explicitly measured at seasonal or annual scales, we refer to the non-seasonal models for all outcomes as "annual" for consistency.

4.5.2 Dyad-level models

To examine how relative group size shapes between-group interactions, we used an extension of the hierarchical Social Relations Model (SRM) [50]. SRMs separate group-level and dyadic-level variation while modeling their correlation, enabling efficient partial pooling and improving parameter estimation [51]. While traditionally applied to social behavior among individuals or human households [e.g., 112–114], we extend this framework to spatial interactions between animal social groups.

We modeled proportional overlap (PO_{fn}) using a zero-augmented (hurdle) SRM implemented in the `rethinking` package [115]. The hurdle component separates the probability of non-zero overlap (Bernoulli distribution) from the degree of overlap when present (Beta distribution). Key predictors included focal and neighbor group size (as group-level fixed effects) and their interaction (as a dyad-level fixed effect). Seasonal models included a three-way interaction between season, focal group size, and neighbor group size. To account for non-independence across dyads, we included varying effects for focal group ID, neighbor group ID, and dyad ID, modeled jointly via a multivariate distribution with a shared correlation structure. This structure allows, for instance, inference about whether a group that overlaps more with one neighbor also overlaps more with others— capturing cross-dyad patterns more flexibly than standard random effects. See subsection S1.5 for full statistical notation of our SRMs.

We modeled encounter probabilities using a related set of Gaussian-distributed dyadic models (after log-transforming the response), implemented in `brms`. While based on the same dyadic framework, these models used a different varying effects structure than the SRM described above (sensu [112, 116]), omitting correlated focal–neighbor effects. This was appropriate because encounter rate is a symmetric response— interactions between groups i and j are equivalent regardless of order— making the focal–neighbor distinction neither identifiable nor meaningful. To reflect the symmetrical nature of the data, we included two sources of random variation: a dyad-level effect, capturing dyad-specific tendencies in encounter rates, and a group-level multiple membership structure, allowing each observation to be jointly attributed to both groups involved. This approach preserves the exchangeability of group identities within dyads and appropriately partitions variance between individual group tendencies and unique dyadic relationships. All predictors were also

symmetric: group size difference, overlap zone area, and vegetation greenness in the overlap zone (measured by mean NDVI). As with the home range and path length models, we accounted for uncertainty in encounter rates using measurement error modeling. To assess seasonal variation in encounters, we included separate interaction terms between season and each predictor— testing whether the influence of group size asymmetries and habitat characteristics on intergroup encounters varied by season.

We applied weakly regularizing priors to all model parameters. All models showed good convergence ($\hat{R} \approx 1.00$), adequate effective sample sizes, and reliable fit based on posterior predictive checks. We summarize effect sizes of parameter estimates using 89% Highest Posterior Density Intervals (HPDIs) and the proportion of the posterior greater than zero (PP>0). See subsection S1.4 for additional model details and assumptions using a causal inference framework.

5 Data availability

Location data are restricted to protect the precise whereabouts of habituated, threatened primates vulnerable to the pet trade. They are archived in a limited-access Movebank repository, and available upon reasonable request to SEP. All code necessary to reproduce our analyses are openly available on Edmond [117]. All demographic and behavioral data will be openly available on Dryad [118] following acceptance.

6 Ethics statement

The study was purely observational, with GPS units carried by observers rather than attached to animals. Research protocols were approved by UCLA's Animal Care Committee (protocol 2016–2022), and all required permits from SINAC and MINAE (the Costa Rican agencies overseeing wildlife research) were secured and renewed every six months. The most recent authorizations include scientific passport #1012-2024-ACAT and permit Resolución #M-P-SINAC-PNI-ACAT-0010-2024. All procedures complied with the Animal Behavior Society's Guidelines for the Use of Animals in Research [119].

7 Author Contributions

We use the Contributor Roles Taxonomy (CRediT) to detail author contributions: Conceptualization (OTJ, BJB, MCC, SEP); Data curation (OTJ, SEP, BJB); Formal Analysis (OTJ, BJB); Funding acquisition (SEP, MCC, BJB); Investigation (SEP, OTJ, BJB); Methodology (OTJ, BJB, SEP, GEF);

Project administration (SEP, BJB, OTJ); Resources (SEP, BJB, MCC); Software (OTJ, BJB, GEF); Supervision (BJB, SEP, MCC, GEF); Visualization (OTJ); Writing – original draft (OTJ, BJB, SEP); Writing – review & editing (OTJ, SEP, BJB, GEF, MCC).

8 Acknowledgments

Thanks to Kate Tiedeman and Alison Ashbury for feedback on remote-sensing and writing respectively. Thank you to Cody Ross and Jeremy Koster for feedback on model structure, and to Richard Berl for establishing the GPS protocols used for location data collection at Lomas (see subsection S1.1 for list of all contributing field assistants). Thanks to Don Cohen for assistance with maintaining the LBMP database. We thank the Costa Rican Park Service (SINAC, Área de Conservación Arenal Tempisque for permission to work in Lomas Barbudal Biological Reserve, and the private landowners who have granted us permission to work on their land (especially Hacienda Pelon, Brin d'Amor and the community of San Ramon de Bagaces).

Data collection was funded primarily by grants to SEP from the National Science Foundation (grants BCS-1919649, BCS-1638428, BCS-0613226, BCS-848360, DDIG 1232371 (co-PI I Godoy), 9633991, SES9870429 and an NSF graduate fellowship), the National Geographic Society (grants 7968-06,8671–09, 9058-12, 9795–15, 45176R-18 and a grant with co-PI B Smuts), the L.S.B. Leakey Foundation (9 grants), the Templeton World Charity Foundation, Inc. (grant 0208), 2 Wenner-Gren grants (one with co-PI I. Godoy), various UCLA COR grants and internal grants from the University of Michigan, Sigma Xi, 5 years of funding by MPI-EVAN, and logistic support from the Wild Capuchin Foundation. BJB supplemented data collection via funds from the American Society of Primatologists, ARCS Foundation and an NSF GRF (grant no. 1650042). This work was supported by the Alexander von Humboldt-Stiftung through funds awarded to MCC.

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