



Diet and polyspecific associations affect spatial patterns among redbtail monkeys (*Cercopithecus ascanius*)

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Abstract

Animals are predicted to be in closer conspecific proximity during feeding on clumped resources, such as fruits in a tropical rain forest, than when feeding on more dispersed resources, such as leaves or insects. Polyspecific associations are also predicted to affect inter-individual distance because the close proximity of more individuals presumably provides increased protection against predators. We examined the effects of food type and polyspecific association on nearest-neighbor distances of redbtail monkeys (*Cercopithecus ascanius*) in the rain forest of Kibale National Park, Uganda. When redbtails consumed fruit, they were closer to conspecific nearest neighbors than when they consumed leaves or insects. When any of the other five monkey species were close or intermingled, redbtail monkeys were farther from conspecific nearest neighbors than when they were not in polyspecific associations; however, this effect was apparently driven by redbtail associations with grey-cheeked mangabeys (*Lophocebus albigena*). The aggression mangabeys exhibit to aerial predators may explain this observation. Our results imply a complex relationship between food distribution, predation risk, polyspecific association and spatial patterns that can be explored further in multiple taxa.

Keywords

guenon, mixed-species association, nearest-neighbor distance, food distribution.

1. Introduction

Food distribution and the risk of predation are important factors that affect group formation and size in animals (Clutton-Brock, 1975; Clark & Mangel, 1984; Krause & Ruxton, 2002; Majolo et al., 2008). For example, food

distributed heterogeneously in rich patches is hard for a lone individual to exploit, but can be acquired more easily and effectively by individuals as part of a group (Alexander, 1974; Johnson et al., 2002). However, group foraging can be costly, as animals face intraspecific competition (Sibly, 1983; Isbell, 1991; Krause & Ruxton, 2002). Group living can also protect animals from predation as increased group size leads to collective vigilance (Treherne & Foster, 1980; van Schaik, 1983; Roberts, 1996), as well as dilution (Hamilton, 1971), and enables proactive mobbing or defense (Pulliam, 1973; van Schaik, 1983; Krams et al., 2009). Predation risk favors group living in ways that complement or oppose the selective pressures exerted by resource distribution.

Group size is often considered a function of the number of individuals capable of foraging without reaching a threshold of reduced foraging efficiency due to feeding competition and the number of individuals needed to decrease predation risk (van Schaik & van Hooff, 1983; Romey, 1995). This tradeoff between the costs and benefits of group living affects group spatial patterns (Krause & Ruxton, 2002). As a result, inter-individual distances and group cohesion can vary among species and within taxa over time and space based on predation risk, diet, and intragroup competition patterns (Wrangham, 1980; Isbell, 1991; Sogard & Olla, 1997).

The 'food distribution' hypothesis (*sensu* Brown & Orians, 1970; Isbell & Enstam, 2002) suggests that conspecifics will affect inter-individual distances according to the spatial distribution of their food resources. The hypothesis predicts that when food is clustered or clumped, inter-individual distance will be shorter, corresponding to the spatial distribution of the food. In contrast, when food is more widely distributed, inter-individual distance will be greater. Inter-individual distance and group spread of sympatric vervet (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) in Kenya, under similar predation pressure, were greater when they foraged on more widely distributed than clumped resources (Isbell & Enstam, 2002). Similarly, when researchers provisioned voles (*Clethrionomys rufocanus*) at food stations, the voles aggregated at the clumped food more than when feeding on non-provisioned more widely distributed resources (Ims, 1987).

Intragroup spatial patterns are also influenced by perceived predation risk: animals alter their position within a group and in relation to one another when they identify a predator. Bottlenose dolphins (*Tursiops aduncus*) restricted their habitat use to internal areas of shallow waters or deep water

areas, instead of the edges of shallow waters where food resources are rich, when tiger sharks (*Galeocerdo cuvier*) were present (Heithaus & Dill, 2006). When nearest neighbors were farther away, cowbirds (*Molothrus ater*) spent more time scanning for predators and less time foraging (Fernández-Juricic et al., 2007). When in a social group, the proximity of more individuals seemingly provides protection from predators, while separation from other individuals renders an animal more vulnerable to attack.

Polyspecific association, also known as mixed species groups, effectively increases the group size of single-species groups with respect to some benefits of group living, while typically not being permanent and not incurring the same level of foraging costs (Terborgh, 1990; Chapman & Chapman, 2000). These associations occur across many taxa, including birds, fish, mammals, and invertebrates (Heymann & Buchanan-Smith, 2000; Frantzis & Herzog, 2002; Stensland et al., 2003; Sridhar et al., 2009). Benefits of polyspecific association, like the benefits of group living, are thought to primarily take two forms: foraging and anti-predation. Even when associates have similar diets, increased foraging efficiency may occur in co-feeding mixed species groups. For example, during feeding, moustached tamarins (*Saguinus mystax pileatus*) flushed arthropod prey, to the foraging benefit of saddle-back tamarins (*S. fuscicollis avilapirensi*) (Peres, 1992).

Although polyspecific associations can form by chance (Waser, 1984), the anti-predation (sometimes referred to as protector-species) hypothesis proposes that they provide protection from predators for at least one member (Pius & Leberg, 1998). Interspecific groups of Thomson's gazelles (*Gazella thomsoni*) and Grant's gazelles (*G. granti*) detected and potentially deterred predators earlier because of the larger group size than monospecific groups (FitzGibbon, 1990). Red colobus (*Procolobus badius*) and Diana monkeys (*Cercopithecus diana*) were most likely to associate during the peak of the chimpanzee hunting season, when risk of attack, especially to red colobus, was highest (Noë & Bshary, 1997).

Polyspecific association also affects group cohesion through similar mechanisms as a single-species group. Sympatric flying prions and diving petrels maintained closer inter-individual distance than predicted by chance to gain foraging information from one another, indicating a foraging benefit to close proximity between species (Silverman et al., 2004). Campbell's monkeys (*Cercopithecus campbelli*) were more dispersed when in association with Diana monkeys (*C. diana*) than when only with conspecifics due to

an increased perception of safety from predators when in the presence of Diana monkeys (Wolters & Zuberbühler, 2003). Thus, polyspecific associates, through ability to protect a larger geographic area (or, in other cases, through particular anti-predator capabilities) can affect conspecific inter-individual distance as well.

Our study focuses on redbtail monkeys (*Cercopithecus ascanius*), an excellent species with which to examine the conspecific spatial effects of feeding and polyspecific associations because of their diverse diet and frequent association with sympatric monkey species (Cords, 1986; Chapman & Chapman, 1996). We examined the factors that influence spacing behavior, indexed as nearest-neighbor distance, in a group of redbtail monkeys in Kibale National Park, Uganda. Redtails are small bodied frugivores (males: 3.7 kg, females: 2.8 kg; Gevaerts, 1992) that also eat insects and, to a lesser extent, young leaves, seeds, and flower parts (Struhsaker, 1981; Chapman et al., 2002; Lambert, 2002; Rode et al., 2006).

Redtails in Kibale associate primarily with red colobus monkeys (*Procolobus rufomitratu*s, time in association = 30.6%), blue monkeys (*Cercopithecus mitis*, 27.6%), grey-cheeked mangabeys (*Lophocebus albigena*, 3.8%), black-and-white colobus (*Colobus guereza*, 2.6%) and l'Hoest's monkeys (*Cercopithecus lhoesti*, 0.2%) (Waser, 1987; Chapman & Chapman, 2000). Redtail diets overlap considerably with those of mangabeys and blue monkeys because all three species eat many of the same fruit species (Wrangham et al., 1998). Houle et al. (2010) quantified that when redbtails, blue monkeys, and mangabeys are feeding in one fruiting tree, mangabeys are dominant and redbtails are most subordinate as determined by the outcomes of aggressive interactions over fruit. The redbtail diet overlaps to a lesser extent with the two folivorous colobus monkey species (Chapman et al., 2010), though previous research at Kanyawara reported an overlap of 25.1% with red colobus (Chapman & Chapman, 2000).

Crowned hawk-eagles (*Stephanoaetus coronatus*) are redbtails' primary predator; at Kanyawara, bones from the six primate species discussed have been found in two monitored eagle nests (Struhsaker & Leakey, 1990). Mangabeys and red colobus in Kibale have both been observed acting aggressively when faced with aerial predators: high-ranking adult male mangabeys and red colobus chased crowned hawk-eagles (Arlet & Isbell, 2009; Chapman unpublished data) and adult male red colobus even climb onto and bite chimpanzees in defense of the group (Stanford, 1995). Red

colobus are the preferred prey of chimpanzees (*Pan troglodytes*) at numerous study sites (Stanford et al., 1994; Mitani & Watts, 1999). In contrast to red colobus and mangabeys, redtails retreat and hide in response to predators (Ihobe & Uehara, 1999). Red colobus and mangabey defense strategies may be a protective buffer for other monkey species present at the time of a chimpanzee or eagle attack. Thus, red colobus and mangabeys may deter predators and provide a benefit to species that are associating with them in mixed-species groups (Chapman & Chapman, 1996).

We tested three predictions. First, given that fruits in forests are typically in patches (i.e., one fruiting tree is a patch) and the distance to the next patch is usually long, while insects and leaves are more widely distributed throughout the habitat (Wrangham, 1980; Isbell, 1991; Janson & Chapman, 1999), we predicted that redtails would have shorter nearest-neighbor distances when feeding on fruit than when feeding on insects and leaves. Second, we predicted that redtail monkeys would be more widely spaced when surrounded by polyspecific associates because of perceived predator protection. Third, given red colobus and mangabey aggressive behavior towards predators, we predicted that nearest-neighbor distance would be greater particularly when red colobus and/or mangabeys were with the redtails.

2. Methods

2.1. Study site and subjects

The study took place in Kibale National Park, in western Uganda (0°13'–0°41'N and 30°19'–30°32'E), a 795 km² mid-altitude evergreen forest. The study group was found near the Kanyawara village, in a 282 ha area with an elevation of 1500 m. The area has an average annual rainfall of 1696 mm (data from 1990–2011; Chapman unpublished data; Chapman & Lambert, 2000; Stampone et al., 2011). Redtail monkeys are a common species in the area, with a density of about 184 individuals per km² (Chapman et al., 2010).

The study group consists of approximately 40 individuals and has been habituated since 2008. At the time of this study, 23 adult females and 7 adult males were individually identified by tail, facial, nipple, and/or body-size characteristics. Thirteen species of primates are present in Kibale, though the polyspecific associates of the redtails typically included only red colobus, mangabeys, black-and-white colobus, blue monkeys, and l'Hoest's monkeys. Of these species, l'Hoest's monkeys are the only species that has not been

systematically habituated and studied in Kanyawara and they were observed in polyspecific association with redbtails the least.

2.2. Data collection

From November 2008 to May 2010, the authors and two field assistants collected 1958 hours of behavioral data (3916 scan samples) on adult redbtails. Scans were collected on up to 5 individuals every 30 min from 9:00 to 16:00 during 10 days per month. We recorded data on the first five individuals we observed and then moved within the group between scan samples so as not to resample the same individual. For each individual, we recorded age/sex; activity; if eating, plant species and part of food item (unripe fruit, ripe fruit, young leaf, mature leaf, leaf bud, flower) or insect by Order; the age/sex of and distance to the individual's conspecific nearest neighbor; DBH of the food tree; and species of polyspecific associate(s), if applicable. We defined polyspecific association as when another primate species was within 50 m of the group (Struhsaker, 1981). Group spread was estimated where possible by pacing the length and width of the social group (Snaith et al., 2008). The observers estimated conspecific nearest-neighbor distance and group spread by eye. Distance estimations were verified using a parallel laser technique we developed (Rothman et al., 2008). Inter-observer reliability was assessed every three months during the study to ensure that estimations were precise and accurate.

2.3. Data analysis

We reduced the original 1958 hours of data (3916 scans) for analysis by restricting the data to adult dyads that were individually identifiable, to ensure that our dataset was not biased towards certain individuals. The reduced data set consists of 1282 hours (2564 scans) on 24 individually identifiable adult redbtails, 18 females and 6 males. The greater number of females than males is due to the skewed sex ratio of redbtail social groups. To examine whether nearest-neighbor distances were affected by polyspecific associations and diet, we used a Generalized Linear Model (GLM) with squared-root transformed nearest-neighbor distance as our response, with food type and presence of each polyspecific associate as predictors, and their interactions. In this model, we considered individual a repeated measure and incorporated Generalized Estimating Equation (GEE) fit criteria (PROC GENMOD; SAS

Enterprise Guide 4.3). This procedure generates a *Z*-statistic (the ratio of estimate and standard error) and a corresponding *p* value (Molenberghs & Verbeke, 2005). We contrasted reproductive parts (ripe and unripe fruits, flowers, seeds, seed pods), leaves (young leaves, mature leaves, leaf buds, leaf petioles, pith), and insects for analysis and used a Chi-Square test to investigate whether individuals ate more of these food items while in polyspecific association than while not in association. Standardized residuals greater than an absolute value of three indicated a lack of fit to the null model (Agresti, 1996). To examine if nearest-neighbor distance was a result of wider group spread in larger fruiting trees, we ran a one-tailed Pearson's correlation between DBH, previously used as a proxy for fruit biomass (Chapman et al., 1992), and group spread.

3. Results

In total, redtails spent $71.4 \pm 2.5\%$ of their time feeding and ate a diet of mainly insects, but they also consumed fruit and young leaves (Figure 1). The majority of the leaves consumed were young leaves: 83% young leaves ($N = 429$), 13% mature leaves ($N = 69$), 2% leaf buds ($N = 10$) and 1% leaf petioles ($N = 6$). Flowers, seeds and fruit of unknown ripeness together only made up 16% ($N = 39$) of reproductive part consumption, indicating

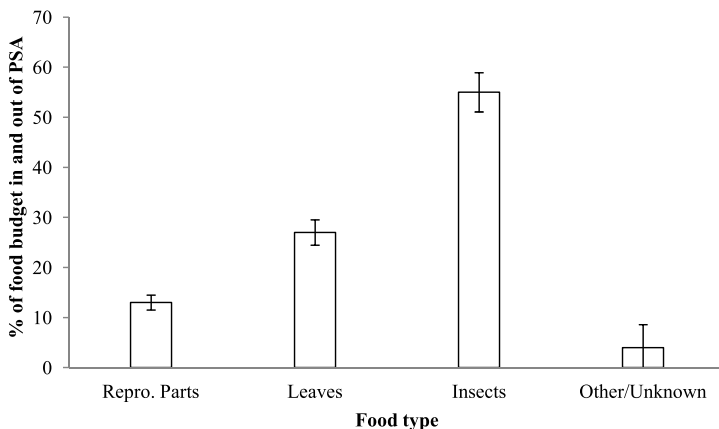
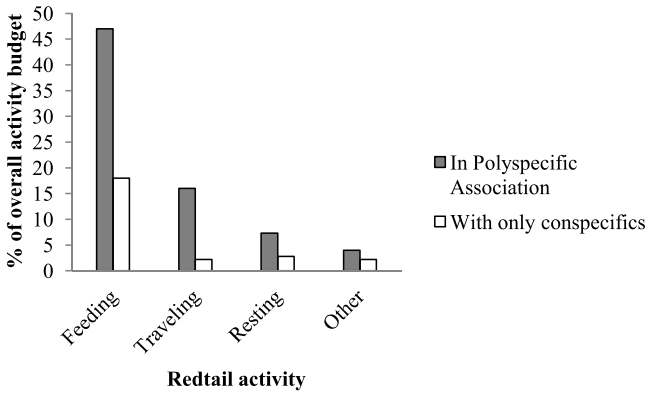
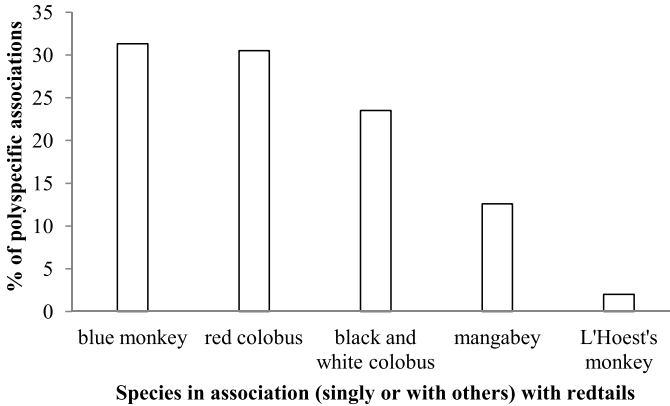


Figure 1. The foraging effort of redtail monkeys in Kibale National Park, Uganda, based on the percentage of time spent feeding on plant reproductive parts, leaves, insects, and other/unknown items (\pm SE). ‘Other/Unknown’ includes unusual items like mushrooms and moss, and difficult to identify food items, often due to lack of visibility.



(a)



(b)

Figure 2. (a) Redtail activity budget in polyspecific association, and with conspecifics. (b) All instances of redbtail polyspecific association with each of 4 polyspecific associates. Please note that this figure indicates all instances and therefore overlaps among species.

emphasis on ripe (38%) and unripe (46%) fruits when consuming reproductive parts. The group spent 73% of their time in polyspecific association ($N = 1869$ scans) and 27% alone ($N = 695$ scans). While in polyspecific association, redbtails associated with between one and four other species, spent most of their activity budget feeding (Figure 2a, b) and ate more fruit and fewer leaves and insects than when with only conspecifics ($df = 2$, $\chi^2 = 41.32$, $p < 0.0001$).

A redbtail's conspecific nearest-neighbor when consuming fruit was closer (mean = 9.88 ± 6.38 m; $N = 242$; $Z = -2.39$; $p = 0.017$) than when con-

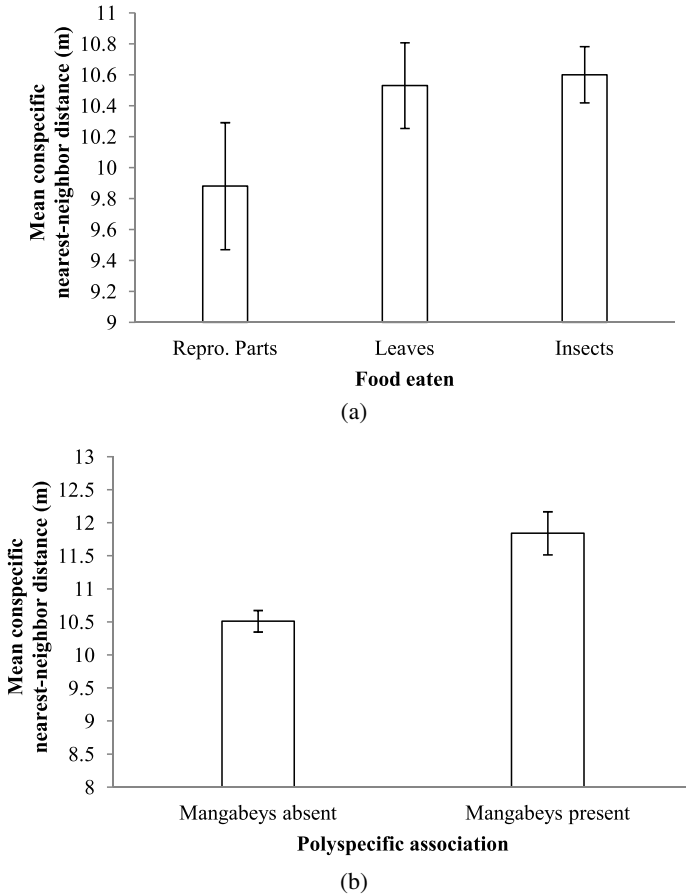


Figure 3. Redtail mean nearest-neighbor distance \pm SE (a) for each food type (reproductive parts, leaves, and insects) in and out of polyspecific association, (b) in polyspecific association when mangabeys are present versus when in polyspecific association with other species with no mangabeys present and (c) for each food type with conspecifics versus in polyspecific association when mangabeys were absent versus present.

suming leaves (mean = 10.53 ± 6.22 m; $N = 506$; $Z = 0.7$; $p = 0.484$) or when consuming insects (mean = 10.60 ± 5.77 m; $N = 1010$; $p > 0.5$) (Figure 3a). When redtails were not in association with another species, individuals were closer to their nearest neighbors (mean = 9.78 ± 5.69 m; $N = 694$) than when any of the other three species was present (mean = 10.83 ± 6.35 m; $N = 1869$). However, this effect was driven by association with mangabeys: a redtail's nearest neighbor was farther when mangabeys were

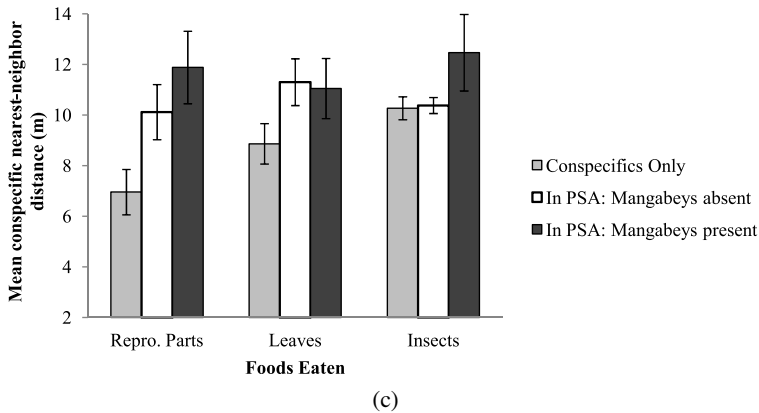


Figure 3. (Continued.)

present (mean = 11.84 ± 6.91 m; $Z = 2.85$; $p = 0.0044$) than when redbtails were alone (mean = 9.78 m) or when any three of the other associates were present (Figure 3b). There was no difference between a redbtail's conspecific nearest-neighbor distance when the group was in association with black and white colobus monkeys (mean = 10.93 ± 6.24 m; $N = 838$; $Z = 1.24$; $p = 0.22$), red colobus (mean = 10.74 ± 6.34 m; $N = 1086$; $Z = 1.52$; $p = 0.13$) and/or blue monkeys (mean = 10.91 ± 6.54 m; $N = 1116$) ($Z = -0.2$; $p = 0.84$). The sample size of l'Hoest's monkey association with redbtails was too small for meaningful results ($N = 70$). No relationship was found between DBH and group spread for the overall dataset (Pearson's correlation coefficient, $r = -0.074$, $p = 0.172$) and for when mangabeys were present ($r = 0.098$, $p = 0.345$).

4. Discussion

Inter-individual distance among group members is in large part dictated by predator protection and the nature of food distribution (Krause & Ruxton, 2002). As predicted, we found that when redbtails consumed fruit, they were closer to conspecifics than when feeding on dispersed leaves or insects, suggesting that the clumped nature of their food resource affected nearest-neighbor distance. Prior research demonstrates that, when feeding on clumped resources, inter-individual distance between group members decreases (Hirsch, 2007; Sugiura et al., 2011). Raccoons (*Procyon lotor*) provisioned with clumped resources were closer to conspecifics when foraging than when feeding on dispersed resources (Wright & Gompper, 2005).

Similarly, squirrel monkeys (*Saimiri sciureus*) feeding on fruit had a closer nearest neighbor and more individuals within 5 m than when feeding on more widely dispersed insects (Stone, 2007). Comparisons between inter-individual distances among patas (*Erythrocebus patas*) and among vervet monkeys (*Cercopithecus aethiops*) in Kenya illustrated that variation in the distribution of *Acacia* food tree species affected spatial cohesion, whereby vervets, who ate from more clumped foods were more spatially cohesive than patas, whose food trees were more dispersed (Isbell & Enstam, 2002). Our results, along with these studies, thus suggest that within-group spatial patterns are affected by food resource distribution.

Our prediction that polyspecific associations with red colobus and mangabeys would affect inter-individual distances was supported for mangabeys, but not for red colobus. Previous research indicated that the proportion of time spent in polyspecific association was positively related to monkey species density (Chapman & Chapman, 2000), but mangabeys and redbills were in association more often than would be predicted by chance based on their population densities (Waser, 1982). Mangabey group densities were much lower than the folivores during the time of our study (Chapman et al., 2010). Thus, redbills' less frequent association with mangabeys compared to, for example, red colobus (see Figure 2b), is not necessarily indicative of a lack of potential benefit of redbill-mangabey association. Waser (1982) suggested that the attraction between mangabeys and redbills might be due to dietary overlap, and this also could be the case for blue monkey-redbill associations, because they eat the same fruit resources and were in frequent association despite the low density of blue monkeys (Chapman et al., 2010). We found that redbills ate more fruit, the main food of mangabeys (Waser, 1975; Olupot, 1998), and fewer leaves when in polyspecific associations, so redbills may be gaining foraging benefits from polyspecific associations, despite any interspecific competition (Houle et al., 2010).

Despite the fact that redbills ate more fruit, a clumped resource, when in polyspecific association, the mangabey-redbill polyspecific associations increased nearest-neighbor distance between redbills (Figure 3c), indicating that mangabeys may provide protective effects against predators. This increase was in comparison to nearest-neighbor distance in polyspecific association when no mangabeys were present and to when only conspecifics were present. As we found no correlation between DBH and group spread, we argue that the increase in nearest-neighbor distance in the presence of

mangabeys was not due to increase in patch size. There are few documented cases of chimpanzees hunting redbtails (Wrangham & Riss, 1990; Watts & Mitani, 2002); however, eagle predation on redbtails occurred more frequently than chance (Struhsaker & Leakey, 1990; Mitani et al., 2001). When this risk of eagle predation is combined with the aggressive reactions by mangabeys towards eagles (Arlet & Isbell, 2009), mangabey association may be especially beneficial to redbtail safety. Red colobus monkeys are the preferred prey of chimpanzees at multiple sites in Kibale (Chapman & Chapman, 1996; Mitani & Watts, 1999) and red colobus anti-predator tactics may be more specialized to these primarily terrestrial group hunters (Stanford, 1995). As redbtails are more prone to aerial attack from eagles, these red colobus defense tactics may not be as relevant to redbtail safety as mangabey defense tactics, even as a temporary buffer.

Our study supports the hypothesis that predation risk affects conspecific spatial relations in mixed species groups. Previous research has shown that predation affects inter-individual distance in single and mixed species groups across taxa. In a monospecific proboscis monkey (*Nasalis larvatus*) group, monkeys maintained close inter-individual distances prior to and during river crossings when the threat of predation by gavials (*Tomistoma schlegeli*) was highest, probably to improve vigilance and predator detection (Yeager, 1991). The predator protection hypothesis was supported in mixed-species groups of orioles (*Icterus galbula bullockii*) and magpies (*Pica nuttalli*); oriole nest density increased in closer proximity to magpie nests. Conspecific inter-individual distance shortened as orioles nested closer to another species better able to defend against nest predators under high predation pressure (Richardson & Bolen, 1999).

Our results demonstrate that conspecific spatial patterns of individuals within a group are influenced by both food distribution and predation risk, and that polyspecific associations can affect these spatial patterns further depending on the costs and benefits of a particular sympatric species' presence. Though the significant differences in distance were as low as 1 m, such distances are considerable ecologically and socially for small arboreal animals. Of particular interest are the differences documented with response to mangabeys and red colobus; both species attack aerial predators. This suggests that a species' response to the composition of the polyspecific association it is a member of is complex and potentially does not just involve the benefit that is obtained from the species it is associating with. This

points to a number of different avenues for future research. For example, since red colobus dominate redbills, the influence of red colobus on redbill conspecific nearest-neighbor distance may depend on if the two species are feeding on the same young leaf resource or not. Since redbill dietary overlap with mangabeys and red colobus differs, nearest-neighbor distance may be strongly influenced by the nature of food resources being used by the redbills at a specific time, and further by the possibility that they can profitably fall back and forage on insects if displaced from a food patch. Additionally, the speculation that the differential spatial response of redbills to mangabeys and red colobus is a result of different predator defense strategies by these associates could be tested with playback experiments of crowned hawk-eagle calls. Our results call for further study across taxa on relationships between predation risk, food distribution, polyspecific association and resulting spatial patterns.

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