Socio-ecological determinants of movement behaviour in red-tailed monkeys (*Cercopithecus ascanius schmidti*)

Edward McLester

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Contents

Abstract

In group-living primates, costs and benefits of sociality are reflected in movement behaviour: where groups move in their environment, and how individuals maintain cohesive groups while moving. Establishing environmental and social determinants of movement behaviour reveals adaptive responses that characterise primate sociality. For primates in different habitats, intra-specific behavioural variation provides insight into ecological pressures that drive habitat-specific adaptive responses. I investigated how group ranging and two individual behaviours that mediate intra-group cohesion – spatial positioning and contact calling – relate to food availability, weather, and social contexts in red-tailed monkeys (*Cercopithecus ascanius*), a forest guenon that also lives in forest scarce savanna-woodland environments. I predicted food availability and weather would have stronger effects on ranging in more seasonal savanna mosaics than forests, and individuals would 1) adjust inter-individual distances in response to increased feeding competition, and 2) adjust contact call acoustic structure to maximise propagation when neighbours were further away. I collected behavioural and ecological data at Ngogo, Uganda, a predominantly forested habitat with small patches of secondary forest, and Issa, Tanzania, a woodland-dominated mosaic with thin strips of riparian forest. Larger home ranges sizes and longer travel distances at Issa reflected lower food availability and hotter temperatures than at Ngogo. Behavioural responses to thermal conditions in secondary forest and woodland suggested comparable environmental heterogeneity across sites at fine spatial scales. Ngogo monkeys increased inter-individual distances where food availability was low and when travelling slower. Individual cohesion indicates trade-offs between reducing feeding competition and social foraging. Ngogo monkeys also adjusted call structures to match expected propagation to conspecifics depending if neighbours produced preceding grunts (i.e. antiphony). Environmental and social drivers of intra-specific movement behaviour reveal adaptive behavioural responses through which primates maintain sociality. Habitat-specific behaviour in red-tailed monkeys also improves our understanding of adaptations in hominins distributed across similar vegetation gradients.

Declaration

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

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Author contributions

Chapter 1

EM designed and wrote the manuscript.

Chapter 2

EM designed the study, collected ranging data, analysed all data, and wrote the manuscript with edits from MB, FS, and AP. MB collected ranging and vegetation plot data. FS and AP collected ranging, vegetation plot, phenology, and weather station data.

Chapter 3

EM designed the study, collected ranging, behavioural, and weather station data, analysed all data, and wrote the manuscript with edits from MB, FS, and AP. MB collected ranging and vegetation plot data. FS and AP collected ranging, behavioural, vegetation plot, phenology, and weather station data.

Chapter 4

EM designed the study, collected ranging and behavioural data, analysed all data, and wrote the manuscript. MB collected vegetation plot data.

Chapter 5

EM designed the study, collected and analysed all data, and wrote the manuscript.

Chapter 6

EM designed and wrote the manuscript.

“Tebetebe was king of the forest and had three children: the Red-tailed Monkey, the Colobus, and the Baboon. When he was dying he sent for them, but the Colobus and the Baboon at first refused to come. Thus the Red-tailed Monkey arrived first and was named by Tebetebe as his successor, being given a white nose, white whiskers and a red tail to mark his rank.”

– Bakonjo folk tale, Rwenzori, Uganda [1]

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[1] Adapted from Haddow, A. J. (1952) Field and laboratory studies on an African monkey, *Cercopithecus ascanius schmidti* Matschie. *Journal of Zoology*. 122: 388.

Introduction

Group-living among primates

Social systems in many primates consist of extended periods spent in stable groups of two or more individuals (Lindenfors 2018). For group-living to be selected for, the benefits of sociality to individual fitness must outweigh the costs (Andrews and Rosenblum 1995; Majolo *et al.* 2008; Ward and Webster 2016). For primates, the fitness benefits of group-living are typically described under three broad hypotheses. First, foraging effort should be more efficient and greater overall due to collective resource detection (Janson and Di Bitetti 1997; Chapman and Chapman 2000a; Chapman and Chapman 2000b). Group-living individuals can allocate more time to foraging than other behaviours (e.g. vigilance for threats or searching for resources otherwise unknown to have been depleted – Isbell and Young 1996; Treves 1998). Larger groups should also be more effective at defending resources from con- and heterospecifics (Thompson *et al.* 2012; Brown 2013; Majolo *et al.* 2020). Second, predation risk should be lower in groups due to collective vigilance and the possibility of cooperative defence against predators (Isbell and Young 1996; Treves 2000; Beauchamp 2017). In the event of an attack, the dilution effect predicts individual risk should decrease as group size increases (e.g. due to greater predator confusion – Elgar 1989; Treves 2000; Beauchamp 2017). Third, group-living should improve reproductive success. Individuals may benefit from greater access to potential mates (depending on social structure; van Noordwijk and van Schaik 1999). More indirectly, females may benefit from lower risk of infanticide in groups by confusing paternity through promiscuity (Boyko and Marshall 2009), and through collective defence against infanticidal extra-group conspecifics (Treves and Chapman 1996).

These benefits may be offset by costs associated with sociality, resulting in trade-offs. For example, group-living results in greater intra-group competition, both for food (Janson and Goldsmith 1995; Chapman and Chapman 2000a; Chapman and Chapman 2000b) and mating opportunities (Mitani *et al.* 1996). In addition, closer proximity and higher rates of interaction between individuals can lead to faster disease transmission (Ward and Webster 2016; e.g. Springer *et al.* 2016).

The extent to which these cost-benefit trade-offs promote sociality are not distributed equally among all individuals in a group, resulting in a diversity of group sizes, social organizations, and social behaviours that vary between and within species. Establishing determinants of this variation is important for understanding not only why primates live in groups, but also how and through which mechanisms these animals maintain groups (Clutton-Brock and Janson 2012).

Group-living as an adaptive response

Investigations into the determinants of primate group-living behaviour have primarily focused on phylogenetic and ecological factors (Ward and Webster 2016). Some group-living characteristics retain strong phylogenetic signatures. For example, social structure is typically conserved between closely related species, particularly among cercopithecoids that exhibit similar social organisation irrespective of habitat dissimilarity (Hill and Lee 1998; Shultz *et al.* 2011; Ward and Webster 2016).

In contrast, other group-living characteristics vary considerably within some species, suggesting an adaptive rather than phylogenetic origin. For example, group size can differ by almost an order of magnitude in some species (e.g. 30 – >200 individuals in chimpanzees, *Pan troglodytes* – Pruetz and Bertolani 2009); Negrey and Langergraber 2020; 25 – 220 individuals in geladas, *Theropithecus gelada* – Kifle *et al.* 2013; 2 – >300 in Angolan black-and-white colobus, *Colobus angolensis* – Fashing *et al.* 2007). Ecological determinants of group size have been studied extensively (e.g. reviewed in Chapman and Chapman 2000b; Snaith and Chapman 2007; Majolo *et al.* 2008; see above). When the number of individuals in a group increases such that the costs of sociality outweigh fitness benefits to individuals, a smaller group size should become advantageous. In some species, smaller group sizes result from lower spatial cohesion (the relative proximity of group members, where more cohesive groups exhibit smaller inter-individual distances – King and Sueur 2011; Heesen *et al.* 2015); that is, groups become temporarily smaller through fission-fusion events that facilitate wide separation between individuals or sub-groups in response to short-term changes in ecological or social conditions (Aureli *et al.* 2008; Sugiura *et al.* 2011; Grove 2012). Well-studied examples of highly fission-fusion species include chimpanzees, bonobos, and spider monkeys (*Pan* and *Ateles* spp. – e.g. Chapman *et al.* 1995; Lehmann *et al.* 2007; reviewed in Aureli *et al.* 2008). More commonly, primates live in highly cohesive groups. In both cases, if ecological or social conditions strongly favour smaller group sizes for long periods, groups will fission permanently (e.g. chimpanzees – Goodall 1983; red-tailed monkeys, *Cercopithecus ascanius* – Struhsaker and Leland 1988; blue monkeys, *C. mitis* – Cords and Rowell 1986; Japanese macaques, *Macaca fuscata* – Sugiyama 1960; Moor macaques, *M. maurus* – Okamoto and Matsumura 2001).

At fine spatial and temporal scales, group- and individual-level behaviours can reveal ecological and social drivers of group-living strategies (Fichtel *et al.* 2011). For example, movement behaviour refers to where animals range and the mechanisms that maintain group cohesion during travel (Trillmich *et al.* 2004). At the group level, ranging patterns reflect compromises between group members for which cost-benefit trade-offs will differ based on individual traits such as age, sex, or nutritional requirements (Trillmich *et al.* 2004; Conradt and Roper 2005; Fichtel *et al.* 2011; Fischer and Zinner 2011). How these trade-offs result in group ranging patterns is therefore of interest in species that exhibit large, highly cohesive groups (i.e. minimal fission-fusion), where many individuals must efficiently coordinate group movements as ecological conditions change (King and Sueur 2011).

Drivers of group ranging

Individuals should adjust group movements in response to variation in environmental conditions. Ranging patterns should reflect changes in food abundance because individuals should travel further or expand home ranges to find new food patches when food availability is low. For example, mountain gorillas (*Gorilla beringei beringei*) exhibit longer daily travel distances and larger home range sizes in areas of lower fruit availability (Ganas and Robbins 2005) and samango monkeys (*C. albogularis* *schwarzi*) reduce monthly home ranges and travel distances in areas of high plant productivity (a proxy of food availability – Parker *et al.* 2020). This pattern may be exacerbated in larger primate groups because of greater feeding competition and faster rates of food patch depletion (Chapman and Chapman 2000a; Chapman and Chapman 2000b; e.g. Olupot *et al.* 1994). Alternatively, individuals may reduce travel distances and switch to fallback foods to conserve energy when food is scarce (Chapman and Chapman 2000b; Hemingway and Bynum 2005). For example, when fruit is not available, chimpanzees and western gorillas (*Gorilla gorilla gorilla*) consume more leaves and reduce travel distances (Doran 1997; Doran-Sheehy *et al.* 2004) and L'Hoest's monkeys (*Allochrocebus lhoesti*) reduce home ranges and consume more seeds (Kaplin 2001; see also Chapman 1988; Green *et al.* 2020).

Hetero- and conspecific animals may also influence group movements. Individuals should avoid predators or areas of high perceived predation risk (Boinski *et al.* 2000; Willems and Hill 2009). In addition, individuals may travel further to defend home ranges from conspecifics that compete for food or access to polyspecific associations (Brown 2013). By associating in close proximity with other species, primates can improve foraging efficiency and predator detection (e.g. Smith *et al.* 2005; Bryer *et al.* 2013; see below). As such, primates may travel further or faster – particularly where heterospecifics exhibit larger home ranges and daily travel distances – to keep up with and maintain associations, as long as benefits conferred by polyspecific associations outweigh costs of energy expenditure (Chapman and Chapman 1996).

Abiotic conditions such as weather should also influence group movements. Individuals may reduce activity in areas and times of thermal stress (e.g. in exposed areas or during peak daytime temperatures – Hill 2006; Johnson *et al.* 2015) and adjust travel speed to avoid energy loss from cold during rainfall (Rudran 1978; Ganas and Robbins 2005). While group movements are the product of both abiotic and biotic factors, disentangling how group members respond collectively to individual ecological factors should be more straightforward in very heterogeneous environments or for primates living across more contrasting gradients of environmental conditions, where intra- and inter-habitat variation in ranging responses should be increasingly observable (e.g. Green *et al.* 2020).

Drivers of group cohesion at the individual level

At the individual level, costs and benefits of group-living are reflected in spatial cohesion. The relative positioning of individuals within groups should reflect trade-offs between a range of environmental and social factors. Individuals may spread out to maximise foraging efficiency by reducing intra-group competition (Cowlishaw 1994; Chapman and Chapman 2000b). Alternatively, individuals may increase cohesion and shorten inter-individual distances to exploit food locations known or found by conspecifics (Garber 2000). These patterns should be modulated by local food availability and individual physiologies, such as nutritional requirements that vary between individuals (Chapman and Chapman 2000b; Felton *et al.* 2009). Forming polyspecific associations may also provide foraging benefits, which should reduce effects of competition and food abundance on individual cohesion. For example, red-tailed monkeys may benefit from associating with larger bodied blue monkeys (*C. mitis*) and grey-cheeked mangabeys (*Lophocebus albigena*) that dislodge insects into more obtainable locations or are able to supplant other competing species (e.g. chimpanzees; hornbills, *Bycanistes* spp. – Struhsaker 1981).

Predation risk is also influenced by polyspecific associations, which in turn should affect how individuals position themselves within groups. Positioning in group cores or close to other group members should reduce predation risk (Treves 2000; reviewed in Boinski *et al.* 2000). Predation risk may be perceived as a function of various ecological conditions, including proximity of heterospecifics, irrespective of actual predation rates (Hill and Cowlishaw 2002). For example, red-tailed monkeys associate with grey-cheeked mangabeys that are able to deter raptors (Bryer *et al.* 2013; reviewed in Terborgh 1990) and Diana monkeys (*C. diana*) similarly associate with red colobus monkeys (*Procolobus badius*) that afford each other protection from raptors and chimpanzees (Noë and Bshary 1997; see also Teelen 2007; reviewed in Treves 1999). Alternatively, some polyspecific associations may increase predation risk because associating with noisy or conspicuous heterospecifics may inadvertently attract predators or mean that species that rely on crypsis or hiding to avoid predation are unable to do so (Gautier-Hion *et al.* 1983; Buzzard 2010). Landscape features, such as vegetation cover and topography also likely influence predation risk. Primates that range in open canopy vegetation may be more vulnerable to aerial predators, while group that travel in particularly dense vegetation may be at greater risk of ambush from terrestrial predators (Willems and Hill 2009; Coleman and Hill 2014). In contrast, use of habitat features that are inaccessible to predators (e.g. cliffs) may reduce predation risk, in turn meaning other factors such as competition are stronger drivers of spatial cohesion at these locations (e.g. Hamilton III 1982).

Social factors, such as the behaviour of close neighbours, should also influence individual spatial cohesion (Heesen *et al.* 2015). Foraging behaviour of other group members should provide visual cues to other individuals that indicate food that could be shared or competition to be avoided (Garber 2000; King *et al.* 2011). While some studies have shown empirically that primates appear to exploit such cues (i.e. social foraging – Galef and Giraldeau 2001; e.g. di Bitetti and Janson 2001), there have been few studies of whether primates are more likely to use these cues depending on other factors, such as changes in environmental conditions. For example, yellow baboons (*Papio cynocephalus*) are more likely to “scrounge” from conspecifics when food availability is higher (King *et al.* 2009). Effects of environmental conditions on social foraging may also change with social contexts – for example, whether certain group members are more reputable sources of food locations based on age and assumed experience of food locations within home ranges (e.g. Pyritz *et al.* 2011). As groups navigate their environments, these fine scale changes in ecological and social conditions should further modulate how group members balance individual motivations that result in continuous changes in individual spatial cohesion.

Bidirectional communication as a mechanism of spatial cohesion

As long as group-living is advantageous for individuals, animals must keep track of at least one other group member to maintain a cohesive group, even while maintaining potentially wide inter-individual distances. As such, individuals must communicate efficiently to mediate cohesion as their immediate ecological and social environment changes. To this end, bidirectional communication is an important adaptation that helps maximise signal detection while limiting signal redundancy (Endler 1993; Oliphant and Batali 1997). A variety of primates exhibit various modalities of bidirectional communication, including visual (e.g. facial expressions in Rhesus macaques, *Macaca mulatta* – Ferrari et al. 2009; gestural greetings in chimpanzees – Luef and Pika 2017, tactile e.g. touching in grey langurs, *Semnopithecus* spp. – Weber 1973), and auditory signals (e.g. pant grunts in chimpanzees – Laporte and Zuberbühler 2010; Luef and Pika 2017).

For primates that live in densely vegetated forests, bidirectional vocalisations are more effective than visual, olfactory, or tactile signals, especially when group members are spread out over large areas (Brown and Waser 2017). In these environments, individuals may preferentially direct contact calls at other individuals that are more likely to detect the call and respond, including those that produced a preceding call (i.e. antiphony – Yoshida and Okanoya 2005). Antiphonal exchanges improve communication efficiency because individuals can better adjust acoustic properties of calls to maximise propagation to the intended target if the target has already called and revealed their location. In addition, antiphony reduces overlap with conspecific calls, thereby avoiding redundant calls that are otherwise energetically expensive to produce (Yoshida and Okanoya 2005).

Studies of antiphonal calling in primates usually focus on loud, long-distance vocalisations that are associated with mediating intra- and inter-group spacing across wide scales. For example, chimpanzees use pant hoots to communicate between parties that can be separated throughout home ranges (e.g. Mitani and Nishida 1993), while grey-cheeked mangabeys use whoop-gobbles to adjust intra-group spatial cohesion and avoid nearby conspecifics (Waser 1976; Waser and Waser 1977; Brown and Waser 2018). Other examples of antiphonal loud calling include blue monkeys (Fuller *et al.* 2019), Milne-Edwards' sportive lemurs (*Lepilemur edwardsi* – Rasoloharijaona *et al.* 2006), mantled howler monkeys (*Alouatta palliata* – Whitehead 1987), and Müller's gibbons (*Hylobates muelleri* – Mitani 1985; reviewed in Mitani and Stuht 1998).

Alternatively, in large, non-fission-fusion groups where many individuals must communicate frequently and concurrently, short-range contact calls are an important modality of communication. Fewer studies have quantified or empirically established antiphonal contact calling, compared to loud calling, in primates (e.g. common marmosets, *Callithrix jacchus* – Miller *et al.* 2010; Miller and Wren Thomas 2012; squirrel monkeys, *Saimiri sciureus* – Biben *et al.* 1986; Biben 1993), and fewer still in wild groups (e.g. Japanese macaques, *Macaca fuscata* – Sugiura 1993). Moreover, individuals may vary the target group member to which contact calls are directed depending on social factors, such as target age (given adults should call more reliably in response than juveniles – Briseno-Jaramillo *et al.* 2018) and group travel speed (given difficulty of locating more distant group members with faster travel – Koda *et al.* 2008). Studies of contact call behaviour should therefore provide insight into an important adaptive mechanism of mediating spatial cohesion.

Inter-habitat and intra-specific variation in group-living behaviour

Examining how environmental and social factors relate to behaviour that reflects fitness benefits of group-living can improve our understanding of primate adaptive behaviour. While social factors such as intra-group demography vary over relatively small spatial scales, environmental conditions such as vegetation cover, weather, and seasonality can vary over wide spatial scales (e.g. between biomes), which should exacerbate inter- and intra-specific variation in adaptive responses. Phylogeny can confound inter-specific comparisons across habitats however, making it difficult to discern adapted and adaptive behaviour when comparing behaviour between primate species that live in different environments (Clutton-Brock and Harvey 1979).

The effect of phylogeny can be negated through intra-specific comparisons for primates distributed across multiple habitats, such as both forests and savanna-woodland mosaics in West and East Africa (e.g. *Pan* spp. – Pruetz and Bertolani 2009; Piel *et al.* 2015; *Cercopithecus* spp. – Sarmiento *et al.* 2001; Korstjens 2019). In savanna mosaics, conditions differ considerably compared to forests. With a minimum of forest and majority of open grassland and woodland cover, food distribution is more heterogeneous and abundance lower overall (Copeland 2009; Piel *et al.* 2017). Higher proportions of open canopy cover and different compositions of predators (e.g. lions, *Panthera leo*; African wild dogs, *Lycaon pictus*) suggest predation risk varies for primates across these landscapes as well (McLester *et al.* 2016; McLester *et al.* 2018). Behavioural studies of primates that live in forests and savanna mosaics often focus on food-rich forests, where these species typically live at highest densities (e.g. Piel *et al.* 2015; McLester *et al.* 2019). As such, the lack of a broader understanding of how primates have adapted to environmental extremes means there is a need to expand studies of behavioural responses to include the margins of species distributions, particularly where primates live across a gradient of habitat types and environmental conditions.

Inter-habitat comparisons can reveal selective pressures that have shaped the behaviour of not only extant, but also extinct primates. Forests and savanna-woodland mosaics resemble two extremes of the Mio-Pliocene transition from closed forests to woodland-dominated mosaics (Antón *et al.* 2014). Open savanna-woodland mosaics were hotter, more seasonal, and had more heterogeneously distributed food than the forests they replaced (Isbell and Young 1996; Passey *et al.* 2010; Cerling *et al.* 2011). The transition from predominantly forested environments to more open mosaics has been associated with a number of key adaptations that characterize hominin evolution (e.g. obligate bipedalism; encephalization – reviewed in Potts 2013). As such, studies of primate behaviour in extant habitats that are similar to these paleoenvironment reconstructions provide an opportunity to assess the environmental pressures under which hominins likely would have evolved (Moore 1996; Pickering and Domínguez-Rodrigo 2010). While extant primate behaviour is not always likely analogous to hominin behaviour, especially in more phylogenetically-distant species (e.g. cercopithecines), such data can help inform hypotheses of environmental conditions that drove hominin adaptations in more open and more seasonal mosaic environments (Foley 1993; Elton 2006).

The red-tailed monkey (*C. ascanius schmidti*) is a social primate that can be used to investigate intra-specific behavioural variation between contrasting habitat types. This species lives in large groups (typically ~10 – 30 individuals) that are typically highly cohesive with minimal fission-fusion (Cords and Sarmiento 2013; but see Detwiler 2018). Red-tailed monkeys live primarily in wide expanses of forest, as well as smaller forest fragments (e.g. Baranga 2004a, 2004b). Previous research on this species has been largely conducted in predominantly forested environments (e.g. Cords 1987; Brown 2013). Nonetheless, red-tailed monkeys are one of the few primarily forest-dwelling primates also found in savanna-mosaic environments (Sarmiento *et al.* 2001; McLester *et al.* 2019; Tapper *et al.* 2019). As such, red-tailed monkeys should exhibit a high degree of behavioural variation between these environments given ecological differences between forest and savanna-mosaic habitats.

Thesis outline

In this thesis, I aimed to establish how environmental and social factors influence primate group-living behaviour by studying movement behaviour in the red-tailed monkey. I collected data from red-tailed monkey groups at two sites with differing ecological conditions – a wet predominantly forest (~60% cover – Wing and Buss 1970) environment at Ngogo, Kibale National Park, Uganda (Figure 1), and a drier, more seasonal savanna-woodland mosaic with minimal riparian forest (~4% cover – McLester *et al.* 2019) at the Issa Valley, Tanzania (Figure 1).

First, to investigate how group-level movements reflect habitat-specific environmental conditions, I compared the influence of food abundance (Ch. 2) and weather (Ch. 2; Ch. 3) on group ranging patterns between sites. I predicted monkeys at Issa would adjust ranging patterns in response to food availability and weather more strongly than at Ngogo, given more seasonal changes in food availability and weather extremes in savanna mosaics than forests.

Second, to investigate how group members maintain cohesion during group movements, I examined how two individual-level behaviours – spatial cohesion (i.e. inter-individual distances; Ch. 4) and contact calling (Ch. 5) – in groups at Ngogo reflect fine-scale changes in social and environmental conditions. I predicted individuals would reduce cohesion and spread out in areas of low food availability or when feeding competition was high, including as an alternative to increasing group travel to acquire food. I also tested the hypothesis that individuals adjust contact call acoustic structure for optimal propagation to the intended target, which in turn should vary depending on whether monkeys were calling in response to a preceding call or social contexts such as neighbour identities and how fast groups were travelling.

I discuss how results demonstrate intra-specific variation in movement behaviour at different spatial scales, and the extents to which results provide evidence for habitat-specific behavioural adaptations. To conclude, I first summarise how understanding primate movement behaviour can contribute to effective conservation strategies. Second, I discuss how comparing monkey behaviour in forest and savanna mosaics against hypotheses of hominin behaviour can improve our understanding of environmental pressures that may have driven hominin adaptations during the Mio-Plicoene transition from similarly closed to open mosaic environments.

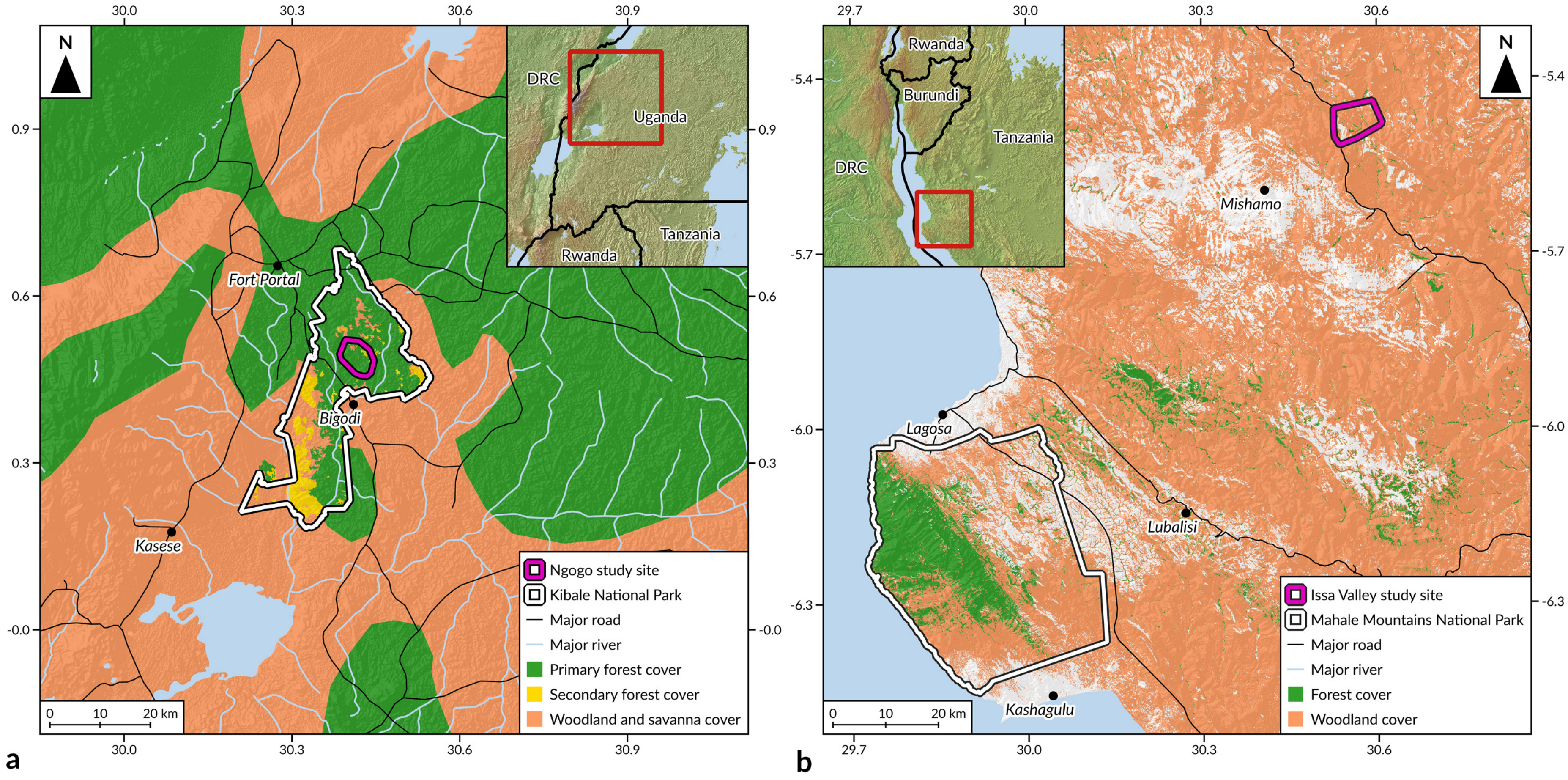

Figure 1 Locations of Ngogo, Kibale National Park, Uganda (a) and the Issa Valley, Tanzania (b) in relation to major landscape features and vegetation cover.

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Title: Food abundance and weather influence habitat-specific ranging patterns in forest- and savanna mosaic-dwelling red-tailed monkeys (*Cercopithecus ascanius*)

Edward McLester [a], Michelle Brown [b], Fiona A. Stewart [a, c] & Alex K. Piel [a, c]

[a] School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK
[b] Department of Anthropology, University of California, Santa Barbara, USA
[c] Greater Mahale Ecosystem Research and Conservation Project, Box 60118, Dar es Salaam, Tanzania

Abstract

Primates that live in predominantly forested habitats and open, savanna mosaics should exhibit behavioral responses to differing food distributions and weather. We compared ecological constraints on red-tailed monkey ranging behavior in forest and savanna mosaic environments. Intra-specific variation in adaptations to these conditions may reflect similar pressures faced by hominins during the Plio-Pleistocene. We followed six groups in moist evergreen forest at Ngogo (Uganda), and one group in a savanna-woodland mosaic at the Issa Valley (Tanzania). We used spatial analyses to compare home range sizes and daily travel distances (DTD) between sites. We used measures of vegetation density and phenology to interpolate spatially explicit indices of food (fruit, flower, and leaves) abundance. We modeled DTD and range use against food abundance. We modeled DTD and at Issa hourly travel distances (HTD), against temperature and rainfall. Compared to Issa, monkeys at Ngogo exhibited significantly smaller home ranges and less variation in DTD. DTD related negatively to fruit abundance, which had a stronger effect at Issa. DTD and HTD related negatively to temperature but not rainfall. This effect did not differ significantly between sites. Home range use did not relate to food abundance at either site. Our results indicate food availability and thermoregulatory constraints influence red-tailed monkey ranging patterns. Intra-specific variation in home range sizes and DTD likely reflects different food distributions in closed and open habitats. We compare our results with hypotheses of evolved hominin behavior associated with the Plio-Pleistocene shift from similar closed to open environments.

Introduction

Hominin evolution is characterized by responses to environmental shifts that resulted in drier, more heterogeneous landscapes during Mio-Pliocene cooling. Specifically, behavioral and morphological adaptations such as obligate bipedalism (Rodman and McHenry 1980; Isbell and Young 1996), increased encephalization (Stanley 1992; Potts 1998), and changes in dental morphology (Teaford and Ungar 2000; Grine *et al.* 2012) have been ascribed to hominin adaptations to the retraction of forests and a transition to open mosaics (White *et al.* 2009; Cerling *et al.* 2011; reviewed in Potts 2013). Compared to the closed, more homogeneous forests they replaced, these open mosaic environments were hotter and more arid (Bromage and Schrenk 1995; Potts 1998; Passey *et al.* 2010), more seasonal (Foley *et al.* 1993), and exhibited a wider, less abundant distribution of food (Isbell and Young 1996). Establishing the extent to which these changes in environmental conditions could have selected for hominin adaptations is of primary interest (Antón *et al.* 2014).

Comparisons of extant primate behavior in closed, primarily forested habitats (hereafter, “forests”) and open, savanna-woodland mosaic (hereafter, “savanna mosaic”) habitats can be used to reconstruct environmental pressures under which hominins likely would have evolved because these environments resemble the two extremes of the Miocene paleoclimate (Moore 1996; Hernandez-Aguilar 2009; Pickering and Domínguez-Rodrigo 2010). For forest primates that also live in savanna mosaic habitats, such studies are rare, however, and still fewer studies have directly compared habitat-specific behavior. Nonetheless, where behavioral comparisons can be made between these habitat types, ranging patterns can provide evidence of adaptations to ecological conditions (Boinski 1987; Doran-Sheehy *et al.* 2004). These adaptations include feeding strategies (Kaplin 2001), social and grouping patterns (Wrangham *et al.* 1993), and physiological and energetic adaptations (Nunn and Barton 2000); all of which inform on how primates utilize and respond to the environment. Ranging patterns are also quantifiable using several well-established metrics (e.g. home range size, daily and hourly travel distances – DTD and HTD – and home range use) that can be directly compared between forests and savanna mosaic habitats.

Variation in a number of biotic (e.g. food abundance; predation risk; polyspecific associations) and abiotic (e.g. temperature; rainfall) factors between habitat types should influence ranging patterns. For example, when key foods are scarce, primates may increase home range size and / or daily travel distances to locate high quality foods, (Chapman and Chapman 2000b; Hemingway and Bynum 2005). Chimpanzees (*Pan troglodytes*) in forest at Taï, Côte d'Ivoire, reduce DTD when concentrated patches of dietary important nuts are ripe and switch to feeding on leaves when both fruit and nuts are scarce (Doran 1997). Alternatively, instead of increasing search effort primates may reduce travel and spend more time feeding on lower quality foods. For primates with flexible diets or in comparatively food-rich environments, fallback foods may still be diverse or abundant enough that ranging patterns do not alter significantly (Alberts *et al.* 2005; Buzzard 2006). For example, forest mangabeys and guenons do not adjust DTD (*Lophocebus albigena* at Kibale, Uganda – Olupot *et al.* 1997; *Cercopithecus mitis* and *C. lhoesti* at Nyungwe, Rwanda – Kaplin 2001) or range use (*C. campbelli*, *C. petaurista*, and *C. diana* also at Taï – Buzzard 2006) in response to changes in fruit availability.

Food abundance should have a greater influence on ranging behavior for forest primates in savanna mosaic habitats given the wider spatio-temporal distribution of resources in these environments (Chapman and Chapman 2000a; Copeland 2009). This is particularly the case where the quality and diversity of available resources is low enough that diet switching is a less effective alternative than expanding home ranges or increasing DTD, even for species with diverse diets. For example, Piel *et al.* (2017) observed chimpanzees in savanna-woodland at the Issa Valley, Tanzania, to consume only 77 plant species compared to mean 112 species for forest populations. As such, a narrow diet and the low density of resources in open savanna mosaics is associated with extremely large home range sizes for chimpanzees (e.g. 80-200km^2 in savanna mosaics – Baldwin *et al.* 1982; compared to 6-20km^2 in forests – Newton-Fisher 2003; Pruetz and Bertolani 2009; Rudicell *et al.* 2011; Samson and Hunt 2012; Nakamura *et al.* 2013). Wide seasonal variation in resource abundance between different vegetation types in savanna mosaic habitats has also been implicated in patterns of home range use. Chimpanzees in savanna mosaics range farther and preferentially exploit woodland species during dry seasons when fruit is most abundant in woodland compared to other vegetation types (Hernandez-Aguilar 2009; Piel *et al.* 2017).

Interactions with sympatric taxa should also affect group ranging. Groups should avoid areas of high predation risk, which can vary substantially throughout home ranges depending on predator density and diversity, and habitat type (Willems and Hill 2009). Polyspecific associations can reduce predation risk, as well as increase foraging efficiency (reviewed in Teelen 2007). Because these benefits are not always conferred equally by each species within an association, some species preferentially seek out heterospecifics. Maintaining associations may therefore require increasing DTD (Chapman and Chapman 1996) or adjusting patterns of home range use (Cords 1987) to coordinate group movements. Similarly, groups may divert travel routes towards or away from conspecifics to initiate or avoid inter-group competition (e.g. over food patches; access to heterospecifics – Brown 2013).

Abiotic factors influence ranging (Hill and Dunbar 2002; Baoping *et al.* 2009) as individuals thermoregulate to avoid overheating in hot temperatures and energy loss from cold during rainfall (Stelzner and Hausfater 1986). Across habitats, high temperatures are associated with reduced travel speeds and duration (yellow baboons, *P. cynocephalus* – Stelzner 1988; white-faced capuchins, *Cebus capucinus* – Campos and Fedigan 2009; Johnson *et al.* 2015) and determine activity schedules (yellow baboons – Hill 2005; Hill 2006; chimpanzees – Kosheleff and Anderson 2009). DTD relates negatively to rainfall in both forests (siamangs, *Hylobates syndactylus*, and lar gibbons, *H. lar* – Raemaekers 1980; red colobus, *Piliocolobus tephrosceles* – Isbell 1983; gorillas, *Gorilla beringei beringei* – Ganas and Robbins 2005; proboscis monkeys, *Nasalis larvatus* – Matsuda *et al.* 2009) and more heterogeneous mosaic habitats (baboons, *Papio* spp. – Johnson *et al.* 2015). Given that temperature and rainfall ranges are more seasonally variable in savanna mosaic habitats that exhibit longer, hotter dry seasons than forests (McGrew *et al.* 1981), these conditions should be especially strong constraints on primate movement in open environments (Hill 2005; Wessling *et al.* 2018).

Previous investigations of primate ranging support the hypothesis that ranging patterns are shaped by food distribution and weather. As such, species living in both forests and savanna mosaic habitats should exhibit intra-specific variation in ranging. We tested this hypothesis in the red-tailed monkey (*Cercopithecus ascanius*), a forest guenon that lives in wide expanses of forest as well as forest-scarce fragments and mosaics (Sarmiento *et al.* 2001). Specifically, we investigated red-tailed monkeys living in two contrasting environments: a predominantly forested landscape at Ngogo, Uganda; and a comparatively heterogeneous savanna-woodland mosaic at the Issa Valley, Tanzania. First, we predicted that red-tailed monkeys at Issa exhibit larger home range sizes than at Ngogo. Second, we predicted that while food abundance and rainfall and temperature should constrain HTD and DTD at both sites, these effects are stronger at Issa than at Ngogo. Specifically, we expected Issa monkeys to exhibit shorter DTD in dry seasons and longer DTD in wet seasons compared to Ngogo monkeys in all months. Finally, we predicted that home range use at Issa is more strongly associated with spatio-temporal changes in food abundance than at Ngogo.

Methods

Study sites

The Ngogo study site is located in the approximate center of Kibale National Park in southwestern Uganda at elevations spanning 1110 – 1590m. The site comprises a *ca.* 40km^2 mosaic of mostly primary forest (*ca.* 60% cover – Wing and Buss 1970) interspersed with isolated patches of secondary forest, woodland, swamp, and grassland (Struhsaker 1997). Rainfall varies substantially between months and years (1977 – 1984 yearly $\bar{x}$: 1500mm – Chapman *et al.* 1999). Consequently, wet and dry seasons are inconsistent between years, which makes identifying other seasonal patterns difficult (e.g. plant phenology – Struhsaker 1997). Predators of red-tailed monkeys at Ngogo include raptors (e.g. crowned hawk-eagles, *Stephanoaetus coronatus* – Mitani *et al.* 2001) and chimpanzees (Watts and Mitani 2002). African golden cats (*Caracal aurata*) are presumed predators but are rarely encountered (Struhsaker 1981). We followed six habituated red-tailed monkey groups at Ngogo: groups R1 through R6 comprised between 10 and *ca.* 35 individuals including one adult male per group, except for R6 which included two adult males (see supplementary Table S1 for detailed demographics). All six groups frequently formed polyspecific associations (≥2 heterospecifics within the periphery of the study group) with habituated gray-cheeked mangabeys (*Cercocebus albigena*) and blue monkeys (*C. mitis*; except for R5 who we never observed to associate with blue monkeys during the study period) and infrequently with unhabituated black and white colobus (*Colobus guereza*), L'Hoest's monkeys (*C. lhoestii*), and olive baboons (*P. anubis*),

The Issa Valley is located *ca.* 668km from Ngogo in the north of the Greater Mahale Ecosystem in western Tanzania (Piel *et al.* 2017). Research centers around a *ca.* 60km^2 area of five major valleys and surrounding flat plateaus at elevations spanning 1150 – 1712m. Vegetation is a mosaic of mostly deciduous *Brachystegia* and *Julbernadia* spp. miombo woodland, grassland, swamp, and minimal evergreen riparian forest (4% cover – EM unpublished data). Compared to the relatively continuous expanse of forest at Ngogo, forest at Issa is restricted to riverine strips that measure <10m wide at some locations. The region is characterized by two distinct seasons: wet from November to April and dry (<100mm monthly rainfall) from May to October (Piel *et al.* 2017; see Results). Chimpanzees also prey upon red-tailed monkeys at Issa (C. Giuliano unpublished data) and possible predators include both crowned-hawk eagles and five large carnivores: leopards (*Panthera. pardus*), lions (*P. leo*), African wild dogs (*Lycaon pictus*), East Africa black-backed jackal (*Canis mesomelas schmidti*), and spotted hyenas (*Crocuta crocuta*; McLester *et al.* 2018). We followed one habituated group at Issa: K0 included between one and four adult males at any one time and increased from *ca.* 35 to 55 total individuals during the study. Red-tailed monkeys at Issa form polyspecific associations with three unhabituated species, although associations are rare compared to Ngogo (red colobus, *P. tephrosceles*; yellow baboons, *P. cynocephalus* – *n* = 2 observations; vervet monkeys, *Chlorocebus pygerythrus* – *n* = 2 observations; EM unpublished data).

Data collection

Ranging data

We collected ranging data at Ngogo from January 2008 to December 2008 (R1 – R4), March to June 2017 (R6), and July to October 2017 (R5), and at Issa from January 2013 to March 2016 (K0). At Ngogo, we followed R1 – R4 for six consecutive days separated by five days (see Brown 2011), and we followed R5 and R6 every day as far as was possible. At Issa, we followed K0 for 5 consecutive days twice monthly from January 2013 to May 2015, and for 10 consecutive days each month from June 2015 to March 2016. For each group, one researcher or at least two trained field assistants arrived at the sleeping site and followed the group from 0700 – 1900 h. During follows at Ngogo, we recorded group locations by estimating the group center-of-mass within a 50 x 50 m gridded map at 30-minute intervals (see Brown 2013) or by recording GPS coordinates automatically at 1-minute intervals using a Garmin Rino 650 GPS unit (R6 and R5). At Issa, we recorded GPS coordinates automatically at 5-minute intervals using Garmin Rino 650 and Garmin Rino 520 GPS units. To account for the difference in location intervals for R1 – R4 compared to R5 and R6, we analyzed these groups separately. Unless otherwise stated, we used only all-day follows (≥9 hour continuous duration) in analyses, as per Kaplin (2001).

Climate data

At Ngogo, temperature and rainfall data were collected daily by the Ngogo Chimpanzee Project using an analogue mercury thermometer and an Onset digital rain gauge, respectively. At Issa, we recorded temperature at 30-minute intervals using a HOBO H8 Pro logger in forest vegetation. We recorded rainfall continuously from January 2013 – July 2014 and September 2014 – March 2016 using a HOBO RG3 rain gauge in woodland.

Food abundance

In 2009, 2012 and 2013 at Ngogo, we sampled 272 50 x 50m plots located at 50m intervals in primary forest across the extent of R6, R5, and four neighboring group home ranges. Within each plot, we identified stems of 34 plant species that were ≥1% of the red-tailed monkey or grey-cheeked mangabey diet (see Brown 2013), and recorded the number of stems for each plant species and diameter at breast height (DBH) of each stem. We ignored stems of diameter <10cm, except for lianas which were measured regardless of size.

Plant phenology data at Ngogo were collected from March – October 2017 by trained field assistants from the Ngogo Chimpanzee Project who walked trails monthly (see Potts *et al.* 2009; Watts *et al.* 2012). Marked plants (*n* = 511 stems; supplementary Table S2) identified to species level were examined for presence-absence of the following: ripe and unripe fruit; new, young, and mature leaves; flowers.

From 2013 – 2016 at Issa, we sampled 155 20 x 20m plots located randomly across the extent of the study site and in both forest and woodland vegetation classes (*n* = 90 forest plots; *n* = 57 woodland plots; *n* = 8 forest-woodland boundary plots). Without data on red-tailed monkey diet at Issa, within each plot we identified all stems >10 cm to species level where possible and recorded the number of stems for each plant species and DBH of each stem. Unidentifiable stems were sampled and identified by a trained botanist – Yahya Abeid – at the National Herbarium of Tanzania.

Plant phenology was sampled at Issa by trained field assistants. Three trails (lengths: 623 – 2608m; *n* = 2 woodland trails; *n* = 1 forest trail) were walked monthly in 2013 – 2015. From 2016, trails were replaced with marked stems distributed across the site identified as the fifteen plant species most consumed by chimpanzees. Observers examined marked plants of at least 10cm DBH and one meter tall (*n* = 1431 total stems; supplementary Table S3) identified to species level and counted the following: ripe and unripe fruit; new, mature and old leaves; flower buds and mature flowers.

Data analyses

Home range size

We used QGIS 2.18.6 (QGIS Development Team, 2018) to calculate paths of Euclidean distance between GPS coordinates for each follow day. For R1 – R6, we used follows of any duration (minimum: R1 = 1 hour; R2 = 0.5 hours; R3 = 2 hours; R4 = 0.5 hours; R5 = 1.5 hours; R6 = 2.25 hours) to increase the sample size relative to K0. To provide parity with previous studies of primate home range sizes, we then calculated 1) the one hundred percent minimum convex polygon (MCP) of these paths, and 2) the number of grid cells intersected by these paths and the sum of this area (grid cell analysis – GCA). For GCA, we used 50 x 50m cells for R6 and R5 and 75 x 75m cells for K0 to account for increased group spread with larger group sizes, as per Kaplin (2001).

Hourly and daily travel distances

To calculate DTD, we measured DTD as the total path length for each all-day follow. To control for overestimation of path length due to variation in GPS accuracy, for R5, R6 and K0 we used only GPS coordinates at 5-minute intervals (mean of 1-minute interval coordinates for R5 and R6) and minimum 5m travelled between consecutive coordinates.

We calculated HTD for K0 as the cumulative Euclidean distance between all GPS points for each complete follow hour (≥50 minutes). To model HTD, we calculated mean temperature and binary occurrence of rain per follow hour. To model DTD, we calculated maximum temperature and total rainfall per day.

Range use and food abundance

We calculated range use as the proportion of GPS points in each grid cell across each group's home range each month (combined across years for K0). We used only all-day follows with consistent 1-minute (for R6 and R5) or 5-minute (for K0) intervals between GPS points in this analysis. Only one all-day follow of K0 in October met this criterion, which we excluded from the analysis.

We calculated two indices of food abundance for primary forest at Ngogo and forest and woodland at Issa. In both indices, we used only plant species for which both phenology and density data were available (*n* = 27 species at Ngogo; *n* = 65 species at Issa). For each sample plot we converted DBH into basal area for each stem and calculated total basal area density for each species within each plot (unit: m^2 basal area / m^2 area sampled). We used these measurements as an initial index of site-wide variation in basal area density for each species. To create a second, spatially explicit index of basal area density, we then used a spatial interpolation in GRASS GIS 7.4 to interpolate home range-wide distributions of basal area density for each plant species in each vegetation class (see supplementary material S1; Table S2; Table S3).

We categorized phenology observations into three plant parts (fruit; flowers; leaves – as per Bryer *et al.* 2013). We used binary presence-absence measures of each plant part 1) to remove observer error relating to absolute counts, and 2) because fruit crop size and number of flowers and leaves are typically proportional to basal area (e.g. Rimbach *et al.* 2014). For both our site-wide and spatially explicit indices of basal area density, we multiplied basal area densities for each species in sample plots and grid cells, respectively, at each site by monthly proportions (0-1; at Issa, the mean monthly proportion) of stems with each plant part present. For our spatially explicit index, we summed these weighted measurements for each plant part across all species and resampled the resulting distributions to the grids of range use for each group (Ngogo: 50m cells, Issa: 75m cells) using maximum plant part abundance for each species (see supplementary material S1).

Statistical analyses

We conducted all statistical analyses in R v3.5.1 (R Core Team 2020; see supplementary Table S4 for a summary of model formulas). To investigate the relationship between HTD and DTD and temperature and rainfall, we used the package *nlme* (Pinheiro *et al.* 2019) to build generalized linear mixed models (GLMM) with Gaussian error distribution. To analyze HTD, we fitted HTD as the response; mean hourly temperature and hourly rainfall (binary) as predictors; and month as a random intercept effect. To analyze DTD, we fitted DTD as the response; interactions between site and maximum daily temperature and daily rainfall (binary), alongside individual main effects, as predictors; and group ID as a random intercept effect to control for variation in group size and composition. We visually inspected the correlogram and plotted residuals of HTD over time to confirm that temporal autocorrelation was not present.

To investigate the relationship between DTD and food abundance, we built a linear model with DTD as the response and interactions, including individual main effects, between group ID and monthly mean fruit and flower abundance in primary forest at Ngogo and riparian forest and woodland combined at Issa, as predictors. We did not include leaf abundance as a predictor because it was collinear with group ID (see below).

To investigate the relationship between home range use and food abundance, we used the package *spaMM* (Rousset *et al.* 2018) to build a GLMM with negative binomial distribution to account for overdispersion. We fitted count of GPS points per grid cell as the response; total number of GPS points per month as a log-transformed offset; and interactions, including individual main effects, between group ID and fruit, flower, and leaf abundance, as predictors. To control for spatial autocorrelation in range use, we fitted a binary adjacency matrix for grid cells used each month as a random intercept effect.

For all models, we manually checked plots of residuals and fitted values, and QQ-plots to check that assumptions of normally distributed residuals and homogeneity of variance had been met. We tested predictors for collinearity by calculating variation inflation factors (VIF) using the package *car* (Fox *et al.* 2018) in an equivalent linear model including only the fixed effects from each model. Multicollinearity was not present in any model (maximum VIF: HTD = 1.05; DTD vs. weather = 1.23; DTD vs. food abundance = 7.35, after removing leaf abundance; range use = 2.06). We centered all predictors to a mean of zero and scaled continuous predictors to a standard deviation of one to improve interpretation of main effects included in interactions, as per Schielzeth (2010). For the mixed models, we used likelihood ratio tests to test significant differences between full and null models without fixed effects, and we interpreted *t* values as *z*-scores to calculate *p* values for individual effects.

Results

At Ngogo, we followed R1 – R4 for 1 – 71 days for each month across the follow period, including days on which multiple groups were followed; except R1 and R3 which we did not follow in December (Table 1). We followed R5 and R6 for four consecutive months each (R6: 9 – 24 days per month; R5: 14 – 27 days per month). At Issa, we followed K0 for 1 – 11 days per month, except for 3 months in which we could not locate the group.

Home range sizes

Home range estimates approached an asymptote after *ca.* 60 days for Ngogo groups and *ca.* 110 days for K0 at Issa (Figure 1). The Ngogo groups exhibited total home ranges of 0.44 – 0.65km^2 (MCP), and 0.46 – 0.65km^2 (50m GCA), respectively (Figure 2; Table 1). Compared to home ranges reported from forest environments, all six Ngogo groups exhibited home ranges larger than the average, but only R5 exhibited a home range larger than the maximum ($\bar{x}$: 0.27km^2; maximum: 0.63km^2 also at Ngogo; Table 2).

Compared to the Ngogo groups, K0 exhibited a substantially larger total home range of 3.93km^2 (75m GCA) and 16.0km^2 (MCP; Figure 3). K0 exhibited a GCA measure 14.1 times greater than the average and 6.2 times greater than the maximum home range sizes reported from any other previous study (Table 2).

The extent of home range used per month for R6 and R5 ranged from 0.38km^2 to 0.51km^2 for R6 and 0.34km^2 to 0.43km^2 for R5 (59 – 79% of R6 home range; 60 – 76% of R5 home range; Figure 4). For K0, monthly home range use ranged from 0.06 – 1.02km^2 (1.5 – 26% of K0 home range; Figure 4). K0 used a significantly greater monthly extent of its home range during the wet seasons compared to the dry seasons (Mann-Whitney: *U* = 93.5, *p* = 0.036).

Table 1 Follow periods, home range sizes calculated using one hundred percent minimum convex polygon (MCP) and grid cell analysis (GCA) methods, and daily travel distances (DTD) for each group.

Study site	**Group**	**Follow period [follow days; all-day follows]**	**Home range size (km^2)**		**Daily travel distance**	
			MCP	**GCA [cell size]**	**Mean [range] (km)**	**Location interval**
Ngogo	R1	Jan 2008 – Sep 2018 [*n* = 225; 123]	0.58	0.52 [50m]	0.97 [0.35 – 2.04]	30 minutes
	R2	Jan 2008 – Aug 2016 [*n* = 352; 250]	0.44	0.56 [50m]	1.01 [0.27 – 2.01]	
	R3	Jan 2008 – Aug 2016 [*n* = 255; 159]	0.54	0.52 [50m]	0.98 [0.34 – 1.71]	
	R4	Jun 2008 – Aug 2016 [*n* = 158; 99]	0.59	0.46 [50m]	1.04 [0.51 – 1.99]	
	R5	Jul – Oct 2017 [*n* = 89; 64]	0.65	0.65 [50m]	1.70 [0.80 - 2.55]	5 minutes; minimum 5m
	R6	Mar – Jun 2017 [*n* = 71; 50]	0.58	0.56 [50m]	1.76 [0.94 - 2.54]	
Issa Valley	K0	Jan 2013 – Mar 2016 [*n* = 237; 175]	16	3.93 [75m]	1.90 [0.36 – 4.13] (wet season); 1.55 [0.68 – 3.42] (dry season)	

Table 2 Comparison of red-tailed monkey ranging patterns, population densities and group sizes from previous studies with the results of this study (CI = confidence interval; SD = standard deviation; SE = standard error; adapted in part from (CI = confidence interval; SD = standard deviation; SE = standard error; adapted in part from Tapper *et al.* 2019).

Country	**Study site**	**Primary vegetation**	**Number of study groups**	**Follow duration (months/group)**	**Mean DTD (km) [range]**	**Home range size**			**Population density**			**Reference**
						Mean area (km^2) [range]	**Method**	**% of Issa Valley GCA**	**Individuals /km^2**	**Groups/ km^2**	**Group size [range]**	
Central African Republic	Bangui	Lowland degraded deciduous rain forest	1	23		0.15	GCA (50m)	3.8	117		17-23	1
Democratic Republic of Congo	Ituri Forest	Medium-altitude primary and secondary evergreen rain forest	Results from transects	6					18.9 [±4.4SE]	5.4 [±0.9SE]	3-11	2
Kenya	Kakamega (Buyangu)	Lowland primary and degraded semi-deciduous rain forest and scrub	2	12	1.80 [1.10-2.80]	0.23 [0.19-0.26]	GCA (50m)	5.9	176	5.9	31 [30-32]	3
	Kakamega (Isecheno)	Lowland primary and regenerating semi-deciduous rain forest	4	11	1.50 [0.90-2.40]	0.36 [±0.13SD]	GCA (50m)	9.2	72	5.2	23-26 [±9SD]	4; 5
Tanzania	Issa Valley	Medium-altitude primary woodland and evergreen riparian forest	1	39	1.75 [0.36-4.13]	3.93	GCA (75m)	-	32 [25.5-40.9 95% CI]	4.5 [3.6-5.7 95% CI]	35-55	This study; 6
						16	MCP	-				
Uganda	Budongo (N15)	Medium-altitude primary semi-deciduous rain forest	1	4	0.96	0.2	GCA (25m)	5.1	4.2	19.2	14 [12-18; *n* = 3]	7
	Budongo (N15; KP11; KP13)	Medium-altitude primary semi-deciduous rain forest	2	16	2.50 [2.43-2.56]	0.45 [0.40-0.49]	MCP	11.5	8.3		$\bar{x}$ = 13	8; 9
	Budongo (N3)	Medium-altitude logged semi-deciduous rain forest	1	4	1.3	0.2	GCA (25m)	5.1	13.3	60	16 [13-18; *n* = 3]	7
	Budongo (N3; N11; B1; B4; W21; K4)	Medium-altitude logged semi-deciduous rain forest	3	16	2.25 [2.16-2.42]	0.21 [0.19-0.22]	MCP	5.3	46.4		$\bar{x}$ = 16 [14-18]	8; 9
	Kibale (K-15 & Mikana)	Medium-altitude logged evergreen rain forest	3	13	0.64	0.37 [±0.12]	Unknown	9.4	38.1	1	15 [±1]	10; 11
	Kibale (K-30)	Medium-altitude primary evergreen rain forest	3	13	0.62	0.26 [±0.04]	Unknown	6.6	135.1	4.8	28 [±1]	10; 11
	Kibale (Kanyawara)	Medium-altitude primary and secondary evergreen rain forest	>1		1.45	0.24 [0.2-0.28]	GCA (50m)	6.1		$\bar{x}$ = 4.6	$\bar{x}$ = 35 [30-35]	12; 13; 14
			1-7	13-23	1.45 [1.09-2.03]	0.2-0.28	GCA (50m)	5.1-7.1	140-175	4.5	$\bar{x}$ = 33 [28-35]	15; 16; 17; 18
			3	4-16		0.21 [0.16-0.25]	MCP	5.3	70-158	2.8-6.3	23 [19-29]	19; 20; 21
	Kibale (Ngogo)	Medium-altitude primary and secondary evergreen rain forest	4 †	37-63	1.57 [1.12-2.3]	0.23 [0.28-0.57]	GCA (50m)	5.9	131.5		26 [14-35]	16; 17

			3		1.69 [±0.38]					2	$\bar{x}$ = 37 [35-40]	T. Struhsaker (unpublished data – see 4; 18)
			2 ‡	29	1.00 [0.77-1.41]	0.55 [0.47-0.63]	Unknown	14			$\bar{x}$ = 36 [25-50]	22
			6	4-37	1.72 [0.80-2.55; R5 and R6]	0.56 [0.44-0.65]	MCP	14.2			$\bar{x}$ = 17 [10-35]	This study; 23

† After one group (size: 35 – 50 individuals) fissioned during the study.

‡ After one group (size: 50 individuals) fissioned during the study.

[1] Galat-Luong (1975); [2] Thomas (1991); [3] Gathua (2000); [4] Cords (1987); [5] Cords (1990); [6] EM unpublished data; [7] Sheppard (2000); [8] Plumptre and Reynolds (1994); [9] Plumptre *et al.* (1997); [10] Rode *et al.* (2006); [11] Chapman and Lambert (2000); [12] Struhsaker (1975); [13] Struhsaker (1978); [14] Struhsaker and Leland (1979); [15] Struhsaker (1980); [16] Struhsaker (1988); [17] Struhsaker and Leland (1988); [18] Butynski (1990); [19] Struhsaker (1997); [20] Treves (1998); [21] Wrangham *et al.* (2007); [22] Windfelder and Lwanga (2002); [23] Brown (2013)

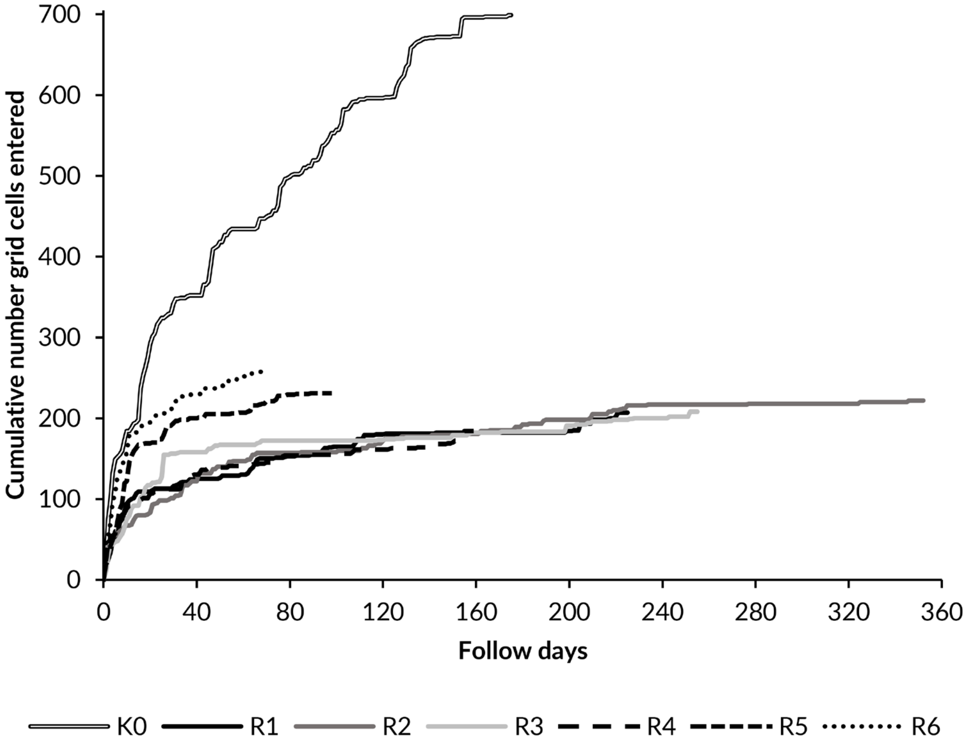

Figure 1 Cumulative use of home range by groups at Ngogo and Issa, calculated as number of unique 50 x 50m grid cells and 75 x 75m grid cells, respectively, entered per follow day.

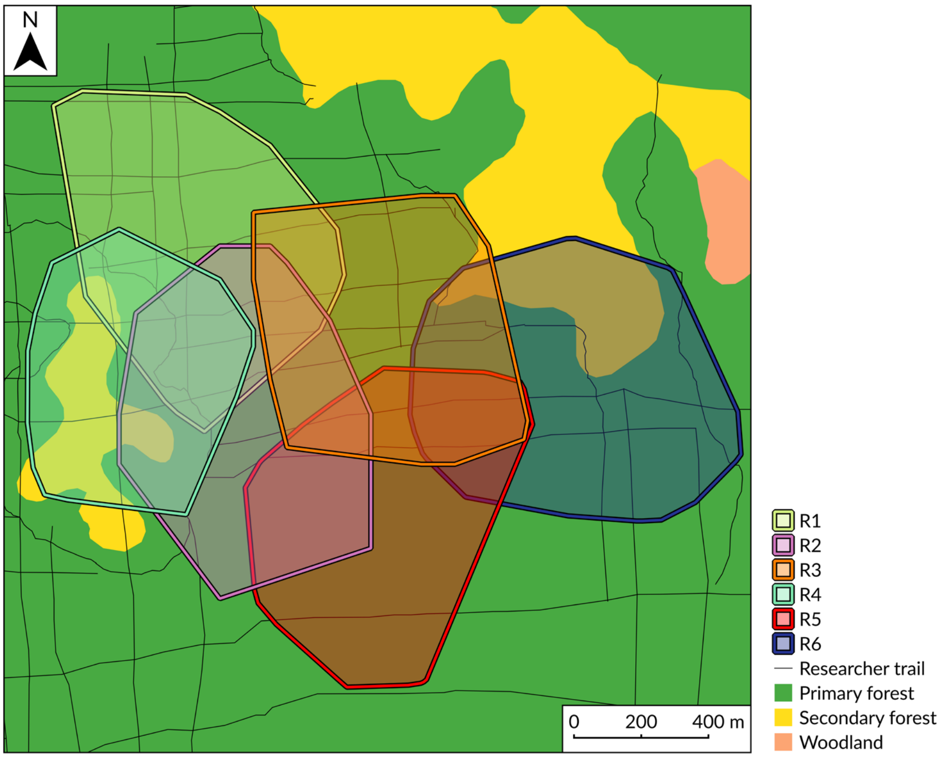

Figure 2 Home range sizes for Ngogo groups for the entire study period, calculated using one hundred percent minimum convex polygons (MCP). Colored shading indicates vegetation cover. Black lines indicate selected researcher trails, included for reference.

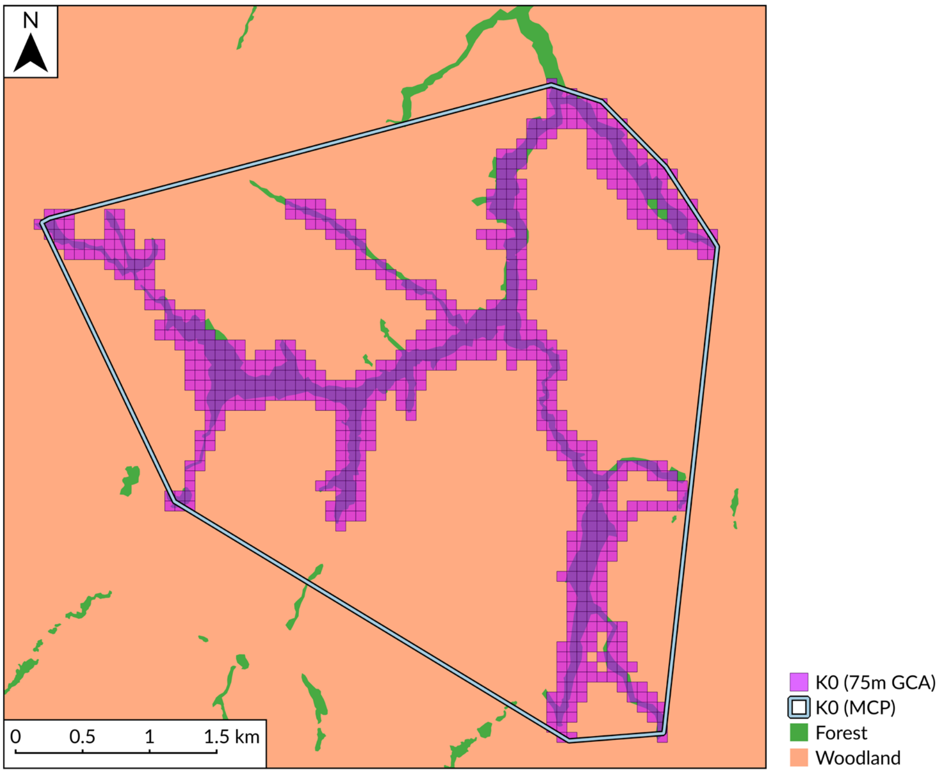

Figure 3 K0 home range size at Issa for the entire study period, calculated using one hundred percent minimum convex polygon (MCP) and 75m grid cell analysis (GCA) methods. Colored shading indicates vegetation cover.

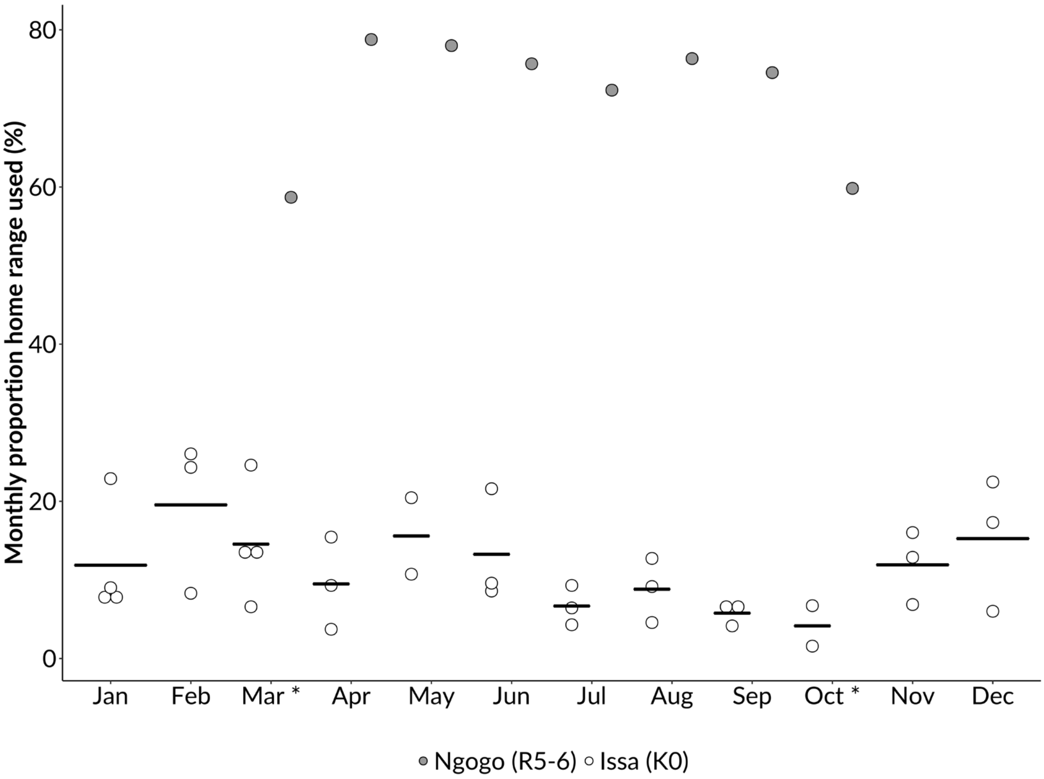

Figure 4 Monthly proportion of home range used by groups at Ngogo and Issa. Proportions calculated using 50m GCA method for R6 and R5 at Ngogo and 75m GCA method for K0 at Issa. Black bars indicate mean values. Asterisks indicate half months for follows for Ngogo groups.

Daily travel distances

At Ngogo, DTD did not differ significantly between groups for R1 – R4 (Kruskal-Wallis: H = 4.851, p = 0.183) or R5 and R6 (*t*-test: -0.916, p = 0.362). DTD differed significantly between months for R1 – R4 pooled (Kruskal-Wallis: H = 82.616, p < 0.001; Figure 5) but not for R5 and R6 pooled (one-way ANOVA: $F_{7, 106}$ = 1.178, p = 0.322). K0 exhibited a significantly wider range of DTD in both wet and dry seasons than R5 and R6 (Kruskal-Wallis: H = 16.006, p < 0.001; Figure 5; Table 1) and R1 – R4 (Kruskal-Wallis: H = 214.620, p < 0.001), although minimum DTD for R1 – R4 was shorter than that for K0 in both seasons.

Mean DTD for R5 and R6 was longer than those reported in other studies for this species in forests, but maximum DTD was not (R5 and R6 $\bar{x}$ 1.72km cf. $\bar{x}$ 1.28km; R5 and R6 maximum 2.55km cf. maximum 2.8km at Buyangu, Kenya; Table 1; Table 2). In contrast, mean wet and dry season DTD and maximum DTD for K0 were all substantially longer (1.5, 1.2, and 1.5 times longer, respectively) than the mean and maximum DTD reported from previous studies (Table 1; Table 2).

Hourly and daily travel distances in response to weather

During the study period at Ngogo, annual rainfall averaged 1409mm (mean monthly rainfall range: 33 – 207mm). At Issa, annual rainfall averaged 1012mm (mean monthly rainfall range: 0 – 204mm). Ngogo temperatures ranged from 14 – 34°C, with a mean daily maximum temperature of 24.4°C across all months. Issa temperatures ranged from 9.9 – 33.2°C, with a mean daily maximum temperature of 24.7°C in wet seasons and 28.0°C in dry seasons.

On average, HTD for K0 peaked during from 7 – 10am and 6 – 7pm, corresponding with highest daily temperatures from 1 – 4pm (Figure 6). Temperature had a significant negative effect on HTD but rainfall did not (GLMM: n = 1228 hours; temperature – estimate = -25.075, p < 0.001; rainfall – estimate = -32.004, p = 0.062; supplementary Table S5). Similarly, on average across both sites temperature had a significant negative effect on DTD but rainfall did not (GLMM: n = 425 days at Ngogo; n = 158 days at Issa; temperature – estimate = -69.222, p < 0.001; rainfall – estimate = -11.444, p = 0.770; supplementary Table S6). Neither the effect of temperature nor rainfall on DTD differed significantly between sites (GLMM: temperature – χ^2 = 3.353, df = 1, p = 0.143; rainfall – χ^2 = 0.644, df = 1, p = 0.422).

Daily travel distances and home range use in response to food abundance

Fruit, flowers, and leaves were substantially more abundant in primary forest at Ngogo than in forest or woodland at Issa, except for woodland flower abundance in the dry season (Figure 7). Mean fruit and flower, but not leaf, abundance differed significantly between months in all three vegetation classes (supplementary Table S7). At Issa, fruit and flower abundance exhibited substantial monthly variation, with peak abundance in the mid and late dry season.

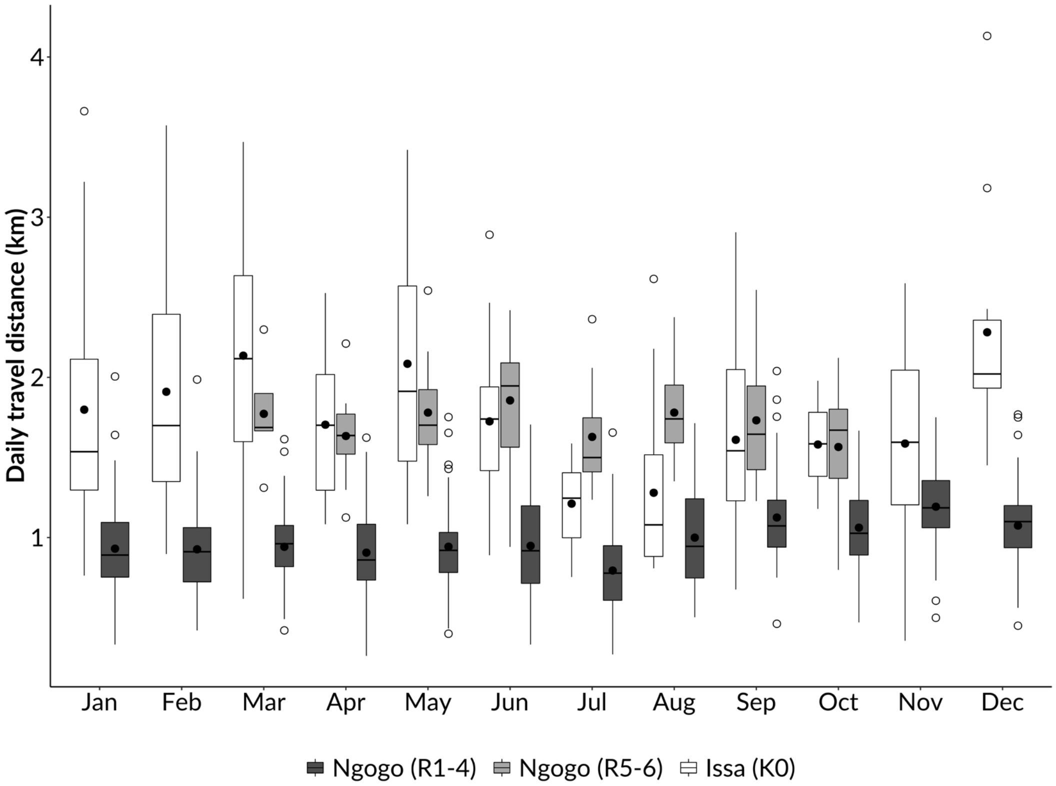

Figure 5 Group mean daily travel distance at Ngogo and Issa by month. Values are grouped by site and GPS interval (R1 – R4: 30-minute intervals; R5, R6, and K0: 5-minute intervals). Black dots and circles indicate mean and outlying values, respectively.

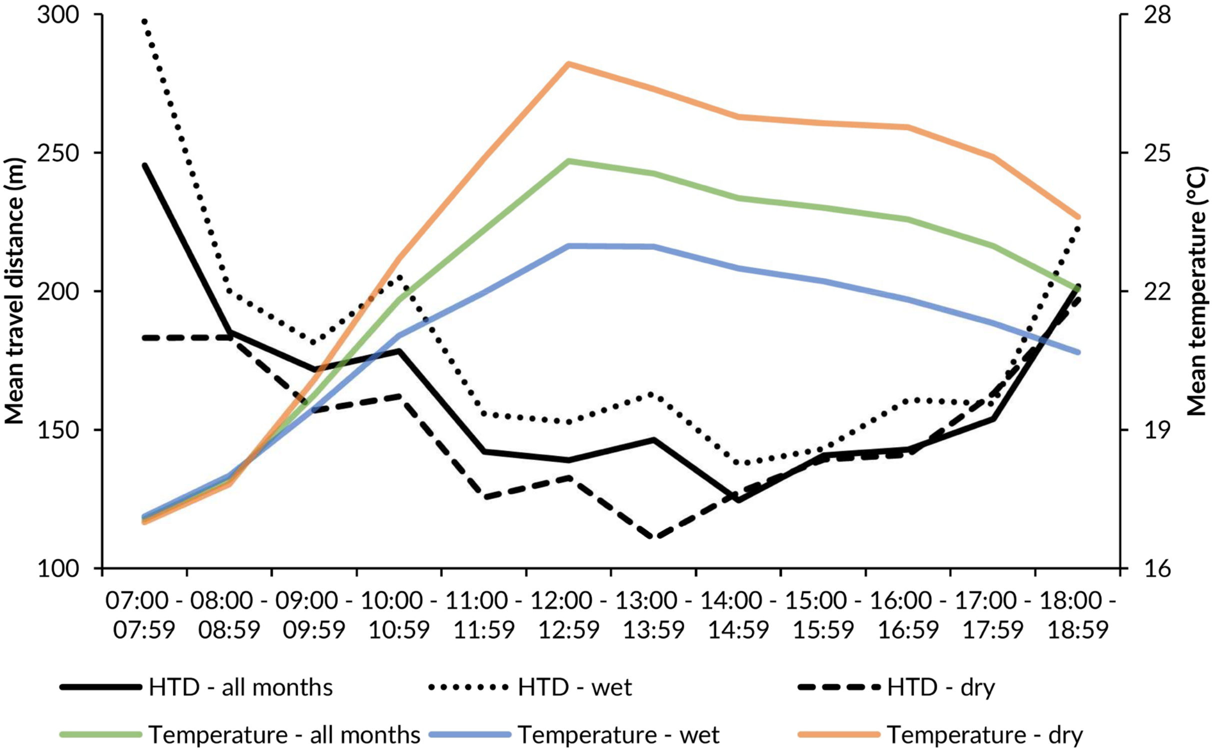

Figure 6 Mean hourly travel distance exhibited by K0 in wet and dry seasons and in all months combined. Colored lines indicate mean hourly temperature in wet and dry seasons and in all months combined.

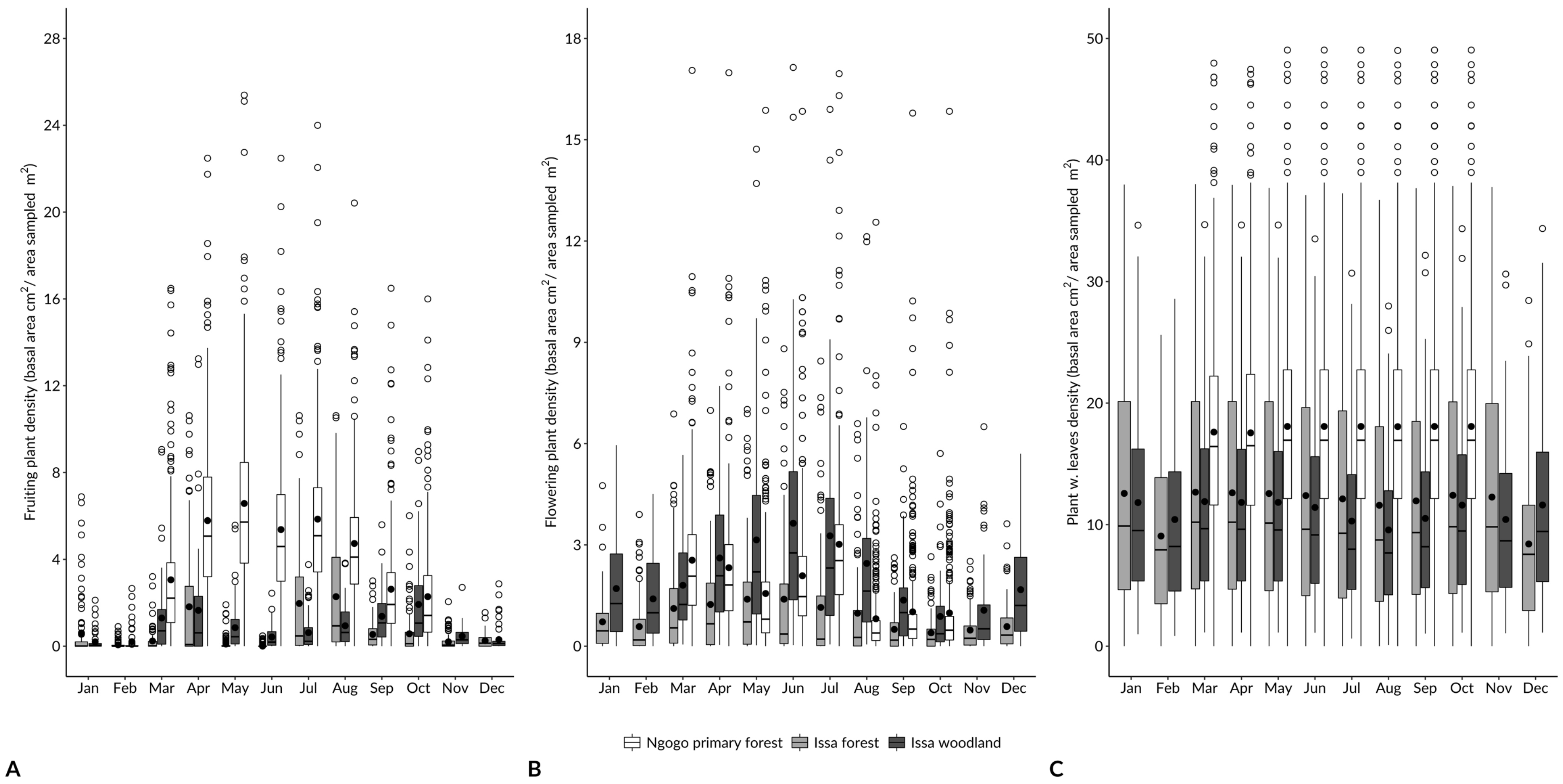

Figure 7 Site-wide indices of food abundance measured in sample plots at Ngogo and Issa. Shown are fruiting plant density (A), flowering plant density (B), and plant with leaves density (C) by vegetation class and month. Black dots and circles indicate mean and outlying values, respectively.

On average across all groups, fruit abundance had a significant negative effect on DTD (linear model: n = 114 days at Ngogo; n = 158 days at Issa; fruit – estimate = -453.550, $p < 0.001$; supplementary Table S8). More specifically, fruit had a significantly stronger negative effect on DTD for K0 compared to R5, but not R6 (interactions between fruit and group ID: R5 – estimate = 858.250, $p < 0.001$; R6 – estimate = 549.160, $p = 0.090$). Flower abundance had no effect on DTD across all groups on average (estimate = -41.020, $p = 0.481$).

GPS intervals were consistent enough for analysis of home range use in 46 all-days follows of R6 (range = 5 – 19 per month), 57 all-day follows of R5 (range = 10 – 20 per month), and 92 all-days follows of K0 (range = 4 – 15 per month). We did not find the effects of fruit, flower, or leaf abundance on range use to differ significantly between either group (GLMM: n = 1017 grid cells at Nggo; n = 964 grid cells at Issa; interactions between food and group ID: fruit – χ^2 = 4.122, df = 2, $p = 0.127$; flowers – χ^2 = 0.139, df = 2, $p = 0.933$; leaves – χ^2 = 0.187, df = 2, $p = 0.911$), nor did we find these predictors to have a significant effect on range use on average across all groups (fruit – estimate = 0.053, p = 0.465; flowers – estimate = -0.004, $p = 0.916$; leaves – estimate = -0.026, $p = 0.473$).

Discussion

Home range sizes and DTD reflect food abundance

Our results indicate substantial intra-specific variation in red-tailed monkey ranging patterns between primarily forested and savanna mosaic habitats in response to both food abundance and weather. As predicted, Issa monkeys exhibited a significantly larger home range than either Ngogo group or any previously studied group. The lower abundance of at least two major dietary components in riparian forest at Issa compared to Ngogo (fruit and leaves – Figure 7) should be a primary explanation for this difference. While Issa monkeys use both riparian forest and woodland, they are dependent on forest foods for longer periods of the year due to the relative paucity of woodland foods outside of dry months (e.g. time spent in forest cf. woodland: adult males 46% cf. 35%; adult females, subadults, juveniles 77% cf. 9%; n = 25 follow days November – December 2017 – EM unpublished data). As such, the irregular spatial geometry of forest at Issa alone should lead to a larger estimate of home range size. This effect is clearly illustrated by the bias in the MCP estimate for K0, which is far larger than the GCA estimate due to including areas of woodland that the group did not use (Figure 3). Nonetheless, even when measured at a finer spatial scale (75m grid cells), Issa monkeys still exhibited a far larger home range than forest groups. Similarly, with only a single group at Issa against which to compare, the larger group size of K0 compared to the Ngogo study groups could be expected to explain a larger home range. However, in a previous study of K0 in 2012 when the group comprised *ca.* 35 individuals, Tapper *et al.* (2019) reported a home range of 0.78 – 1.93km^2 after only three months of follows – already disproportionately larger than estimates for forest groups of similar sizes (Table 1).

In addition to a larger home range, Issa monkeys also exhibited a longer maximum DTD compared to the Ngogo groups. Reduced, more heterogeneous forest cover at Issa may result in smaller patches of fruit and flowers (Chapman and Chapman 2000b) that are also less food-rich than at Ngogo. These patches are likely to be more rapidly depleted by monkeys at Issa – particularly given the larger group size of K0 – resulting in greater daily search effort and a larger home range to meet subsistence needs (Wrangham *et al.* 1993). Similar to other sites, insects likely comprise an important component of red-tailed monkey diet at Issa (Bryer *et al.* 2015; AP unpublished data). Insects are typically more uniformly distributed but harder to locate than fruit, flowers, and leaves (Chapman and Chapman 2000b). Increasing DTD may be the most efficient strategy for obtaining insects in narrow forest strips at Issa if alternatives such as expanding group spread are not possible (Isbell 2012).

Increased food abundance should result in shorter DTD as inter-group feeding competition and rates of food depletion are reduced (Janson and Goldsmith 1995; Chapman and Chapman 2000b). Unlike previous studies (e.g. Kaplin 2001; Buzzard 2006), we found a negative effect of fruit abundance on DTD across both sites that corroborates this hypothesis. Specifically, fruit was significantly more abundant in dry seasons, which also likely explains the smaller proportions of home range used in these months. Moreover, this effect was only significantly stronger for K0 at Issa compared to the smaller Ngogo group (R5). Similar effect sizes for the two larger study groups across both sites supports the hypothesis that increased intra-group feeding competition with larger group sizes influences primate DTD to a greater extent than variation in food abundance alone.

Thermal constraints on travel distances

We also found evidence that temperature negatively influences HTD and DTD. Issa monkeys exhibited smallest monthly DTD ranges in dry season months when maximum temperatures were highest, and lowest travel speeds during highest hourly temperatures at 13 – 16h. These patterns corroborate the hypothesis that temperature should constrain the utilization of open vegetation (e.g. woodland) for forest primates (Pruetz 2018; Wessling *et al.* 2018). As such, behavioral responses (e.g. seeking shade; reducing time spent travelling) should vary between forests and savanna mosaics (Hill 2005). For example, savanna chimpanzees at Fongoli, Senegal, shelter in caves when temperatures are hottest (Pruetz 2007) and preferentially utilize forest patches that provide the only sources of shade and water (Pruetz and Bertolani 2009). Although fruit may provide most water, red-tailed monkeys drink from streams and arboreal water holes at both Ngogo and Issa. Given the lack of rain and drying up of streams for substantial periods (*ca.* three months) in the late dry season at Issa, water requirements could also limit monkey ranging. In the absence of higher resolution weather data from Ngogo, behavioral responses to heat stress at small temporal scales (eg. hourly or minute by minute variation) remain to be compared between forest and savanna mosaic habitats.

In contrast to our third prediction, neither HTD nor DTD related to rainfall. At Issa, microhabitat variation in rainfall means that light rainfall measured in one part of the study area may not reflect heavy rainfall elsewhere that results in localized flooding (AP personal observation). Flooding rivers can restrict access to forest patches that are only reachable to monkeys by travelling terrestrially through woodland (EM unpublished data). Conversely, in patches with more continuous canopy cover red-tailed monkey groups travel in all but the heaviest of rainfall, when visibility and vocal communication between individuals are likely limited (EM personal observation). Although primates should reduce travel in rain to minimize energy loss (Stelzner 1988), in savanna mosaics the difficulty of meeting daily nutritional requirements may mean that in food-rich areas monkeys prioritize travelling and foraging during rainfall only until maintaining group cohesion becomes difficult.

Determinants of home range use

While home range sizes and DTD reflected differences in food availability between sites, range use did not relate to food abundance at Ngogo or Issa despite significant monthly variation in fruit and flower availability. At Ngogo, the relatively high availability of food may mean that resource depletion does not significantly limit time spent at a patch; similar to the consistent patterns of DTD and proportions of home range used. At Issa, higher resolution data on diet composition may be needed to investigate the effect of other foods, such as insects. Insects comprise an important component of red-tailed monkey diet at Ngogo (Struhsaker 2017), particularly as fallback foods (Rothman *et al.* 2014). If insects are distributed more heterogeneously than fruit, flowers, and leaves then insect abundance should influence range use to a greater extent than these plant parts. This relationship should also vary between forests and more open environments given inter-habitat differences in insect availability. At Issa for example, insect abundance likely varies between vegetation types given that monkeys are known to exploit woodland locusts driven into riparian forest by dry season fires (FS personal observation).

We included all identifiable plant species in our measures of food abundance at Issa because the species that comprise monkey diet are not yet identified. This approach could have led to overestimations of food availability, masking an effect on range use. At Ngogo, food abundance indexed with similar phenology methods does not relate to energy balance (urinary c-peptide levels) in red-tailed monkeys either (MB unpublished data), suggesting that controlling for species-specific diet composition is also important even in food-rich forests. For example, while we averaged variation in plant part presence for each species per month, future studies should account for intra-specific phenological variation across even relatively small spatial scales at Ngogo (Brown 2011). Competition from six other larger-bodied primates may also have negated the influence of plant parts that we identified as present but were consumed by other species or ignored due to diet switching (Brown 2013).

Range use may also be influenced by factors other than food abundance. In our models we considered all patches (grid cells) equally regardless of vegetation type or position in the home range (periphery vs. core). At Issa however, forest configuration and a large home range mean that monkeys may not travel to distant patches if reducing DTD and increasing group spread are more efficient alternatives (Ganas and Robbins 2005). Potential predators are frequently encountered by red-tailed monkeys at both sites (e.g. chimpanzees; crowned-hawk eagles – Mitani *et al.* 2001; Watts and Mitani 2002; McLester *et al.* 2018). Anti-predator responses include hiding or changing group travel direction (Cords 1987), which affect time spent in an area. Moreover, predation risk should differ between savanna mosaic and forest habitats (Dunbar 1988). For example, Issa monkeys use isolated forest patches that are only accessible by travelling terrestrially through woodland. Groups pause travel at forest peripheries for substantial periods of time while scanning the immediate area or waiting for predators to leave before moving between patches, typically running without stopping (EM personal observation). Similarly, inter-group encounters – frequently over access to blue monkeys and grey-cheeked mangabeys (Brown 2011) – occur along home range peripheries, which can result in abrupt changes of direction depending on the outcome or preemptive avoidance (Brown 2013).

Hominin adaptations to savanna mosaic environments

Our results provide insight into environmental pressures that hominins (e.g. *Ardipithecus, Paranthropus,* and early *Homo* spp.) would have faced in similar paleoenvironments (Leonard and Robertson 1997; Antón *et al.* 2014). Furthermore, while red-tailed monkeys are phylogenetically distant to hominins, our results indicate similarities between strategies exhibited by monkeys and those predicted for later hominins (e.g. *Homo*) in coping with these pressures. For example, thermoregulation has been implicated as an important driver of hominin evolution (e.g. Wheeler 1992, 1994; Passey *et al.* 2010). Exploiting open vegetation (e.g. woodland) foods should have resulted in increased thermal stress due to reduced shade and greater travel distances to obtain scarcely-distributed resources (Ruxton and Wilkinson 2011). While monkeys primarily use riparian forest at Issa, we found temperature still negatively affected travel speed. This relationship is similar to that predicted for hominins, which should have reduced activity and sought shade during peak daily temperatures (Wheeler 1994).

Food distribution should also have been a significant determinant in the behavior of early *Homo* species, given the substantial increase in energy expenditure in *H. erectus* compared to the australopithecines (Leonard and Robertson 1997). We ascribed the larger home range size and range of DTD for Issa monkeys to the less abundant and more seasonally-variable distribution of food in a savanna mosaic habitat. These results reflect hypothesized increases in hominin home range sizes and DTD that would have been necessary to support foraging effort for scarcer resources in savanna mosaic environments (Rose and Marshall 1996). Such differences in spatial requirements for primates in forests and savanna mosaics also support predicted decreases in hominin population density with the expansion of open environments (Grove *et al.* 2012), as illustrated by extant variation (Table 1).

In addition to increasing home range, primates may also expand dietary breadth to cope with the wide distribution of resources that characterize drier, mosaic habitats. In a comparative study of hominin dietary niches, Nelson and Hamilton (2018) showed that early hominins (e.g. *Ardipithecus*) most closely resemble modern chimpanzee niche-space in the types and amounts of resources they consume, whereas later hominin species may have exploited aquatic sources (see also Braun *et al.* 2010) to meet subsistence requirements, expanding their dietary niche and gradually becoming more generalist over time (Roberts and Stewart 2018). Subsequent analyses that incorporate red-tailed monkey food source distribution and diversity should reveal whether dietary composition, in addition to home range sizes, also differs between forest and savanna mosaic populations. Moreover, dental microwear and isotopic comparison of the available plants in these forests should provide extant analogues for comparisons of especially contemporaneous fossil hominins (*sensu* Lee-Thorp *et al.* 2003). Comparing these data from more groups across a finer vegetation gradient should further clarify the extent to which ecological conditions have influenced both extant and extinct primate behavioral adaptations.

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Supplementary material

S1 Modelling food abundance for each study site

Selection of spatial interpolation method

We used an inverse distance weighting (IDW) interpolation to spatially interpolate measures of basal area density for each plant species between sampled plots. We found a relative paucity of previous studies that used spatial interpolation techniques to predict biotic factors (e.g. plant species richness and diversity – Grytnes and Vetaas 2002; Hernandez-Stefanoni and Ponce-Hernandez 2006), compared to abiotic factors (e.g. rainfall – Sun *et al.* 2003; soil pH and salinity – Robinson and Metternicht 2006). Data on potential predictor variables of food abundance (e.g. NDVI values; soil composition) were not available at either Ngogo or Issa. This made regression techniques such as multiple regression Kriging (e.g. as per Essens and Hernández-Stefanoni 2013) unfeasible. We sampled and aimed to index a relatively stationary factor (basal area density of mature plant stems), compared to factors in which sampling does not provide such an absolute measure of that factor at that exact location. For example, a measure of slow-growing plant stems should be expected to remain representative of that location for a longer period of time than a measure of insect abundance. As such, we selected a conservative interpolation method that would reflect actual sampled measures at sampling plots as closely as possible. We did not choose a Kriging method for this reason. Spline interpolations can be fitted to pass exactly through the interpolated values; however, we did not find the smooth gradients produced by spline interpolations to accurately reflect the frequently sharp changes in plant species diversity and abundance that we observed between close-proximity plots. IDW has been shown to produce satisfactory results (e.g. in comparison to Kriging) when the metric to be interpolated is stratified by an appropriate category (e.g. plant diversity stratified by vegetation class – Hernandez-Stefanoni and Ponce-Hernandez 2006).

Selection of IDW parameters and mask

We investigated optimal interpolation parameters for each site by cross-validating interpolations of basal area density in GRASS GIS 7.4. For these preliminary investigations, we used only measures of *Diospyros abyssinica* at Ngogo and *Monopetalanthus richardsiae* at Issa. We used these species because they were present in the highest numbers of plots at each site, and we aimed to improve the reliability of our cross-validations by investigating an interpolation with the fewest number of plots with no or unknown values. We compared parameter fits using the root mean squared error (RSME) of predicted values, as per Hernandez-Stefanoni and Ponce-Hernandez (2006).

We first used a ten-fold jacknife cross-validation to establish optimal values for nearest neighbour and power parameters in each interpolation. For each site, we tested four values for the nearest neighbour parameter (3, 5, 10, 20) and three values for the power parameter (1,2,3). We chose the range of values for the nearest neighbour parameter to test based on how evenly distributed sample plots were across both sites. We chose the range of power parameters to test as per Hernandez-Stefanoni and Ponce-Hernandez (2006). We ran each combination of parameters three times and repartitioned the data at random before each run. RSME did not differ significantly by number of nearest neighbours at either Ngogo (Kruskal-Wallis: $H = 5.456$, $p = 0.141$) or Issa (Kruskal-Wallis: $H = 3.795$, $p = 0.285$). We therefore selected the value with the lowest mean RSME across all runs at each site for use as the nearest neighbour parameter (at Ngogo: 5 – Fig. 9.1; at Issa: 3 – Fig. 9.2). RSME differed significantly by power at Ngogo (Kruskal-Wallis: $H = 4.727$, $p = 0.094$) but not at Issa (Kruskal-Wallis: $H = 0.172$, $p = 0.918$). We used 3 as the power parameter at Ngogo. We used 1 as the power parameter at Issa, as the value with the lowest mean RSME across all runs (Fig. 9.2).

Second, we used an *n*-fold jacknife cross-validation to establish a mask for interpolations of the above parameters at each site. Sampling plots were not evenly distributed across either study site, and may not have reflected small-scale variation in plant density. As such, we masked these interpolations because we aimed to improve the reliability of predicted cells in our interpolation by excluding cells for which values were predicted using plots that were located disproportionately far away. Interpolated value error was not significantly correlated with distance to nearest sampling plot at Ngogo (Spearman rank correlation: $r_s = -0.055$, $p = 0.363$; Fig. 9.3). Nonetheless, given the low proportion of locations tested in this analysis that were substantially isolated (e.g. >100m; Fig. 9.3) from the nearest sample plot, we used a maximum distance of 150m from each interpolated cell to the nearest sample plot to mask interpolations for Ngogo to reduce error. Interpolated value error was significantly correlated with distance to nearest sampling plot at Issa (Spearman rank correlation: $r_s = 0.276$, $p = 0.006$; Fig. 9.4). We used a maximum distance of 200m from each interpolated cell to the nearest sample plot to mask interpolations for Issa.

Interpolation of sample plots

Before interpolating basal area density, we log-transformed this measure to normalize the distribution. At Ngogo, we only sampled plots in primary forest; therefore, we interpolated basal area density only within the extent of primary forest cover. At Issa, we found a high degree of variation in plant species composition between the two vegetation classes (forest and woodland; post hoc Bray-Curtis dissimilarity index: $B = 0.859$). Hernandez-Stefanoni and Ponce-Hernandez (2006) demonstrated that stratifying interpolations by vegetation classes improves interpolation accuracy; therefore, we stratified our index of food abundance for Issa by vegetation class. We classified each plant species at Issa as forest- or woodland-only (for species with 100% of stems present in only one vegetation class), or home range-wide (for species with stems present in both vegetation classes). For forest-only species and the distribution of home range-wide species in forest, we interpolated basal area density only within the extent of forest cover. For woodland-only species and the distribution of home range-wide species in woodland, we found sample plots in woodland to be too unevenly distributed to produce reliable results from a spatial interpolation. We therefore substituted mean species basal area density for these species in woodland in each 20m cell (see below). We established vegetation class extents at each site by 1) mapping out forest and woodland cover at Issa using satellite imagery

(Google & DigitalGlobe – accessed January 2016) in QGIS 2.18.6, and 2) using a vegetation class map of Ngogo produced by the Uganda Biomass Survey.

Sample plots at Ngogo were 50 x 50m in size. Given the relatively small home ranges of the study groups and subsequent fine scale at which interpolations were made at Ngogo, we interpolated using a cell (raster pixel) size of 10m to allow for interpolations to reflect potentially sharp gradients in species abundance. We resampled these 10m interpolations by maximum value to 50m resolution for analysis of home range use at Ngogo. Sample plots at Issa were 20 x 20m in size and we used 20m cells for interpolations for this site. We resampled these 20m interpolations by maximum value to 75m resolution for analysis of home range use at Issa. Before resampling interpolations for both sites, we replaced corresponding interpolated cells with actual observed values of total species basal area density from sample plots. For Issa, following resampling we used only 75 x 75m range use cells that had a minimum of 12 (of a possible 16) interpolated cells from which to resample. Given predicted differences in food abundance between forest and woodland, this was to remove errors resulting from range use cells spanning both forest and woodland that would otherwise have incorrectly been resampled from only one vegetation class.

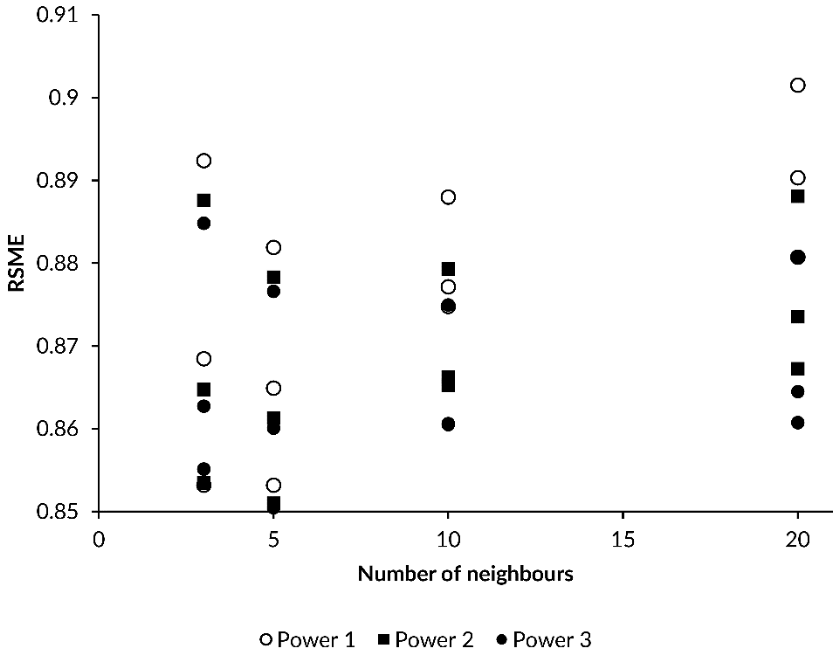

Figure S1 Effect of varying values for nearest neighbour and power parameters on RSME for interpolations of *D. abyssinica* at Ngogo.

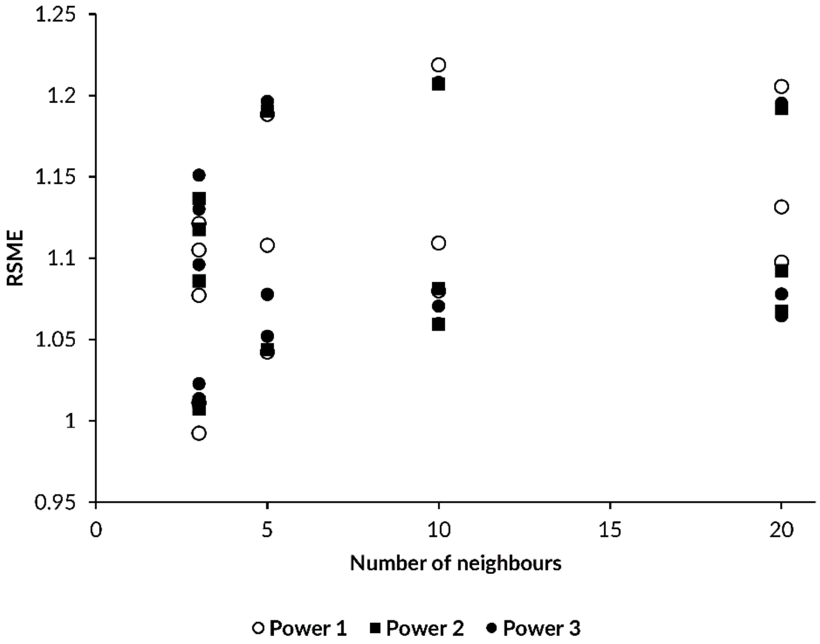

Figure S2 Effect of varying values for nearest neighbour and power parameters on RSME for interpolations of *M. richardsiae* at Issa.

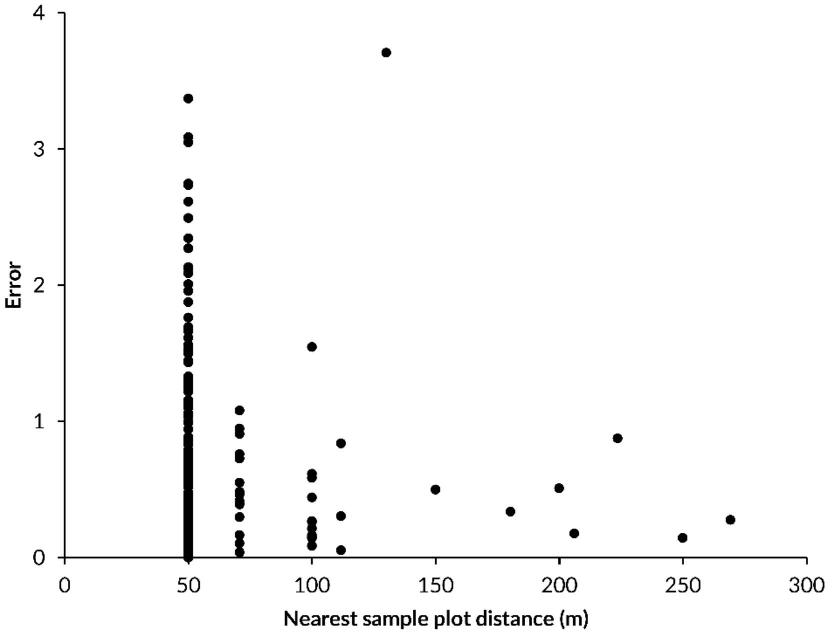

Figure S3 Relationship between nearest sample plot distance and error for interpolations of *D. abyssinica* at Ngogo.

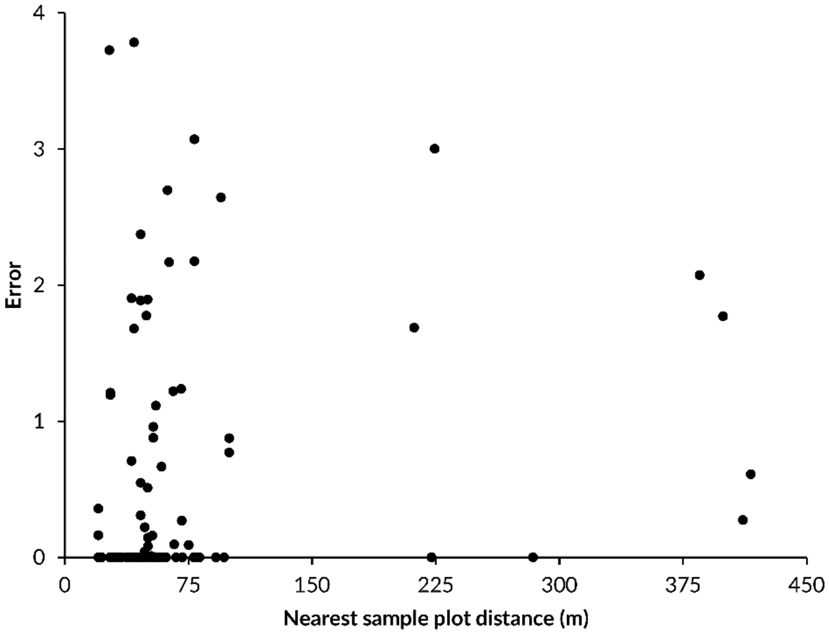

Figure S4 Relationship between nearest sample plot distance and error for interpolations of *M. richardsiae* at Issa.

Table S1 Demographic composition of each study group, adapted from Brown (2011). Ranges indicate fluctuating numbers over duration of study. Tildes indicate approximate counts.

Study site	**Group**	**Group composition**				
		Total size	**Adult males**	**Adult females [with dependent infants]**	**Subadults**	**Juveniles**
Ngogo	R1	12 – 13	1	8 [0 – 3]	3 – 4	8 – 10
	R2	10 – 11	1	7 [1 – 7]	2 – 3	5 – 7
	R3	10 – 11	1	7 [2 – 4]	2 – 3	7 – 8
	R4	10	1	7 [1 – 3]	2	6
	R5	~25	1	~16 [1] adult females and subadults		~5
	R6	~35	2	~20 [3] adult females and subadults		~8
Issa	K0	~35 – ~55	2 – 4	-	-	-

Table S2 List of plant species for which both abundance and phenology data were available and included in the model of food abundance at Ngogo.

Family	**Species**
Anacardiaceae	*Pseudospondias microcarpa*
Annonaceae	*Monodora myristica*
Annonaceae	*Uvariopsis congensis*
Apocynaceae	*Tabernaemontana* spp.
Bignoniaceae	*Spathodea campanulata*
Canellaceae	*Warburgia ugandensis*
Cannabaceae	*Celtis durandii*
Ebenaceae	*Diospyros abyssinica*
Fabaceae	*Erythrina excelsa*
Fabaceae	*Millettia dura*
Flacourtiaceae	*Dasylepis eggelingii*
Meliaceae	*Trichilia dregeana*
Moraceae	*Bosqueia phoberos*
Moraceae	*Ficus brachylepis*
Moraceae	*Ficus dawei*
Moraceae	*Ficus mucuso*
Moraceae	*Ficus natalensis*
Moraceae	*Morus lactea*
Moraceae	*Treculia africana*
Rutaceae	*Teclea nobilis*
Sapindaceae	*Aphania senegalensis*
Sapindaceae	*Blighia unijugata*
Sapindaceae	*Zanha golungensis*
Sapotaceae	*Aningeria altissima*
Sapotaceae	*Chrysophyllum albidum*
Sapotaceae	*Mimusops bagshawei*
Verbenaceae	*Premna angolensis*

Table S3 List of plant species for which both abundance and phenology data were available and included in the model of food abundance at Issa. Vegetation class indicates the vegetation class(es) in which stems of each species were sampled.

Family	**Species**	**Vegetation class**
Achariaceae	*Rawsonia lucida*	Forest
Annonaceae	*Xylopia odoratissima*	Forest
Apocynaceae	*Pleiocarpa pycnantha*	Forest
Apocynaceae	*Tabernaemontana pachysiphon*	Forest
Bignoniaceae	*Kigelia africana*	Forest
Clusiaceae	*Garcinia buchananii*	Forest
Ebenaceae	*Diospyros gabunensis*	Forest
Euphorbiaceae	*Croton megalocarpus*	Forest
Euphorbiaceae	*Drypetes gerrardii*	Forest
Fabaceae	*Baikiaea insignis*	Forest
Fabaceae	*Julbernardia unijugata*	Forest
Fabaceae	*Monopetalanthus richardsiae*	Forest
Fabaceae	*Piliostigma thonningii*	Forest
Malvaceae	*Thespesia garckeana*	Forest
Melianthaceae	*Bersama abyssinica*	Forest
Rhamnaceae	*Ziziphus abyssinica*	Forest
Rhizophoraceae	*Cassipourea malosana*	Forest
Rubiaceae	*Rothmannia urcelliformis*	Forest
Rutaceae	*Citropsis gabunensis*	Forest
Rutaceae	*Vepris grandifolia*	Forest
Rutaceae	*Vepris trichocarpa*	Forest
Sapindaceae	*Haplocoelum foliolosum*	Forest
Annonaceae	*Hexalobus monopetalus*	Woodland
Bignoniaceae	*Stereospermum kunthianum*	Woodland
Chrysobalanaceae	*Parinari curatellifolia*	Woodland
Combretaceae	*Terminalia mollis*	Woodland
Dipterocarpaceae	*Monotes africana*	Woodland
Dipterocarpaceae	*Monotes elegans*	Woodland
Fabaceae	*Dalbergia nitidula*	Woodland
Fabaceae	*Isoberlinia angolensis*	Woodland
Loganiaceae	*Strychnos cocculoides*	Woodland
Ochnaceae	*Ochna mossambicensis*	Woodland
Olacaceae	*Ximenia americana*	Woodland
Passifloraceae	*Faurea saligna*	Woodland
Phyllanthaceae	*Hymenocardia acida*	Woodland
Rubiaceae	*Canthium burthii*	Woodland
Rubiaceae	*Multidentia crassa*	Woodland
Rubiaceae	*Rothmannia engleriana*	Woodland
Verbenaceae	*Vitex mombassae*	Woodland
Anacardiaceae	*Lannea schimperi*	Both
Anisophylleaceae	*Anisophyllea boehmii*	Both
Annonaceae	*Annona senegalensis*	Both
Apocynaceae	*Diplorhynchus condylocarpon*	Both
Bignoniaceae	*Markhamia obtusifolia*	Both
Combretaceae	*Combretum molle*	Both
Combretaceae	*Combretum pentagonum*	Both
Combretaceae	*Terminalia servicea*	Both
Euphorbiaceae	*Pseudolachnostylis maprouneifolia*	Both
Euphorbiaceae	*Uapaca nitida*	Both
Fabaceae	*Albizia antunesiana*	Both
Fabaceae	*Brachystegia boehmii*	Both
Fabaceae	*Brachystegia longifolia*	Both
Fabaceae	*Brachystegia microphylla*	Both
Fabaceae	*Brachystegia spiciformis*	Both
Fabaceae	*Julbernardia globiflora*	Both
Fabaceae	*Newtonia buchananii*	Both
Fabaceae	*Pericopsis angolensis*	Both
Fabaceae	*Pterocarpus angolensis*	Both
Fabaceae	*Pterocarpus tinctorius*	Both
Loganiaceae	*Strychnos madagascariensis*	Both
Loganiaceae	*Strychnos spinosa*	Both
Oleaceae	*Schrebera trichoclada*	Both
Proteaceae	*Faurea rochetiana*	Both
Rhamnaceae	*Erythrina abyssinica*	Both
Verbenaceae	*Vitex doniana*	Both

Table S4 Model formulas used in statistical analyses. Interaction terms "*" indicate inclusion of both main and interaction terms "x + y + x:y".

Package::function	**Model type**	**Error**	**Response**	**Predictors**	**Random intercept effect "(1|x)"**
nlme 3.1::*lme*	Generalized linear mixed model	Gaussian	Hourly travel distance	mean hourly temperature + hourly rainfall (binary)	Month
			Daily travel distance	max. daily temperature*study site + daily rainfall (binary)*study site	Group ID
base R 3.5.1::*lm*	Linear model		Daily travel distance	fruit abundance*group ID + flower abundance*group ID	-
spaMM 2.5.11::*corrHLfit*	Generalized linear mixed model	Poisson	Count GPS points per grid cell per month + total GPS points per month (log transformed offset)	fruit abundance*group ID + flower abundance *group ID + leaf abundance *group ID	Adjacency matrix (monthly grid cell ID)

Table S5 Results of the linear mixed model detailing effects of temperature and rainfall on hourly travel distance for K0 at Issa (SE = standard error; * = *p* value < 0.05).

Fixed effect	**Estimate**	**SE**	***t***	***p***
Intercept	165.077	7.940	20.789	-
Hourly mean temperature	-25.075	4.271	-5.871	< 0.001 *
Hourly rainfall	-32.004	17.076	-1.874	0.062

Comparison of null and full model likelihood ratio test: $\chi^2 = 34.420$, DF = 2, $p < 0.001$

Table S6 Results of the linear mixed model detailing effects of temperature and rainfall on daily travel distance groups at Ngogo and Issa (SE = standard error; * = significant *p* value < 0.05).

Fixed effect	**Estimate**	**SE**	***t***	***p***
Intercept	1366.211	145.564	9.386	-
Maximum daily temperature	-69.222	20.647	-3.353	< 0.001 *
Daily rainfall	-11.444	39.178	-0.292	0.770
Site †	656.583	388.196	1.691	0.152
Interaction: site*maximum daily temperature	-80.182	43.944	-1.825	0.067
Interaction: site*daily rainfall	73.283	91.781	0.798	0.422

Comparison of null and full model likelihood ratio test: $\chi^2 = 23.997$, DF = 5, $p < 0.001$

† Binary factor: Ngogo = 0; Issa = 1

Table S7 Results of Kruskal-Wallis tests of variation in monthly food abundance at Ngogo and Issa (Figure 7). In all tests *p*-values were corrected by Bonferroni correction (* = significant *p* value < 0.05).

Study site	**Vegetation class**	**Resource**	***H***	***p***
Ngogo	Primary forest	Fruit	545.520	< 0.001 *
		Flowers	623.550	< 0.001 *
		Leaves	1.929	1.0
Issa	Riparian forest	Fruit	239.940	< 0.001 *
		Flowers	40.375	< 0.001 *
		Leaves	19.513	0.630
	Woodland	Fruit	155.630	< 0.001 *
		Flowers	110.780	< 0.001 *
		Leaves	6.738	1.0
	Riparian forest & woodland combined	Fruit	293.51	< 0.001 *
		Flowers	109.600	< 0.001 *
		Leaves	17.320	1.0

Table S8 Results of the linear model detailing effects of mean monthly food abundance on daily travel distance groups at Ngogo and Issa (SE = standard error; * = significant *p* value < 0.05).

Fixed effect	**Estimate**	**SE**	***t***	***p***
Intercept	1507.070	140.340	10.739	-
Fruit	-453.550	123.370	-3.676	< 0.001 *
Flowers	-41.020	58.070	-0.707	0.481
Group (R5) †	393.770	193.110	2.039	0.042 *
Group (R6) †	1065.960	608.750	1.751	0.081
Interaction: fruit*group (R5) †	858.250	233.210	3.680	< 0.001 *
Interaction: fruit*group (R6) †	549.160	323.040	1.700	0.090
Interaction: flowers*group (R5) †	-82.680	92.230	-0.897	0.371
Interaction: flowers*group (R6) †	-236.270	245.800	-0.961	0.337

Respective comparison for fruit*group for R6 cf. reference R5: estimate ±SE = -309.090 ±297.980; *t* = -1.037; *p* = 0.301

Respective comparison for flowers*group for R6 cf. reference R5: estimate ±SE = -153.590 ±249.0; *t* = -0.617; *p* = 0.538

† Reference: K0

Table S9 Results of linear mixed model detailing effects of food abundance on proportion of time spent per grid cell (SE = standard error; * = significant *p* value < 0.05).

Predictor	**Estimate**	**SE**	***t***	***p***
Intercept	-5.683	0.067	-85.108	-
Fruit	0.053	0.072	0.730	0.465
Flowers	-0.004	0.035	-0.105	0.916
Leaves	-0.026	0.036	-0.717	0.473
Group (R5) †	-1.079	0.157	-6.851	< 0.001 *
Group (R6) †	-0.632	0.153	-4.127	< 0.001 *
Interaction: fruit*group (R5) †	-0.175	0.155	-1.132	0.258
Interaction: fruit*group (R6) †	-0.166	0.155	-1.072	0.284
Interaction: flowers*group (R5) †	-0.103	0.079	-1.311	0.190
Interaction: flowers*group (R6) †	-0.029	0.088	-0.328	0.743
Interaction: leaves*group (R5) †	0.108	0.088	1.233	0.217
Interaction: leaves*group (R6) †	0.084	0.090	0.936	0.349

Comparison of null and full model likelihood ratio test: χ^2 = 97.585, DF = 11, *p* < 0.001

Respective comparison for fruit*group for R6 cf. reference R5: estimate ±SE = 0.009 ±0.097; *t* = 0.097; *p* = 0.923

Overall test for interaction fruit*group: χ^2 = 4.122, DF = 2, *p* = 0.127

Respective comparison for flowers*group for R6 cf. reference R5: estimate ±SE = 0.074 ±0.086; *t* = 0.866; *p* = 0.386

Overall test for interaction flowers*group: χ^2 = 0.139, DF = 2, *p* = 0.933

Respective comparison for leaves*group for R6 cf. reference R5: estimate ±SE = -0.024 ±0.105; *t* = -0.226; *p* = 0.822

Overall test for interaction leaves*group: χ^2 = 0.187, DF = 2, *p* = 0.911

† Reference: K0

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Title: Thermal conditions constrain group movements and habitat use in forest- and savanna woodland-dwelling red-tailed monkeys (*Cercopithecus ascanius*)

Edward McLester [a], Michelle Brown [b], Fiona A. Stewart [a c] & Alex K. Piel [a c]

[a] School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK
[b] Department of Anthropology, University of California, Santa Barbara, USA
[c] Greater Mahale Ecosystem Research and Conservation Project, Box 60118, Dar es Salaam, Tanzania

Abstract

As forests transitioned to hotter open environments in the late Miocene, thermal conditions were likely important selection pressures on early hominins. For extant primates living in forest and savanna mosaics, behavioural responses to habitat-specific thermal conditions can reveal environmental pressures under which hominins may have evolved. Primates in savanna mosaics with less abundant, widely distributed food may tolerate greater heat exposure than forest groups to obtain sufficient food. We compared ranging responses to ambient temperature, solar irradiance, and food abundance in red-tailed monkeys (*Cercopithecus ascanius*) at Ngogo (Uganda), a relatively food-rich mosaic of closed canopy forest and patches of open canopy secondary vegetation, and Issa (Tanzania), an open woodland-dominated mosaic with minimal closed forest and lower food availability. We predicted that first, hourly travel speed relates more negatively to temperature at Ngogo than Issa, and second, Issa monkeys use open vegetation during higher temperatures and greater solar irradiance than Ngogo 1) as closed vegetation food availability decreases, and 2) when foraging *cf.* resting. We collected focal scans and group ranging patterns during all-day follows. We used HOBO and Kestrel loggers to record hourly temperature in each vegetation class, and we used a GIS to estimate hourly, spatially-explicit solar irradiance. Temperature gradients between forest and open vegetation were similar at both sites. Temperature had a stronger negative effect on travel speed at Ngogo. When closed vegetation food was lower, Issa groups used open vegetation during higher temperatures and solar irradiance than Ngogo groups. Monkeys at both sites travelled and rested in similar temperatures and irradiance. Monkeys reduced behavioural responses to high temperature and irradiance in savanna mosaics, likely to prioritise meeting foraging requirements. Comparable responses to intra-habitat thermal heterogeneity reinforce the importance of considering thermal conditions at fine spatial scales in hypotheses of extant and extinct primate thermoregulatory behaviour.

Introduction

The transition from closed forests to more heterogeneous savanna mosaics during the Mio-Pliocene is considered a substantial driver of hominin evolution (Bromage and Schrenk 1995; Antón *et al.* 2014; Alemseged *et al.* 2020). Savanna-woodland mosaics were more arid and seasonal than densely vegetated, primarily closed canopy forest environments (Passey *et al.* 2010; Cerling *et al.* 2011). Changes in thermal conditions (e.g. temperature; solar irradiance) between these environments were likely selection pressures for hominins, such as *Australopithecus* and early *Homo* spp., because these abiotic factors can vary across spatial (e.g. regional; microclimates) and temporal scales (e.g. seasonal; hourly). Specifically, open canopy cover would have resulted in less shade and greater heat exposure, while longer hotter dry seasons would have led to more seasonally variable temperature ranges (McGrew *et al.* 1981; Hill 2005; Pruetz and Bertolani 2009; Wessling *et al.* 2018b). For hominins, thermal conditions have therefore been associated with morphological (e.g. hair loss; bipedality – Ruxton and Wilkinson 2011), physiological (e.g. variable core body temperature;

sweating – Wheeler 1992; Ruxton and Wilkinson 2011), and behavioural adaptations (e.g. activity budgets; ranging patterns – Wheeler 1994).

Given limitations of using the fossil record to reconstruct hominin adaptations (Byrne 1995), comparing extant primate behaviour between environments – especially species living in forest and savanna mosaics that resemble hominin paleoenvironments – can help reconstruct environmental pressures that may have influenced hominin behaviour (e.g. *Pan* spp. – Moore 1996; Wessling *et al.* 2018b; cercopithecoids – Leonard and Robertson 1997; Isbell *et al.* 1998; McLester *et al.* 2019a). Landscape- or biome-level comparisons of primate behaviour typically contrast study sites that are broadly classified as either heterogeneous or homogenous depending on vegetation cover (see Wessling *et al.* 2018a). These site-wide characterisations may not reflect microclimates within habitats that can vary substantially between vegetation classes (e.g. Frost 1996), however. Instead, intra-specific comparisons of primates distributed across both forest and savanna mosaic environments avoid phylogenetic bias and can reveal both inter- and intra-habitat variation in adaptive responses to thermal heterogeneity.

Primate behavioural responses to changes in thermal conditions are primarily mechanisms of energy conservation (Stelzner and Hausfater 1986; Morland 1993; Hanya 2004). As such, thermoregulatory behaviour is often reflected in ranging patterns. For example, behavioural responses to higher ambient temperatures include reduced travel speeds and duration (chacma baboons, *Papio ursinus* – Stoltz and Saayman 1970; yellow baboons, *P. cynocephalus* – Stelzner 1988; Johnson *et al.* 2015; Yunnan snub-nosed monkeys, *Rhinopithecus bieti* – Baoping *et al.* 2009; white-faced capuchins, *Cebus capucinus* – Campos and Fedigan 2009) and increased rates of individual thermoregulatory behaviour such as resting (chacma baboons – Hill 2005; chimpanzees, *Pan troglodytes* – Kosheleff and Anderson 2009; reviewed in Terrien *et al.* 2011). These behaviours often correlate with patterns of habitat use, where animals preferentially travel to cooler, shadier areas (e.g. Hill 2006) or shelter in caves (e.g. Barrett *et al.* 2004; Pruetz 2007). Methodologically, ranging patterns are useful because they reveal thermoregulatory behaviour at multiple scales (e.g. group-level *cf.* individual animals) through well-established metrics (e.g. travel speed; hotspots of home range use) that enable direct comparisons between study species and sites.

We investigated ranging responses to thermal conditions in the red-tailed monkey (*Cercopithecus ascanius schmidti*), which lives primarily in expanses of closed canopy forest as well as woodland-dominated mosaics (Sarmiento *et al.* 2001; McLester *et al.* 2019a). We compared behaviour between two mosaic environments with contrasting proportions of closed canopy forest. At Ngogo (Uganda), wide expanses of rainforest are interspersed with isolated patches of mixed canopy cover, regenerating, secondary forest (Figure 1; see Methods). At the Issa Valley (Tanzania), most vegetation is open canopy miombo woodland, with closed canopy forest restricted to thin riparian strips (Figure 1). At Issa and for some groups at Ngogo, home ranges include large proportions of woodland and secondary forest (e.g. >20% – Table 1; hereafter, “open vegetation”) in addition to riparian and primary forest (hereafter, “closed vegetation”). Savanna-mosaic environments should exhibit wider daily ambient temperature ranges, in addition to lower proportions of closed canopy

Table 1 Follow days, age-sex class compositions, and model inclusion for each study group. Home range are illustrated in Figure 2; see McLester *et al.* (2019a) for details of estimate methods. Home range sizes for K1 and K2 at Issa are preliminary estimates (HTD = hourly travel distance; OVU = open vegetation use; tilde = approximate count).

Study site	**Group**	**Follow period [follow days]**	**Inclusion in analysis (method)**	**Home range size (km^2)**	**Proportion home range comprising open vegetation (%)**	**Follow days open vegetation used (%)**	**Group composition**				
							Total size	**Adult males**	**Adult females [with infants]**	**Subadults**	**Juveniles**
Ngogo	R4	Jun 2008 – Jul 2014 [*n* = 151]	OVU (grid cells)	0.40 [2]	24.9	138 (91.4)	10	1	7	2	6
	R6	Mar – Jun 2017 [*n* = 71]	OVU (grid cells)	0.65 [2]	21.9	50 (70.4)	~35	1 – 2	~20 [2] adult females and subadults		~8
	R5	Jan – Feb 2019 [*n* = 23]	HTD (60-minute paths)	0.60 [2] [3]	0.0	-	~30	1	14 – 16 [5 – 6]	9 – 10	4 – 5
	R2	Jan – Mar 2019 [*n* = 24]	HTD (60-minute paths)	0.24 [2]	0.0	-	16	1	7 [~3 – ~5]	6	2
	RSW	Jan – Apr 2019 [*n* = 22]	HTD (60-minute paths)	0.41 [2]	1.4	2 (9.1)	16 – 19	1	9 [4 – 6]	6 – 7	0 – 2
	RGS	Apr – Jun 2019 [*n* = 72]	HTD (60-minute paths); OVU (20-minute paths)	0.30 [2]	24.2	62 (86.1)	17 – 19	1	5 [1 – 2]	7	4 – 6
Issa Valley	K0	Jan 2013 – Mar 2016 [*n* = 175]	HTD (60-minute paths)	16.0 [2]; 3.93 [4]	96.3 [6]	Daily	~35 – ~55	2 – 4	-	-	-
	K1 [1]	Nov 2017 – Dec 2019 [*n* = 102]	OVU (focal scans)	7.54 [2]; 1.76 [4]			~30 [7]	1	- [~3]	-	-
	K2 [1]	Nov 2017 – Dec 2019 [*n* = 86]	OVU (focal scans)	0.74 [2]; 0.47 [5]			10 – 11 [7]	1	7 [3]	1 – 2	1

[1] Daughter groups resulting from fission of K0 during 2016 – 2017

[2] Calculated using minimum convex polygon

[3] Calculated from both follows in 2017 and additional follows in 2019 (see McLester *et al.* 2019a)

[4] Calculated using 75m grid cell analysis (grid resolution accounts for group size and spread)

[5] Calculated using 50m grid cell analysis (grid resolution accounts for group size and spread)

[6] Site-wide mean (McLester *et al.* 2019b). See Figure 2 for an illustration of forest and woodland cover across K0’s home range

[7] Composition in 2017

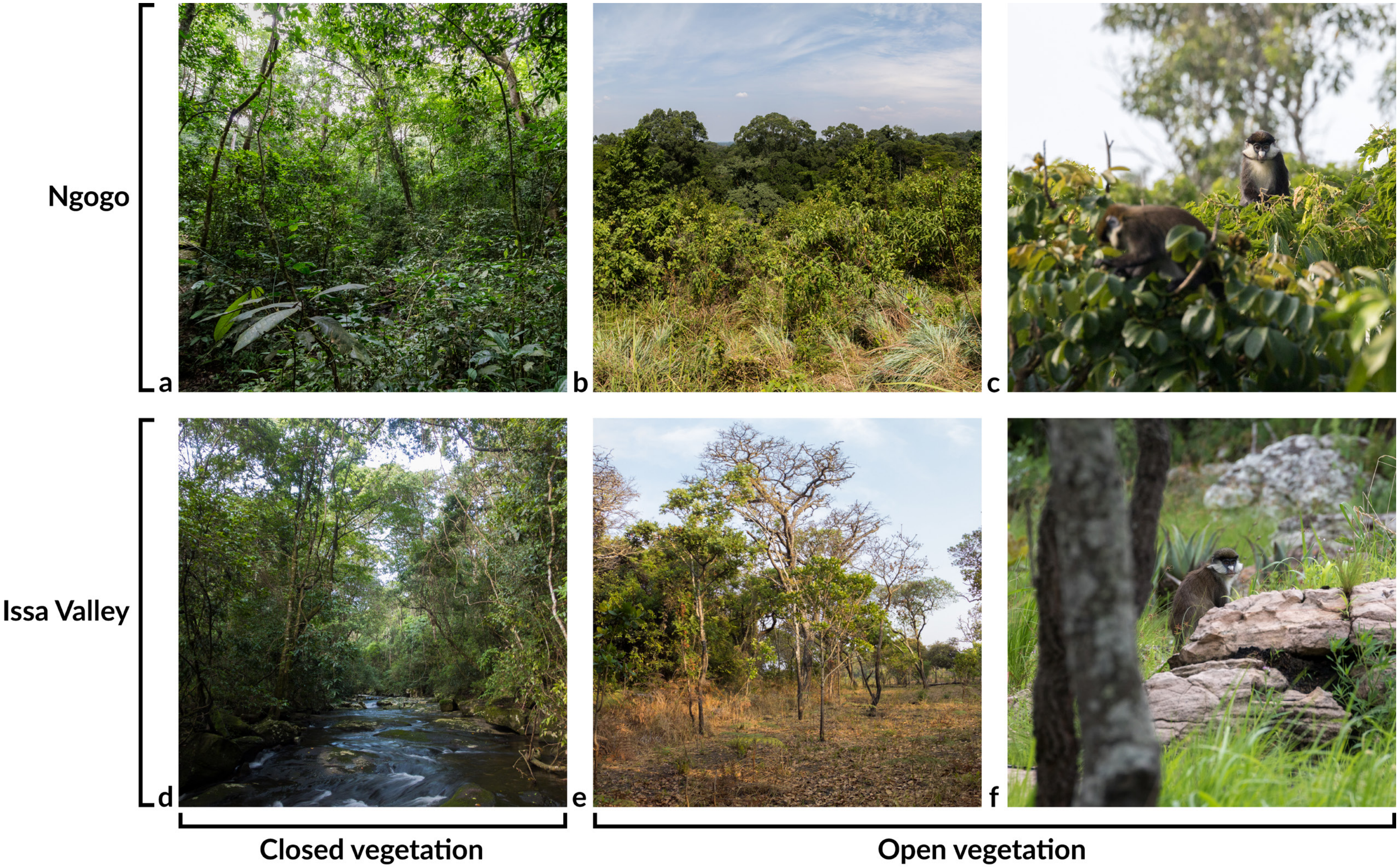

Figure 1 Vegetation classes comprising red-tailed monkey habitat at each study site. At Ngogo: (a) closed-canopy primary forest; (b) secondary forest (foreground, with primary forest in background; (c) adult female in R6 group feeding arboreally in open-canopy secondary forest. At Issa: (d) closed-canopy riparian forest; (e) miombo woodland during dry season (foreground, with riparian forest strip in background left side); (f) adult female in K2 group travelling terrestrially through woodland during wet season. Photos: EM.

cover that result in larger areas exposed to solar irradiance, than primarily forested environments (McGrew *et al.* 1981; Hill *et al.* 2004).

Expected differences in thermal conditions between Issa and Ngogo may result in trade-offs related to open vegetation use. For example, similar to savanna mosaic paleoenvironments that had more widely scattered food patches than the forests they replaced (Isbell and Young 1996), food abundance (fruit, flowers, and leaves) at Issa is highly variable across months and between open and closed vegetation, and less abundant overall than at Ngogo (McLester *et al.* 2019a; Figure S1). A previous study of red-tailed monkeys at Issa found that temperature negatively affects group travel speed (McLester *et al.* 2019a). It is unknown, however, whether the same relationship exists elsewhere. At Ngogo, the greater proportion of closed vegetation means this relationship may be stronger because of the reduced need to travel during hotter temperatures to acquire sufficient food. Similarly, Issa monkeys may forage more in hot open vegetation to acquire enough food, while food in closed vegetation at Ngogo may be sufficient such that foraging during higher temperatures in open vegetation is unnecessary.

To test the hypothesis that thermal heterogeneity influences intra-specific variation in ranging patterns, we investigated habitat-specific variation in two behavioural responses to temperature and solar irradiance: group travel speed and open vegetation use. First, we compared inter-site differences in 1) monthly and daily temperature ranges in open and closed vegetation, and 2) hourly solar irradiance ranges in open vegetation. Second, we predicted that monkeys would reduce group travel speed (measured through hourly travel distance – HTD) as ambient temperatures increased, and that this effect would be stronger at Ngogo. Third, we predicted that monkeys at Issa would be more likely than Ngogo monkeys to use open vegetation during higher temperatures and greater solar irradiance as food availability declined in closed vegetation. As such, we expected Issa groups to use open vegetation during higher temperatures when foraging (groups travelling *cf.* stationary) than Ngogo groups. Within groups at Issa, we expected individuals to use open vegetation during lower temperatures when foraging (*cf.* resting or engaged in social behaviour).

Methods

Study sites & groups

We collected data from red-tailed monkey groups at two study sites. Ngogo (Kibale National Park, Uganda) comprises a ~40 km^2 mosaic of mostly primary forest (*ca.* 60% cover – Wing and Buss 1970) interspersed with isolated patches of secondary forest, woodland, swamp, and grassland (Struhsaker 1997; Figure 2; elevation: 1,110 – 1,590m). Primary forest canopy cover is almost all closed (defined as >50% tree crown cover) and *ca.* 25-30m high on average, with the tallest trees reaching >55m (Butynski 1990; Figure 1). In the core of the study site, secondary forest has resulted from succession following the end of human clearing and burning from *ca.* 1975 onwards (Struhsaker 1997; T. Struhsaker personal communication). Vegetation consists of early- to mid-growth bushes and trees with understorey characterised by dense, often impenetrable thicket. In secondary forest,

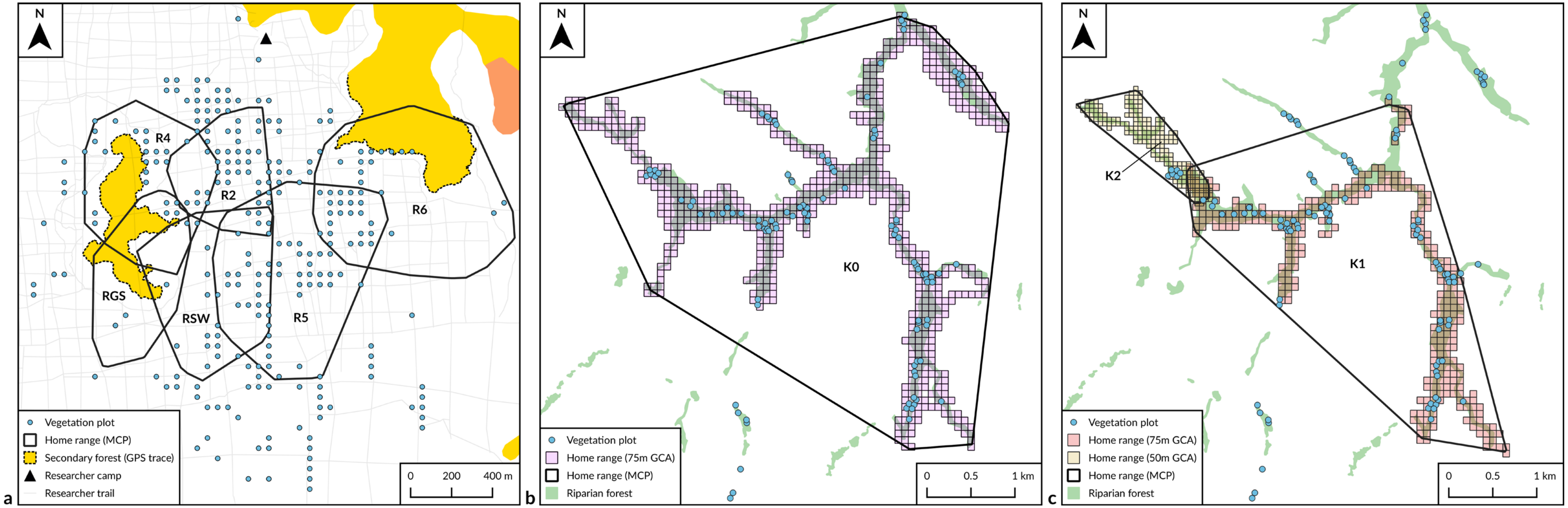

Figure 2 Locations of home ranges for red-tailed monkey study groups at Ngogo (a) and Issa (b, c) in relation to vegetation cover and vegetation plots. At Ngogo, blank white indicates primary forest. Dotted lines indicate secondary forest that we mapped at high resolution using GPS traces; remaining secondary forest and woodland cover were mapped by the Uganda Biomass Survey. Researcher trails and camp are shown for reference. At Issa, blank white indicates miombo woodland (MCP = minimum convex polygon; GCA = grid cell analysis).

tree height is lower (*ca.* 5 – 15m high on average), canopy cover is more open and results in increased sunlight exposure, and moisture levels are more variable than primary forest (Struhsaker 1997). Wet seasons are approximately bimodal annually (mean annual rainfall 1977 – 1984: 1500mm), although substantial monthly and yearly variation in rainfall means the onset of wet and dry seasons changes each year (Potts *et al.* 2020). We followed six habituated red-tailed monkey groups at Ngogo for varying periods between 2008 and 2019, each comprising between 10 and ~35 individuals in total (see Table 1 for detailed demographics).

The Issa Valley (Tanzania) is ~670 km from Ngogo and comprises a ~60 km^2 area of five major valleys and surrounding flat plateaus (elevation: 1,150 – 1,712m). Vegetation is a mosaic of mostly deciduous *Brachystegia* and *Julbernadia* spp. miombo woodland, grassland, swamp, and minimal evergreen riparian forest (4% cover – McLester *et al.* 2019b; Figure 1). Woodland consists of scattered deciduous trees (primarily *Brachystegia* and *Julbernardia* spp.) with a savanna grass understorey (>2m in wet seasons) that burns during late dry seasons due to human ignitions. Compared to the expanse of forest at Ngogo, forest at Issa is restricted to relatively thin riverine strips (<10m wide, in parts) surrounded by woodland (Figure 1; Figure 2). Dry seasons (<100 mm monthly rainfall) are from May to October (Stewart 2011; McLester *et al.* 2019a). We followed three habituated groups at Issa – initially a single group (K0) that increased in size from ~35 to ~55 individuals from 2013 – 2016, which split into two daughter groups that we followed from 2017 – 2019 after K0 fissioned (K1 and K2 – Table 1). K1 and K2 home ranges comprise smaller overlapping areas within the extent of K0's previous home range (Figure 2).

Data collection

Temperature and relative humidity data

We collected temperature data using loggers located in open and closed vegetation at both study sites. At Ngogo, we used two Kestrel Drop D1 loggers to record temperature in primary and secondary forest at 20-minute intervals from March – November 2019. Loggers were located 2 – 3m high in trees with canopy cover of 100% in forest and 25% in secondary forest. At Issa, we recorded temperature at 30-minute intervals using HOBO H8 Pro (2013 – 2016) and HOBO 8K Pendant (2017 – 2019) loggers in riparian forest, and a HOBO U30 station (2015 – 2016, 2014 – 2019) and HOBO 8K Pendant logger (2013 – 2014) in woodland. The HOBO U30 station in woodland also recorded relative humidity at the same 30-minute intervals as temperature measurements. Pendant loggers were located 3 – 5m high in trees, and the U30 and H8 stations were located at ground-level.

Behavioural data

At both sites, at least one researcher or two trained field assistants followed groups from 0700 to 1900 hr. From 2008 – 2016 at Ngogo, we recorded group locations at 30-minute intervals by mapping group centre-of-mass to the nearest grid cell of a 50m x 50m grid laid over the site. From 2017 – 2019 at Ngogo and 2013 – 2019 at Issa, we collected ranging data using Garmin Rino 650 GPS units that recorded coordinates (typically <4m accuracy) automatically at 5-minute intervals during follows.

During group follows, we collected 15-minute interval scans of focal individuals, for which we recorded: focal vegetation class and behaviour; whether the group was travelling (binary: travelling or not travelling); and at Ngogo, whether the group was in a polyspecific association (≥2 conspecifics of a different species within the periphery of the study group). For Ngogo groups, we also recorded *ad libitum* observations of potential predator presence (chimpanzees, *Pan troglodytes*; crowned hawk-eagles, *Stephanoaetus coronatus*) when visible to groups. Because we could not always know how long a potential predator was in proximity, we made conservative estimates by extending durations by 30 minutes before and after observations. We alternated identities (or age-sex class, if identity was unknown) of focal individuals in consecutive scans to minimise temporal autocorrelation.

Mapping secondary forest at Ngogo

We traced secondary forest patches at Ngogo in 2019 by walking around patch perimeters while recording GPS coordinates at automatic 5-second intervals. We created polygons for patches in QGIS 3.10 (QGIS Development Team 2019) by joining consecutive coordinates by Euclidean distances. We traced patches at least once in each direction to corroborate GPS coordinates and then cross-referenced polygons with a vegetation class map produced in 2017 as part of the Uganda Biomass Study. See Table 1 and Figure 2 for proportions of secondary forest cover in group home ranges (calculated using secondary forest traces in this study and minimum convex polygon home range estimates in McLester *et al.* 2019a).

Data analyses

Hourly travel distance

We analysed HTD for four groups at Ngogo for which both ranging and temperature data were available (Table 1). We used QGIS to calculate HTD as the total Euclidean distance between consecutive coordinates per follow hour (≥50 minutes). At Issa, we used measures of HTD calculated previously for K0 by McLester *et al.* (2019a) using the same method. To reduce overestimates of path length resulting from variation in GPS accuracy, we used only coordinates with at least 5m distance between consecutive coordinates.

We matched HTD to mean hourly temperature recorded in closed vegetation except for HTD at Ngogo where >50% length overlapped our traces of open vegetation, which we matched to temperature recorded in open vegetation. We disregarded HTD that overlapped with predator presence. We also noted whether the group was in a polyspecific association at any point during each HTD. Red-tailed monkeys at Ngogo associate with six other primate species, of which two are habituated to researchers (grey-cheeked mangabey, *Lophocebus albigena*; blue monkey, *C. mitis*). Unlike blue monkeys, mangabeys associated with each red-tailed monkey group in this study, and mangabey associations are more likely to influence red-tailed monkey ranging patterns (Brown 2013; EM personal observation). We therefore re-classified polyspecific associations for each HTD from at least one corresponding scan, as follows: in association with mangabey; in association with other species; not in association. Although data on polyspecific associations and predator presence at Issa were not available from 2013 – 2016 for our analysis of HTD, associations and predator encounter rates at Issa are infrequent compared to Ngogo, partly due to the low densities exhibited by most primate species at this site (see rates in McLester *et al.* 2019a).

Thermal conditions, food abundance, and group travel during open vegetation use

To investigate whether monkeys used open vegetation during significantly different thermal conditions at each site, we tested two predictors (food abundance in closed vegetation and group travel) of ambient temperature and solar irradiance during open vegetation use. At Ngogo, we identified open vegetation use from group ranging patterns (grid cells for groups followed 2008 – 2016, and 20-minute paths for groups followed 2017 – 2019) that overlapped our traces of secondary forest patches. We used the same method as HTD to calculate 20-minute travel distance, matching the 20-minute intervals of our temperature loggers. We considered only grid cells that overlapped ≥50% in area with secondary forest, and 20-minute paths for which ≥50% of length was spent in secondary forest, as indicative of time spent in secondary forest by groups.

At Issa, riparian forest patches are thin enough in places that a group is frequently spread across forest and woodland simultaneously and discerning the vegetation class(es) a group was in from GPS coordinates alone was not possible. We therefore identified open vegetation use from focal scans of individuals. For each scan, we also re-categorised focal behaviour as either "active" or "non-active" depending on its association with foraging effort (Table S1; as per Starr *et al.* 2012).

We matched each observation of open vegetation use (20-minute paths and 30-minute grid cells at Ngogo; 15-minute focal scans at Issa) to measures of ambient temperature and solar irradiance in open vegetation, food abundance in closed vegetation, and whether the group was travelling. We matched open vegetation temperature to paths and focal scans by date and time (mean hourly temperature for focal scans). Where relative humidity data were available at Issa, we weighted temperature by relative humidity to provide an index that more closely reflects heat exposure perceived by the monkeys. We weighted temperature measurements above 24°C using the formula derived by Mather (1974), as described by Hill *et al.* (2004; see supplementary material S1).

We estimated hourly solar beam irradiance (watts/m^2) for 92.5 x 92.5m grid cells across the extent of monkey home ranges at each site (including control for cloud cover; see supplementary material S2). We matched values of solar irradiance to corresponding paths, grid cells, and focal scans by coordinates, dates, and times of observations. For 20-minute paths that passed through multiple 92.5m grid cells, we used the maximum value of solar irradiance intersected.

We indexed monthly food abundance (fruit, flowers, and leaves) in closed vegetation across all monkey home ranges at each site from 2017 – 2019 (i.e. except for R4, for which necessary phenology data were not available). We measured plant stem basal area (m^2) in vegetation plots sampled in closed vegetation across the extent of red-tailed monkey home ranges (*n* = 272 2500m^2 plots sampled 2009 – 2013 at Ngogo; *n* = 118 400m^2 plots sampled 2013 – 2019 at Issa). For each plant species per plot, we weighted basal area density by the proportions (scale: 0 – 1) of stems with fruit, flower, and leaf presence, as measured from monthly phenology transects (at Ngogo, collected by the Ngogo Chimpanzee Project). We summed fruiting stem, flowering stem, and stem with leaf density for each plot. For each plant part, we scaled the mean across all plots, weighted each measurement by proportion of red-tailed monkey diet at Ngogo ($\bar{x}$: fruit = 79%; flowers = 11%; leaves = 10% – MB unpublished data), and summed all three measurements for a single index of monthly food abundance (see Table S2 for plant species included at each site; see McLester *et al.* 2019a for details of vegetation plot and phenology data collection).

For 20-minute paths at Ngogo and focal scans at Issa, we used focal scans to identify whether groups were travelling. For grid cells at Ngogo for which corresponding focal data were not available, we identified group travel as whether grid cells were different (travelling) or the same (not travelling) between consecutive observations.

Statistical analyses

We conducted all statistical analyses in R 3.6.3 (R Core Team 2020). To investigate HTD and open vegetation use at each site, we built Bayesian linear mixed models with Gaussian error distributions (package: *MCMCglmm*). To investigate HTD, we fitted interactions between temperature and focal group (*n* = 5 groups) and polyspecific association as predictors. To investigate whether monkeys used open vegetation during significantly different temperatures or in areas of significantly different solar irradiance depending on study site, we built two models with temperature and solar irradiance as response variables and interactions between focal group (*n* = 3 – 5 groups) and 1) closed vegetation food abundance, and 2) group travelling (binary), as predictors.

We centred variables to a mean of zero and a standard deviation of one to improve model fitting and interpretation of continuous main effects in interactions (Schielzeth 2010). There were no confounding effects of predictor multicollinearity (maximum variance inflation factor: HTD = 1.11, temperature = 1.55, solar irradiance = 2.60). We fitted models with the default *MCMCglmm* priors for fixed effects, weakly informative priors for random effects (*V* = 1; *n* = 0.002), and the standard inverse-gamma prior for residual variance. We ran Markov chains (Monte Carlo) for 800,000 iterations with a burn-in of 100,000 iterations and a thinning interval of 100 iterations. After running each model, we checked trace plots to confirm autocorrelation was not an issue and that effective sample sizes were adequate (HTD: minimum = 6969, mean = 8017; temperature: minimum =7180, mean = 7928; solar irradiance: minimum = 7539, mean = 8047). We calculated the Gelman-Rubin diagnostic for three other equivalent models to confirm chain convergence (maximum point estimate for all models = 1.0).

For each response, we compared the deviance information criterion (DIC) between models with each combination of fixed interaction effects, a model with only fixed main effects, and a null model with no fixed effects. Lower DIC and higher corresponding weights indicate better relative model fit – differences of ≥5 DIC substantially so (e.g. Dutton *et al.* 2014). For each response, we selected the model with the lowest DIC compared to the null model and inferred fixed effect sizes by examining posterior distributions (widths and overlap of 95% credible intervals with zero) and posterior probabilities (how likely a predictor relates to the response – calculated as proportion of samples in each distribution with the same sign as the mean).

Using focal scans at Issa, we also compared differences in temperature and solar irradiance during open vegetation use between 1) age-sex classes (adult male; adult female; adult female with dependent infant; subadult and juvenile) using Kruskal-Wallis tests with post-hoc Dunn's tests (Bonferroni corrected) to identify pair-wise differences, and 2) focal behaviour (active; non-active) using Mann-Whitney tests.

Results

Hourly temperatures and solar irradiance

At both sites, daily temperature in closed vegetation peaked between 12 – 14hr (Figure 3). Maximum daily temperatures in open vegetation occurred earlier in the day at Ngogo (peaking 10 – 11hr) than at Issa, where high temperatures peaked around 13hr and remained high until after 16hr. Monthly mean and maximum hourly temperatures in open vegetation were highest at Ngogo during March – May (late dry season).

In open vegetation, mean daily maximum temperature was slightly higher at Issa than at Ngogo ($\bar{x}$ 28.5°C at Ngogo *cf.* $\bar{x}$ 29.6°C at Issa; Figure S2). The highest temperatures we recorded during the study period were in open vegetation (45.3°C in March 2019 at Ngogo; 40.5°C in September 2013 at Issa). At both sites, daily mean and minimum temperatures were similar in open (daily mean: $\bar{x}$ 22.4°C at Ngogo *cf.* $\bar{x}$ 22.8°C at Issa; daily minimum: $\bar{x}$ 16.5°C at Ngogo *cf.* $\bar{x}$ 16.5°C at Issa) and closed vegetation (daily mean: $\bar{x}$ 21.0°C at Ngogo *cf.* $\bar{x}$ 21.6°C at Issa; daily minimum: $\bar{x}$ 16.3°C at Ngogo *cf.* $\bar{x}$ 16.5°C at Issa). Hourly solar irradiance was similar on average between both closed vegetation patches at Ngogo and Issa, although ranges were wider at Issa (Figure S3).

Hourly travel distance

HTD related negatively to temperature for all groups, and this effect was stronger for each Ngogo study group compared to K0 at Issa (linear model: n = 1051 hr at Ngogo; n = 993 hr at Issa; R5 *cf.* K0 – posterior density $\bar{x}$ = -0.393, posterior probability = 100.0; RSW *cf.* K0 – PD $\bar{x}$ = -0.327, PP = 100.0; R2 *cf.* K0 – PD $\bar{x}$ = -0.330, PP = 100.0; RGS *cf.* K0 – PD $\bar{x}$ = -0.203, PP = 100.0; Figure S4; Table S3; Table S6). Ngogo groups travelled further per hour when in polyspecific association than when not, particularly with grey-cheeked mangabeys (PD $\bar{x}$ = 0.298, PP = 100.0; other species – PD $\bar{x}$ = 0.286, PP = 97.7). The effect of temperature on HTD did not vary when groups were in association, irrespective of species (Table S3).

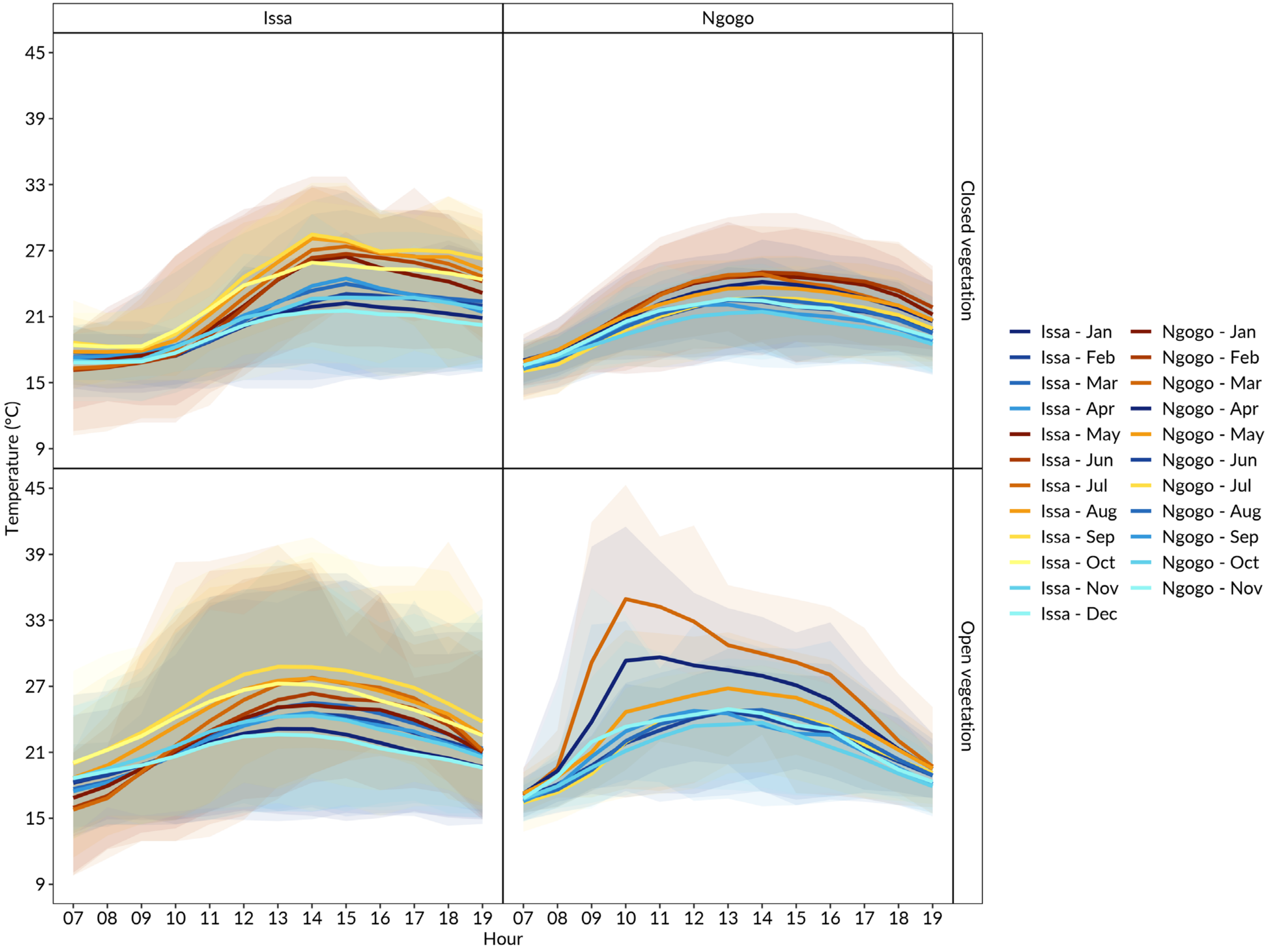

Figure 3 Monthly mean (lines) and minimum and maximum temperatures (7am – 7pm; shading) in closed vegetation (primary forest at Ngogo; riparian forest at Issa) and open vegetation (secondary forest at Ngogo; miombo woodland at Issa) by site. Blue colours indicate wet season months and orange colours indicate dry season months (<100mm mean monthly rainfall) during the study period.

Temperatures during open vegetation use

As food abundance in closed vegetation decreased, K1 and K2 at Issa were more likely to use open vegetation during hotter temperatures than RGS at Ngogo (linear model: $n = 653$ observations at Ngogo; $n = 489$ observations at Issa; RGS *cf.* K1 – posterior density $\bar{x} = 0.506$, posterior probability = 98.2; RGS *cf.* K2 – PD $\bar{x} = 1.591$, PP = 100.0; Figure S5a; Figure S5b; Table S4; Table S7). K2 also used open vegetation during hotter temperatures than K1 as closed vegetation food abundance fell (PD: -1.080 [-1.657 – -0.473], PP = 100.0).

RGS at Ngogo and K1 at Issa travelled during cooler temperatures than when stationary (PD $\bar{x} = 0.109$, PP = 70.4; Figure S5c; Table S7). In contrast, K2 did not rest or travel during substantially different temperatures in open vegetation (K2 *cf.* K1 – PD $\bar{x} = 0.570$, PP = 98.6).

Solar irradiance during open vegetation use

As food abundance in closed vegetation decreased, K1 and K2 at Issa were more likely to use areas of open vegetation exposed to higher solar irradiance than RGS, and to a lesser extent R6, at Ngogo (linear model: $n = 2203$ observations at Ngogo; $n = 442$ observations at Issa; RGS *cf.* K1 – posterior density $\bar{x} = 1.085$, posterior probability = 100.0; RGS *cf.* K2 – PD $\bar{x} = 0.628$, PP = 97.8; R6 *cf.* K1 – PD $\bar{x} = 0.846$, PP = 96.9; R6 *cf.* K2 – PD $\bar{x} = 0.390$, PP = 80.1; Figure S6a; Figure S6b; Table S5; Table S8).

K1, K2, and RGS did not travel in areas of open vegetation with lower solar irradiance than when stationary (K2 *cf.* K1 – PD $\bar{x} = 0.200$, PP = 71.4; RGS *cf.* K1 – PD $\bar{x} = -0.083$, PP = 63.7; Figure S6c; Table S8). R6 and R4 were more likely to travel in areas of higher solar irradiance compared to K1 (R6 *cf.* K1 – PD $\bar{x} = 0.525$, PP = 93.9; R4 *cf.* K1 – PD $\bar{x} = 0.547$, PP = 95.9).

Intra-group variation in open vegetation use at Issa

At Issa, age-sex classes in K1 and K2 used open vegetation during significantly different temperature ranges (Kruskal-Wallis: $H = 23.584$, $p < 0.001$; Figure 4a) but not in areas of significantly different solar irradiance (Kruskal-Wallis: $H = 2.511$, $p = 0.473$; Figure 4b). Adult males used open vegetation during significantly higher temperatures compared to adult females (Dunn's test: $Z = 3.571$, $p < 0.001$) and adult females with dependent infants ($Z = 3.721$, $p = 0.001$). Subadults also used open vegetation during significantly higher temperatures than adult females with infants ($Z = 2.911$, $p = 0.004$).

Issa monkeys did not exhibit active and non-active behaviours during significantly different temperatures (Mann-Whitney: $U = 16281$, $p = 0.079$; Figure 4c). In contrast, monkeys that were actively foraging or travelling used areas of open vegetation with significantly lower solar irradiance than when non-active ($U = 16229$, $p = 0.001$; Figure 4d).

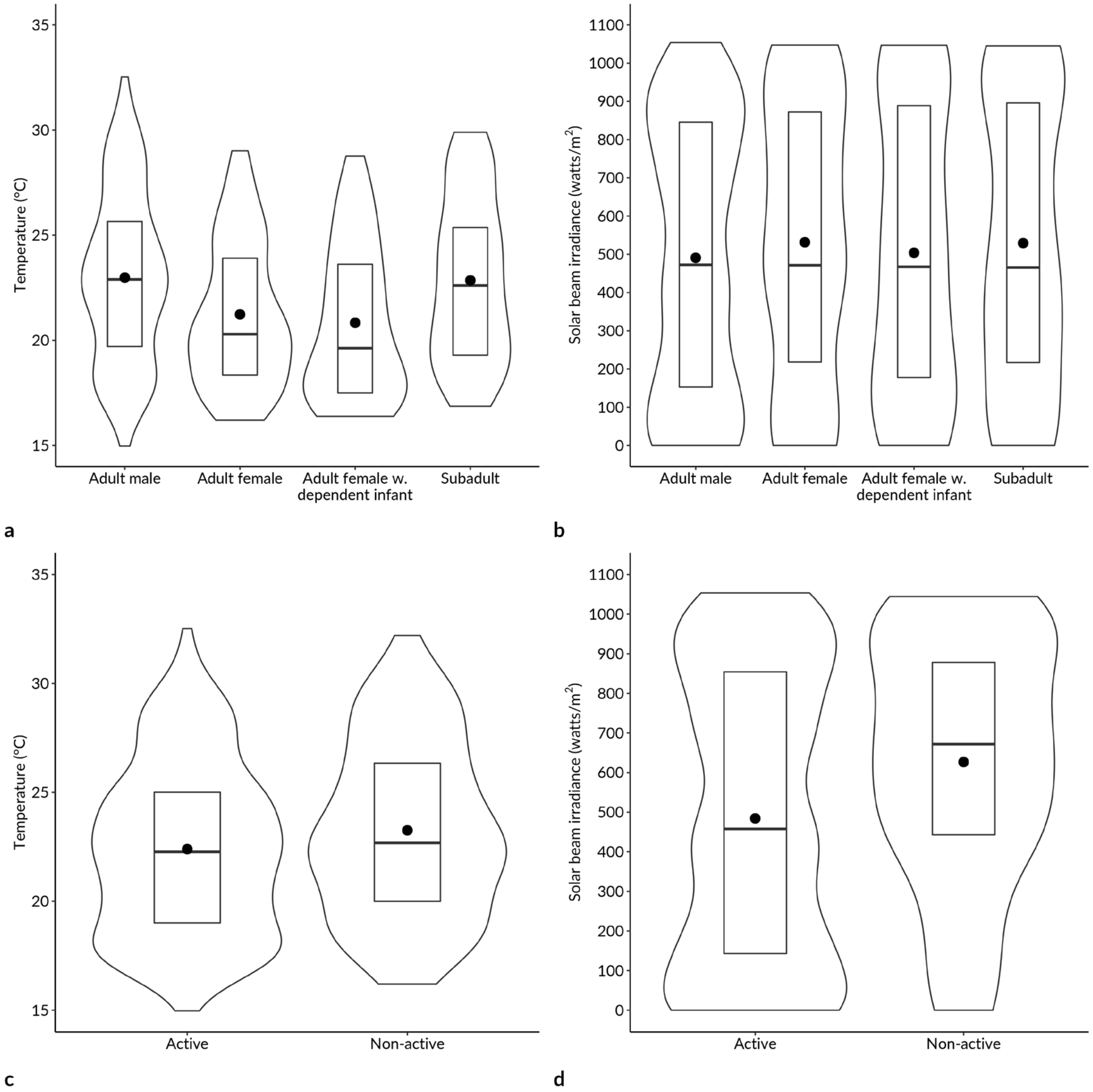

Figure 4 Temperatures and solar irradiance during miombo woodland use by red-tailed monkeys in K1 and K2 groups at Issa. Measures are stratified by focal individual age-sex class (a, b) and activity (c, d; bars = median values; dots = mean values; boxes = inter-quartile range; outlines = sample distribution).

Discussion

Thermal conditions in forest and savanna-woodland mosaics

Temperatures were higher in open than closed vegetation at both sites. Open vegetation temperatures were also higher than expected (>40°C during the dry season) at Ngogo than Issa. Average hourly solar irradiance was similar at both sites (Figure S3). Because this index was primarily a function of elevation, the wider ranges for irradiance at Issa mostly reflect the higher elevation of the site and steeper valleys that result in wider expanses of shade throughout the day. For both indices, we were able to satisfy a key assumption for this study – that ranges for thermal conditions at Ngogo were in fact comparable to those at Issa – so that we could directly compare open vegetation use by monkeys at each site under a null hypothesis that temperature and solar irradiance influence open vegetation use equally at both sites.

Temperature constrains travel speed across habitats

As temperatures increased, red-tailed monkeys at both sites reduced HTD. Furthermore, temperature was a stronger constraint on HTD for groups at Ngogo than at Issa, as predicted. McLester *et al.* (2019a) found daily travel distance related negatively to temperature across both Ngogo and Issa, but this effect did not differ significantly between sites. Instead, the effect of temperature on travel distance may only be observable at fine temporal (e.g. hourly) scales. For example, temperature ranges fluctuated more strongly in open than closed vegetation (Figure 3), especially during drier months at Ngogo, which should influence more rapid behavioural responses as groups travel between open and closed vegetation multiple times per day.

While temperature had the same effect on HTD irrespective of if groups were in polyspecific associations, travel speeds for all Ngogo groups were significantly higher when in association, and more so with grey-cheeked mangabeys. Associating with mangabeys is advantageous for red-tailed monkeys because mangabey males are more effective at deterring aerial predators, to the extent that red-tailed monkeys compete with conspecific groups for access to mangabeys (Brown 2013; Bryer *et al.* 2013). As such, red-tailed monkeys may expend more energy travelling to maintain these associations while mangabeys are within their home ranges (Chapman and Chapman 1996).

Thermal tolerance in open vegetation

During periods of low food (fruit, flowers, and leaves) availability, Issa monkeys used open vegetation during hotter temperatures and in areas of greater exposure to solar irradiance than at Ngogo, as we predicted. All three foods types were more variable across months at Issa than at Ngogo, with highest fruit and flower abundance found in open vegetation during late dry seasons when temperatures were highest (Figure S1). As such, Issa monkeys likely tolerated more challenging thermal conditions than groups at Ngogo to access food in open vegetation. In contrast, Ngogo monkeys may have been less dependent on open vegetation food given higher food availability in closed vegetation.

When in open vegetation, groups travelled during lower temperatures, as we expected, but this relationship was not stronger at Ngogo than at Issa. The exception was K2 at Issa, which travelled and stayed stationary during similar temperatures. Temperature ranges during observations of K2 were much lower than other groups, however (Figure S5c), meaning temperatures may not have been hot enough to significantly constrain group travel.

Groups in open vegetation were also not more likely to travel in areas of lower solar irradiance, irrespective of site. Compared to ambient temperature, we measured solar irradiance as a spatially-explicit metric of heat exposure that may be better explained by more spatially variable factors than our binary index of group travel. For example, predation risk may constrain foraging behaviour in open vegetation more than heat exposure. Monkeys at both sites may be comparably susceptible to predation from aerial predators in open canopy vegetation, while at Issa travelling terrestrially or foraging in low-lying woodland vegetation may increase vulnerability to carnivores (Cords 2002; McLester *et al.* 2018). Perceived predation risk is more likely a function of conditions that increase vulnerability than predator presence, meaning predation risk should influence open vegetation use similarly at both sites irrespective of inter-site differences in rates of predation attempts (Hill and Cowlishaw 2002). Diet may also influence fine-scale variation in open vegetation use if monkeys forage in areas of heat exposure only to obtain high-quality foods (see also Lile *et al.* 2020). For example, Cords (2002) found blue monkeys (*C. mitis*) were more likely to forage for protein-rich invertebrates in open tree crowns that were more exposed to both aerial predators and sunlight. Incorporating dietary preferences, especially for relatively heterogeneously distributed foods such as insects, should better inform the spatial dimensions of trade-offs influencing activity budgets in open vegetation.

At the individual level, Issa monkeys did not exhibit active and non-active behaviours during significantly different temperatures, but they foraged and travelled in areas of lower solar irradiance than when resting or exhibiting social behaviours, as expected. This discrepancy may reflect fine-scale, intra-group variation in thermoregulatory behaviour. For example, some individuals may increase inter-individual distances to access open vegetation while other group members remain stationary in closed vegetation, as a more energetically efficient alternative to increasing travel speed (Chapman and Chapman 2000; Ganas and Robbins 2005). At Issa, adult males and subadults were more likely to use open vegetation during hotter temperatures than females, supporting this hypothesis, especially as adult males exhibit higher inter-individual distances and spend more time in miombo woodland than other individuals (McLester *et al.* 2019a; Ch. 4). In contrast, we would expect future studies to find less intra-group variation in thermoregulatory behaviour at Ngogo. Ngogo monkeys travelled in and out of open vegetation patches as highly-cohesive groups and rarely spent time with group members spread across both vegetation classes (EM personal observation; see Methods). At the individual level, behavioural synchrony has important fitness benefits for group-living primates. For example, individuals that spread out to acquire food while other group members are resting or engaged in social interactions in close proximity may become isolated and at greater risk of predation at group edges (King and Cowlishaw 2009). As such, a relative abundance of food at Ngogo – at least in closed vegetation (Figure S1) – may mean group members are more likely to match thermoregulatory behaviour of conspecifics, such as prioritising resting over foraging, compared to Issa.

Forest loss can cause long-lasting thermal heterogeneity

At Ngogo, we found stronger effects of temperature on HTD, and weaker effects of food abundance on challenging conditions during open vegetation use, than at Issa. These results support characterisations of forests as relatively food-rich environments in which thermal conditions constrain group movements more strongly than food abundance; in contrast to savanna-mosaic environments, in which highly seasonal food availability means primates trade thermal exposure for food acquisition more often. At finer home range-wide scales, however, we found similarities in thermal conditions and monkey responses at both sites. We sampled temperature for one year at Ngogo and more data are required to determine if our measurements are outlying values, either compared to other years or to other patches of open vegetation. Nonetheless, during our study period, temperature ranges were similarly higher in open than closed vegetation at both sites. In addition, group-level responses (travelling *cf.* resting) to thermal conditions in open vegetation were similar at both sites. Comparable responses to harsher thermal conditions in open vegetation at both sites support previous hypotheses that heat exposure is an important driver of primate behaviour (e.g. reviewed in Hill *et al.* 2004). While such broad patterns can be hypothesized based on data from a single site or group, comparative studies are essential for testing their generality.

Unlike naturally occurring miombo woodland at Issa, secondary forest at Ngogo is the result of human activity (Lwanga 2003). Compared to old-growth primary forest, secondary forest at Kibale supports different community composition and densities of primates (e.g. Weisenseel *et al.* 1993; Lwanga 2006), likely due to lower plant food availability (Rode *et al.* 2006). Diet, activity budgets, ranging, and polyspecific associations of blue monkeys in secondary forest at Ngogo are associated with different arthropod communities and increased vulnerability to aerial predators compared to primary forest (Angedakin 2010). Our results provide further evidence that even after human deforestation has stopped, clearings have been protected, and vegetation has been allowed to recolonize, the ecology of subsequent regrowth may remain different to unlogged forest for multiple decades (e.g. in line with Chapman and Chapman 1999; Nummelin and Zilihona 2004). On average, each Ngogo group used secondary forest in significantly higher temperatures and solar irradiance than at least one of two groups in open vegetation at Issa. We collected our data as recently as 2019, indicating that after *ca.* 35 years of succession, thermal conditions likely still substantially affect how primates use secondary forest. How well primates can adapt to this vegetation over longer periods remains to be tested. It is currently unknown, for example, whether home ranges remain stable over time for groups that use secondary forest, or if other ecological factors (e.g. food abundance, which remains to be quantified in secondary forest at Ngogo) may drive long-term home range shifts if groups compete for access to primary forest.

Hominin responses to changing thermal conditions

Comparing primate adaptive responses to thermal conditions in environments that resemble paleohabitats can offer insight into how thermal pressures may have selected for extinct primate adaptations. While great apes are typically used to model hominin behaviour and ecology, cercopithecoid monkeys distributed across forest and savanna-woodland environments can also provide useful models for reconstructing environmental pressures that may have selected for behavioural adaptations in early hominins (Foley 1993; reviewed in Elton 2006). Thermoregulation would have been an important adaptive response in hominins as cooler forests contracted and were replaced by hotter mosaic environments in the Mio-Pliocene (Wheeler 1992, 1994; Passey *et al.* 2010). In these open environments, reduced canopy cover and lower water availability would have resulted in greater thermal stress than in forests (Wessling *et al.* 2018b).

The thermoregulatory behaviour that we observed in red-tailed monkeys resembles that predicted for hominins. For example, groups reduced travel speeds with hotter temperatures, and this effect was exacerbated in a savanna-mosaic with higher proportions of open vegetation. Hominins should also have optimised activity budgets by foraging during cooler temperatures and moving to shade during extreme heat (Wheeler 1994). Extant guenon survivability (presence / absence in a given location) is predicted by activity budgets; specifically, guenons are absent from sites where individuals are predicted to spend more time resting and travelling at the expense of foraging (Korstjens *et al.* 2018). The effect of thermal conditions on where and for how long hominins would have able to forage in open conditions would also likely have been an important constraint on hominin expansion into hotter, drier environments.

We also found savanna-mosaic dwelling red-tailed monkeys were more likely to use open vegetation during hotter temperatures and exposure to solar irradiance as food abundance in closed forest decreased, which we ascribed to the necessity of obtaining food that was more heterogeneously distributed and less abundant overall than in a predominantly forest environment. Thermal stress for hominins in hotter savanna-woodland mosaics would have been compounded by a scarcer distribution of food that required greater search effort and energetic expenditure to exploit (Isbell and Young 1996; Copeland 2009). For example, stable isotope and faunal fossil deposit data indicate that hominins (especially *Paranthropus* spp.) exhibited behavioural flexibility to access food in a diversity of paleohabitats, such as woodland-forest gradients and grasslands that separated forest patches (Lüdecke *et al.* 2018). Integrating both diet and ranging data into future studies should further disentangle trade-offs between food acquisition and avoidance of thermal stress in both extant and extinct primates.

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Supplementary material

S1 Calculation of temperature-humidity index

We weighted temperature measurements (>24°C) using the following formula (see Hill *et al.* 2004):

$$a = -8.784694756 + 1.61139411(b) + 2.338548839(c) - 0.14611605(b).(c) - 0.012308093(b)^2 - 0.016424827(c)^2 + 0.002211731667(b)^2.(c) + 0.00072546(b).(c)^2 - 0.000003582(b)^2.(c)^2$$

where a = heat-humidity index; b = temperature (degrees Celsius); c = relative humidity (%)

S2 Estimation of solar irradiance

We estimated solar beam irradiance (watts/m^2) per hour for grid cells across the extent of monkey home ranges at each site. We used the function *r.sun.incidout* in GRASS 7.8.1 (GRASS Development Team 2018), which estimates solar irradiance as a function of time of day, terrain aspect (angle), and terrain relief (e.g. shadowing caused by valleys or hills). We used the SRTM v4.1 digital elevation model (resolution = 92.5m; Jarvis *et al.* 2008) as the basis for aspect and slope inputs (calculated using the function *r.slope.aspect*). For each 92.5m grid cell, we calculated hourly solar irradiance from 7am – 7pm for each day of the year (1 – 365; not year-specific).

Because the output of *r.sun.incidout* assumes clear sky (i.e. no cloud cover that would otherwise block or reduce solar irradiance), we weighted our measures of solar irradiance using an index of cloud optical thickness. Cloud cover with greater optical thickness is more likely to block or reflect solar radiation (see e.g. Bishop & Rossow, 1991). We extracted values of cloud optical thickness recorded by NASA MODIS Aqua (MYD06_L2) and Terra (MOD06_L2) satellites (Platnick *et al.* 2015). Cloud optical thickness was recorded by each satellite once daily between 07:20 – 12:35h at a resolution (pixel size) of 1km and on a scale of 0 – 15,000. For each red-tailed monkey follow day, we sampled cloud optical thickness from 49 pixels (representative of a 49km^2 area) overlapping each study site. We reclassified the maximum sampled value for each day to a categorical scale with five bins:

Cloud optical thickness (pixel value)	**Weight**
0	1.0
1 – 3750	0.8
3751 – 7500	0.6
7501 – 11250	0.4
11251 – 15000	0.2

We multiplied each value of solar irradiance by the corresponding weight for that date. MODIS data were not available for dates prior to 2010; therefore, we did not weight solar irradiance values for follow days from 2008 – 2009 (n = 24).

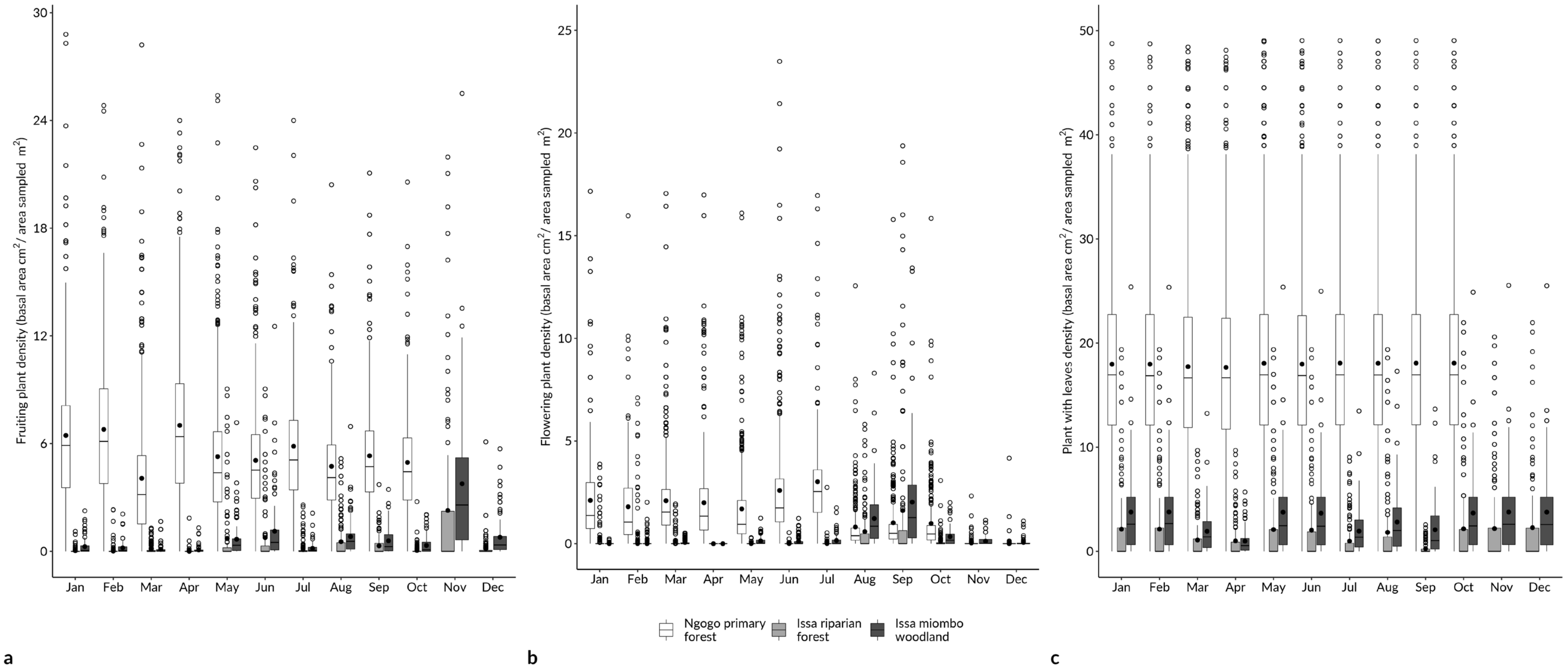

Figure S1 Site-wide indices of food abundance measured in vegetation sample plots in primary forest at Ngogo and riparian forest and miombo woodland at Issa. Values for fruiting plant density (a), flowering plant density (b), and plant with leaves density (c) are summarised by month for the duration of the study period at each site (black dots = mean values; circles = outlying values).

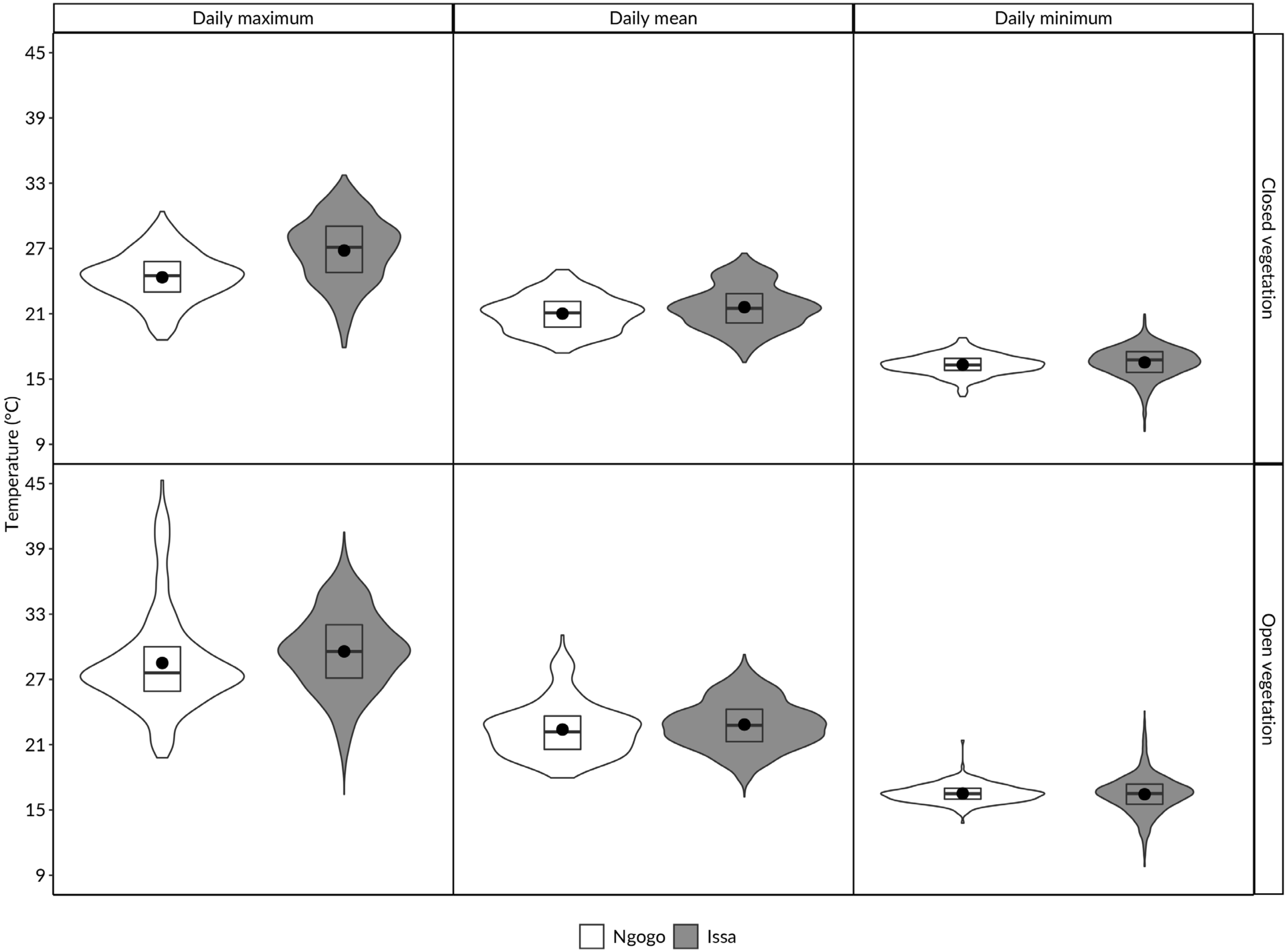

Figure S2 Daily mean, minimum, and maximum temperatures (7am – 7pm inclusive) for closed and open vegetation at both sites (bars = median values; dots = mean values; boxes = inter-quartile range; outlines = sample distribution).

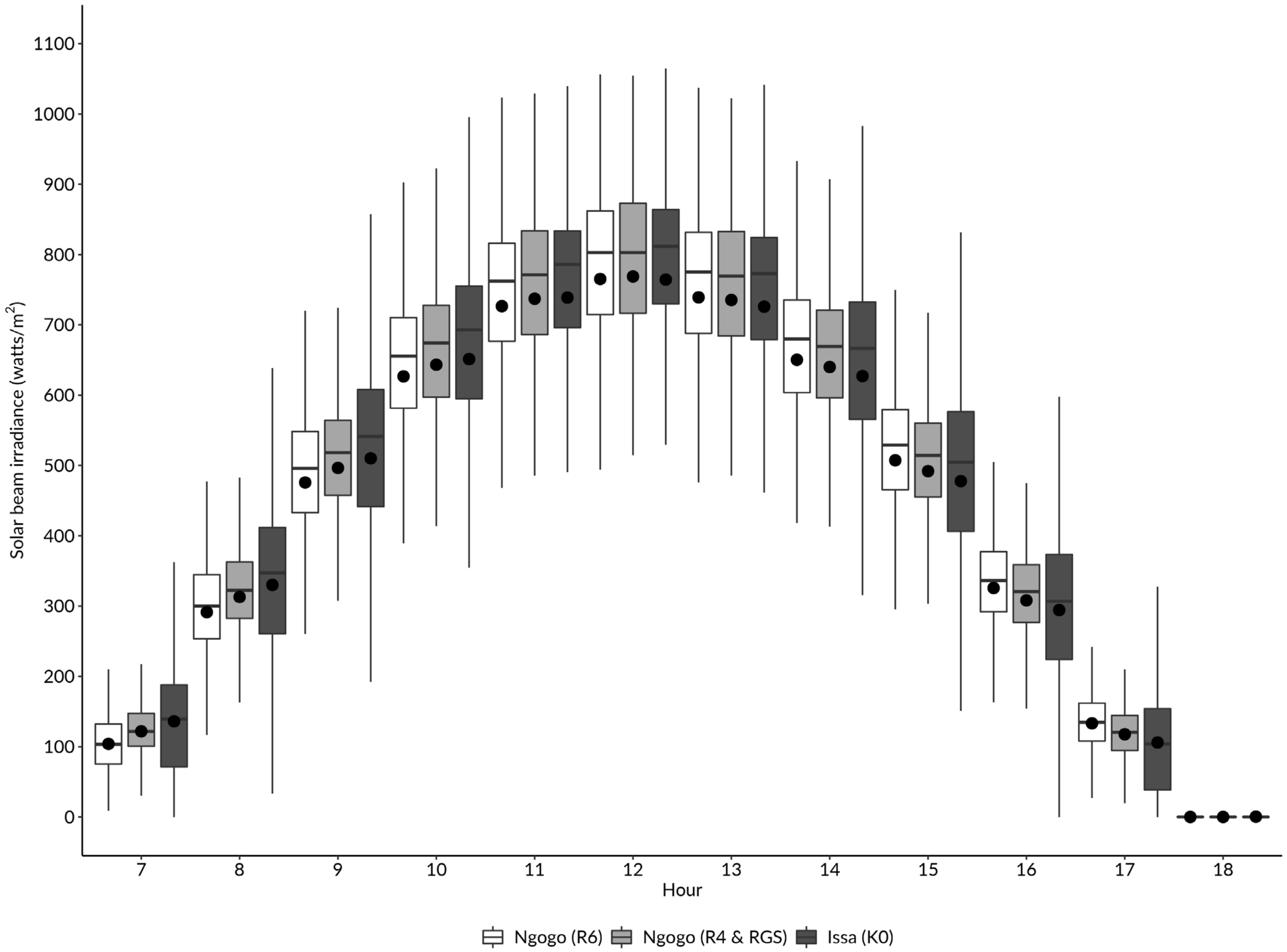

Figure S3 Hourly solar irradiance (7am – 7pm) for all days of the year (1 – 365) weighted by cloud cover in open vegetation at Ngogo and Issa. Measurements at Ngogo are shown separately for the secondary forest used by R6 compared to that used by R4 and RGS (Figure 2). Measurements at Issa are shown for miombo woodland across the extent of K0’s home range (bars = median values; dots = mean values; boxes = inter-quartile range; vertical lines = minimum and maximum values).

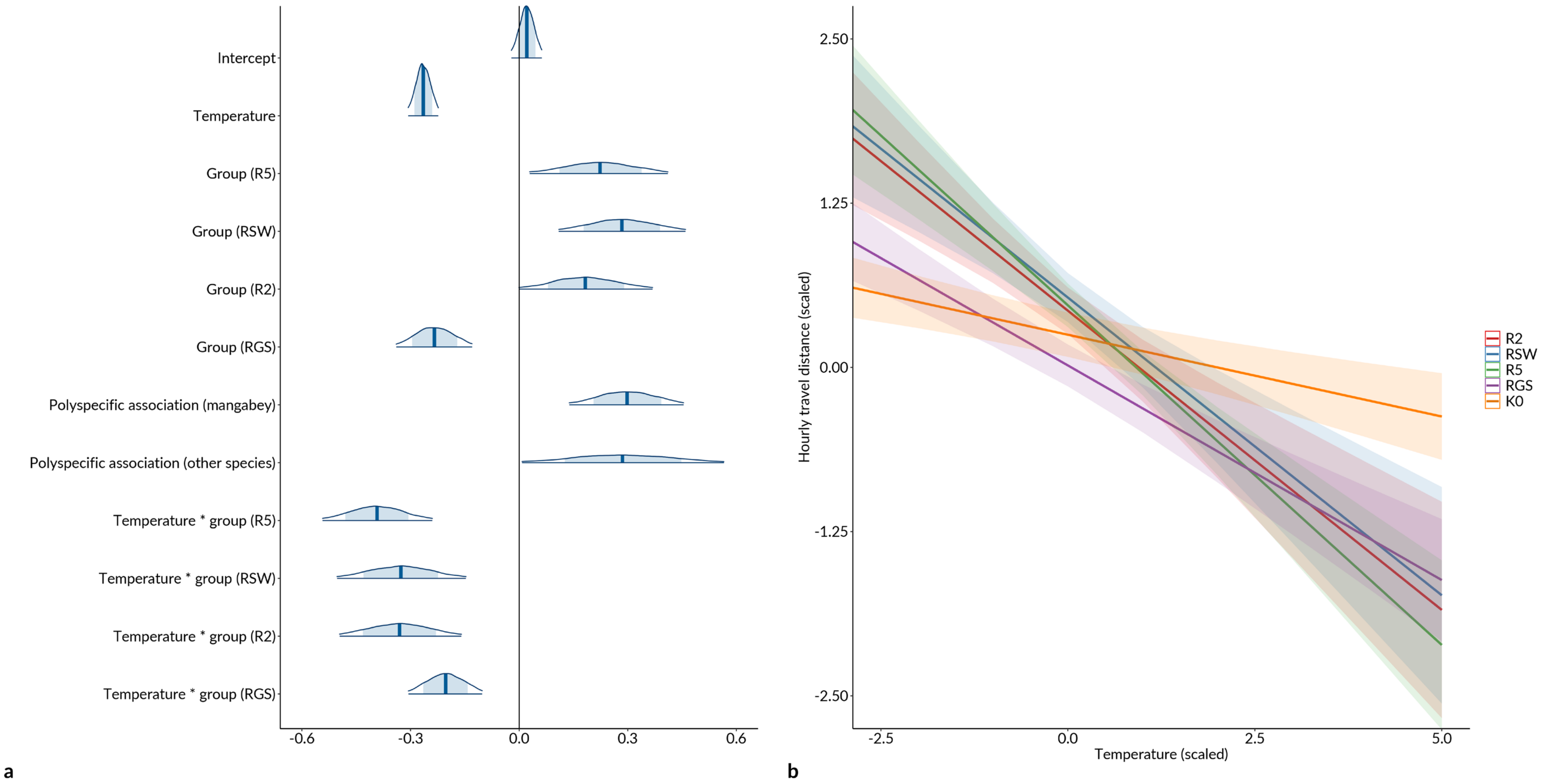

Figure S4 Fixed effects in model of hourly travel distance (Table S6). (a) Upper and lower 95% (distributions) and 75% (blue shading) highest posterior density intervals. (b) Interaction between temperature and group. Bands indicate confidence intervals derived from equivalent generalized least squares regression. Reference levels: group = “K0”; polyspecific association = “not in association”.

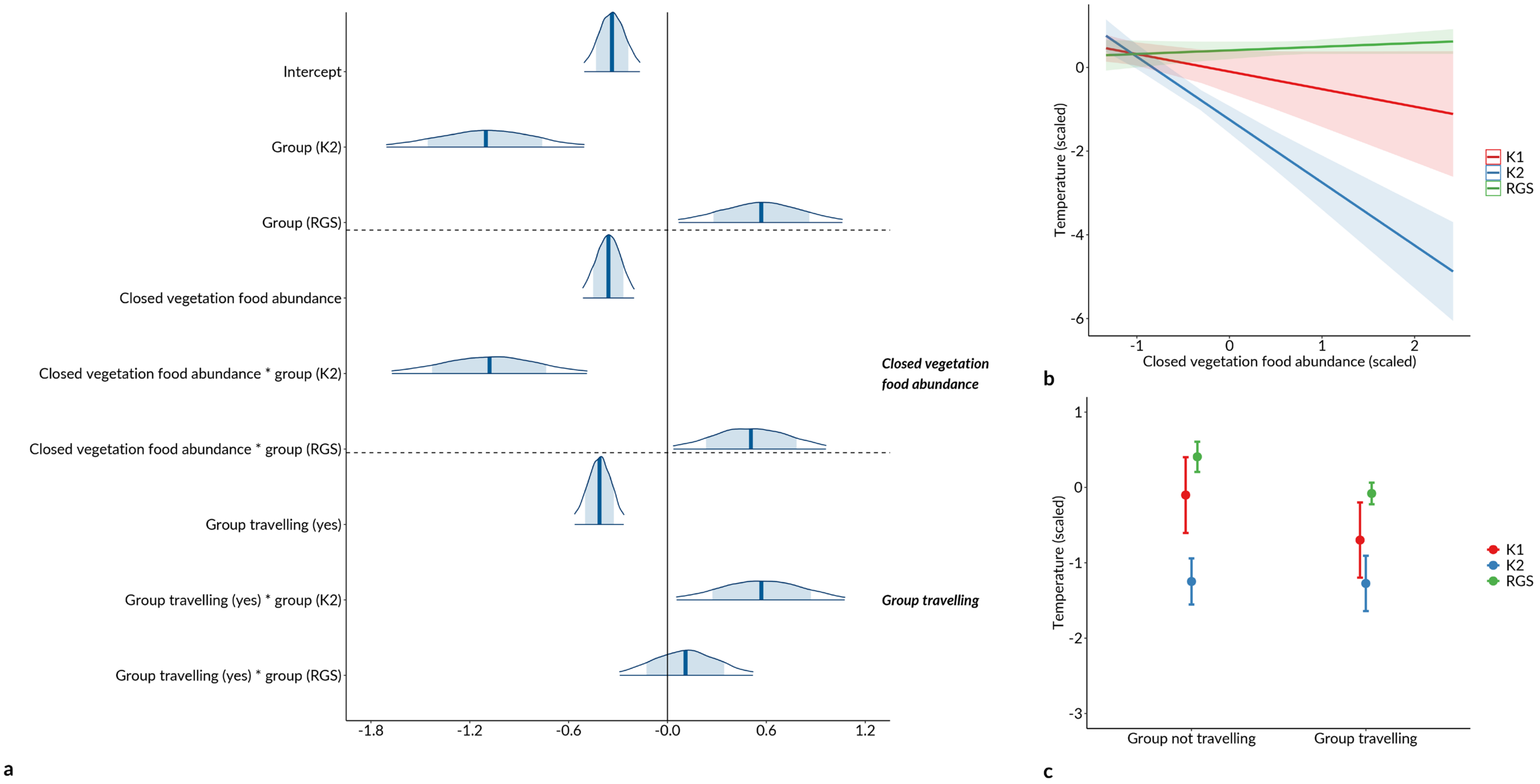

Figure S5 Fixed effects in model of temperature during open vegetation use (Table S7). (a) Upper and lower 95% (distributions) and 75% (blue shading) highest posterior density intervals grouped by hypothesis (dashed lines). (b) Interaction between food abundance in closed vegetation and group. Bands indicate confidence intervals derived from equivalent generalized least squares regression. (c) Interaction between group travelling and group. Reference levels: group = “K1”; group travelling = “group not travelling”.

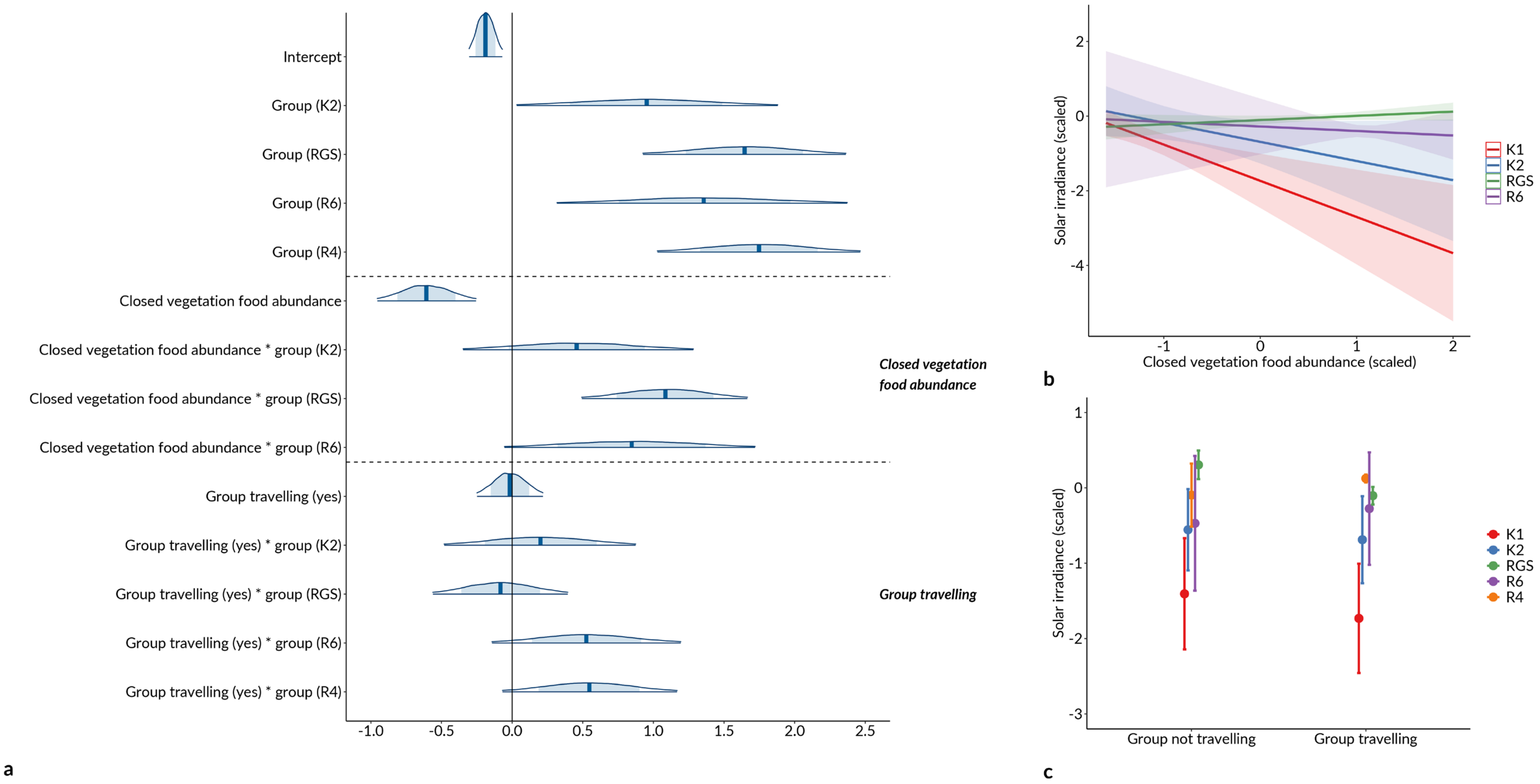

Figure S6 Fixed effects in model of solar irradiance during open vegetation use (Table S8). (a) Upper and lower 95% (distributions) and 75% (blue shading) highest posterior density intervals grouped by hypothesis (dashed lines). (b) Interaction between food abundance in closed vegetation and group. Bands indicate confidence intervals derived from equivalent generalized least squares regression. (c) Interaction between group travelling and group. Reference levels: group = “K1”; group travelling = “group not travelling”.

Table S1 Re-classification of focal individual ethogram as either “active” (associated with foraging) or “non-active” (social or resting) behaviour.

Focal behaviour	**Re-classification**
Eating	Active
Drinking	
Travelling	
Scanning ("visual scanning directed beyond arm's reach" in any context – Treves, 1998)	
Resting	Non-active
Grooming	
Self-grooming	
Playing	
Copulating	
Conspecific aggression	

Table S2 List of plant species at each study site for which basal area and phenology measures were available and used to estimate fruiting stem, flowering stem, and stem with leaves abundance.

Study site	**Family**	**Species**
Ngogo	Anacardiaceae	*Pseudospondias microcarpa*
Ngogo	Annonaceae	*Monodora myristica*
Ngogo	Annonaceae	*Uvariopsis congensis*
Ngogo	Apocynaceae	*Tabernaemontana spp.*
Ngogo	Bignoniaceae	*Spathodea campanulata*
Ngogo	Canellaceae	*Warburgia ugandensis*
Ngogo	Cannabaceae	*Celtis durandii*
Ngogo	Ebenaceae	*Diospyros abyssinica*
Ngogo	Fabaceae	*Erythrina excelsa*
Ngogo	Fabaceae	*Millettia dura*
Ngogo	Flacourtiaceae	*Dasylepis eggelingii*
Ngogo	Meliaceae	*Trichilia dregeana*
Ngogo	Moraceae	*Bosqueia phoberos*
Ngogo	Moraceae	*Ficus brachylepis*
Ngogo	Moraceae	*Ficus dawei*
Ngogo	Moraceae	*Ficus mucuso*
Ngogo	Moraceae	*Ficus natalensis*
Ngogo	Moraceae	*Morus lactea*
Ngogo	Moraceae	*Treculia africana*
Ngogo	Rutaceae	*Teclea nobilis*
Ngogo	Sapindaceae	*Aphania senegalensis*
Ngogo	Sapindaceae	*Blighia unijugata*
Ngogo	Sapindaceae	*Zanha golungensis*
Ngogo	Sapotaceae	*Aningeria altissima*
Ngogo	Sapotaceae	*Chrysophyllum albidum*
Ngogo	Sapotaceae	*Mimusops bagshawei*
Ngogo	Verbenaceae	*Premna angolensis*
Issa Valley	Anacardiaceae	*Lannea schimperi*
Issa Valley	Anisophylleaceae	*Anisophyllea boehmii*
Issa Valley	Annonaceae	*Annona senegalensis*
Issa Valley	Apocynaceae	*Diplorhynchus condylocarpon*
Issa Valley	Apocynaceae	*Saba comorensis*
Issa Valley	Chrysobalanaceae	*Parinari curatellifolia*
Issa Valley	Clusiaceae	*Garcinia huillensis*
Issa Valley	Combretaceae	*Combretum molle*
Issa Valley	Combretaceae	*Terminalia mollis*
Issa Valley	Euphorbiaceae	*Pseudolachnostylis maprouneifolia*
Issa Valley	Fabaceae	*Brachystegia spiciformis*
Issa Valley	Fabaceae	*Isoberlinia angolensis*
Issa Valley	Fabaceae	*Julbernardia unijugata*
Issa Valley	Fabaceae	*Piliostigma thonningii*
Issa Valley	Fabaceae	*Pterocarpus tinctorius*
Issa Valley	Flacourtiaceae	*Flacourtia indica*
Issa Valley	Loganiaceae	*Strychnos cocculoides*
Issa Valley	Loganiaceae	*Strychnos madagascariensis*
Issa Valley	Loganiaceae	*Strychnos spinosa*
Issa Valley	Olacaceae	*Ximenia americana*
Issa Valley	Phyllanthaceae	*Uapaca nitida*
Issa Valley	Rhamnaceae	*Ziziphus abyssinica*
Issa Valley	Rubiaceae	*Canthium burthii*
Issa Valley	Verbenaceae	*Vitex mombassae*

Table S3 HTD model selection using deviance information criterion (DIC) ranks. Models comprise each possible combination of fixed interaction and main effects, a model with only interaction main effects, and a null model with no fixed effects. Model structures indicate included interactions (bold italics = selected best fitting model).

Model structure	**Degrees of freedom**	**DIC**	**DIC ∆ null model**	**Weight**
Null (no fixed effects)	2	5803.63	-	<0.01
Main effects only	10	5594.98	-208.65	<0.01
A	***14***	5554.60	-249.03	***0.73***
B	13	5576.88	-226.75	<0.01
AB	17	5556.64	-246.99	0.27

A = temperature * group

B = temperature * polyspecific association

Table S4 Temperature during open vegetation use model selection using deviance information criterion (DIC) ranks. Models comprise each possible combination of fixed interaction and main effects, a model with only interaction main effects, and a null model with no fixed effects. Model structures indicate included interactions (bold italics = selected best fitting model).

Model structure	**Degrees of freedom**	**DIC**	**DIC ∆ null model**	**Weight**
Null (no fixed effects)	2	3243.86	-	<0.01
Main effects only	7	3143.20	-100.66	<0.01
A	9	3119.49	-124.37	<0.01
B	10	3133.40	-110.46	<0.01
AB	***12***	***3082.20***	***-161.66***	***1.00***

A = group * closed vegetation food abundance

B = group * group travelling

Table S5 Solar irradiance during open vegetation use model selection using deviance information criterion (DIC) ranks. Models comprise each possible combination of fixed interaction and main effects, a model with only interaction main effects, and a null model with no fixed effects. Model structures indicate included interactions (bold italics = selected best fitting model).

Model structure	**Degrees of freedom**	**DIC**	**DIC ∆ null model**	**Weight**
Null (no fixed effects)	2	7509.18	-	<0.01
Main effects only	9	7423.21	-85.96	<0.01
A	12	7413.02	-96.16	0.07
B	14	7418.43	-90.75	<0.01
AB	***17***	***7407.95***	***-101.23***	***0.92***

A = group * closed vegetation food abundance

B = group * group travelling

Table S6 Summary output for the best fitting model of HTD, as selected in Table S3 (parentheses = categorical variable levels; CI = credible interval).

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	Posterior probability
Intercept	0.021	-0.021	0.063	84.0
Temperature	-0.265	-0.306	-0.223	100.0
Group (R5) †	0.223	0.025	0.404	98.9
Group (RSW) †	0.284	0.109	0.459	99.9
Group (R2) †	0.183	-0.003	0.367	97.4
Group (RGS) †	-0.234	-0.335	-0.126	100.0
Polyspecific association (mangabey) ‡	0.298	0.139	0.454	100.0
Polyspecific association (other species) ‡	0.286	0.009	0.566	97.7
Interaction: temperature*group (R5) †	-0.393	-0.547	-0.246	100.0
Interaction: temperature*group (RSW) †	-0.327	-0.502	-0.147	100.0
Interaction: temperature*group (R2) †	-0.330	-0.499	-0.164	100.0
Interaction: temperature*group (RGS) †	-0.203	-0.306	-0.102	100.0

† Reference: K0

‡ Reference: not in polyspecific association

Table S7 Summary output for the best fitting model of temperature during open vegetation use, as selected in Table S4 (parentheses = categorical variable levels; CI = credible interval).

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	Posterior probability
Intercept	-0.337	-0.501	-0.164	100.0
Closed vegetation food abundance	-0.359	-0.515	-0.206	100.0
Group travelling (yes) †	-0.413	-0.565	-0.267	100.0
Group (K2) ‡	-1.102	-1.671	-0.477	100.0
Group (RGS) ‡	0.569	0.062	1.055	98.7
Interaction: closed vegetation food abundance*group (K2) ‡	-1.080	-1.657	-0.473	100.0
Interaction: closed vegetation food abundance*group (RGS) ‡	0.506	0.049	0.973	98.2
Interaction: group travelling (yes)*group (K2) †	0.570	0.040	1.051	98.6
Interaction: group travelling (yes)*group (RGS) †	0.109	-0.297	0.509	70.4

† Reference: group not travelling

‡ Reference: K1

Table S8 Summary output for the best fitting model of solar irradiance during open vegetation use, as selected in Table S5 (parentheses = categorical variable levels; CI = credible interval).

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	Posterior probability
Intercept	-0.189	-0.305	-0.071	99.9
Closed vegetation food abundance	-0.607	-0.944	-0.246	100.0
Group travelling (yes) †	-0.016	-0.254	0.210	55.5
Group (K2) ‡	0.953	0.053	1.894	97.8
Group (RGS) ‡	1.646	0.910	2.345	100.0
Group (R4) ‡	1.357	0.317	2.373	99.3
Group (R6) ‡	1.748	1.021	2.455	100.0
Interaction: closed vegetation food abundance*group (K2)	0.457	-0.367	1.248	86.3
Interaction: closed vegetation food abundance*group (RGS)	1.085	0.502	1.672	100.0
Interaction: closed vegetation food abundance*group (R6)	0.846	-0.026	1.741	96.9
Interaction: group travelling (yes)*group (K2)	0.200	-0.479	0.875	71.4
Interaction: group travelling (yes)*group (RGS)	-0.083	-0.538	0.413	63.7
Interaction: group travelling (yes)*group (R6)	0.525	-0.136	1.198	93.9
Interaction: group travelling (yes)*group (R4)	0.547	-0.085	1.151	95.9

† Reference: group not travelling

‡ Reference: K1

Supplementary references

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Title: Food availability influences strategies of intra-group cohesion in red-tailed monkeys (*Cercopithecus ascanius*)

Edward McLester [a] & Michelle Brown [b]

[a] School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK
[b] Department of Anthropology, University of California, Santa Barbara, USA

Abstract

A key trade-off for group-living animals is balancing increased collective foraging effort against intra-group feeding competition. In non-fission-fusion groups, this trade-off should be reflected in intra-group spatial cohesion (relative spatial proximity among individuals). When food is scarce, individuals may increase cohesion to benefit from social foraging or spread out to acquire resources as an alternative to increasing group travel. Moreover, age-sex classes with greater expected nutritional requirements and foraging individuals should spread out further to reduce competition. We investigated how food abundance influences spatial cohesion in red-tailed monkeys (*Cercopithecus ascanius*) at Ngogo (Uganda), depending on three factors: group travel speed; individual age-sex class; and individual behaviour (foraging *cf.* resting or social behaviour). We collected 15-minute interval scans of inter-individual distances and 1-minute interval GPS coordinates from six groups over 13 months. We modelled two indices of cohesion for focal individuals – 1) nearest neighbour distance, and 2) area of Voronoi tessellations ("domains") calculated from ≥3 nearest neighbour distances – against group travel speed (per 15 minutes) and a spatio-temporal model of food abundance (fruit; flowers; leaves). When food abundance was low, monkeys increased nearest neighbour distance as groups travelled slower, and domain sizes were smaller. Nearest neighbour distance related negatively to food abundance for adult males, adult females with infants, and juveniles and positively for subadults and adult females without infants. Individuals increased nearest neighbour distance and domain size when they or neighbours were actively foraging, irrespective of food abundance. Spreading out to reach new food patches may be an effective alternative to increasing group travel. At the individual level, variation in cohesion between age-sex classes and foraging *cf.* non-foraging individuals may reflect trade-offs between reducing competition and social foraging.

Introduction

To benefit from group-living, animals must maintain sociality while minimising costs associated with gregariousness (Andrews and Rosenblum 1995; Ward and Webster 2016). For example, optimal foraging efficiency reflects a trade-off between greater collective search effort, but increased intra-group competition, as gregariousness increases (Janson and Goldsmith 1995; Chapman and Chapman 2000a; Chapman and Chapman 2000b). Among primates, this trade-off is an important selective pressure on social structure, which comprises varying degrees of spatial cohesion across the Order (Wrangham 1980). Spatial cohesion refers to how closely individuals position themselves to other group members, where greater cohesion reflects denser clumping of individuals (Boinski *et al.* 2000; LaBarge *et al.* 2020; synonymous with "group spread" in Smith *et al.* 2005). Some species exhibit fluid, fission-fusion systems that facilitate complete separation between individuals over large spatial and temporal scales (Aureli *et al.* 2008; Grove 2012). More commonly, primates live in stable, cohesive groups that exhibit little or no fission-fusion dynamics. For these species, strategies of maximising foraging efficiency are reflected in spatial cohesion at the individual level. How and where individuals position themselves relative to other group members should be a function of both social and ecological factors that influence foraging efficiency, including food availability (reviewed in Clutton-Brock and Janson 2012), group ranging (Chapman and Chapman 2000b), identities of neighbouring con- and heterospecifics (Janson 1990; Bryer *et al.* 2013), and predation risk (Isbell and Enstam 2002; reviewed in Hirsch 2007). As such, investigating intra-group spatial cohesion can provide insight into how group members both maintain cohesive groups and meet individual energetic requirements while environmental conditions vary over time.

Food abundance and distribution are important drivers of intra-group feeding competition that have been investigated extensively at the group level as determinants of group-living. For example, groups should forage over an area with sufficient food to meet individual energetic requirements or a smaller group size will become advantageous (Chapman and Chapman 2000a). Empirically, intra-group feeding competition relates negatively to group size among numerous primate species (Garber 1987; Wrangham *et al.* 1993; Janson and Goldsmith 1995; see also Korstjens *et al.* 2018). Social structure is also associated with food abundance, particularly in species that exhibit high fission-fusion. For example, spider monkeys (*Ateles* spp.) exhibit smaller party sizes when food is scarce, likely to mitigate greater feeding competition (Garber 1987; McFarland Symington 1988). Chimpanzees (*Pan troglodytes*) also exhibit higher rates of fission and smaller party sizes when food is more patchily distributed (Newton-Fisher *et al.* 2000; Basabose 2004). Despite the generality of these hypotheses, there have been fewer studies of how food abundance may similarly influence group cohesion at the individual level (e.g. Irwin 2007; Samuni *et al.* 2019). For example, as food abundance decreases and food patch depletion increases, groups could increase travel distances to discover new patches. Group travel is an energetically expensive behaviour that requires all group members to move collectively, irrespective of individual motivations (Chapman 1988; King and Sueur 2011). Instead, group members may improve foraging effort by reducing cohesion at the individual level. Spreading out should allow individuals to increase their own search fields and reduce intra-group competition (Chapman and Chapman 2000a). As such, reducing cohesion may be an alternative to group travel, especially in large groups in which collective travel requires compromises between many individuals, or when food is scarce or widely scattered (Gillespie and Chapman 2001; Isbell 2012).

Not all individuals in a group may respond similarly to feeding competition, leading to variation in spatial cohesion among individuals as food abundance decreases. For example, nutritional requirements differ between broad age-sex classes. Fast-growing juveniles and lactating females with dependent infants usually have higher nutritional requirements than other individuals (Felton *et al.* 2009) but are typically most vulnerable to predation (Boinski *et al.* 2000). In areas of low food availability, these individuals may be more likely to increase otherwise short inter-individual distances that diffuse predation risk (Treves 2000). The location and behaviour of individuals also indirectly provide information to other group members as to food location (Garber 2000; Fischer and Zinner 2011). As such, cohesion may increase for some individuals as they or neighbours reduce inter-individual distances to exploit visual cues that improve foraging success (Vickery *et al.* 1991; Garber 2000; Galef and Giraldeau 2001; see also Chauvin and Thierry 2005). For example, foraging behaviour can indicate either a source of food to be joined, or potential feeding competition to avoid (Garber 2000; Garber *et al.* 2009; King *et al.* 2009; reviewed in Hirsch 2007). Older individuals with more experience of food locations should be more likely to attract other individuals, especially when food is scarcer (King 1991; Zuberbühler and Janmaat 2010; Pyritz *et al.* 2011).

We investigated the influence of food availability on intra-group spatial cohesion in the red-tailed monkey (*Cercopithecus ascanius*). At Ngogo, Uganda, this species lives in uni-male groups that exhibit minimal fission-fusion, while fruiting and flowering plant abundance vary substantially across small spatial (50m) and temporal (monthly) scales (Struhsaker 1997; McLester *et al.* 2019). We tested the hypothesis that individuals adjust spatial cohesion (distances to neighbouring individuals) in response to variation in food abundance, depending on three social factors. First, when food abundance is low we predicted that individuals are more likely to spread out as groups travel slower. Second, we predicted that as food abundance decreases, individuals with higher nutritional requirements (e.g. juveniles and females with dependent infants) are more likely to spread out than other individuals. Third, we predicted that individuals actively foraging (*cf.* resting or engaged in social behaviours) spread out further when neighbours are also foraging, and this effect is stronger when food abundance is lower.

Methods

Data collection

We collected data at Ngogo, Kibale National Park (Uganda), a mosaic of predominantly closed canopy primary forest and small patches of mixed canopy cover secondary forest (Struhsaker 1997). We followed six habituated red-tailed monkey groups between March – October 2017 and January – June 2019 (6 – 112 follow days per group; Table 1). Groups each comprised one adult male and multiple adult females, subadults, and juveniles, and ranged in size from 16 – 35 total individuals (see Table 1 for detailed group compositions). At Ngogo, red-tailed monkeys associate with six other primates (grey-cheeked mangabey, *Lophocebus albigena*; blue monkey, *C. mitis*; L'Hoest's monkey, *Allochrocebus lhoesti*; black and white colobus, *Colobus guereza*; red colobus, *Piliocolobus tephrosceles*; olive baboon, *Papio anubis*), of which some mangabey and blue monkey groups were habituated to researcher presence.

We collected behavioural data during all-day (7am-7pm) follows of groups. We recorded 15-minute interval scans of focal individuals using ODK Collect on ASUS Z130C Android tablets. To minimise temporal autocorrelation, we did not record scans from consecutive individuals of the same identity (or age-sex class, if identity was unknown). For each scan, we noted the following: focal age-sex class, behaviour, and vegetation class; distance to the nearest six neighbours; neighbour age-sex classes and behaviours (or species, for heterospecifics). We also recorded whether the focal was in the group core or periphery (an outermost individual located beyond any other group member – Morrell *et al.* 2010). We categorised age-sex classes as adult male (testicles fully descended and typically blue coloured), adult female (nipples clearly visible), adult female with dependent infant (in

Table 1 Details of follow days, age-sex class compositions, and proportion of time spent in association with other species (*n* = 38 – 2428 focal scans per group) for each study group.

Group	Follow period [follow days]	Sample size (*n* focal scans)		Group composition					Time in polyspecific association (%)			
		Nearest neighbour distance	**Domain size**	**Total size**	**Adult males**	**Adult females [with dependent infants]**	**Subadults**	**Juveniles**	**Grey-cheeked mangabey (*Lophocebus albigena*)**	**Blue monkey (*Cercopithecus mitis*)**	**Other species**	**Not in association**
R6	Mar – Jun 2017 [*n* = 71]	1026	363	~35	2	~20 [3] adult females and subadults		~8	35.9	69.9	1.1	15.7
R5	Jul – Oct 2017 [*n* = 89]	1984	371	~25	1	~16 [1] adult females and subadults		~5	37.6	0.2	1.4	61.3
	Jan – Feb 2019 [*n* = 23]			~30	1	14-16 [5-6]	9-10	4-5				
R2	Jan – Mar 2019 [*n* = 24]	376	16	16	1	7 [5]	6	2	38.0	25.5	9.2	43.1
RSW	Jan 2019 [*n* = 9]	294	26	16-17	1	9 [4]	6-7	0	32.0	2.3	4.9	63.7
	Mar – Apr 2019 [*n* = 13]			18-19	1	9 [7]	6-7	2				
RB	Mar – May 2019 [*n* = 6]	27	-	~20	1	≥7	≥3	?	21.1	0.0	0.0	78.9
RGS	Apr – May 2019 [*n* = 46]	635	26	17	1	5 [2]	7	4	8.9	1.0	4.1	88.0
	Jun 2019 [*n* = 26]			19	1	5 [0]	7	6				

>50% of incidences female carries infant between trees, infant spends >50% of time in close association [<2m] with female, and infant suckles frequently), subadult (testicles and nipples paler and shorter than adults, if visible), and juvenile (body size substantially smaller than subadults; following Cords 1987; Brown 2013). During follows we also recorded GPS coordinates at automatic 1-minute intervals using a Garmin Rino 650 unit.

We paused data collection while groups were in proximity (<30m) to conspecific groups because inter-group interactions in red-tailed monkeys are often antagonistic (Brown 2013) and likely influence spatial cohesion (e.g. LaBarge *et al.* 2020). Similarly, we did not collect focal data during group alarm responses to potential threats – typified by fleeing, alarm vocalising, and increases in vigilance behaviour – because these behaviours are more likely to be individual responses than coordinated among group members (Cords 1987; Boinski *et al.* 2000). We resumed data collection only when most (*ca.* >75%) individuals had resumed normal foraging or social behaviours. The presence alone of a potential predator (most frequently chimpanzees, *Pan troglodytes* and crowned hawk-eagles, *Stephanoaetus coronatus*) did not always elicit a visible alarm response from any or all group members. To control for predation risk in analyses, we therefore also recorded *ad libitum* when potential predators encountered and moved away from groups (and vice versa). Because we could not always accurately identify how long a potential predator was in proximity or detectable by monkeys, we made conservative estimates by extending durations of known potential predator presence by 30 minutes before and after observations.

We measured food abundance following McLester *et al.* (2019). In 2009 and 2012-13 we sampled 272 50 x 50 m vegetation plots located at 50 m intervals in primary forest across the extent of study group home ranges. Within each plot, we identified stems of 34 plant species (selected as comprising ≥1% of the red-tailed monkey or grey-cheeked mangabey diet – see Brown 2013) and recorded diameter at breast height (DBH) of each stem. We ignored stems of diameter <10 cm, except for lianas which were measured regardless of size. Corresponding phenology data were collected by Ngogo Chimpanzee Project field assistants using monthly trails, along which marked plants (n = 511 stems) identified to species level were examined for presence of ripe and unripe fruit, flowers, and new, young, and mature leaves.

Data analyses

We calculated two indices of spatial cohesion. First, we used distance from the focal individual to the nearest neighbour to test effects of neighbour identity and behaviour. Second, to test a more spatially explicit measure of cohesion, we used scans for which at least the three nearest neighbours were visible to calculate the area of a three-dimensional Voronoi tessellation for the focal individual (hereafter, “domain”; unit = m^3; following Hamilton 1971; see also Morrell *et al.* 2010; Josephs *et al.* 2016). Because it was not possible to record angles or bearings of neighbours relative to the focal individual, we used NetLogo 3D 6.1.1 (Wilensky 1999) to calculate mean domain size based on 2500 random permutations of neighbour positions at their observed distances. We set the limit for infinite tessellations as 15m for individuals in the group periphery (the 99th percentile of maximum neighbour distance for all scans and based on typical visibility at Ngogo – following Josephs *et al.* 2016) and as the maximum neighbour distance recorded per scan for individuals in the group core (see Figure 1 for an example permutation; see supplementary material S1 for NetLogo code).

We re-categorised behaviour as either "active" or "non-active" depending on its association with foraging effort (Table S1; following Starr *et al.* 2012). Where monkeys were engaged in social behaviour with one or more other individuals directly next to them (grooming, playing, suckling, copulating, or aggression), we considered these monkeys as a single entity and used one distance to all of the individuals in the interaction combined. In all scans, focal individuals were arboreal. We used QGIS v3.10 (QGIS Development Team 2019) to calculate group travel speed for each scan as the summed Euclidean distance between the 16 consecutive 1-minute GPS coordinates immediately preceding the scan.

We calculated a spatio-temporal index of food abundance (*n* = 27 plant species), detailed in full in McLester *et al.* (2019). For each sample plot, we converted stem DBH into basal area. We used spatial interpolations in GRASS GIS 7.4 (GRASS Development Team 2018) to interpolate distributions of basal area for each plant species in primary forest across the extent of study group home ranges. We categorized phenology observations into binary presence-absence measures of three plant parts (fruit; flowers; leaves). For each interpolated grid cell, we multiplied basal area for each species by monthly proportions (0–1) of stems with each plant part present. We summed these weighted measurements for each plant part across all species and resampled the resulting distributions to a 50 x 50m grid laid over the study site using maximum plant part abundance for each species. We scaled fruit, flower, and leaf abundance, weighted each measurement by proportion of red-tailed monkey diet at Ngogo ($\bar{x}$: fruit = 79%; flowers = 11%; leaves = 10% – MB unpublished data), and summed all three measurements for a single index of food abundance that we matched to scans by corresponding grid cell and month.

Statistical analyses

We used the package *MCMCglmm* in R 3.6.3 (R Core Team 2020) to build Bayesian linear mixed models with Gaussian error distributions for our two response variables, nearest neighbour distance and domain size. To analyse nearest neighbour distance, we fitted interactions between food abundance and 1) group travel speed, 2) focal age-sex class, 3) neighbour age-sex class, and 4) focal behaviour and neighbour behaviour (three-way interaction) as predictors. To analyse domain size, we fitted interactions between food abundance and 1) group travel speed, 2) focal age-sex class, and 3) focal behaviour as predictors.

For all models, we fitted vegetation class (categorical: primary forest or edge) and potential predator presence (binary) as fixed control effects, and group ID as a random intercept effect to control for variation in group size and polyspecific association rates (Table 1). We centred variables to a mean of zero and a standard deviation of one to improve model fitting and interpretation of continuous main effects in interactions (Schielzeth 2010). There were no confounding effects of independent variable multicollinearity (maximum variance inflation factor: nearest neighbour distance

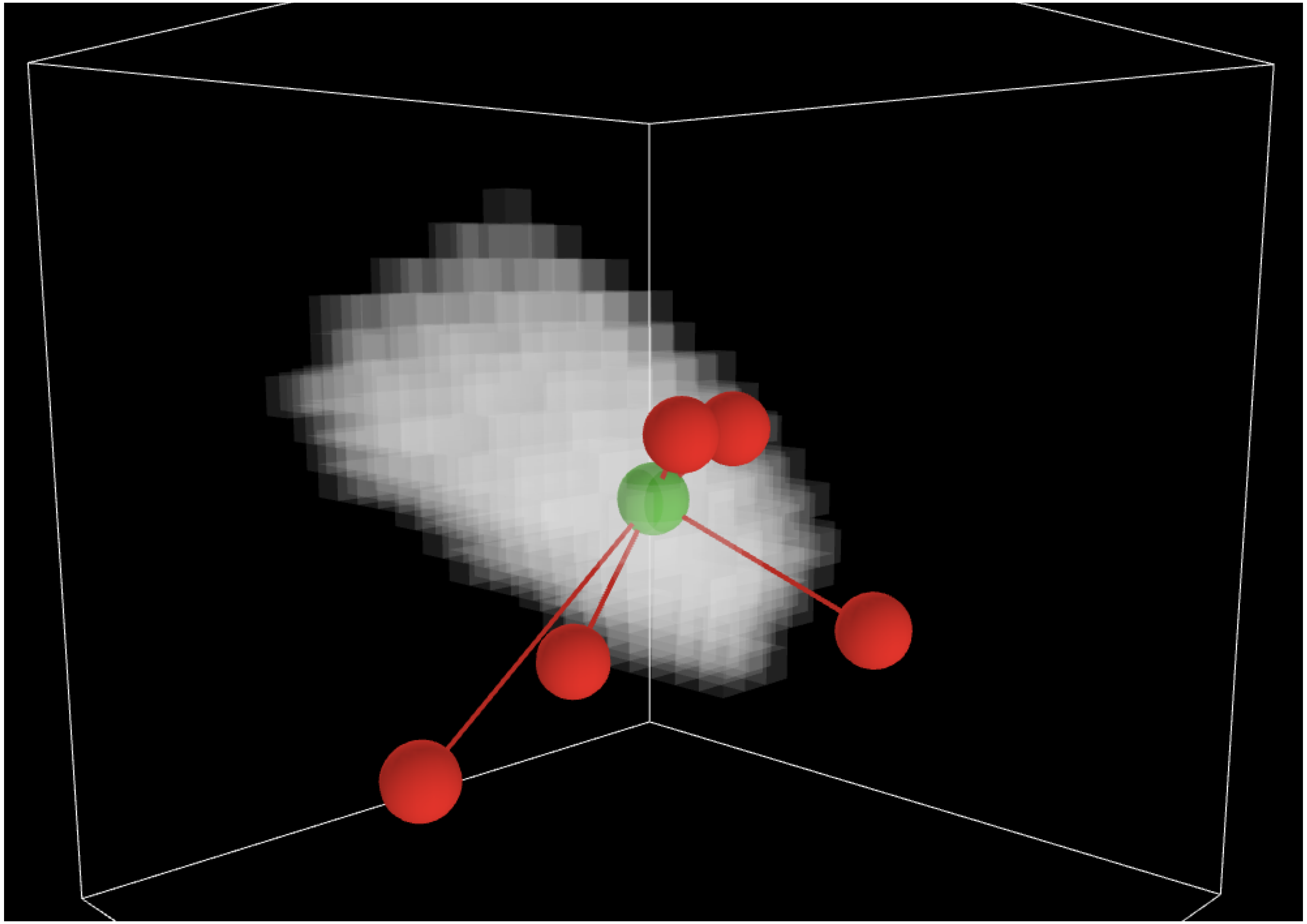

Figure 1 Example permutation of distances between a focal individual (green sphere) in the group core and the five nearest neighbours (red spheres; highlighted by red lines) to calculate domain size. The resulting Voronoi tessellation (domain) belonging to the focal individual is indicated by white shading of 1m^3 cubes. White border lines indicate X, Y, and Z dimensions.

= 1.12, domain size = 1.12). We fitted models with the default *MCMCglmm* priors for fixed effects, weakly informative priors for random effects (V = 1; n = 0.002), and the standard inverse-gamma prior for residual variance. We ran Markov chains (Monte Carlo) for 800,000 iterations with a burn-in of 100,000 iterations and a thinning interval of 100 iterations. After running each model, we checked trace plots to confirm autocorrelation was not an issue and that effective sample sizes were adequate (nearest neighbour distance: minimum = 6102, mean = 8003; domain size: minimum = 6033, mean = 8023). We calculated the Gelman-Rubin diagnostic for three other equivalent models to confirm chain convergence (maximum point estimate: nearest neighbour distance = 1.0, domain size = 1.0).

For each response, we compared the deviance information criterion (DIC) between models with each combination of fixed interaction effects, a model with only fixed main effects, and a null model fitted with only the control effects. Lower DIC and corresponding weights indicate better model fit – differences of ≥5 DIC substantially so (e.g. Dutton *et al.* 2014) – and probabilities that a model is the best relative fit, respectively. We selected the model with the lowest DIC compared to the null model and inferred fixed effect sizes by examining posterior distributions (widths and overlap of 95% credible intervals with zero) and posterior probabilities (how likely a predictor relates to the response – calculated as proportion of samples in each distribution with the same sign as the mean).

Results

We modelled 27 – 1984 scans per group to analyse nearest neighbour distance and 26 – 371 scans per group to analyse domain size (Table 1). The best fitting model of nearest neighbour distance included interactions between food abundance and group travel speed and focal age-sex class, but not between food abundance and neighbour age-sex class, or between food abundance and focal behaviour and neighbour behaviour (DIC Δ *cf.* null model: -666.23; DIC weight 95% – Table S2). The best fitting model of domain size included only main effects without interactions between food abundance and group travel speed, focal age-sex class, and focal behaviour (DIC Δ *cf.* null model: -40.42; DIC weight 27% – Table S3).

Spatial cohesion in relation to group travel speed

The effect of group travel speed on nearest neighbour distance depended on food abundance. In areas of mean and greater food abundance, nearest neighbour distance related positively to group travel speed (linear mixed model: n = 4342 scans; posterior density $\bar{x}$ = 0.028, posterior probability = 97.2 – Figure 2b; Table S4). When food abundance was low however, monkeys were more likely to increase nearest neighbour distance as groups travelled slower (PD $\bar{x}$ = 0.048, PP = 100.0). Domain size did not relate substantially to travel speed (linear mixed model: n = 802 scans; PD $\bar{x}$ = -0.037, PP = 83.7 – Figure 3; Table S5) but related positively to food abundance (PD $\bar{x}$ = 0.099, PP = 99.7).

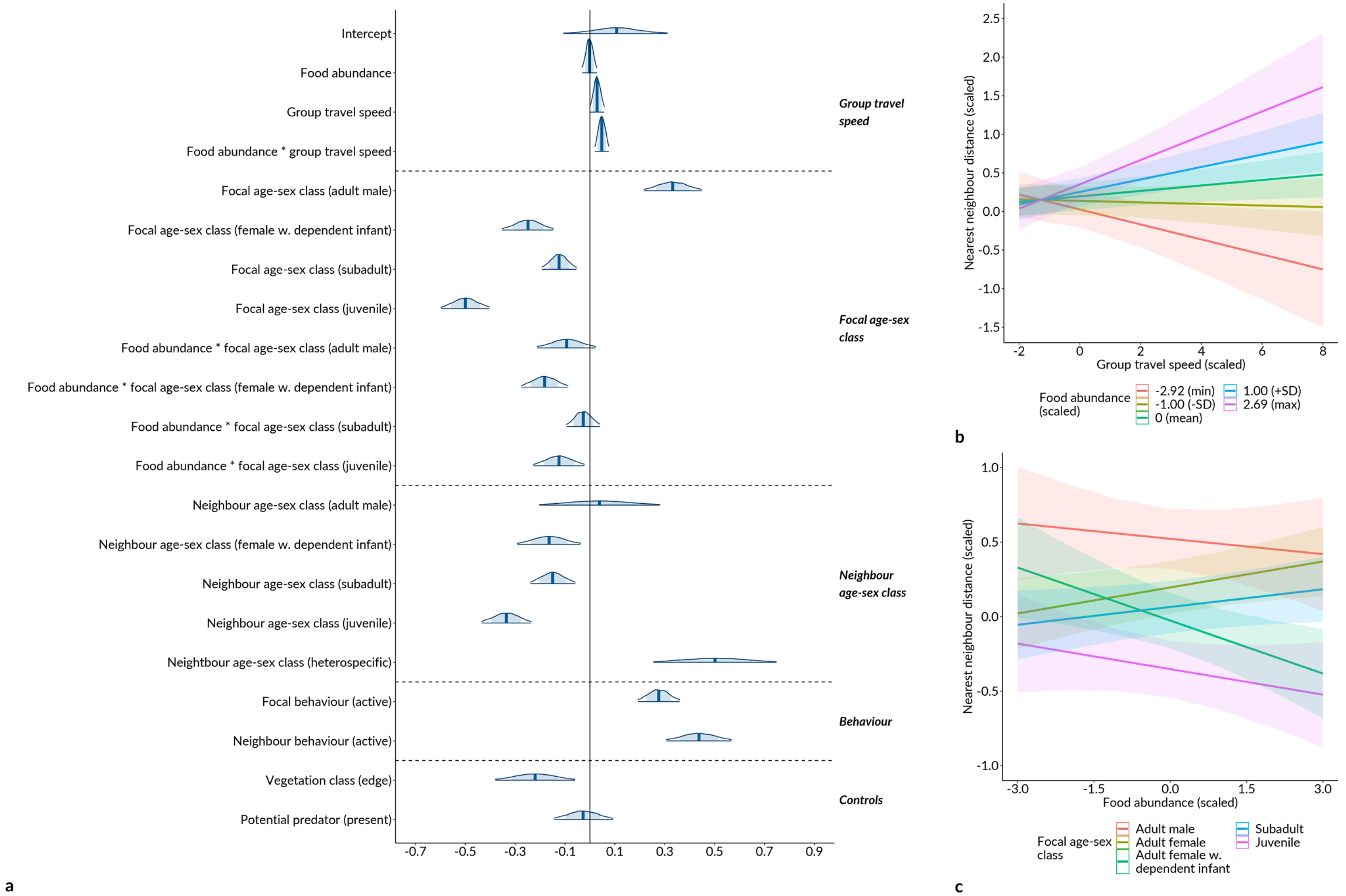

Figure 2 Fixed effects in model of nearest neighbour distance (Table S4). (a) Upper and lower 95% (distributions) and 75% (blue shading) highest posterior density intervals grouped by hypothesis (dashed lines). (b) Interaction between group travel speed and food abundance (select levels of food abundance shown). (c) Interaction between focal age-sex class and food abundance. Bands indicate confidence intervals derived from equivalent generalized least squares regression. Reference levels: focal and nearest neighbour age-sex class = “adult female”; focal and nearest neighbour behaviour = “non-active”; vegetation class = “forest”; potential predator = “absent”.

Spatial cohesion in relation to focal and nearest neighbour age-sex class

The effect of food abundance on nearest neighbour distance also differed by focal age-sex class (Figure 2c; Table S4). In areas of lower food abundance, adult females and subadults exhibited shorter nearest neighbour distances (*cf.* adult females – posterior density $\bar{x}$ = -0.027, posterior probability = 78.3). In contrast, adult males (PD $\bar{x}$ = -0.093, PP = 94.1), adult females with dependent infants (PD $\bar{x}$ = -0.182, PP = 100.0), and juveniles (PD $\bar{x}$ = -0.124, PP = 99.2) were more likely to increase nearest neighbour distance when food abundance was low, compared to adult females without dependent infants.

Irrespective of food abundance, nearest neighbour distance was shorter when the neighbour was an adult female with dependent infant (PD $\bar{x}$ = -0.164, PP = 99.4), subadult (PD $\bar{x}$ = -0.149, PP = 100.0), or juvenile (PD $\bar{x}$ = -0.335, PP = 100.0), compared to adult females without dependent infants. For all focal individuals, nearest neighbour distance was also larger when the neighbour was a heterospecific (PD $\bar{x}$ = 0.502, PP = 100.0).

Adult males exhibited larger domains (PD $\bar{x}$ = 0.361, PP = 99.4 – Figure 3; Table S5) than adult females. Juveniles exhibited smaller domain sizes than adult females (PD $\bar{x}$ = -0.213, PP = 97.9) but adult females with dependent infants (PD $\bar{x}$ = 0.012, PP = 53.2) and subadults (PD $\bar{x}$ = 0.049, PP = 70.6) did not.

Spatial cohesion in relation to individual behaviour

Monkeys distanced themselves further from their nearest neighbour when they or their neighbour were exhibiting active behaviour (feeding, travelling, or scanning *cf.* focal non-active – posterior density $\bar{x}$ = 0.276, posterior probability = 100.0; *cf.* neighbour non-active – PD $\bar{x}$ = 0.437, PP = 100.0 – Figure 2; Table S4). DIC scores for models of nearest neighbour distance did not support two- or three-way interactions between focal behaviour, neighbour behaviour, and food abundance (minimum DIC when in model: 11678.11 *cf.* minimum DIC overall: 11658.85 – Table S2). As such, individuals exhibited greater nearest neighbour distance when active irrespective of the neighbour's behaviour, and vice versa. Domain sizes were also substantially larger when the focal individual was active (PD $\bar{x}$ = 0.318, PP = 100.0 – Figure 3; Table S5).

Discussion

Individual spatial cohesion as an alternative to group travel

Red-tailed monkeys varied spatial cohesion as they travelled slower depending on local food abundance. Where food was abundant, monkeys increased cohesion at slower travel speeds. Higher food availability should reduce the influence of intra-group feeding competition and lead to social factors driving inter-individual spacing. Primates typically exhibit higher rates of close-proximity social behaviour than foraging behaviour when groups are travelling slowly or resting. This effect may be

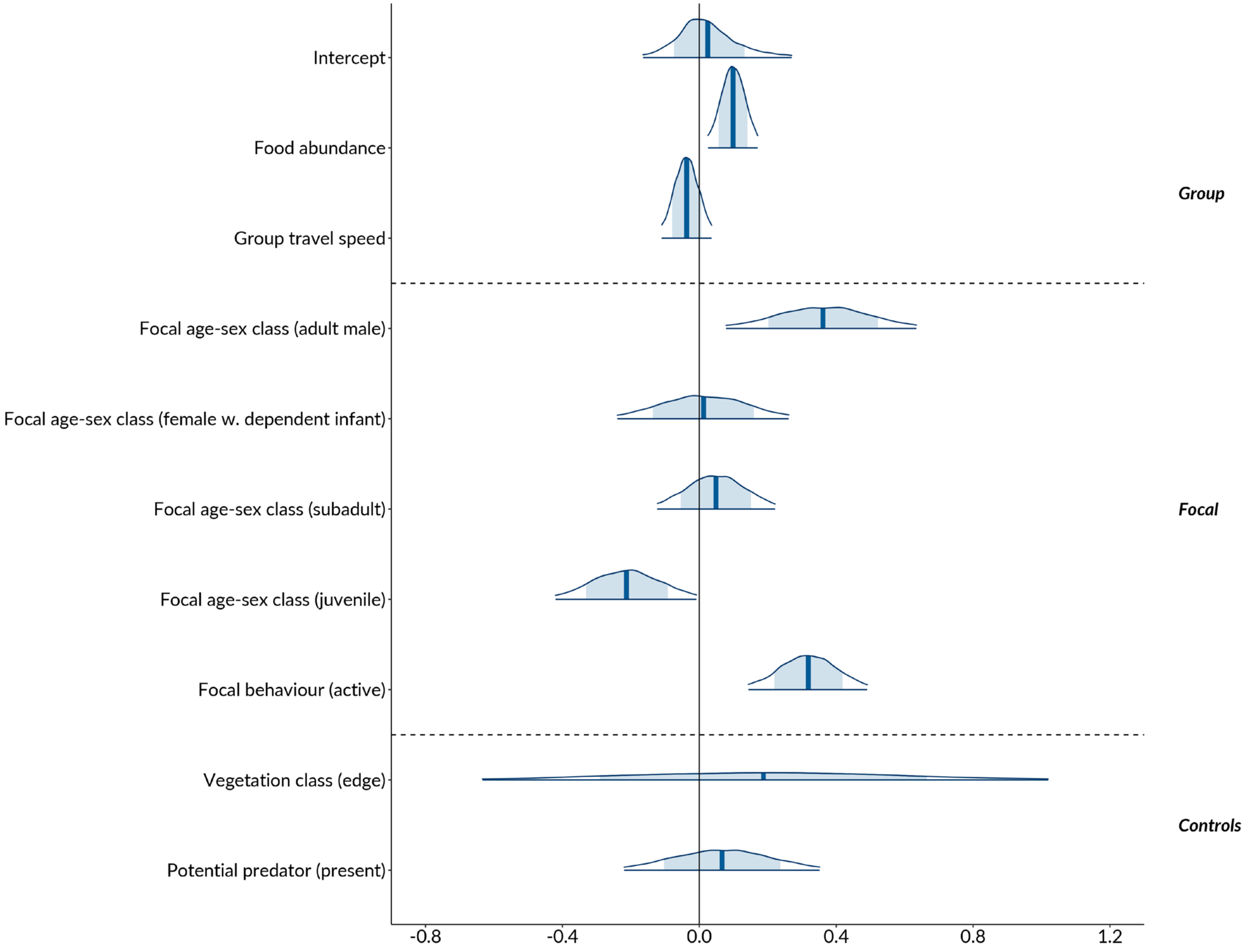

Figure 3 Upper and lower 95% (distributions) and 75% (blue shading) highest posterior density intervals for fixed effects in model of domain size, grouped by hypothesis (dashed lines). Reference levels: focal and nearest neighbour age-sex class = “adult female”; focal and nearest neighbour behaviour = “non-active”; vegetation class = “forest”; potential predator = “absent”.

stronger when food is abundant because there may be less need to prioritise foraging over social behaviour (e.g. van Doorn *et al.* 2010).

In areas of low food abundance red-tailed monkeys increased nearest neighbour distance as groups travelled slower, as predicted. When food availability is low, individuals should either find new patches or reduce feeding competition (Chapman and Chapman 2000b). To this end, reducing cohesion and spreading out may be a more effective alternative than increasing travel distance. For example, collective group travel in some locations may not be possible unless all individuals are prepared to tolerate the same costs of travel to acquire food, such as entering territory of a conspecific group or using habitat types that increase vulnerability to predation (Boinski *et al.* 2000). Moreover, increasing group travel to acquire food restricts patch choice for individuals because they must follow the rest of the group. Individuals with highest nutritional requirements may drive further travel, resulting in greater energy expenditure for all group members (a "funnelling effect" – Isbell 2012). These costs of group travel are experienced by all group members, particularly in large groups (Chapman and Chapman 2000b). Instead, an individual that spreads out to increase foraging efficiency will mostly incur trade-off costs themselves (e.g. greater predation risk – Hamilton 1971; Boinski *et al.* 2000). Because nutritional demands are rarely the same for all group members at any one time (Felton *et al.* 2009; see also Cords 1986), flexible intra-group spatial cohesion could therefore be a more efficient strategy for individuals to meet foraging requirements when increasing group-wide travel does not suffice or is not possible.

Spatial cohesion reflects individual cost-benefit ratios

Variation in spatial cohesion among age-sex classes broadly matched our expectations of energetic and social requirements among individuals. Juveniles spread out the least and adult males spread out the most, consistent with previous studies. Juveniles prefer close spatial affiliations and central positions, likely to reduce predation risk and mediate social bonds (Robinson 1981; Collins 1984; Waser 1985; Boinski *et al.* 2000; Teichroeb *et al.* 2015). In contrast, relatively large-bodied individuals (e.g. adult males) often exhibit wider inter-individual distances because of a tendency to tolerate increased predation risk at group peripheries in exchange for lower feeding competition (Cowlishaw 1994; Boinski *et al.* 2000; Schmitt and Di Fiore 2015; Teichroeb *et al.* 2015). For female philopatric red-tailed monkeys that live in uni-male groups, adult males may also be deterred from spending less time in close association with unrelated adult females in the group core, especially if they are infanticidal.

Adult females with dependent infants and juveniles exhibited greater nearest neighbour distances as food abundance decreased compared to other individuals. Females with young infants attract more social interactions than other group members (Garber 1987), while juveniles must develop social bonds (e.g. through play – Palagi *et al.* 2004) that mean most time is spent in highly cohesive spatial affiliations with mothers or other juveniles. Given lactating females and fast-growing juveniles typically have relatively high nutritional demands (Felton *et al.* 2009), increasing spacing when food is scarce may reduce social interference, thereby mitigating feeding competition and maximising time spent feeding (Collins 1984; Heesen *et al.* 2013).

Red-tailed monkeys also spread out when the nearest neighbour was a heterospecific. Inter-specific social interactions (e.g. grooming) are less frequent than intra-specific interactions, which may be reflected in less cohesive spatial affiliations (EM personal observation). In addition, red-tailed monkeys are smaller than other species they associated with (except for some L'Hoest's monkeys), which may result in greater perceived feeding competition from these animals. Red-tailed monkeys at Kanyawara (also Kibale National Park) also increased inter-individual spacing when in polyspecific association with grey-cheeked mangabeys – the species most commonly associated with in this study (Table 1) – partly because mangabey males aggressively defend mixed-species groups against aerial predators (e.g. crowned hawk-eagles, *Stephanoaetus coronatus* – Bryer *et al.* 2013).

Spatial dimensions of intra-group feeding competition

Unlike nearest neighbour distance, and in contrast to our prediction, individuals exhibited smaller domain sizes as food abundance decreased, irrespective of group travel speed or age-sex class. This contrasting effect of food abundance on spatial cohesion at two different scales (dyads *cf.* clusters of up to seven individuals) may reflect spatial variation in feeding competition perceived by individuals. The likelihood of an occupied food patch being depleted should increase with distance to an individual. As such, when groups are widely spread out, individuals may perceive feeding competition to be strongest from, and only reduce distances to, the most immediate neighbour, because subsequent neighbours are more likely to compete with their own nearest neighbour (di Bitetti and Janson 2001; Beauchamp 2008).

Monkeys may also only spread out when feeding on heterogeneously distributed food (e.g. invertebrates) because patches of more densely distributed food (e.g. fruit, leaves) are usually large enough to support multiple individuals feeding over short time periods without intense feeding competition (Beauchamp 2008; Sugiura *et al.* 2011; Heesen *et al.* 2015). As such, some variation in individual cohesion may be associated food types consumed by monkeys – which we were not able to record – because diet composition likely varies between age-sex classes (e.g. Cords 1986). Similarly, adult red-tailed monkeys at Kanyawara increased nearest neighbour distance more when feeding on scattered insects than densely distributed fruit (Bryer *et al.* 2013). For highly insectivorous red-tailed monkeys at Ngogo ($\bar{x}$: 34% of diet – Struhsaker 2017), the distribution of individual foods may also explain additional variation in cohesion, especially as we were not able to index insect availability.

Spatial cohesion and social foraging

Smaller domain sizes indicate increased cohesion as distances reduce between focal individuals and both nearest neighbours and other group members beyond them. Monkey domain sizes were smaller in areas of lower food availability, which may reflect the increasing importance of visual communication. Behavioural cues are important visual signals that communicate information on feeding competitors and food locations to any observers in sight (King *et al.* 2009; Fischer and Zinner 2011). For primates in relatively densely vegetated forest environments, reducing proximity should improve how effectively individuals can observe and exploit these signals to avoid competitors or join more efficient foragers. When acquiring such information, group members actively discriminate between individuals to identify the most reliable sources of information (Andrews and Rosenblum 1995; King *et al.* 2011). For example, subadults and adult females without dependent infants exhibited shorter nearest neighbour distance as food abundance decreased. Older and philopatric individuals should be more reliable sources of information because they have more experience of food quality and locations within their home range (Pyritz *et al.* 2011).

We also found individuals increased nearest neighbour distances when they or their nearest neighbour were foraging, irrespective of food availability. Low rates of aggression and similar cortisol levels among adult female red-tailed monkeys at Ngogo suggest intra-group feeding competition may be relatively low (MB unpublished data). As such, foraging individuals may not avoid other individuals significantly more even when food is scarce.

Similarly, our models did not support an interaction effect between focal and neighbour behaviours on nearest neighbour distance. For example, foraging focal individuals did not spread out more if the nearest neighbour was also foraging, which we expected would be perceived as feeding competition to avoid (*cf.* resting or exhibiting social behaviour). While individuals may cue off foraging behaviour to avoid competition where neighbours can be observed, reduced visibility in dense vegetation or over wide distances may restrict how often individuals can see and respond to conspecific behaviour. In addition, two of the three behaviours that we expected to reflect foraging behaviour – feeding, travelling, and scanning – may not always have been associated with foraging. It was not always possible to determine whether monkeys were scanning or travelling to find food, or to initiate social interactions (e.g. grooming) or avoid predators. The contexts of these behaviours – such as the identities of individuals exhibiting them – should also influence conspecific responses. Kinship and social affiliations may indirectly influence spatial positioning as individuals should have more experience of how effective at foraging or tolerable of food sharing related or closely bonded group members are (Sueur and Petit 2008; King *et al.* 2009). Future studies from groups of known individuals and life histories should continue to disentangle the trade-offs that mediate spatial cohesion and provide insight into fine-scale ecological and social pressures that drive sociality.

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Supplementary material

S1 Calculation of domain size

Code for NetLogo 3D 6.1.1 using world dimensions X=21 by Y=21 by Z=21. We performed 2500 runs for each scan in BehaviorSpace using the variable “raw.input” that follows the format: scan number; whether focal was in the core or periphery of the group; distances to the six nearest neighbours, including heterospecifics (each delimited by the character “|”). We input unknown distances as “NA”. Example input: “Scan649|Core|1|2|3|4|NA|NA”. Output in BehaviorSpace used the expression “mean domain.list”.

```
breed[focals focal]
breed[nns nn]

turtles-own
[
  domain
]

globals
[
  domain.list
  scan.iteration
  cutoff
  delimited
  scan.code
  focal.position
  distance.list
  distance.no.na.list
]

to setup
  clear-all
  reset-ticks
  reset-timer
  set scan.iteration 0
  set domain.list (list)
  set distance.no.na.list (list)
  set delimited split-string raw.input "|"
  set scan.code (item 0 delimited)
  set focal.position (item 0 but-first delimited)
  set distance.list but-first but-first delimited
  foreach distance.list [ [x] ->
    ifelse x = "NA" []
    [set distance.no.na.list lput read-from-string x
distance.no.na.list]]
  ifelse focal.position = "Core" [set cutoff max
distance.no.na.list] [set cutoff 15]
end

to-report split-string [ input delimiter ]
  let result []
  let dlen length delimiter
  while [ (position delimiter input) != false ]
  [ let pos position delimiter input
    let sub substring input 0 pos
    if sub != "" [ set result lput sub result ]
    set input substring input (pos + dlen) length input
  ]
  if length input > 0
  [ set result lput input result ]
  report result
end

to add.focal
  create-turtles 1
      [set breed focals
        set shape "circle"
        set color green
        set size 2
        setxyz 0 0 0]
end

to add.neighbour
  foreach distance.list [ [metres] ->
    ifelse metres = "NA" []
    [create-turtles 1
      [set breed nns
        set shape "circle"
        set color red
        set size 2
        let nearest-focal min-one-of other focals [distance
myself]
        move-to one-of patches with [distance nearest-focal =
read-from-string metres]
  ]]]
end

to voronoi
  ask focals [
    set domain patches in-radius cutoff with [min-one-of
turtles [distance myself] = myself]
    set domain.list lput count domain domain.list
  ]
end

to go
  setup
  loop [
    clear-turtles
    clear-patches
    add.focal
    add.neighbour
    voronoi
    set scan.iteration (scan.iteration + 1)
    if scan.iteration = 2500 [stop]
  ]
End
```

Table S1 Re-classification of behaviour as either “active” (associated with foraging) or “non-active” (social or resting) behaviour.

Focal behaviour	**Re-classification**
Eating Drinking Travelling Scanning ("visual scanning directed beyond arm's reach" in any context – Treves, 1998)	Active
Resting Grooming Self-grooming Playing Copulating Conspecific aggression	Non-active

Table S2 Nearest neighbour distance model selection using deviance information criterion (DIC) ranks. Models comprise random effects and each possible combination of fixed interaction and main effects, a model with only interaction main effects, and a null model with no fixed effects. Model structures indicate included interactions (bold italics = selected best fitting model).

Model structure	**Degrees of freedom**	**DIC**	**DIC ∆ null model**	**Weight**
Null (no fixed effects)	2	12325.06	-	<0.01
Main effects only	24	11679.22	645.84	<0.01
A	25	11669.58	655.48	<0.01
B	29	11668.03	657.03	0.01
C	30	11687.86	637.20	<0.01
D	30	11686.83	638.23	<0.01
AB	***30***	***11658.83***	***666.23***	***0.95***
AC	31	11677.75	647.31	<0.01
AD	31	11677.16	647.90	<0.01
BC	35	11677.25	647.81	<0.01
BD	35	11675.44	649.62	<0.01
CD	36	11695.04	630.02	<0.01
DE	41	11694.27	630.79	<0.01
ABC	36	11667.47	657.59	0.01
ABD	36	11666.15	658.91	0.02
ACD	37	11684.78	640.28	<0.01
ADE	42	11686.72	638.34	<0.01
BCD	41	11684.11	640.95	<0.01
BDE	46	11686.25	638.81	<0.01
CDE	46	11702.25	622.81	<0.01
ABCD	42	11674.18	650.88	<0.01
ABDE	47	11678.13	646.93	<0.01
ACDE	47	11694.29	630.77	<0.01
BCDE	51	11694.40	630.66	<0.01
ABCDE	52	11685.94	639.12	<0.01

A = food abundance * group travel speed

B = food abundance * focal age-sex class

C = food abundance * neighbour age-sex class

D = focal behaviour * neighbour behaviour

DE = food abundance * focal behaviour * neighbour behaviour

Table S3 Domain size model selection using deviance information criterion (DIC) ranks. Models comprise random effects and each possible combination of fixed interaction and main effects, a model with only interaction main effects, and a null model with no fixed effects. Model structures indicate included interactions (bold italics = selected best fitting model).

Model structure	**Degrees of freedom**	**DIC**	**DIC ∆ null model**	**Weight**
Null (no fixed effects)	2	2278.98	-	0.00
Main effects only	***16***	***2238.55***	***-40.42***	***0.27***
A	17	2238.78	-40.19	0.24
B	21	2239.99	-38.99	0.13
C	18	2241.51	-37.47	0.06
AB	22	2239.64	-39.34	0.16
AC	19	2241.08	-37.90	0.08
BC	23	2243.65	-35.33	0.02
ABC	24	2242.93	-36.05	0.03

A = food abundance * group travel speed

B = food abundance * focal age-sex class

C = food abundance * focal behaviour

Table S4 Summary output for the best fitting model of nearest neighbour distance selected in Table S2 (parentheses = categorical variable levels; CI = credible interval).

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	Posterior probability
Intercept	0.107	-0.096	0.318	87.2
Food abundance	-0.002	-0.031	0.028	54.9
Group travel speed	0.028	0.000	0.058	97.2
Interaction: food abundance * group travel speed	0.048	0.020	0.076	100.0
Focal age-sex class (adult male) †	0.332	0.221	0.452	100.0
Focal age-sex class (adult female w. dependent infant) †	-0.249	-0.351	-0.147	100.0
Focal age-sex class (subadult) †	-0.124	-0.193	-0.055	100.0
Focal age-sex class (juvenile) †	-0.500	-0.591	-0.399	100.0
Interaction: food abundance * focal age-sex class (adult male) †	-0.093	-0.211	0.022	94.1
Interaction: food abundance * focal age-sex class (adult female w. dependent infant) †	-0.182	-0.277	-0.090	100.0
Interaction: food abundance * focal age-sex class (subadult) †	-0.027	-0.093	0.040	78.3
Interaction: food abundance * focal age-sex class (juvenile) †	-0.124	-0.228	-0.023	99.2
Neighbour age-sex class (adult male) †	0.038	-0.197	0.285	61.5
Neighbour age-sex class (adult female w. dependent infant) †	-0.164	-0.290	-0.037	99.4
Neighbour age-sex class (subadult) †	-0.149	-0.238	-0.058	100.0
Neighbour age-sex class (juvenile) †	-0.335	-0.436	-0.237	100.0
Neighbour age-sex class (heterospecific) †	0.502	0.262	0.753	100.0
Focal behaviour (active) ‡	0.276	0.195	0.361	100.0
Neighbour behaviour (active) ‡	0.437	0.305	0.565	100.0
[Control] Vegetation class (edge) §	-0.220	-0.382	-0.067	99.6
[Control] Potential predator (present) ǀ	-0.027	-0.149	0.086	67.4

† Reference: "adult female"

‡ Reference: "non-active"

§ Reference: "primary forest"

ǀ Reference: "absent"

Table S5 Summary output for the best fitting model of domain size selected in Table S3 (parentheses = categorical variable levels; CI = credible interval).

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	Posterior probability
Intercept	0.025	-0.167	0.264	57.3
Food abundance	0.099	0.024	0.169	99.7
Group travel speed	-0.037	-0.112	0.033	83.7
Focal age-sex class (adult male) †	0.361	0.088	0.639	99.4
Focal age-sex class (adult female w. dependent infant) †	0.012	-0.236	0.265	53.2
Focal age-sex class (subadult) †	0.049	-0.134	0.209	70.6
Focal age-sex class (juvenile) †	-0.213	-0.412	-0.002	97.9
Focal behaviour (active) ‡	0.318	0.139	0.485	100.0
[Control] Vegetation class (edge) §	0.187	-0.644	1.007	67.0
[Control] Potential predator (present) ǀ	0.066	-0.218	0.353	67.6

† Reference: "adult female"

‡ Reference: "non-active"

§ Reference: "primary forest"

ǀ Reference: "absent"

Supplementary references

Treves, A. (1998). The influence of group size and neighbors on vigilance in two species of arboreal monkeys. *Behaviour*, 135, 453-481.

Title: Contact call acoustic structure reflects antiphony in a wild primate (*Cercopithecus ascanius*)

Edward McLester [a]

[a] School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK

Abstract

Contact calls are an important mechanism of maintaining group cohesion when visibility is restricted. To maximise call detection, animals should direct calls at nearest neighbours or individuals that have produced preceding calls (i.e. antiphony). Individuals should also direct calls at neighbours who respond more reliably or are closest when groups are travelling. Because animals adjust call acoustic structure to optimise propagation, call structure may reflect distance to (and identity) of the intended receiver. I investigated whether the acoustic structure of red-tailed monkey (*Cercopithecus ascanius*) contact grunts reflected nearest neighbour distances depending on 1) if preceded by another grunt, 2) neighbour age-sex class, or 3) group travel speed. For grunts recorded from five groups, I measured six acoustic parameters associated with sound propagation. Mean grunt entropy and frequency related negatively to neighbour distance when the neighbour grunted prior or when there was no preceding grunt, but not when a more distant individual had previously grunted. Neighbour age-sex class and group travel speed did not influence whether grunts reflected neighbour distance, but mean entropy and frequency increased as groups travelled faster. Variation in grunt acoustic structure provides evidence for antiphonal calling in this species and may reflect call flexibility that counteracts increased ambient noise when groups travel faster.

Introduction

Benefits of sociality are contingent on group-living animals' abilities to maintain and adjust group cohesion (relative spatial positioning of individuals; Trillmich *et al.* 2004; Ward and Webster 2016). Group members must communicate rapidly and over wide spatial scales to mediate inter-individual distances and track locations of specific individuals (e.g. to maintain social bonds; Cheney *et al.* 1996; Oda 1996). As such, behavioural mechanisms through which animals exchange information should reflect social and ecological pressures that drive adaptive communication behaviour (Ord *et al.* 2010).

Bidirectional vocalising is an important adaptation that maximises call detection while limiting call redundancy (Endler 1993; Oliphant and Batali 1997). By responding to a preceding call, individuals can validate successful transmission of information (Schleidt 1973), increase call precision (e.g. using a preceding caller's location – Snowdon 2001), and reduce overlap that degrades information transmission (Yoshida and Okanoya 2005; Inoue *et al.* 2013). Bidirectional vocalising may be especially important where environmental conditions such as rain, dense vegetation, or darkness restrict visual or tactile communication (Marler 1967; Brown and Waser 2017). Investigating bidirectional calling, and determinants of reciprocity, therefore provides insight into how individuals maintain cohesive groups, even when conspecifics are not visible.

Bidirectional calling should be influenced by social factors, particularly in species that exhibit long-term bonds (e.g. primates – Miller and Wren Thomas 2012). For example, where contact calls transmit individual-specific information such as caller location (Boinski 1991), individuals may direct calls at certain group members either in response to a preceding call or to elicit a response (i.e. antiphony – ≥2 animals calling in response to preceding calls – Cheney *et al.* 1996; Yoshida and

Okanoya 2005). Which individuals engage in antiphonal exchanges may depend on individual identity (e.g. older individuals may be more reputable sources of information or more likely to respond – Briseno-Jaramillo *et al.* 2018) or group travel speed (e.g. more widely-spaced individuals may be less likely to detect calls as groups travel faster – Koda *et al.* 2008). Individuals adjust call acoustic structure to maximise chances of detection (Ey *et al.* 2009; Table 1). Acoustic parameters associated with increasing sound propagation should therefore reflect distance to, and identity of, the intended recipient (e.g. broadly, the closest neighbour *cf.* an individual beyond), especially in large groups or where individuals are widely spaced (Sugiura 2007).

I investigated bidirectional calling in the red-tailed monkey (*Cercopithecus ascanius*), a social primate that lives primarily in densely-vegetated forests (Sarmiento *et al.* 2001). Groups are typically large (>15 individuals) and exhibit wide inter-individual distances (e.g. >50m group diameter). Adult females and subadults and juveniles of both sexes produce two contact calls, of which the phrased grunt is most clearly associated with maintaining group cohesion (Marler 1973; reviewed in Cords and Sarmiento 2013). I tested the hypothesis that contact call acoustic structure reflects propagation to the nearest neighbour, depending on three factors: whether a different individual produces a preceding call; nearest neighbour age-sex class; and group travel speed. I predicted that the relationship between grunt structure and nearest neighbour distance is strongest when 1) a preceding grunt is produced by the nearest neighbour (*cf.* an individual further away); 2) the nearest neighbour is an adult female (*cf.* subadult or juvenile); 3) groups are travelling faster (see Tables 1 and 2 for summaries of predictions).

Methods

Data collection

I collected data at Ngogo, Kibale National Park (Uganda), a mosaic of predominantly closed canopy primary forest and mixed canopy secondary forest (Struhsaker 1997). I followed five habituated red-tailed monkey groups between March – October 2017 and January – June 2019 (*n* = 24 – 112 follow days per group; Table S1). Groups each comprised one adult male and multiple adult females, subadults, and juveniles (*n* = 16 – 35 total individuals per group; see Table S1 for detailed group compositions).

I recorded grunts *ad libitum* using a Sennheiser MKH 416-P48U directional microphone and a Marantz PMD661MKII solid-state recorder (channels: mono; bit depth: 24-bit PCM; sampling rate: 96kHz). I did not record consecutive grunts from the same focal individual to minimise temporal autocorrelation. I recorded grunts from individuals within 12m of the microphone and with a clear (i.e. of vegetation) line of sight, following Fischer *et al.* (2013). For each grunt, I noted the following: caller age-sex class (adult male or female, subadult, or juvenile; or identity if known) and vegetation class (primary forest, secondary forest, or edge); nearest neighbour age-sex class and distance from focal (metres); if a different individual had grunted in the preceding five seconds, and if so, preceding caller identity (binary: nearest neighbour to focal or not). I used five seconds as the window for identifying

Table 1 Acoustic parameters selected for analysis with justifications of predicted relationships with call propagation.

Acoustic parameter	**Definition (this study)**	**Unit**	**Predicted relationship with call propagation distance**	**Justification**
Duration	Total duration of call	Time (ms)	Positive	Sounds with longer durations should attenuate over distance more slowly, depending on the environment. For example, optimal sound duration for propagation should last long enough to be reverberated by reflective surfaces in the environment (Nemeth *et al.* 2006). Neighbour proximity relates to increased duration of contact calls in Japanese macaques (*Macaca fuscata* – Sugiura 2007) and isolation calls in squirrel monkeys (*Saimiri sciureus* – Masataka and Symmes 1986; see also Brumm *et al.* 2004; Ey *et al.* 2009; but see Oda 1996).
Maximum time	Duration until maximum power (dB / sample unit) of call occurs	Time (ms)	Negative	Sounds that reach maximum power more quickly should attenuate over distance more slowly over short distances (<100m; e.g. primate loud calls – Waser and Waser 1977).
Mean entropy	Function of energy distribution across frequencies, with purer, narrowband sounds having lower entropy than noisier, broadband sounds	Bits	Negative	Sounds with lower entropy should attenuate over distance more slowly than noisier sounds, depending on frequency. For example, in dense forest, pure tones below 500Hz attenuate substantially slower than pure tones at higher frequencies (Waser and Waser 1977), while Morton (1975) found no significant difference between pure and noisy tone attenuation at frequencies up to 15kHz. Lower entropy may also reflect higher amplitude (Ríos-Chelén *et al.* 2020; see also Liao *et al.* 2018; Fuong and Blumstein 2020).
Maximum frequency	Frequency at which maximum power (dB / sample unit) of call occurs	Hz	Negative	Sounds with concentrations of energy at lower frequencies attenuate over distance more slowly and propagate further (Chapuis 1971; Marten *et al.* 1977; Waser and Waser 1977; Waser and Brown 1986; Brown and Handford 2000; Ey *et al.* 2009; see also Morton 1975), depending on the environment. For example, sounds are reflected more effectively by objects with reflective surface diameters at least equal to the sound wavelength, which lengthens as frequency decreases (e.g. ≥33cm diameter to increase reflectivity of a 1000Hz sound at 20°C ambient temperature; ≥69cm for a 500Hz sound at 20°C – Naguib 2003).
Mean frequency	Mean of centre frequency* ("the frequency that divides the spectrogram slice into two frequency intervals of equal energy" – Charif *et al.* 2010) across duration of call	Hz	Negative	
Minimum frequency	Minimum centre frequency* across duration of call	Hz	Negative	

* I measured minimum and mean frequency from the 50% frequency contour, which compared to e.g. the peak frequency contour best ignored gaps within the structure of grunts that would otherwise have led to measurements including sections of ambient noise.

Table 2 Predicted modulation of relationship between nearest neighbour (NN) distance and call propagation by three social factors. Individual levels are shown for categorical fixed effects included in statistical models (see Methods; Table S3).

Effect	**Levels**	**Predicted effect of NN distance on call propagation [relative strength]**
Preceding grunt	No preceding grunt	Positive
	Preceding grunt – produced by NN	Positive
	Preceding grunt – unknown if produced by NN	Positive [weakest]
	Preceding grunt – not produced by NN	No relationship
NN age-sex class	Adult female	Positive [strongest]
	Subadult	Positive [weaker]
	Juvenile	Positive [weakest]
	Adult male	No relationship
Group travel speed	[Continuous]	Positive

antiphonal calls because inter-call intervals can vary between individuals (Yoshida and Okanoya 2005; following Oda 1996; Miller *et al.* 2009). During follows, I recorded GPS coordinates at automatic 1-minute intervals using a Garmin Rino 650 unit.

Data analyses

I analysed recordings in Raven Pro v1.6 (Center for Conservation Bioacoustics 2019). I discarded recordings in which I could not distinguish the focal grunt against ambient noise or grunts from other monkeys, or in which grunts overlapped with loud ambient sounds in the same frequency range (e.g. bird and cicada vocalisations; snapping branches). To reduce interference from ambient noise, I used only recordings with a signal-noise ratio of ≥6dB, calculated as the difference in inband power (dB) between each grunt spectrogram sample and an identically sized (duration and frequency bounds) sample comprising only ambient noise within 500ms (mean = 50.1ms) of the corresponding grunt, following Charif *et al.* (2010).

For each grunt, I measured six acoustic parameters (spectrograms: Fast Fourier transformation length = 1024 samples, window = Hann, hop size = 0.1ms, frequency resolution = 2.93Hz; see Figure 1 for example spectrograms; see Table 1 for *a priori* selection of acoustic parameters). I used QGIS v3.10 to calculate 15-minute group travel speed as the summed Euclidean distance between the 16 consecutive 1-minute GPS coordinates preceding the grunt.

Statistical analyses

I used the package *MCMCglmm* in R 3.6.2 (R Core Team 2020) to build Bayesian linear mixed models, with each acoustic parameter as a response and interactions between nearest neighbour distance and 1) grunt in preceding five seconds (hereafter, “preceding grunt”), 2) nearest neighbour age-sex class, and 3) group travel speed, as predictors (Table 2; supplementary material). I fitted vegetation class as a fixed control effect, and focal ID (or age-sex class where identity was unknown) as a random intercept effect. For each response, I compared the deviance information criterion (DIC) between models with each combination of fixed interaction effects and a null model fitted with only the control effects. For each response, I selected the model with the lowest DIC compared to the null

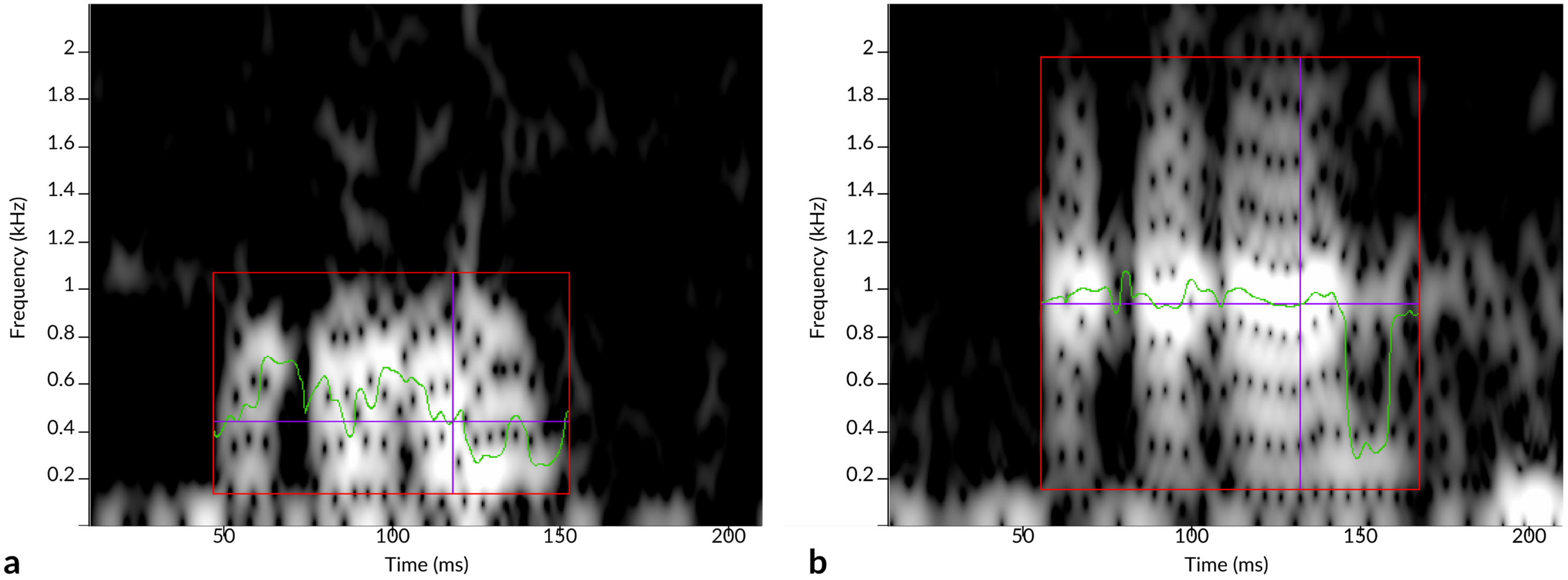

Figure 1 Example spectrograms illustrating grunts from an adult female (a) and a subadult (b). Red border indicates selection box drawn in Raven Pro, from which measurements are extracted: duration (selection box width); maximum time (vertical purple line); maximum frequency (horizontal purple line); 50% frequency contour (green line). The measurement for mean entropy cannot be indicated visually.

model and inferred fixed effect sizes by examining posterior distributions (widths and overlap of 95% credible intervals with zero) and posterior probabilities (probability a predictor relates to the response – calculated as proportion of samples in each distribution with the same sign as the mean).

Results

Model selection per acoustic parameter

I analysed 899 grunts (*n* = 57 – 317 grunts per group – Table S1). For grunt duration, maximum time, maximum frequency, and minimum frequency, none of the predictive models were substantially more likely to fit the data better than the null model (minimum DIC *cf.* null model: +2.86 – 11.5; maximum predictive model DIC weight: 0.3 – 13%; Table S2). For mean entropy and mean frequency, the best fitting model included an interaction between nearest neighbour distance and preceding grunt, although this was less certain for mean frequency (mean entropy – DIC *cf.* null model: -7.14; DIC weight: 55%; mean frequency – DIC *cf.* null model: -0.88; DIC weight: 38%; Table S2).

Modulating effect of preceding grunts

The relationship between nearest neighbour distance and grunt mean entropy, and to a lesser extent mean frequency, depended on whether and by whom a grunt was produced in the preceding five seconds. Monkeys produced calls with substantially lower mean entropy as nearest neighbour distance increased when there was 1) a preceding grunt produced by the nearest neighbour (*n* = 96; posterior density $\bar{x}$ = -0.251, posterior probability = 95.1; Figure 2; Table S3), 2) a preceding grunt produced by either a nearest neighbour or non-nearest neighbour that I could not differentiate (*n* = 266; PD $\bar{x}$ = -0.323, PP = 99.4), or 3) no preceding grunt (*n* = 333; PD $\bar{x}$ = -0.224, PP = 96.6). In contrast, when a preceding grunt was produced by an individual further away than the nearest neighbour, mean entropy did not relate strongly to nearest neighbour distance (*n* = 98; PD $\bar{x}$ = 0.100, PP = 80.8).

Grunt mean frequency related negatively to nearest neighbour distance when a preceding grunt was produced by either a nearest neighbour or non-nearest neighbour that I could not differentiate (PD $\bar{x}$ = -0.280, PP = 98.4; Figure 2; Table S3) but not an individual beyond the nearest neighbour (PD $\bar{x}$ = 0.116, PP = 84.0). Mean frequency related weakly negatively to nearest neighbour distance when a preceding grunt was produced by the nearest neighbour (PD $\bar{x}$ = -0.180, PP = 88.3) or when there was no preceding grunt (PD $\bar{x}$ = -0.140, PP = 86.9).

Modulating effects of nearest neighbour age-sex class and group travel speed

The effect of nearest neighbour distance on either mean entropy or mean frequency did not vary depending on nearest neighbour age-sex class or how fast the group was travelling (Figure 2; Table S3). Mean frequency related positively to group travel speed (posterior density $\bar{x}$ = 0.102, posterior

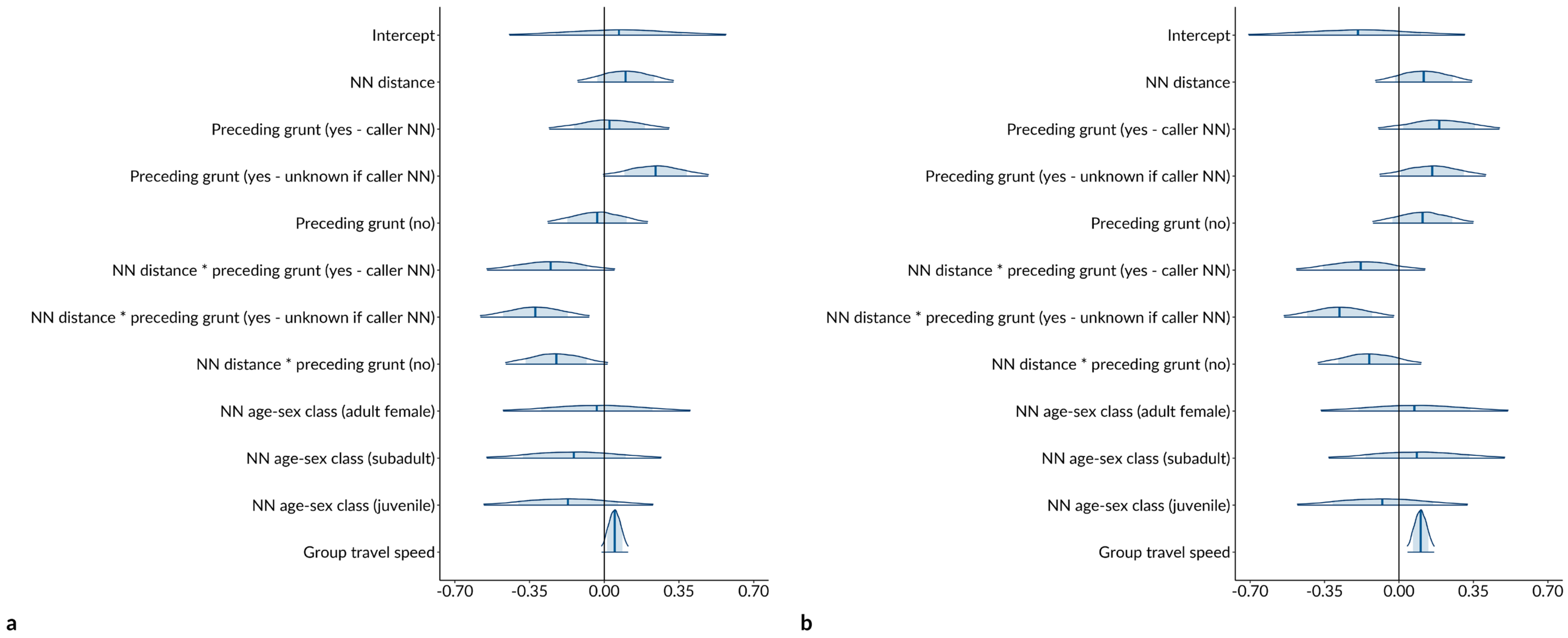

Figure 2 Upper and lower 95% (distributions) and 75% (blue shading) highest posterior density intervals for fixed effects in models of mean entropy (a) and mean peak frequency (b; Table S3). Reference levels: preceding grunt = “yes - caller not nearest neighbour”; nearest neighbour (NN) age-sex class = “adult male”.

probability = 99.9), as did mean entropy although this effect was slightly more variable (PD $\bar{x}$ = 0.049, PP = 94.4).

Discussion

Mean entropy and frequency of red-tailed monkey grunts related to nearest neighbour distance only when the nearest neighbour called in the preceding 5 seconds or when there was no preceding grunt. In these instances, and as predicted, mean entropy and mean frequency both decreased as nearest neighbour distance increased, matching expected call structure for optimal propagation over longer distances (detailed in Table 1). These results suggest red-tailed monkeys exhibit a degree of antiphony when contact calling; that is, monkeys produce calls that appear better optimised for detection by the preceding caller than closer individuals. During the study, monkeys frequently exhibited wide inter-individual distances (e.g. >20m – Ch. 4) but groups rarely fissioned irrespective of size (*n* = <10 observations in 301 follow days, each lasting <1 hour). Antiphonal calling is an important adaptation that allows animals to track out-of-sight conspecifics over wide expanses of dense vegetation; in this case, thereby allowing monkeys to increase individual distances to neighbours instead of fissioning entirely and losing fitness benefits conferred by larger groups (Ward and Webster 2016).

Grunt structure also related to nearest neighbour distance when there was no preceding grunt, while nearest neighbour age-sex class – which I expected would broadly reflect variation in which individuals monkeys preferentially directed calls at – had no effect. The difficulty of tracking other group members in dense vegetation and over wide group spread means that individuals attempting to communicate with specific individuals would likely expend energy producing calls that propagate the width of the group, without knowing if the target is within hearing range. Without a preceding call to act upon, initial callers may instead target the nearest neighbour to maximise chances of call detection. Initial grunts in antiphonal exchanges therefore likely function foremost to maintain contact between closely-spaced neighbours. Nonetheless, individuals likely associate with related or closely-bonded individuals (e.g. as in *C. mitis* – Cords *et al.* 2018), meaning callers may still be initiating exchanges with specific individuals who are simply more likely to be their nearest neighbour.

I expected individuals would more likely direct calls at their nearest neighbours as groups travelled faster because of the increased difficulty of pinpointing more distant individuals in quicker moving groups. Group travel speed had no effect on whether monkeys adjusted grunt structure to nearest neighbour distance however. In some circumstances (e.g. in areas of high food availability – Ch. 4), groups reduced inter-individual distances when travelling faster, likely resulting in improved call detection for all group members. As such, callers may not always need to direct calls at close neighbours to maximise chances of detection. Furthermore, callers also may not need to adjust grunt structure significantly more to attain optimal propagation for individuals separated only by a few metres. Instead, on average monkeys produced grunts with higher mean frequency and entropy when groups were travelling faster, which should reduce the impact of increased ambient noise on call detection. First, increasing frequency should improve audibility of low frequency grunts (206 – 671Hz; $\bar{x}$ = 576Hz – Figure S1) that are difficult to localise even in favourable environmental conditions (Waser and Waser 1977); and second, increasing entropy through broadband calls should counteract fast-changing attenuation properties of the environment as monkeys travel through forest (Morton 1975; Waser and Waser 1977).

In addition to ambient noise, other environmental conditions may also select for contact calling behaviour. In red-tailed monkeys, inter- and intra-specific competition influence ranging and rates of inter-group aggression (Cords 1987; Brown 2013). Predation risk is also a key driver of vigilance behaviour and group size (Treves 2000; e.g. Mitani *et al.* 2001; Watts and Mitani 2002; McLester *et al.* 2018). Antiphony reduces call redundancy and minimises inadvertent attraction of con- and heterospecifics that could increase competition or predation risk (Yoshida and Okanoya 2005).

Environmental influences on vocalising behaviour also likely vary depending on social contexts. For example, while I was not able to distinguish preceding callers beyond "nearest neighbour or not", it is likely that grunts following a single preceding grunt were directed at the initial caller. Where grunts are preceded by multiple different callers however, future studies could examine whether individuals direct calls at the initial caller, or simply the closest preceding caller (e.g. to maximise detection by at least one other individual while avoiding propagating calls further than necessary). Similarly, cost-benefit ratios of calling (e.g. exchanging information at the risk of increasing group conspicuousness – Boinski *et al.* 2000) may vary depending on caller identity or to whom they are responding. Possible altruistic determinants of call production (e.g. kinship; social centrality – Mitani and Nishida 1993; King and Sueur 2011; Kulahci *et al.* 2015) therefore remain to be tested.

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Supplementary material

Statistical analyses and mixed models

For grunts where GPS coordinates were missing (*n* = 54 grunts; 6.0% of observations), I used the package *mice* in R 3.6.2 to regress (method: predictive mean matching) suitable values of group travel speed from time of day and vegetation class, which are known to correlate to hourly travel speeds in red-tailed monkeys (following van Buuren and Goothuis-Oudshoorn 2011; see McLester *et al.* 2019).

I used the package *MCMCglmm* to build six models (one for each acoustic parameter) with Gaussian error distributions. I centred responses and continuous predictors to a mean of zero and a standard deviation of one to improve model fitting and interpretation of continuous main effects in interactions (Schielzeth 2010). There were no confounding effects of predictor multicollinearity (fixed main effect model – maximum variance inflation factor: 1.04) or response multicollinearity (pairwise Pearson correlation coefficients – maximum *r*: 0.65). I modelled observations with unknown values for categorical predictors but did not analyse effects for these levels unless there was a valid interpretation.

I fitted models with the default *MCMCglmm* priors for fixed effects, weakly informative priors for random effects (*V* = 1; *n* = 0.002), and the standard inverse-gamma prior for residual variance. Markov chains (Monte Carlo) ran for 800,000 iterations with a burn-in of 100,000 iterations and a thinning interval of 100 iterations. After running each model, I checked trace plots to ensure autocorrelation was not an issue and that effective sample sizes were adequate (all models – minimum: 7213; mean: 8012). I calculated the Gelman-Rubin diagnostic for three other equivalent models to confirm chain convergence (maximum point estimate for all models = 1.0).

I compared models with each combination of interactions and selected the best fitting model for each response based on DIC scores. Lower DIC and higher corresponding weights indicate better relative model fit – differences of ≥5 DIC substantially so (e.g. Dutton et al. 2014).

Table S1 Follow days, age-sex class compositions, and recording sample sizes by age-sex class for each focal group

Group	**Follow period [follow days]**	**Group composition**					**Sample size (*n* recorded grunts)**				
		Total size	**Adult males**	**Adult females**	**Subadults**	**Juveniles**	**Adult female**	**Subadult**	**Juvenile**	**Unknown**	**Group total**
R6	Mar – Jun 2017 [*n* = 71]	~35	2	~20 adult females and subadults		~8	141	28	4	4	177
R5	Jul – Oct 2017 [*n* = 89]	~25	1	~16 adult females and subadults		~5	214	44	2	4	264
	Jan – Feb 2019 [*n* = 23]	~30	1	14 – 16	9 – 10	4 – 5					
R2	Jan – Mar 2019 [*n* = 24]	16	1	7	6	2	64	20	-	-	84
RSW	Jan; Mar – Apr 2019 [*n* = 22]	16 – 19	1	9	6 – 7	0 – 2	41	15	-	1	57
RGS	Apr – Jun 2019 [*n* = 72]	17 – 19	1	5	7	4 – 6	217	90	4	6	317
										Total	899

Table S2 Model selection using deviance information criterion (DIC) ranks. For each response, the models tested comprise random effects and each possible combination of fixed interaction and main effects, as well as a null model with no fixed effects (bold italics = selected best fitting model; N = nearest neighbour; DF = degrees of freedom).

	Mean entropy				**Duration**			
Model	**DF**	**DIC**	**DIC Δ null model**	**Weight**	**DF**	**DIC**	**DIC Δ null model**	**Weight**
Null (no fixed effects)	3	2442.25	-	0.02	***3***	***2448.04***	***-***	***0.54***
NN distance * preceding grunt	***20***	***2435.11***	***-7.14***	***0.55***	20	2453.58	5.54	0.03
NN distance * NN age-sex class	20	2443.41	1.16	0.01	20	2450.89	2.86	0.13
NN distance * group travel speed	17	2438.73	-3.52	0.09	17	2452.89	4.85	0.05
NN distance * preceding grunt + NN distance * NN age-sex class	24	2440.73	-1.52	0.03	24	2452.37	4.34	0.06
NN distance * preceding grunt + NN distance * group travel speed	21	2436.50	-5.75	0.28	21	2453.10	5.06	0.04
NN distance * NN age-sex class + NN distance * group travel speed	21	2444.91	2.66	0.00	21	2451.77	3.73	0.08
NN distance * preceding grunt + NN distance * NN age-sex class + NN distance * group travel speed	25	2442.24	-0.01	0.02	25	2452.45	4.41	0.06

Table S2 continued

	Maximum time				**Maximum frequency**			
Model	**DF**	**DIC**	**DIC Δ null model**	**Weight**	**DF**	**DIC**	**DIC Δ null model**	**Weight**
Null (no fixed effects)	***3***	***2459.80***	***-***	***0.98***	***3***	***2539.39***	***-***	***0.99***
NN distance * preceding grunt	20	2473.92	14.12	0.00	20	2553.09	13.70	0.00
NN distance * NN age-sex class	20	2471.51	11.71	0.00	20	2556.91	17.52	0.00
NN distance * group travel speed	17	2467.67	7.87	0.02	17	2550.89	11.50	0.00
NN distance * preceding grunt + NN distance * NN age-sex class	24	2479.13	19.33	0.00	24	2557.86	18.47	0.00
NN distance * preceding grunt + NN distance * group travel speed	21	2475.32	15.52	0.00	21	2553.04	13.65	0.00
NN distance * NN age-sex class + NN distance * group travel speed	21	2473.18	13.38	0.00	21	2557.03	17.64	0.00
NN distance * preceding grunt + NN distance * NN age-sex class + NN distance * group travel speed	25	2480.68	20.88	0.00	25	2558.15	18.76	0.00

Table S2 continued

	Mean frequency				**Minimum frequency**			
Model	**DF**	**DIC**	**DIC Δ null model**	**Weight**	**DF**	**DIC**	**DIC Δ null model**	**Weight**
Null (no fixed effects)	3	2461.44	-	0.24	***3***	***2506.81***	***-***	***0.99***
NN distance * preceding grunt	***20***	***2460.56***	***-0.88***	***0.38***	20	2521.90	15.09	0.00
NN distance * NN age-sex class	20	2465.95	4.51	0.03	20	2520.38	13.57	0.00
NN distance * group travel speed	17	2464.12	2.68	0.06	17	2516.90	10.09	0.01
NN distance * preceding grunt + NN distance * NN age-sex class	24	2463.30	1.86	0.10	24	2526.78	19.98	0.00
NN distance * preceding grunt + NN distance * group travel speed	21	2462.51	1.07	0.14	21	2523.80	17.00	0.00
NN distance * NN age-sex class + NN distance * group travel speed	21	2467.94	6.50	0.01	21	2522.34	15.53	0.00
NN distance * preceding grunt + NN distance * NN age-sex class + NN distance * group travel speed	25	2465.33	3.89	0.03	25	2528.86	22.06	0.00

Table S3 Summary output for models of all six acoustic parameters (mean entropy; call duration; maximum time; maximum, mean, and minimum frequency). Results correspond to the model selected in Table S2 (parentheses = categorical variable levels; NN = nearest neighbour; CI = credible interval).

	Mean entropy				**Duration**			
Fixed effect	**Posterior mean**	**Lower 95% CI**	**Upper 95% CI**	**Posterior probability**	**Posterior mean**	**Lower 95% CI**	**Upper 95% CI**	**Posterior probability**
Intercept	0.069	-0.432	0.578	-	-0.085	-0.255	0.081	-
NN distance	0.100	-0.126	0.322	80.8				
Preceding grunt (no) †	-0.033	-0.262	0.204	60.9				
Preceding grunt (yes - caller NN) †	0.024	-0.256	0.305	56.5				
Preceding grunt (yes - unknown if caller NN) †	0.241	-0.005	0.487	97.3				
Interaction: NN distance*preceding grunt (no) †	-0.224	-0.461	0.016	96.6				
Interaction: NN distance*preceding grunt (yes - NN) †	-0.251	-0.554	0.039	95.1				
Interaction: NN distance*preceding grunt (yes - unknown if NN) †	-0.323	-0.584	-0.075	99.4				
NN (adult female) ‡	-0.170	-0.563	0.229	79.8				
NN (juvenile) ‡	-0.035	-0.472	0.403	55.6				
NN (subadult) ‡	-0.142	-0.548	0.268	75.0				
Group travel speed	0.049	-0.011	0.113	94.4				
[Control] Vegetation class (primary forest) §	0.107	-0.162	0.373	78.3				
[Control] Vegetation class (secondary forest) §	-0.094	-0.404	0.199	73.0				

Table S3 continued

	Maximum time				**Maximum frequency**			
Fixed effect	**Posterior mean**	**Lower 95% CI**	**Upper 95% CI**	**Posterior probability**	**Posterior mean**	**Lower 95% CI**	**Upper 95% CI**	**Posterior probability**
Intercept	-0.040	-0.208	0.130	-	-0.068	-0.207	0.062	-
NN distance								
Preceding grunt (no) †								
Preceding grunt (yes - caller NN) †								
Preceding grunt (yes - unknown if caller NN) †								
Interaction: NN distance*preceding grunt (no) †								
Interaction: NN distance*preceding grunt (yes - NN) †								
Interaction: NN distance*preceding grunt (yes - unknown if NN) †								
NN (adult female) ‡								
NN (juvenile) ‡								
NN (subadult) ‡								
Group travel speed								
[Control] Vegetation class (primary forest) §								
[Control] Vegetation class (secondary forest) §								

Table S3 continued

	Mean frequency				**Minimum frequency**			
Fixed effect	**Posterior mean**	**Lower 95% CI**	**Upper 95% CI**	**Posterior probability**	**Posterior mean**	**Lower 95% CI**	**Upper 95% CI**	**Posterior probability**
Intercept	-0.193	-0.696	0.316	-	0.014	-0.128	0.164	-
NN distance	0.116	-0.110	0.343	84.0				
Preceding grunt (no) †	0.111	-0.121	0.350	82.0				
Preceding grunt (yes - caller NN) †	0.190	-0.099	0.469	90.0				
Preceding grunt (yes - unknown if caller NN) †	0.156	-0.090	0.408	88.8				
Interaction: NN distance*preceding grunt (no) †	-0.140	-0.383	0.102	86.9				
Interaction: NN distance*preceding grunt (yes - NN) †	-0.180	-0.488	0.113	88.3				
Interaction: NN distance*preceding grunt (yes - unknown if NN) †	-0.280	-0.542	-0.027	98.4				
NN (adult female) ‡	-0.079	-0.484	0.315	64.6				
NN (juvenile) ‡	0.072	-0.367	0.511	62.3				
NN (subadult) ‡	0.084	-0.328	0.498	64.8				
Group travel speed	0.102	0.041	0.166	99.9				
[Control] Vegetation class (primary forest) §	0.157	-0.114	0.421	87.7				
[Control] Vegetation class (secondary forest) §	0.055	-0.241	0.372	63.2				

† Reference: “yes - caller not NN”

‡ Reference: “edge”

§ Reference: “adult male”

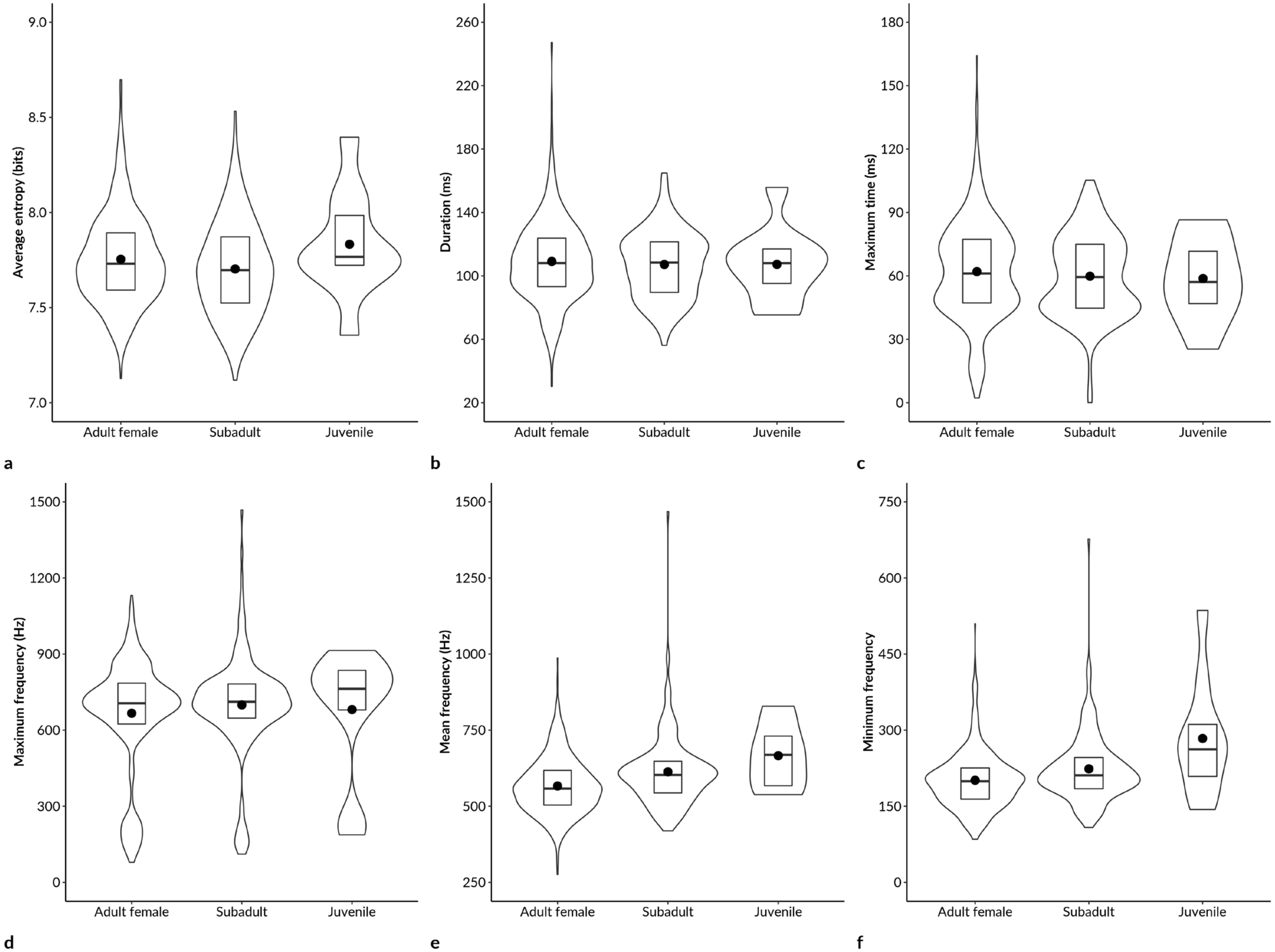

Figure S1 Summary of phrased grunt (*n* = 899) measurements extracted in Raven Pro for six acoustic parameters by each age-sex class: a) mean entropy (bits); b) grunt duration (milliseconds); c) maximum time (milliseconds); d) maximum frequency (Hz); mean frequency (Hz); minimum frequency (Hz; bars = median values; dots = mean values; boxes = inter-quartile range; outlines = sample distribution).

Supplementary references

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Conclusions

In this thesis, I investigated determinants of red-tailed monkey movement behaviour. Specifically, I investigated how three behaviours – group ranging, intra-group spatial cohesion, and contact calling – related to environmental (food abundance; thermal conditions) and social factors (group travel; age-sex classes and behaviours of closest neighbours), at a predominantly forest environment at Ngogo and a savanna-woodland mosaic at the Issa Valley. These relationships can provide evidence for adaptive behavioural responses through which primates maintain sociality.

Environmental influences on movement behaviour

I first examined group ranging responses to biotic (food availability) and abiotic conditions (rainfall, temperature, and solar irradiance). Issa red-tailed monkeys exhibited a larger home range, and more variable daily travel distances than Ngogo (Ch. 2). Groups reduced hourly travel distances more in hotter temperatures at Ngogo than Issa. As food abundance in closed vegetation (primary forest at Ngogo; riparian forest at Issa) decreased, Issa monkeys reduced daily travel distances more than Ngogo monkeys (Ch. 2), and were more likely to use open canopy woodland during higher temperatures and solar irradiance than Ngogo monkeys were in open canopy secondary forest. At both sites, however, monkeys in open vegetation were similarly likely to travel in cooler temperatures and lower solar irradiance than when stationary (Ch. 3).

Environmental influences on movement behaviour were especially observable when compared between sites comprising different habitats. Inter-site variation in environmental determinants of group ranging broadly reflected landscape-level characterisations of savanna-woodland mosaics as hotter, more food-scarce environments that overall present more challenging conditions for forest guenons to adapt to (e.g. following McGrew *et al.* 1981; Wessling *et al.* 2018b). For example, larger home ranges and more variable daily travel distances correlated with a wider, more seasonally variable distribution of resources at Issa than at Ngogo (Ch. 2). Compared to Ngogo, Issa monkeys also travelled faster during hotter temperatures on average in both open and closed vegetation, and tolerated greater heat exposure in open vegetation, likely reflecting a stronger influence of food availability in cooler, closed vegetation in a trade-off between acquiring food – and thereby increasing foraging effort – and avoiding heat exposure and thermal stress (Ch. 3). These responses matched my prediction that broad, linear environmental influences of movement behaviour would be exacerbated over habitat-wide scales, similar to previous studies of group-living behaviour across continent-wide scales (e.g. group ranging in *Papio* spp. – Johnson *et al.* 2015; reviewed in Hill 2005; group size in *Cercopithecus* spp. – Korstjens *et al.* 2018).

Instances in which monkeys exhibited similar responses to environmental heterogeneity across sites reinforce the importance of scale when examining ecological influences on movement behaviour (e.g. Brown 2000). For example, in analyses at finer spatio-temporal scales (i.e. 20-minute interval observations *cf.* daily totals; 50-75m *cf.* home-range wide), Ngogo and Issa monkeys both similarly adjusted range use to changes in food locations and reduced travel during high temperatures and solar irradiance in open canopy vegetation. These responses suggest that at fine scales, heterogeneity in environmental conditions may be similar at sites otherwise typically considered as contrasting habitat types. A previous study of creatinine levels in forest- and savanna-woodland-dwelling chimpanzees (*Pan troglodytes verus*) suggests dehydration pressures are similarly high, if not higher in rainforest, despite lower rainfall in savanna mosaics (Wessling *et al.* 2018a). The authors suggest this discrepancy may be smaller than expected if savanna chimpanzees exhibit habitat-specific behavioural adaptations that negate physiological stress, such as ranging closer to water sources during dry periods. In future studies of red-tailed monkeys, endocrinological data (e.g. creatinine; c-peptide; cortisol levels) may also be useful to test whether similar behavioural responses to thermal conditions across habitats correspond to comparable levels of environment-induced stress. If stress levels are similar in both habitats, despite conditions that should be more challenging in savanna mosaics, it may indicate monkeys exhibit behavioural strategies beyond adjusting ranging for coping with environmental pressures. For example, monkeys may exhibit dietary flexibility to switch to fallback foods in closed canopy riparian forest – which I was not able to measure in this thesis – that would mean savanna mosaic monkeys do not need to increase foraging effort in open vegetation relative to forest-dwelling groups.

Red-tailed monkeys and other guenons distributed across multiple habitat types can provide useful model species to compare effects of fine-scale environmental heterogeneity on behaviour. These primates exhibit much smaller home ranges than chimpanzees and bonobos (*P. paniscus*) for example, which are the focus of many studies of forest primates in savanna-woodland environments (e.g. Pruetz 2006; Serckx *et al.* 2015). Environmental factors that vary over fine spatial scales (e.g. 100m), such as the composition and geometry of vegetation cover, should have stronger effects on movement behaviour for guenons with small home ranges than apes with much larger home ranges. As such, the inter-site comparisons of ranging behaviour in Ch. 2 and Ch. 3 highlight the need to incorporate or control for environmental heterogeneity at a range of scales, particularly in inter-species comparisons of group-living behaviour.

Individual behaviour reflects socio-ecological interactions

In addition to investigating movement behaviour at the group level, I also examined how environmental heterogeneity may be reflected in movement behaviour at the individual level. By investigating movement behaviour among individuals of different age-sex classes, I hoped to gain more insight into how individuals balance costs and benefits of sociality while maintaining group cohesion. For example, daily travel distance related more negatively to food abundance for larger groups at both Ngogo and Issa, suggesting intra-group feeding competition was contributing to longer travel distances when food was scarce (Ch. 2). A similar effect of feeding competition was reflected in how individuals positioned themselves relative to each other. As food abundance decreased, all group members on average reduced cohesion and spread out further when travelling slower but adult males, females with infants, and juveniles spread out further than other age-sex classes (Ch. 4). Additionally, at Issa adult males were most likely to use woodland during hotter temperatures and spent more time in them overall, despite greater heat exposure and likely risk of aerial predation (Ch. 2; Ch. 3).

Despite environmental differences between Ngogo and Issa and clear variation in movement behaviour between age-sex classes, groups at both sites exhibited relatively cohesive, stable groups with minimal fissioning. Cohesive group movements are the products of compromises and trade-offs made by individuals that are ultimately driven by a fitness benefit conferred by group-living (Conradt and Roper 2005; King and Sueur 2011). When the benefits of group-living no longer outweigh the disadvantages, individuals should fission into smaller groups (Chapman and Chapman 2000). At Ngogo, I rarely observed group fissions (*n* = <10 in 301 follow days) and never involving a group splitting into more than two subgroups or for longer than *ca.* one hour. At Issa, I observed groups to fission only once in 6 months of group follows when K0, which at the time was extremely large (*ca.* 50 individuals), split into two subgroups for *ca.* 5 hours. As such, despite inter-site differences in food abundance and thermal conditions between Ngogo and Issa and relatively large group sizes (in particular, K0 numbering 40 – 50 individuals at Issa during 2015 – 2016), compromises between individual motivations rarely resulted in smaller group sizes becoming even temporarily advantageous.

Given group fission was rare and benefits of sociality clearly high, variation in behavioural strategies between individuals matched my expectations that group members would respond differently social and ecological factors as they continuously balanced minimising individual fitness costs against maintaining stable groups. Variation among group members in behaviours such as spatial positioning or vegetation use likely reflects individual physiology and morphology. For example, primate behavioural responses to changes in environmental conditions are primarily driven by energy conservation, as individuals maximise energy expenditure during favourable conditions (e.g. high food availability – Strier 1992; Gerber *et al.* 2012) and minimise energy loss during harsher conditions (e.g. food scarcity – Strier 1992; Fashing 2001; extreme heat and cold – Morland 1993; Hanya 2004; Hill 2006; Pruetz 2007). Behavioural strategies of energy conservation will therefore differ for individuals and age-sex classes with different energetic and nutritional requirements (Felton *et al.* 2009). Similarly, vulnerability to predation should relate to body and group size, which should in turn influence the extents to which different individuals are likely to trade-off predation risk against food acquisition (e.g. by foraging in areas of open canopy or scattered vegetation that increase vulnerability to aerial predation – Zuberbühler and Jenny 2002). For red-tailed monkeys, particularly at Issa where the greatest distribution of food shifts substantially between dense riparian forest and open-canopy miombo woodland by season, I would expect smaller individuals to be more likely to switch to lower quality fallback foods, while bolder or larger individuals (e.g. adult males) might be more likely to continue searching for high quality food in open woodland. While I inferred some of these individual traits based on broad age-sex classes, diet and endocrinological data (e.g. measures of cortisol and testosterone that reflect energetic stress – Jaeggi *et al.* 2018) in individuals could provide more precise explanations of how different group members experience intra-group feeding competition or perceive predation risk in certain areas.

Contact calling behaviour was also likely influenced by environmental conditions. Individuals produced grunts with greater entropy and frequency ranges as groups travelled faster. These patterns could be attributed to rapid variation in environmental surroundings as groups travel, resulting in individuals adjusting grunt structure for optimal propagation over a broader spectrum of conditions such as vegetation density and ambient noise (Waser and Waser 1977). In this thesis, I compared grunts between individuals at Ngogo, and not between Ngogo and Issa. Comparing vocalisations from both Ngogo and Issa monkeys should allow more detailed testing of hypotheses related to environmental influences, given contrasting habitat types and environmental conditions at each site. Biotic and abiotic factors such as vegetation density, topography, temperature, and windspeed influence how sound propagates through the environment (Brown and Waser 2017). Given vocalising is energetically costly, environmental factors should therefore influence how individuals adjust call acoustic structure so that calls optimally propagate to the intended receiver (i.e. the acoustic adaptation hypothesis – Morton 1975; reviewed in Ey and Fischer 2009). Several studies of the acoustic adaptation hypothesis have been conducted in blue monkeys (*Cercopithecus mitis*) and grey-cheeked mangabeys (*Lophocebus albigena*) that are sympatric with red-tailed monkeys at Kibale National Park. Brown *et al.* (1995) found playbacks of forest-dwelling blue monkey loud calls (pyow, trill) and contact calls (grunt, trill) exhibited lower distortion in forest than savannah environments, which the authors ascribed to selection for call structures that propagate more efficiently in forest environments with greater vegetation density (see also Waser and Brown 1986). Waser and Waser (1977) also found loud call rates were typically highest in early mornings, which might reflect temporal windows of coolest temperatures and lowest wind speed that facilitate furthest propagation of long-distance calls (reviewed in Brown and Waser 2017). As such, red-tailed monkeys at Issa may produce contact calls with greater variation in acoustic structure or adjust vocalising behaviour (e.g. increasing call rate or moving to a more arboreal position – Waser and Waser 1977) to account for greater heterogeneity in vegetation cover (dense forest *cf.* open woodland) than Ngogo.

Environmental factors likely mediate social influences on contact calling behaviour. At Ngogo, contact call acoustic structure reflected optimal propagation to nearest neighbours when there was no preceding grunt to respond to. I associated this effect with dense vegetation and low visibility at Ngogo, which may have led to monkeys maximising call detection by the nearest individual regardless of identity, compared to attempting to communicate with a specific individual elsewhere in the group whose location would have been harder to pinpoint. At Issa however, more open vegetation and greater visibility in miombo woodland may mean that individuals are more likely to be able to direct calls at specific individuals that aren't simply the nearest neighbour, or use visual communication to maintain contact with close group members and reserve energetically costly vocalisations for long-distance communication.

In addition, grunt acoustic structure broadly reflected optimal propagation to monkeys that produced preceding grunts. Although neighbour age-sex class did not appear to influence whether monkeys directed contact calls at their nearest neighbour or an individual further away, some individuals, especially adult females, appeared to produce contact calls more often than others (Ch. 5). I was not able to quantify this variation, nor was I able to test whether all individuals responded to calls of other individuals at the same rate. Relatedness is likely to be a strong influence on potentially altruistic interactions, such as calling to reveal location at the risk of attracting predators or providing visual cues to food locations. Genetic data could help reveal whether individuals participate in these interactions to the same extent depending on the identity of other callers or neighbouring individuals.

Paleoecological drivers of primate movement behaviour in the Plio-Pleistocene

Extant cercopithecoids can provide useful referential models to inform hypotheses of hominin adaptation (reviewed in Elton 2006). Investigating environmental determinants of movement behaviour in red-tailed monkeys in both forest and savanna-mosaic environments can reveal environmental pressures that hominins (e.g. *Australopithecus* and early *Homo* spp.) in ecologically similar paleoenvironments would likely have evolved under. In addition, I was able to compare behavioural responses of red-tailed monkeys to these conditions with hypotheses of hominin behavioural adaptations. While acknowledging that red-tailed monkeys are phylogenetically distant to hominins, and therefore behavioural responses may not be entirely analogous to those of hominins, I hoped to demonstrate that red-tailed monkeys living in both forest and savanna-woodland environments can provide a useful system to understand the environmental pressures that may have driven hominin evolution.

Transitions to more open landscapes with more widely distributed food and hotter, more arid conditions are predicted to have influenced hominin ranging patterns (Copeland 2009). I found larger home ranges and longer maximum daily travel distances in savanna-woodland groups than forest groups related primarily to more seasonally variable food abundance, mirroring predicted changes in hominin ranging as forests transitioned to more open mosaics (e.g. Isbell and Young 1996). Scattered resources should also have led to longer daily travel distances, as well as increased energy expenditure, in hominins – particularly in *Homo* spp. that would have travelled further to acquire high quality but scattered resources, such as meat. Moreover, when food abundance in closed forest was low, Issa monkeys were also more likely to tolerate greater heat exposure in open canopy woodland than Ngogo monkeys were in open canopy secondary forest. Hominins may also have had to balance energy loss through heat exposure with obtaining food that in certain seasons was only available in open vegetation (e.g. Wheeler 1994).

Both of these ranging responses in hominins may have been further influenced by competition. For example, the inclusion of meat – a high quality but relatively difficult to obtain food – in the diet would have resulted in greater competition for *Homo* spp. from both conspecific groups and sympatric carnivores (Rose and Marshall 1996). How competition also influenced hominin ranging patterns could be tested in further comparisons of extant cercopithecine ranging patterns. Although most cercopithecines such as guenons rarely consume meat (Lile *et al.* 2020), in savanna-woodland environments with more seasonally variable food availability than forests, competition for preferred food items (e.g. fruit) may be stronger. As such, groups may avoid or compete more strongly with conspecific groups or even heterospecifics (e.g. chimpanzees; hornbills, *Bycanistes* spp.). Alternatively, inter-group and -specific competition may have been offset by larger home ranges, and subsequently lower population densities, that should have occurred in more open environments and could be reflected in densities of extant cercopithecines in savanna-woodland mosaics, which for primarily forest-dwelling species are typically much lower in open mosaics compared to forest populations (e.g. McLester *et al.* 2019).

In addition to ranging, previous studies of cercopithecoids as referential models for hominin adaptation suggest that further comparisons of red-tailed monkeys in forest and savanna-woodland habitats could continue to provide insight into other hominin adaptations. Expanding diet and switching to fallback foods is a common strategy among primates when preferred foods are scarce or unavailable (Lambert and Rothman 2015). Early dietary data from chimpanzees at Issa indicate that diet is much narrower (fewer plant species consumed overall) than conspecifics in predominantly forest habitats at Gombe and Mahale (Piel *et al.* 2017). Diet switching over short temporal (e.g. monthly) scales may be exacerbated compared to forests however, due to considerable seasonality at Issa that results in most fruit in miombo woodland during late dry seasons (Ch. 2; Ch. 3). For late australopithecines and early *Homo* spp. evolving in mosaics with more widely scattered food than forests, diet switching and expansion was also likely an important adaptation to increased seasonal unavailability of fruit (Nelson and Hamilton 2018; see also Hamilton *et al.* 2019). For example, increased consumption of plant underground storage organs (e.g. Hernandez-Aguilar *et al.* 2007) and aquatic plants (e.g. Wrangham *et al.* 2009) have been hypothesised as important steps in the evolution of hominin diet. Although apes are typically used as extant models when assessing hypotheses of hominin diet, cercopithecines with flexible diets (e.g. compared to more specialized folivorous colobines) can also provide appropriate models of hominins (Hemingway and Bynum 2005; Elton 2006; Cerling *et al.* 2013). To this end, investigating how highly omnivorous red-tailed monkeys adjust diet between habitat types may provide further evidence for dietary flexibility as an adaptive response in hominins that also likely evolved diverse diets in response to changes in vegetation cover.

Although I only investigated spatial cohesion and vocalising behaviour in red-tailed monkeys at Ngogo in this thesis, expanding these investigations to groups in savanna-mosaic environments could help inform further hypotheses of key environmental pressures in hominin evolution. Group cohesion and structure in early hominins is not well understood, but food availability would likely have been an important pressure on hominin group structure. Potts (1998) predicted that hominins evolving in mosaic environments should exhibit a flexible social structure, with a trend of increasing fission-fusion structures with the divergence of *Homo* spp. from the australopithecines (Grove *et al.* 2012). Larger party sizes (e.g. >20 individuals) would likely have been constrained by food availability, especially as *Homo* spp. evolved a diet of high quality, more heterogeneously distributed foods (e.g. meat) that may have attracted greater intra-group competition (Foley 1996; Treves and Palmqvist 2007). Predation risk would also likely have influenced hominin group size, given the high density of sympatric carnivores in the Plio-Pleistocene (Rose and Marshall 1996). Primates in large cohesive groups are more conspicuous and more likely to spend time monitoring conspecifics instead of scanning for predators. As such, hominins would have had to balance forming less cohesive or smaller parties that reduced risk of detection against larger parties that travelled quietly and benefitted from more individuals scanning for predators (Treves and Palmqvist 2007; see also Schreier and Swedell 2012). Compared to Ngogo, Issa exhibits lower, more seasonal food availability and a different composition of predators, including four large carnivores not found at Ngogo (leopard, *Panthera pardus*; lion, *P. leo*; African wild dog, *Lycaon pictus*; spotted hyena, *Crocuta crocuta*). The extent to which these factors influence group cohesion more strongly at Issa than Ngogo could provide broad evidence for similar pressures on hominin adaptation.

Antiphonal calling is an important adaptation for avoiding call overlap and reducing call redundancy, which may be driven by ambient noise that increases during fast travel (Yoshida and Okanoya 2005; Ch. 5). Mediating spacing between hominin groups and parties would have required communication, likely including vocalisations. In australopithecines such as *A. afarensis*, air sacs could have served to amplify vocalisations, hinting at a vocal repertoire that included long-distance spacing calls functionally similar to chimpanzee pant hoots (de Boer 2012). In later *Homo* spp., miscommunication may have been sufficient a selection pressure to result in morphological adaptations that improved vocal articulation, including the reduction and eventual absence of air sacs (de Boer 2012; see also Ghazanfar and Rendall 2008; Clark and Henneberg 2017). Contact calls used by red-tailed monkeys at both sites should be under selection for optimal propagation and detection, meaning vocalising behaviour in red-tailed monkeys may provide an interesting reference for environmental influences on hominin vocalising behaviour, particularly where short-range contact calls (e.g. rather than chimpanzee loud calls) are of interest.

Applications of primate movement behaviour in conservation

Given the prevalence of human threats that nearly all non-human primates face (Estrada *et al.* 2017), it is difficult to conduct any study of primate ecology without considering its applications to conservation. The results in this thesis can improve our basic knowledge of red-tailed monkey biology; knowledge without which it is difficult to 1) understand the extent to which these animals will respond to human activities, and 2) subsequently design effective conservation strategies that facilitate human-wildlife coexistence. For example, spatial data, such as variation in home range size, daily ranging, and habitat use described in Ch. 2 and Ch. 3 may be useful when designing reserves and corridors. Home range sizes allow conservationists to predict group densities supported by protected areas (e.g. Brugiere and Fleury 2000; Fashing and Cords 2000). Metrics of home range and habitat use inform how likely these animals are to use protected areas comprising certain habitat types. In particular, I demonstrated that thermal conditions in secondary forest at Ngogo likely constrain the extent to which red-tailed monkeys can forage in this vegetation. More broadly, this result indicates that protecting already deforested areas may not prevent long-lasting changes in ecology that likely affect subsequent primate survivability, reinforcing a need to prevent forest clearance before it occurs.

Primates, including guenons such as red-tailed monkeys, are umbrella species that play important roles in seed dispersal and forest regeneration (Lambert 2011). Red-tailed monkeys are not currently considered endangered; rather, they are classified as “Least Concern” on the IUCN Red List (de Jong and Butynski 2019). Importantly however, these labels are broad distribution-wide classifications that may not reflect either local ecologies or human threats. I demonstrated that red-tailed monkeys living in two different habitat types exhibit substantial variation in behaviour that likely influences their vulnerability to human threats. For example, larger home range sizes, and therefore smaller group and individual densities, in savanna-mosaic monkeys should increase vulnerability to local extinction (Purvis *et al.* 2000; McLester *et al.* 2019). Threats are also likely to vary and increase at different rates between habitat types in the future (McLester *et al.* 2019; see also Boyd *et al.* 2008). As such, my results reinforce the need for habitat-specific data on both behaviour and threats to improve predictions of how these primates may respond to and cope with likely increasing human activity in habitats across their distribution.

Limitations and future studies

The indices of food abundance I used in Ch. 2, 3, and 4 used data on fruit, flowers, and leaf abundance but not insect abundance, which I was unable to sample due to time constraints. Insects are known to be an important dietary component for red-tailed monkeys, as well as many other guenons (e.g. 34% of feeding observations for *C. ascanius* at Ngogo – Struhsaker 2017; reviewed in Chapman *et al.* 2002). Moreover, insects are higher quality (i.e. rich in protein – Bryer *et al.* 2015) resources that are likely to be widely distributed in clumps, similar to fruit (Garber 2000). As such, acquiring and reducing competition for insects may be an important source of variation in movement behaviour. Specifically, in future studies that 1) expand indices of food abundances to include insect abundance, and 2) are able to reclassify foraging behaviour to specify individual food types being consumed, I expect insect availability and consumption to more strongly influence group and individual behaviours, such as ranging and spatial cohesion, than other food types. Sampling insect densities (e.g. following Ozanne *et al.* 2011) and matching sampled species to those actually consumed by red-tailed monkeys are the primary difficulties of incorporating data on insects in behavioural studies. Spatially-explicit indices of insect abundance will likely be hard to calculate, given their heterogeneous distribution in monkey environments, and may require intensive sampling at across study sites if spatial interpolations or other techniques to predict abundance in unsampled locations prove unreliable.

In addition to food abundance, in Ch. 3 I also indexed temperature to investigate if a trade-off between these two conditions was reflected in group ranging at either site. Ambient temperature alone may not be an exact reflection of heat exposure as perceived by primates, because other conditions such as windspeed and relative humidity likely also influence the effect of temperature (Hill *et al.* 2004; see also Thompson *et al.* 2016). At Issa, for example, windspeed may play an important role in reducing heat exposure for primates in miombo woodland given the low density of woodland trees and funnel effects created by steep valleys. I was able to weight temperatures in miombo woodland at Issa by humidity, but humidity and windspeed data were not available for other sites or vegetation classes and should ideally be measured in future studies that compare behaviour against abiotic conditions. A current trial of VHF telemetry collars with Issa monkeys also raises the possibility of fitting temperature loggers on collars in the future in order to quantify thermal environments for individual animals (see e.g. Thompson *et al.* 2014).

In Ch. 4 and 5, I examined spatial cohesion and contact calling behaviour at the individual level. When investigating variation in these behaviours between individuals, I discerned individuals by age-sex class because I could not reliably establish individual identities quickly enough to provide a sufficient sample size to incorporate into models by the end of the study. I used individual identity only as a baseline control in models, where known. Categorising individuals based on metrics such as age-sex class can be useful to some extents, such as informing nutritional requirements (which should typically be highest for young, fast-growing individuals, or lactating females – Felton *et al.* 2009) or predation risk (which should be greater for small-bodied individuals – e.g. Zuberbühler and Jenny 2002). However, these metrics may also risk inadvertently grouping individuals that could otherwise exhibit individual variation in life history traits that explain variation in movement behaviour. For example, strong social affiliations or kinship should increase how likely individuals are to tolerate competition, or even share food (de Waal 1989). Similarly, individuals may not tolerate feeding competition from all other group members equally, which could be reflected in high rates of aggression or avoidance. Incorporating individual identities into future studies would allow movement behaviour to be contextualised against finer resolution metrics – such as social network centrality or networks of grooming and aggression that reflect social affiliations – that can be calculated for each individual in the group. These metrics should allow us to answer questions about how individual animals influence group cohesion. While movement behaviour of individual primates, and therefore groups, is likely the product of a myriad of ecological and social influences that drive trade-offs at a range of spatial and temporal scales, expanding on the results in this thesis by incorporating long-term life history data from individuals should further reveal how these animals maintain group cohesion and the mechanisms through which group members mediate collective movements.

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