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Moving in a Miombo: Ranging Patterns and Habitat Use in Red-Tailed Monkeys (*Cercopithecus ascanius*) From the Issa Valley, Tanzania

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ABSTRACT

Objectives: Guenons are a valuable model for understanding primate adaptability to heterogeneous habitats, similar to the environmental pressures faced during hominin evolution. This study investigates how red-tailed monkeys (*Cercopithecus ascanius*) use two distinct vegetation types, riparian forests and miombo woodlands, within a mosaic habitat in the Issa Valley, Tanzania. We assessed how seasonality impacts core area sizes in both vegetation types, the proportion of spatial overlap between core areas across different seasons and years, and whether woodland use is associated with increased daily path lengths (DPLs) or specific foods.

Methods: We employed kernel density estimates on behavioral observations (2016–2023) to calculate core area sizes and overlaps and linear regressions to assess relationships between woodland use and DPL. We employed logistic regression to analyze associations between food categories and woodland use.

Results: Core area sizes and overlaps did not vary significantly between seasons in either woodlands or forests. DPL showed a trend toward being lower on days when animals spent more time in woodland. Feeding on bark, flowers, and unripe fruit strongly increased the likelihood of woodland use, whereas ripe fruit was associated with forests.

Discussion: We propose several drivers for woodland use as well as what role niche partitioning with sympatric primates may play. Our study indicates that this arboreal primate dynamically utilizes the vegetation matrix, highlighting the importance of behavioral flexibility for Plio-Pleistocene hominins as forests were gradually replaced with wooded landscapes.

1 | Introduction

Guenons (tribe Cercopithecini) are a diverse group of African monkeys that offer crucial insights into primate and human evolution due to their ecological diversity, social complexity, and evolutionary history (Elton 2006; Kingston 2007; Cords 2012; Jensen et al. 2023). Found across sub-Saharan Africa, guenons have radiated into a wide range of habitats, from dense rainforests to savannah woodlands, reflecting adaptive flexibility similar to early hominins (Kingston 2007). Their evolutionary history provides a window into primate diversification during the Miocene and Pliocene epochs, periods critical to understanding human ancestry (Elton 2006). Importantly, guenons exhibit diverse social systems, including female-bonded groups, multi-male units, and even monogamous pairings—offering comparative models for reconstructing early human social behavior (Cords 2012). Moreover, genetic studies of guenons reveal frequent hybridization events, challenging traditional species boundaries and highlighting the role of gene flow in primate evolution (Jensen et al. 2024). Such patterns of interspecific gene flow also provide a useful parallel for understanding the complexity of human evolution, particularly given recent evidence of interbreeding between *Homo sapiens* and other hominins like Neanderthals and Denisovans (e.g., Reilly et al. 2022). Finally, guenons' adaptability to fragmented and changing environments mirrors the environmental pressures faced by early hominins, making them valuable for studying primate resilience and adaptability (Kingston 2007; Elton 2006).

One way that we can understand behavioral responses is to examine movement ecology and the ways that movement dynamics are associated with spatial and temporal environmental change, for example, habitat seasonality, composition, or fragmentation (Millspaugh and Marzluff 2001; Pennec et al. 2020; Semel et al. 2022). Primate ranging behavior is known to be influenced by the spatial distribution of key resources, with different taxa increasing or decreasing their daily path length (DPL) or home range size in response to food availability (Kaplin 2001; Raño et al. 2016; Corrêa et al. 2018). For forest guenons specifically, previous studies proposed that in periods of food scarcity, these primates tend to exhibit diet-switching and far-ranging patterns that facilitate resource monitoring (Kaplin 2001; Chapman et al. 2004; Buzzard 2006). Such strategies may be constrained when the primary habitat is (1) small, potentially making it difficult to sustain the group when switching from, for example, fruits to alternative food sources, and (2) surrounded by the matrix habitat comprised of vegetation that may limit such a far-ranging strategy.

Individuals' ability to navigate different landscape features (e.g., canopy structure, forest edges, etc.) and interact with habitat matrix can be especially important for population survival in highly fragmented, complex, or mosaic habitats. For example, the matrix might supplement their diet by providing resources from secondary vegetation—a phenomenon known as "landscape supplementation" (Dunning et al. 1992; Chaves et al. 2011; Pozo-Montuy et al. 2013). However, the ability of most primate species to move through matrix habitats and exploit different features has not been widely examined (Anderson et al. 2007; Arroyo-Rodríguez and Fahrig 2014). Studies on arboreal marsupial taxa show that certain types of matrix habitats provide enough connectivity (Smith-Ramirez et al. 2010) while others create significant obstacles to arboreal movement (Rodríguez-Cabal et al. 2007).

Among arboreal guenons (*Cercopithecus* spp.), red-tailed monkeys (*C. ascanius*) are one of the most widely distributed species and have been the subject of extensive comparative research. These primates comprise five subspecies (Butynski 2004a) distributed across Central and East Africa, and are found in diverse habitats, including moist tropical, dry evergreen, riverine, and regenerating secondary forests (de Jong and Butynski 2019). Although they are primarily frugivorous, invertebrates comprise a substantial proportion of their diet, in some sites comprising up to 30% of all foods eaten and providing a crucial source of protein, contributing an average of 24% of their daily protein intake (Gathua 2000; Chapman et al. 2004; Bryer et al. 2015).

Despite extensive work into dietary ecology and polyspecific associations (Struhsaker 1978, 2017; Gathua 2000; Tweheyo and Obua 2001; Chapman et al. 2004; Bryer et al. 2015), the movement ecology of red-tailed monkeys remains understudied, with previous research focusing either on one sex only (females; Bektic 2009) and what factors (e.g., female choice) influenced incursions into and out of groups of solitary males (Jones and Bush 1988). In the only detailed study on red-tailed monkey daily travel distances and home ranges in a mosaic environment, McLester et al. (2019) showed that food availability and thermoregulatory constraints due to heat stress influence red-tailed monkey ranging patterns in the Issa valley, especially in contrast to monkeys from Ngogo forest (Uganda), which had smaller ranges and shorter daily travel distances, likely due to more concentrated food sources.

In the Issa Valley, Western Tanzania, red-tailed monkeys inhabit a mosaic woodland habitat (Fornof et al. 2023). Riparian forests account for only approximately ~3% of the study area, with the remaining ~97% being "open" vegetation, consisting of miombo woodland, seasonally inundated grasslands, and rocky outcrops (Drummond-Clarke et al. 2022). As a result, Issa red-tailed monkeys rely on woodlands, although the spatiotemporal patterns of this use remain unknown (Tapper et al. 2019). McLester et al. (2019) provided valuable insights into the movement patterns of Issa red-tailed monkeys, but they did not examine habitat use at a fine spatial scale, distinguish between movements across the two contrasting habitat types at Issa—riparian forests and miombo woodlands—or explore how the use of woodland relates to foraging behavior. These aspects are critical for understanding how monkeys living in a heterogeneous mosaic habitat exploit different vegetation types.

In this study, we used a long-term dataset of behavioral-spatial data of a single red-tailed monkey group (study group hereafter) from Issa to investigate how red-tailed monkeys exploit different vegetation types within this mosaic habitat, and what ecological factors might drive this use. Specifically, we predicted that (P1) season will significantly influence core area sizes in both riparian forests and woodlands, with larger core areas in the wet (fruit-lean) season, and that (P2) woodland core areas will exhibit significant variation in overlap across seasons and years, whereas forest core areas will remain stable.

For Issa red-tailed monkeys, travel ranges were shown to be shorter with increased food abundance (McLester et al. 2019). Assuming that the study group uses woodlands for foraging and that food resources there are broadly distributed, we predicted that (P3) the DPL of the study group increases as the proportion of daytime they spend in woodlands increases. Finally, considering the importance of invertebrates for these primates (Gathua 2000; Chapman et al. 2004), we predicted that (P4) invertebrates will be the only food category positively associated with woodlands, driving woodland use.

The implications of the study have a bearing on conservation practice, paleoecological reconstructions, and niche partitioning in a diverse and faunal-rich landscape. For conservationists, considering the growing threats of habitat loss and fragmentation (Arroyo-Rodríguez and Fahrig 2014; Estrada et al. 2017), future conservation actions will likely be influenced by how animals interact with and respond to habitats of different vegetation compositions and the effects of climate change on habitat suitability (Boyle et al. 2013; Galán-Acedo et al. 2019).

Additionally, the versatility of extant guenon habitat occupation and consequential associated adaptations has implications for how we reconstruct Miocene/Pliocene hominids that occupied and competed within (e.g., Deane et al. 2013) diverse environments (Kingston 2007). Finally, how red-tailed monkeys at Issa minimize competition from larger-bodied sympatric yellow baboons (*Papio cynocephalus*) and both competition and predation risk from chimpanzees (*Pan troglodytes*) has a bearing on how we understand present (Schreier et al. 2009) and past (van Holstein et al. 2024) dimensions of inter-specific competition.

2 | Methods

2.1 | Study Site and Subjects

The Issa Valley lies within the Greater Mahale Ecosystem, situated in Western Tanzania (see Figure 1). The Issa Valley study area is approximately 85 km^2, comprised of several major valleys and adjacent plateaus ranging in elevation from 1150 to 1712 m. (Piel et al. 2017). The region experiences two distinct seasons: a wet season from November to April (> 250 mm monthly rainfall in some months) and a dry season from May to October (< 60 mm monthly rainfall) (Piel et al. 2017).

The habitat is characterized as a mosaic of miombo woodland, dominated by deciduous *Brachystegia* and *Julbernadia* spp., interspersed with seasonally inundated grasslands, rocky outcrops, swamps and evergreen riparian forest (Drummond-Clarke et al. 2022). During the study period, the study group was observed using riparian forest (forest hereafter), woodland, and swamp habitats. For analytical purposes, swamp habitat was grouped with woodland due to its low representation (0.39% of all observations) and its structural similarity to woodland.

We focused on one red-tailed monkey group, habituated since 2012 (McLester et al. 2019). Throughout data collection, group size varied between 27 and 35 individuals and consisted of multiple adult males and females, sub-adults, juveniles, and infants (McLester et al. 2019; Fornof et al. 2023). At Issa, red-tailed monkeys live sympatrically with Eastern chimpanzees and yellow baboons as well as hyenas (*Crocuta crocuta*), African wild dogs (*Lycaon pictus*), and leopards (*Panthera pardus*) (see list in Piel et al. 2019; D'Ammando et al. 2022).

2.2 | Data Collection

We conducted full-day focal follows between 2016 and 2023, typically 6 days per month. Each morning, we selected one focal individual (adult, subadult, or juvenile) and followed it from first contact until the group entered its sleeping tree. We used instantaneous focal animal sampling, recording the selected individual's behavior and location every 5 min throughout the day. If the focal animal became temporarily out of sight, observers attempted to relocate it; the follow was only terminated if the animal remained out of view for ≥ 30 min, at which point a new focal was selected. Where group members

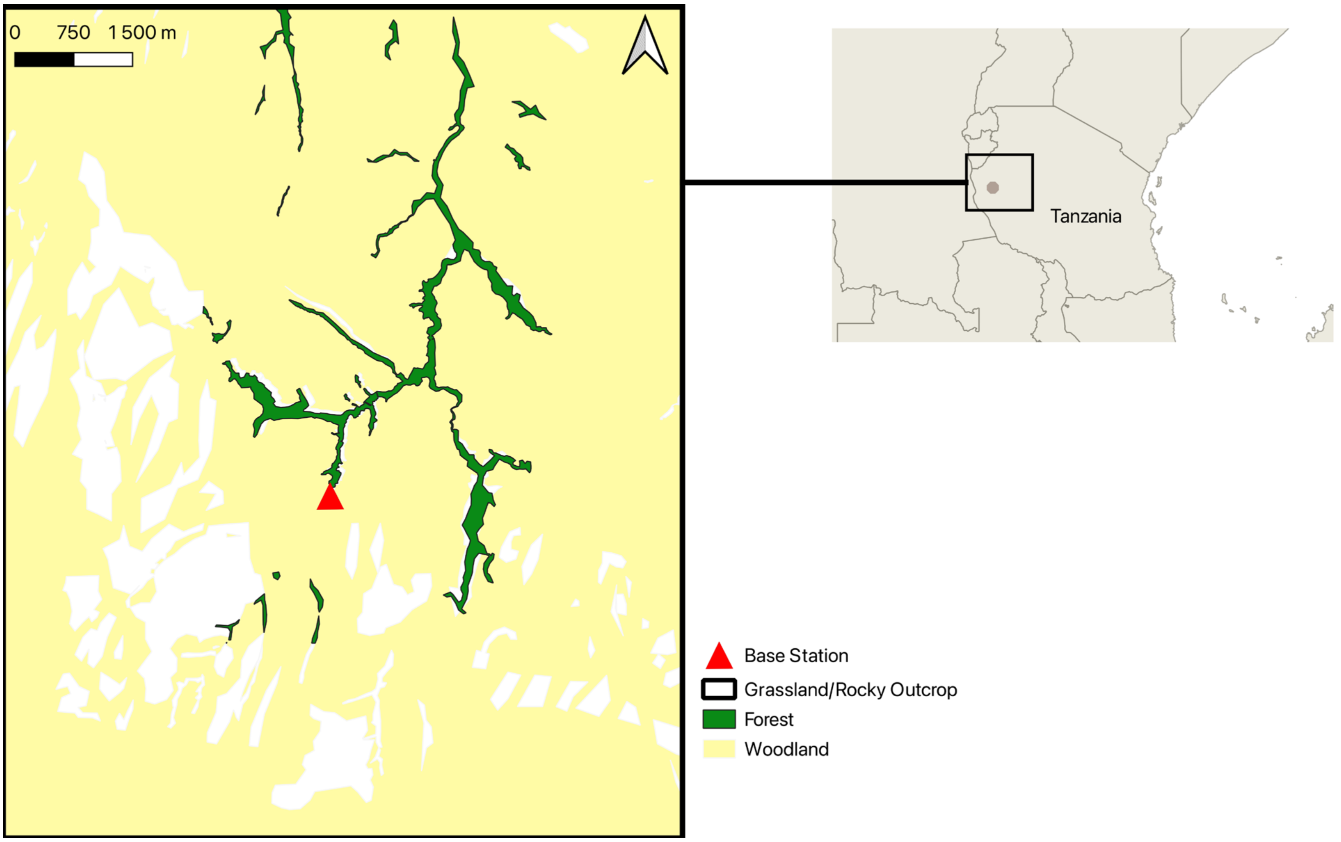

FIGURE 1 | Map of the study site. The map displays Issa Valley's location in western Tanzania and highlights different vegetation types that comprise the study site.

were not individually recognizable, we changed age/sex classes when selecting new focal to minimize the risk of oversampling the same indviduals. At each 5-min sample, we recorded GPS coordinates (latitude and longitude), time and vegetation type (forest or woodland). Additionally, when the focal was feeding (i.e., ingesting food), the food consumed was recorded whenever possible. We grouped food into following categories: ripe fruit, unripe fruit, leaf, flower, stem, sap, bark, invertebrates, and mushroom. Feeding on invertebrates was identified by distinctive motor patterns used by this species when capturing such prey (Cords 1986; Gathua 2000; Struhsaker 2017), although further taxonomic identification of these prey items was not possible. We used Open Data Kit (ODK) forms, tailored to capture parameters relevant to the study. In instances where coordinates could not be captured via ODK forms, coordinates were attempted to be recorded using Garmin GPS units (model: Rino 700 2-way radio/GPS). Any entries for which coordinates could not be obtained using either method were excluded from the analysis.

2.3 | Data Analysis

All data analyses were conducted in RStudio Statistical Software (2024.4.2.764 version; Posit Team 2024). Results with p-values < 0.05 were considered statistically significant, and results with p-values between 0.05 and 0.1 are referred to as trends.

To investigate predictions P1 and P2, we calculated the 50% kernel density estimate (KDE) core areas (hotspots) for each season (dry and wet) and year for both vegetation types. We focused on 50% KDE core areas, as these represent the locations most intensively used by the study animals, meaning those likely to play an important role within the habitat, whereas the 95% KDE may include peripheral movements or rare excursions that are less informative for understanding how the animals rely on the two vegetation types (Worton 1989; Williams et al. 2002).

To evaluate whether sampling effort was sufficient for estimating whole home ranges, we constructed observation–area curves for each stratum (vegetation type × season × year). For each stratum, relocation points were sequentially added, and home-range area was recalculated at each step using the minimum convex polygon enclosing 100% of relocations (Mohr 1947). This produced accumulation curves describing home-range area as a function of sampling effort. A curve was considered to have reached a plateau when the proportional change in estimated area across the final five increments was $< 5\%$ (after Odum and Kuenzler 1955). Observation–area curves indicated that all but three strata with the lowest sample sizes ($n < 40$) reached the plateau criterion. The exceptions were woodland wet-season strata in 2018, 2020, and 2022, suggesting greater uncertainty in their home-range estimates. These cases were retained in analyses but interpreted cautiously (see Section 4).

To assess differences in core area sizes between seasons, we used independent samples t-tests for each vegetation type. We calculated the overlap between core areas across all pairs of season-year combinations within each vegetation type, expressing overlap as the proportion of shared area relative to the mean core area size. Because these pairwise overlaps are not statistically independent, we used an analysis of similarity (ANOSIM) with 999 permutations to test whether overlaps differed between seasons (following Hanya and Bernard 2016). ANOSIM compares the differences between groups to those within groups while accounting for non-independence among observations.

When testing P3, we first excluded any days in which, after removing entries with missing GPS coordinates, gaps in the focal follow data exceeded 120 consecutive minutes (following Johnson et al. 2015). We calculated the DPL for each day by summing the great-circle distances between consecutive GPS points, using GPS locations recorded at 5-min intervals (Dunlap et al. 1972; Johnson et al. 2015). We identified entry and exit points into woodland to compute the total time spent in this vegetation type each day, which we then divided by the total observation time to obtain the proportion of time the study group spent in woodland. To explore the relationship between DPL and the proportion of time spent in woodland, we performed a linear regression analysis. We then created a scatterplot to visualize this relationship and conducted a correlation to quantify association strength.

For P4, we performed logistic regression to quantify the relationship between food categories and vegetation type. The vegetation variable was encoded as a binary outcome (1 for woodland, 0 for forest), and the predictors included food categories. We created separate binary variables for each category (1 if that food was consumed, 0 otherwise). Logistic regression models were fit using a generalized linear modeling approach with a binomial distribution. Odds ratios (OR) and 95% confidence intervals were calculated from the model coefficients to interpret the effects of each food category.

3 | Results

In total, we utilized 4866 GPS entries with identified vegetation type, suitable for spatial analyses of core area sizes and overlaps [P1&P2], (see Table 1). Of these, 24 complete full-day focal follows met the criteria for DPL analysis, representing days in which gaps in the cleaned focal follow data did not exceed 120 consecutive minutes, with 14 days from the dry season and 10 from the wet season [P3]. To test P4, we used 935 observations (495 from the dry season, 440 from the wet) where the focal individual was foraging and the food category was identified.

3.1 | Kernel Density Estimates

Contrary to our predictions (P1 and P2), core area sizes did not differ significantly between seasons in woodlands (dry season mean $= 2.26\,\text{km}^2$, wet season mean $= 3.18\,\text{km}^2$; $t = -0.803$, $\text{df} = 10.94$, $p = 0.439$) or in forests (dry season mean $= 1.86\,\text{km}^2$, wet season mean $= 2.33\,\text{km}^2$; $t = -0.745$, $\text{df} = 10.29$, $p = 0.473$). Differences in core area overlaps were not statistically significant for either woodland (ANOSIM $R = -0.130$, $p = 0.984$; Figure 2) or forests (ANOSIM $R = -0.104$, $p = 0.907$; Figure 3).

3.2 | DPL

Contrary to P3, DPL was lower on days with greater use of woodland, with this relationship showing a trend ($R^2 = 0.126$, $F(1, 22) = 3.16$, $p = 0.089$; Figure 4).

3.3 | Food Categories as Drivers of Woodland Use

Several food categories significantly predicted the use of woodland (see Table 2) [P4]. Specifically, the odds of the study group being in woodland increased by approximately 714% when monkeys fed on bark ($p < 0.001$), 147% when feeding on flowers ($p = 0.024$), and 166% when feeding on unripe fruit ($p = 0.038$). Ripe fruit was the only category negatively associated with woodland, as the odds of individuals being in woodland when consuming this food decreased by 74.6% ($p < 0.01$). Although statistically not significant ($p = 0.291$), the likelihood of primates being in woodland decreased by 55.4% when feeding on invertebrates, thus not supporting P4.

TABLE 1 | Annual observation days by season.

Year	Days observed (wet season, November–April)	Days observed (dry season, May–October)	Total days observed
2016	54	9	63
2017	15	25	40
2018	4	17	21
2020	28	16	44
2021	35	32	67
2022	12	7	19
2023	9	19	28

Note: The table summarizes the number of observation days per year, including a breakdown of days observed during the dry and wet seasons.

4 | Discussion

In this study, we explored habitat use in a troop of red-tailed monkeys that live in a mosaic habitat. We found no evidence that core area sizes differed between seasons in either woodlands or forests. Similarly, core area overlap did not vary significantly between seasons in either vegetation type, providing no support for our predictions (P1 and P2). Contrary to P3, DPL showed a trend toward being lower on days when animals spent more time in woodland. Finally, while the likelihood of individuals being in woodland increased with the consumption of certain foods, we found no support for our P4 that invertebrate consumption would drive the use of this vegetation. Together, these results highlight the complex ways that a forest guenon exploits a mosaic environment.

Previous findings for the same study group (data from 2013 to 2016) reported larger home ranges during the wet season (McLester et al. 2019). This pattern broadly aligns with the results of this study—although seasonal differences were not significant, core area sizes were on average larger during the wet season in both vegetation types. This pattern is likely linked to reduced fruit availability at Issa during the wet season (McLester et al. 2019). When fruit is scarcer and more patchily distributed, individuals may expand their space use to meet dietary requirements, a pattern previously observed in guenons (e.g., *C. mitis* and *C. ascanius*—Struhsaker 1978; *A. l'hoesti* and *C. mitis doggetti*—Kaplin 2001). Alternatively, apparent patterns of broader

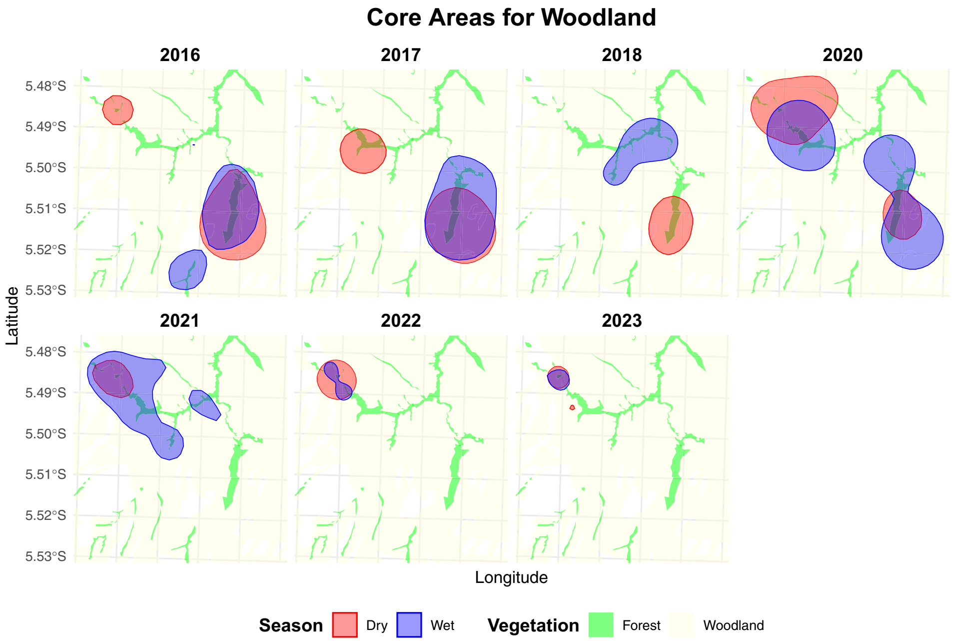

FIGURE 2 | Woodland core areas in different seasons over the years. Maps display the spatial distribution of core areas (areas of 50% utilization distribution) for woodland vegetation, differentiated by the dry and wet seasons. Core areas are represented by kernel density estimate (KDE) contours, and the different seasons and vegetation types within the study site are displayed in contrasting colors as indicated by the legend.

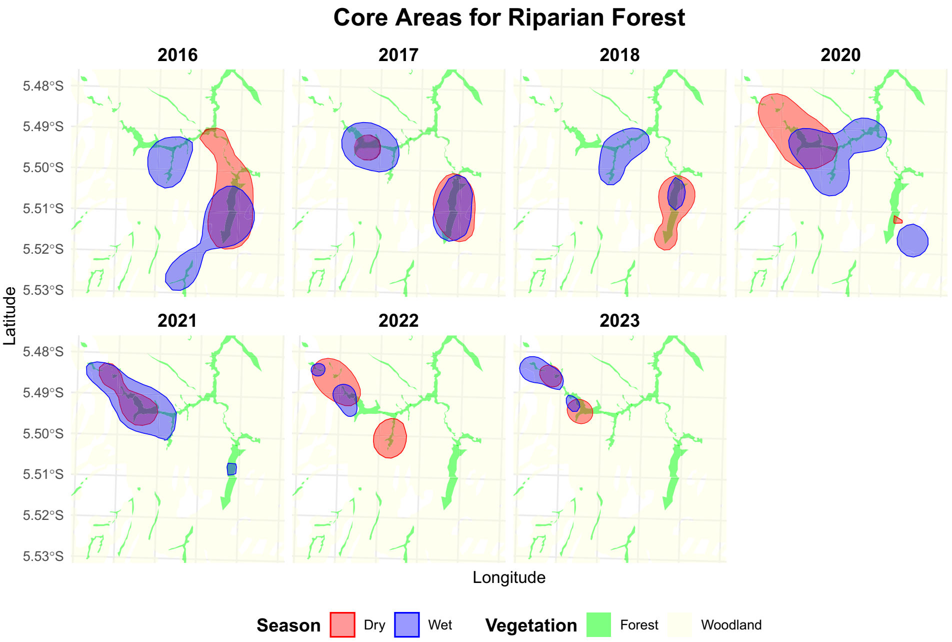

FIGURE 3 | Forest core areas in different seasons over the years. Maps display the spatial distribution of core areas (areas of 50% utilization distribution) for forest vegetation, differentiated by the dry and wet seasons. Core areas are represented by kernel density estimate (KDE) contours, and the different seasons and vegetation types within the study site are displayed in contrasting colors as indicated by the legend.

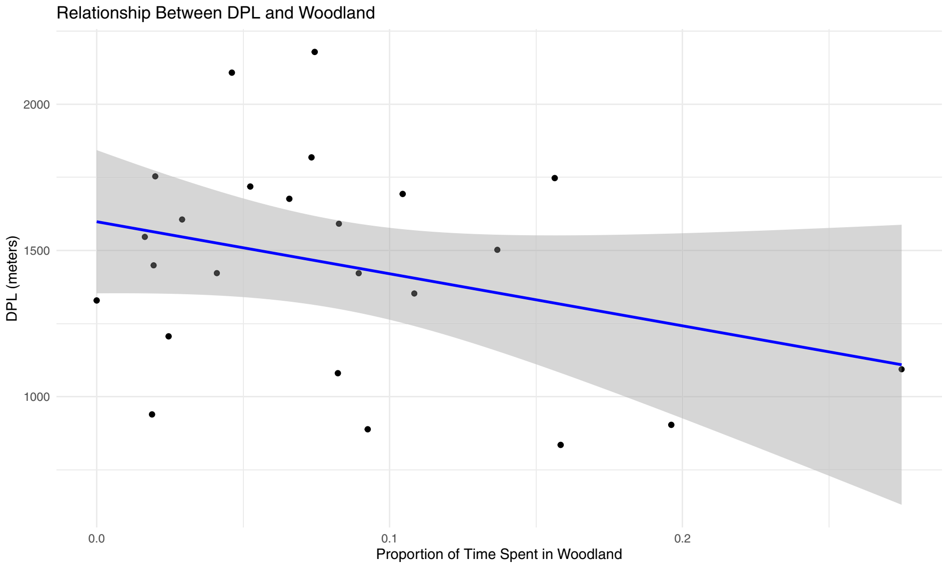

FIGURE 4 | Relationship between daily path length and woodland proportion. The scatter plot shows the relationship between the daily path length of the study group and the proportion of time spent in woodland. The x-axis represents the proportion of daytime spent in woodland (time in woodland divided by total observation time per day), and the y-axis shows DPL (m). The blue line represents the fitted linear regression. DPL tended to decrease with increasing use of woodland ($R^2 = 0.126$, $F(1, 22) = 3.16$, $p = 0.089$), although this relationship was not statistically significant.

space use could be explained by individuals exhibiting "resource monitoring" during periods of food shortage, traveling further not only to meet their dietary requirements but also to limit rival groups' access to resources (Kaplin 2001; Buzzard 2006; Janson and Byrne 2007). The presence of multiple red-tailed monkey groups at Issa (Fornof et al. 2023) makes such a resource monitoring strategy even more plausible.

Our findings that core area sizes in woodland did not increase during the fruit-lean season suggest that monkeys may not rely heavily on this vegetation type for dietary supplementation. Furthermore, the lack of significant differences in core area overlap across seasons and years in woodland indicates that these areas are unlikely to represent locations repeatedly targeted to exploit stable food resources, although these patterns need to be interpreted cautiously given uncertainty associated with lower sample sizes in three woodland wet-season strata. While the absence of persistent core areas in forests is more surprising, it may reflect heterogeneity in fruiting patterns of key feeding trees, especially important food species like *Ficus*

TABLE 2 | Association between food categories and woodland.

Category	Estimate	OR	p
Ripe fruit	−1.41	0.25	< 0.01
Unripe fruit	0.98	2.66	0.038
Bark	2.10	8.14	< 0.001
Flower	0.91	2.47	0.024
Leaf	−0.55	0.58	0.296
Invertebrates	−0.81	0.45	0.291
Mushroom	0.53	1.71	0.577
Stem	−0.04	0.96	0.999
Sap	0.36	1.43	0.617

Note: The table contains a summary of logistic regression results illustrating the relationship between various food categories and the likelihood of the study group being in woodland. For each category, the logistic regression estimate (logit coefficient), odds ratio (OR = exp.(estimate)), and *p*-value are provided.

(Tweheyo and Obua 2001) or mechanisms like diet-switching (Buzzard 2006) to potentially avoid competition and predation from sympatric chimpanzees. Additionally, spatial constraints imposed by intergroup dynamics may contribute to relatively stable patterns of space use, as overlap zones between neighboring primate groups are often underused, including in red-tailed monkeys (Wrangham et al. 2007). Further investigation into how sympatric primate species and another red-tailed monkey group at Issa use space across vegetation types will clarify these patterns.

We were not able to consider invertebrates as a driver of space use, given our lack of data on invertebrate abundance or distribution, yet speculate here given that invertebrates are a key food source wherever red-tailed monkey diet has been studied (Struhsaker 1978; Gathua 2000; Chapman et al. 2004; Bryer et al. 2015). Although insects provide relatively poor energy returns compared to fruits, in the wet season of fruit scarcity they may still be a desirable prey item, as they offer protein levels comparable to leaves and can supply important macro- and micronutrients (Bryer et al. 2015). Further study of invertebrate consumption rates and especially invertebrate seasonal (and spatial) changes in abundance and distribution will be useful.

The three food categories (bark, flower, and unripe fruit) that were positively associated with woodland use may indicate opportunistic or supplementary feeding, as these resources have not been reported to comprise the majority of the diet in previously studied red-tailed monkey populations (Struhsaker 1978; Cords 1986; Chapman et al. 2004; Bryer et al. 2015). However, such comparisons should be made with caution given the high dietary variability documented across populations of this species (Cords 1986; Chapman et al. 2004). While red-tailed monkey bark consumption has not been reported in the literature, sympatric chimpanzees at Issa consume bark during periods of low fruit availability (Piel et al. 2017), and multiple other primate species (e.g., *Macaca fuscata, Gorilla* sp.) have been reported to consume bark as a fallback food (Nishida 1976), although more recent work has argued that "fallback" is not a defining property of a food but instead varies with ecological and physiological context (Lambert and Rothman 2015).

Consuming flowers could be a strategy to obtain a rare, concentrated source of certain macronutrients, as shown in red-tailed monkeys (Ross et al. 2022) and in other primates (e.g., *Ateles geoffroyi*—Griffin 2013). Whether Issa red-tailed monkeys use woodlands to target preferred or alternative foods when no preferred foods are available in forests is not yet known. Given that we were unable to test for seasonal variation in woodland food consumption in this study, future analyses examining both seasonality and the nutritional content of woodland foods are needed to reveal what purpose these foods serve.

Finally, DPL showed a negative trend with increasing woodland use, which suggests that individuals are not ranging further in woodlands than in forests. Considering that food abundance is inversely associated with daily travel distance at Issa (McLester et al. 2019), it may be that the foods red-tailed monkeys seek in woodlands are accessed opportunistically or are adjacent to forests and thus require minimal travel. Higher spatial resolution data on monkey locations in relation to forest edges may resolve this. Furthermore, given the lack of statistical significance, this pattern should be interpreted as suggestive rather than conclusive and could be clarified with greater sampling effort.

5 | Conservation Implications

Current applied conservation efforts often rely on incomplete knowledge of variability in animal movement patterns (Anderson et al. 2007; Semel et al. 2022). While movement ecology research—particularly on foraging behavior and home range size—has shown clear relevance for the design of protected areas (e.g., *Calidris* spp.; Choi et al. 2019), integration of movement ecology and conservation biology remains relatively limited (Angeloni et al. 2008; Arroyo-Rodríguez and Fahrig 2014; Berger-Tal et al. 2016). Given the increasing fragmentation of primate habitats (Arroyo-Rodríguez and Fahrig 2014), knowledge of species adaptability to such fragmented, mixed-type habitats improves predictions for future habitat loss (de Almeida-Rocha et al. 2017) and understanding whether these environments are suitable for their long-term survival (Meijaard 2016).

Responses to fragmentation differ among and within species: chimpanzees in fragmented forests shift diet and grouping patterns but maintain habitat use across seasons (Chancellor et al. 2011), northern pigtailed macaques (*M. leonina*) expand ranging and plantation use during fruit-scarce periods in mixed forest–plantation landscapes (Gazagne et al. 2020), and diademed sifakas (*Propithecus diadema*) reduce home range size, daily travel distances, and avoid forest edges in fragments compared with continuous forest (Irwin 2007). Black and white guereza (*Colobus guereza*) groups in heterogeneous habitats exhibit up to fivefold differences in diet and home range size (Harris and Chapman 2007), illustrating substantial behavioral variation even within a single site.

Red-tailed monkeys are classified as Least Concern on The IUCN Red List (de Jong and Butynski 2019) and are locally abundant, including in disturbed forests, though their responses to disturbance vary (Chapman et al. 2000; Baranga 2004; Mammides et al. 2009). In contrast, most *Cercopithecus* species are classified as Near Threatened by the IUCN (IUCN 2023), with a general lack of ecological data for most threatened species (e.g., *C.mitis kandti*; Tuyisingize et al. 2023). Such long-term data, needed to make robust conservation decisions are typically hard to obtain considering the elusive behavior, restricted ranges, and the scarcity of habituated groups of threatened taxa (Butynski 2004b). Limited past studies have shown that different *Cercopithecus* species often show similarities in response to environmental change (Thom 2023). This suggests that understanding the movement patterns of locally common species as *C. ascanius*—particularly those populations inhabiting heterogeneous environments—could inform conservation actions for range-restricted and, consequently, data-deficient species of the genus (Butynski 2004b).

At Issa, that red-tailed monkeys can maintain similar core area sizes and DPL across forests and woodland despite substantial variation in tree density, canopy cover, and dominant species between those vegetation types, indicating some degree of behavioral flexibility. Whether this flexibility entails trade-offs in micro- or macronutrient intake, inter-individual spacing, or antipredator behavior remains unknown. However, these results highlight the Issa population as a valuable system for future research integrating movement data with measures of nutritional quality, physiological stress, and predation pressure, which may help predict responses of this species—and potentially other arboreal guenons—to habitat heterogeneity.

6 | Implications for Human Evolution

The usefulness of primates for understanding human evolutionary processes is well described elsewhere (Sandel et al. 2024) and includes the use of observations of extant species to inform behavioral inferences from fossil evidence and the importance of phylogenetic reconstructions of key traits. Elton (2006) argues that specifically, the Cercopithecini tribe offers additional key advantages that have direct comparability to hominid evolution: they are a diverse genus with > 25 species, have a geographically wide distribution, live in multi-species groups, and exhibit an array of ecological adaptations (e.g., diet, space use, locomotion) to environmental pressures. Together, these attributes parallel many of the same features that characterize Plio-Pleistocene scenarios of human evolution (Elton 2006; Cords 2012), and allow us opportunities to test hypotheses on inter-specific dynamics, niche-partitioning (Schreier et al. 2009), and exploitation of heterogenous landscapes (Arroyo-Rodríguez and Fahrig 2014; Raño et al. 2016; Corrêa et al. 2018).

In the current study, we assessed ranging and habitat use of an extant guenon species that lives in a mosaic habitat, similar to those reconstructed for key hominid species, for example, *Ardipithecus ramidus* (White et al. 2009). Mosaic habitats were a defining context for much of hominid evolution in Africa. Rather than specializing in a single niche, hominids likely exploited multiple adjacent vegetation types (Beasley and Schoeninger 2019), gaining ecological resilience as diet, locomotion, and cognition responded to environmental variability in resource type, canopy connectivity, and inter-individual visibility among others. Our results of monkeys' exploitation of both forest and woodland vegetation helps explain the variable C3 and C4 isotope data from fossil hominids, for example (Cerling et al. 2011; Sponheimer et al. 2013). Moreover, that we found no differences in core range sizes across vegetation types suggests there would have been minimal energetic cost to shifting between these areas for larger bodied hominids. Our observations of vegetation-specific consumed foods (e.g., bark, flowers in woodland vs. ripe fruit in forests) has bearing on our contextualisation of hominid nutrition and movement patterns reconstructed from paleodietary analyses (Paine et al. 2019).

7 | Limitations and Future Directions

Without data on fruit availability for red-tailed monkey foods as well as the vegetation-specific spatial distribution of other important food resources, especially invertebrates, we can only speculate on the interaction of movement and feeding ecology. Considering that food resources vary significantly in space and time (Nummelin 1989; Butynski 1990; Kaplin et al. 1998), future research should investigate the seasonal distribution and availability of foods within different vegetation types in Issa. Additionally, there are no available data on micro-climatic conditions, which influence the distribution of foods and impact primate movements (Baoping et al. 2009; McLester et al. 2019). We rarely observed the entire troop in the woodland; rather, the troop was more often spread across woodland and forest. As such, it may be there is individual-level variation in woodland use at Issa, with increased predation risk in open areas (*sensu* Fornof et al. 2023) discouraging vulnerable age-sex classes (e.g., juveniles, females with infants), as observed in *M. mulatta* (Anand and Radhakrishna 2022). Finally, group size is also known to affect home range size and DPL in many primate species (Xie et al. 2024). Although we did not account for fluctuations in group size in this study, it could represent an important source of variation in Issa red-tailed monkey movement patterns and warrants further investigation in future research.

We were not able to broadly address the role of insectivory in driving red-tailed behavior. Although the degree of invertebrate predation is challenging to quantify given the diversity of insect morphotypes, developmental stages, and variable distribution of insects consumed by red-tailed monkeys and other guenons (Gathua 2000; Bryer et al. 2015; Struhsaker 2017), capturing invertebrate abundance is possible, if laboriously intensive (Struhsaker 2017). Past studies identified invertebrate prey in guenons by analyzing gut contents (Gautier-Hion 1980), but this requires deceased animals. Alternatively, molecular analysis of fecal DNA using high-throughput DNA sequencing would reveal specific dietary contents more reliably than behavioral observations (*Chlorocebus pygerythrus*—Brun et al. 2022; *C. mitis* and *C. ascanius*—Lyke et al. 2019; *Saguinus weddelli*—Mallott et al. 2014). Importantly, our focal follows did not capture full-day feeding profiles, limiting resolution of dietary patterns and precluding a detailed assessment of red-tailed monkey diet in woodland–forest mosaics.

Finally, we determined core areas using Kernel Density Estimation; however, using more recently developed techniques like Dynamic Brownian Bridge Movement Models could offer a more dynamic representation by incorporating the temporal sequence of movements and behavioral characteristics (Kranstauber et al. 2012; Semel et al. 2022). This would allow us to investigate whether movement patterns shift over time in response to behavioral changes, environmental factors, or interactions with other individuals—metrics that are neglected by static models. Additionally, in this study, the relatively small number of woodland wet-season observations in 3 years ($n < 40$) may have reduced statistical power to detect seasonal differences in space use.

Author Contributions

Justas Ž. Mikulėnas: conceptualization, investigation, writing – original draft, methodology, data curation. **Joram L. Navaya:** data curation, methodology. **Fiona A. Stewart:** writing – review and editing, validation, resources, supervision, project administration. **Alex K. Piel:** writing – review and editing, validation, resources, supervision, project administration.

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Ethics Statement

Permission to conduct research at Issa was granted to J.Ž.M., A.K.P., and F.A.S. by TAWIRI (Tanzanian Wildlife Research Institute), COSTECH (Tanzanian Commission for Science and Technology), and the Tanganyika District.

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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