



Seasonal variation and group size effects in putty-nosed monkeys' (*Cercopithecus nictitans*) heterospecific associations in the Nouabalé-Ndoki National Park

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Abstract

Many non-human primates form heterospecific associations to increase benefits resulting from group living like antipredation defence and increased foraging efficiency while avoiding costly resource competition that usually arises from large conspecific groups. Previous studies provided profound insight into how these benefits are obtained and what behavioural changes might be elicited through association formation. What remains widely unknown are factors that could account for intra-specific variation in association patterns. For instance, we are still widely lacking a comprehensive assessment of how group size and seasonality affect heterospecific associations across larger number of groups within a species. The current study monitored more than 20 groups of putty-nosed monkeys (*Cercopithecus nictitans*), a forest guenon known to be frequently in association with other monkey species, for 37 months in the Nouabalé-Ndoki National Park, Republic of Congo. Amongst the five primate species observed in association with *C. nictitans*, grey-cheeked mangabeys (*Lophocebus albigena*) and crowned monkeys (*C. pogonias*) were the most frequently encountered association partners. We did not find any effect of seasonality on association rates. However, larger *C. nictitans* groups were substantially more in association with *L. albigena* and *C. pogonias* than smaller groups during the main dry season. We argue that our findings suggest a major impact of antipredation benefits of heterospecific troops including *C. nictitans* during periods of increased vulnerability. We discuss how knowledge about variations in association patterns may help to adjust conservation strategies.

Keywords Polyspecific associations · *Cercopithecus nictitans* · Congo

Introduction

Many highly social mammal and bird species form inter-specific associations to navigate in their habitats (ungulates: Fitzgibbon 1990; Beaudrot et al. 2020; primates: Noë and Bshary 1997; Heymann and Buchanan-Smith 2000; cetaceans: Quérouil et al. 2008; Syme et al. 2021; birds: Powell 1985; Greenberg 2000; Sridhar et al. 2009). A conservative measure following Struhsaker (1981) considers two species being in association if any group member of one species is in at most 20 m from a member of another species. Multi-species associations may either occur by chance e.g., as aggregations at a commonly shared food source or they might be actively formed and maintained (Waser 1980; Whitesides 1989). A range of costs and benefits drove the evolution of this phenomenon and the likelihood of such associations to occur. In a nutshell, the formation of heterospecific

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associations centres around benefits from increasing group size without increasing costs that are normally related to larger conspecific groups, e.g., increased competition for food and reproduction (van Schaik 1983; Isbell 2004). Similar to benefits that arise from forming conspecific groups, benefits from forming heterospecific troops usually fall into two classes. First, advantages can be linked to the reduction of predation risk by increasing safety in number effects through dilution and confusion effects (Delm 1990; Schradin et al. 2019). Additionally, vigilance towards predators can be exploited, shared, and increased (Buzzard 2010; Kenward 1978; Bshary and Noë, 1997). After detection, especially heterospecific males often jointly mob predators (McGraw and Zuberbühler 2008). Benefits may result in behavioural changes in associated species. For instance, activity budgets can switch from time spend for vigilance to foraging or to the extension of ecological niches due to a decreased susceptibility to predation (*Cercopithecus campbelli*, *C. diana*, *C. cephus*: Gautier-Hion et al. 1983, Bshary and Noë, 1997, Wolters and Zuberbühler 2003). The extension of vertical use of space to normally inaccessible strata pave the way for broader access to feeding resources, which falls in the second category of potential benefits of associations related to increased foraging efficiency. Associated species were shown to exploit each other's knowledge about fruiting trees and to avoid redundant visits to food patches (*C. mitis* and *C. ascanius*: Cords 1987, Cords 1990). Furthermore, multi-species groups can cooperatively defend shared territories against conspecific neighbours (*Saguinus fuscicollis* and *S. mystax*: Peres 1992). One strategy to circumvent competition over food with overlapping diets is to switch between different food resources and thus to decrease diet overlap, probably through digestive flexibility (in *C. Ascanius* with *C. mitis*, *Lophocebus albigena* and *Procolobus badius*: Lambert 2002).

Although ample empirical investigations substantially increased our understanding of heterospecific associations amongst non-human primates, we still face two major problems. First, observations in natural habitats are often limited to few groups due to the difficult recognition of specific unhabituated groups, missing knowledge about home ranges and limitations in following several unhabituated groups through dense forest habitats. However, different groups may well have different interests in forming associations, e.g., due to variations in group size (e.g., Struhsaker 2000; Patterson et al. 2014; Strier et al. 2014; Beauchamp and Cabana 1990). Group size likely has a strong impact on key benefits from associating such as safety in number effects, on vigilance or resource competition with overlapping diets. Unfortunately, systematic investigations of correlations between intraspecific group size and association indices are widely lacking to date. Second, it often remains difficult to tease apart benefits related to foraging from those

related to predation avoidance. For instance, the extension of an ecological niche to previously unexploited strata could as well be interpreted as the compensation of increased feeding competition between associated species. Hence an apparent benefit from associating could turn into the mitigation of costs arising from associating. Such phenomena seem particularly likely with pronounced niche overlaps in sympatric species. Furthermore, if resources are scarce and shared, resource competition can also lead to the dissolution or avoidance of associations to avoid physical, agonistic interactions and to reassure sufficient access to resources. Systematic investigations of the interaction between group size and seasonal changes in resource availability provide the potential to disentangle predation avoidance from foraging related benefits in promoting the formation of heterospecific aggregations.

Cercopithecus nictitans are mostly arboreal, diurnal guenons that live in groups of 3 to 20 individuals with one adult reproductive male, several related females, and their offspring (Buzzard and Eckardt 2007). Males are often spatially separated in higher canopies or at the periphery of the group and do rarely interact socially with other group members (Gautier-Hion 1980). However, males usually take over the lion's share of group defence during predatory events (Arnold and Zuberbühler 2006; Mehon and Stephan 2021). In Gabon and Cameroon, *C. nictitans* has been reported to be frequently in association with *C. cephus* and to a lesser extent with *C. pogonias* and grey-cheeked mangabey (*Lophocebus albigena*). In the republic of Congo, *C. nictitans* has been also frequently encountered with *C. cephus* and *C. pogonias*, despite considerable dietary overlaps (Gautier-Hion 1980; Gautier-Hion et al. 1983; Eckardt and Zuberbühler 2004). Some groups were consistently found to be more reliable in association than others, although reasons for intergroup variation remain unknown (FGM, CS, personal observation). A possible reason for this heterospecific assemblages despite very similar foraging preferences was suggested by Gautier-Hion (1980), who documented that *C. nictitans* decreased diet overlap with *C. cephus* and *C. pogonias* during two periods. First, during the main dry season when resources were scarce male and female *C. nictitans* increased the intake of mature leaves and decreased fruit consumption. Both *C. cephus* and *C. pogonias* did not considerably switch consumed food type. This suggests that *C. nictitans* may actively seek and maintain association with other species to secure predation avoidance benefits despite nutritional disadvantages. Second, towards the end of the major rainy season, female *C. nictitans* switched from fruits to young leaves and insects, most likely due to changed nutritional needs of pregnant and lactating females (Coelho 1974). Whether this seasonal shift of foraging preferences stabilises heterospecific associations during periods of limited resource availability remains yet unknown.

We continuously monitored 26 identified groups of *C. nictitans* in the Nouabalé-Ndoki National Park, Republic of Congo. Generally, we aim to give a description of *C. nictitans* association patterns both in terms of identifying associated species and quantifying how often different groups were encountered in association. More specifically, we investigate seasonal and inter-group differences to elucidate constituting factors of association patterns. For each encounter with a target group, we identified the present *C. nictitans* group and identified all associated primate species. We collected rain fall data during the study period as a proxy to season and food resource availability. We predict that if the reduction in predation risk was the major driving force for heterospecific associations and *C. nictitans* seek to form heterospecific associations, then smaller groups are supposed to have more benefits from increasing troops size and should show higher rates of association than larger groups of *C. nictitans*. If other primate species actively join *C. nictitans*, we expect the contrary pattern, namely larger *C. nictitans* groups being preferred to increase troop size. In this case, larger groups should be found more often in association than smaller groups that provide less predation avoidance benefits. Because we could not directly identify consumed food types with unhabituated groups, we predict that if *C. nictitans* either switched food resources in the main dry season or food resource availability had no major impact, association rates should not vary across seasons. In contrast, if foraging benefits for *C. nictitans* mainly promote polyspecific associations, larger groups should be encountered less in association during major dry seasons when feeding competition over fruits is supposed to increase.

Methods

Study site and subjects

We collected data on 26 groups of *C. nictitans* in the Nouabalé-Ndoki National Park, Republic of Congo (2°15.50 N 16°24.70 E; altitude about 300 m), between January 2019 and March 2022 (37 months in total due to a break in December 2019 and January 2020). Groups ranged in size from 7 to 22 individuals (S1) and home ranges were spread over an area of about 60 km². The study area was mainly located in a mixed-species forest that is characterised by high diversity both in terms of spatial structure and floral plant species (Harris 2002), providing ample foraging resources for primates and other wildlife. Average home range of single groups was 0.66 km² with moderate inter-group variation due to group size and thus resource competitiveness and season due to resource availability (FGM, CS, unpublished data). Both main forest guenon predators, eagles (*Stephanoaetus coronatus*) and leopards (*Panthera pardus*) are present in

this protected, primary rainforest habitat. Since 2018, groups were identified by individual markings (e.g., broken tails, visible scars) and group size, and the groups' home range was determined and monitored using GPS data. Group size varied between the beginning and the end of data collection for the majority of groups to the amount of ± 2 individuals (due to births and male subadult disappearance). However, relative group size remained stable between groups and none of the groups disintegrated. Groups often considerably overlap in their home ranges with about three adjacent neighbouring groups per focal group (FGM, CS, unpublished data). Additional to chimpanzees (*Pan troglodytes troglodytes*) and western-lowland gorillas (*Gorilla gorilla gorilla*), eight other diurnal monkey species are present in the study area: *C. pogonias*, *C. cephus*, the eastern black-and-white colobus (*Colobus guereza*), the agile mangabey (*Cercocebus agilis*), *L. albigena*, the Oustalet's red colobus (*Piliocolobus oustaleti*), the De Brazza's monkey (*C. neglectus*), and the Allen's swamp monkey (*Allenopithecus nigroviridis*). The latter was only sighted once during the study period and has been previously reported to be exceptionally rare in the area (Maisels et al. 2006), similar as to *P. oustaleti* (Brncic 2018), which is why we excluded both species. *C. neglectus* has strong preferences for riverine and swampy habitats that are rarely visited by *C. nictitans* (Bitty and McGraw 2007; Oates 2011) and generally very rarely form associations with other species (Zeeve 1991; Mugambi et al. 1997). We thus excluded *C. neglectus* from the list of monkey species that are likely to frequently encounter *C. nictitans*. None of the groups has been habituated to human presence and human observers collected data without being noticed from concealed positions. In the area, the major dry season is supposed to range from December to February and the major rainy season is usually from September to November. The minor dry season ranges from June to August and the minor wet season ranges from March to May, which can be subject to annual variability in rainfall (Mitani 1992).

Data collection

Target group choice followed an observational protocol reassuring similar observation effort per month for each group. Four main transects were established around the research camp leading to a balanced number of groups in the north, east and west with the south being limited through the Ndoki river. Observers approached and identified *C. nictitans* groups using information about home range, group composition and specific, individual markings. The primary observer (FGM or DNK) and two experienced Ba'Aka assistants then observed the undisturbed *C. nictitans* group for 5 to 20 min using Nikon Monarch 7 binoculars. Other monkey species that were associated

with the target group were identified and recorded by all three observers using visual and frequently uttered, conspicuous vocal cues. Variation in observation time was caused by different visibility due to e. g. group spread and vegetation. Once all three observers confirmed the presence of at least two individuals from another primate species within 20 m, observational records were stopped. Rainfall data were collected daily during the study period at a close natural forest clearing that was located approximately in the centre of our 60 km² study area using a rain gauge (average distance to closest group: 1.8 km, average distance to the farthest group: 5.4 km: raw data for rainfall are provided in S3).

Data analysis

Two of the 26 groups were encountered less than 10 times (5 and 2 times, respectively) during 37 months of data collection, which is why we excluded them from further analysis resulting in a final sample size of 24 groups. With the remaining 24 groups, we excluded encounters from further analysis in case observations had to be cancelled for the following reasons: observers were detected by the target group ($N=8$), and the arrival of forest elephants or gorilla groups ($N=9$). First, we calculated the percentage that groups were encountered alone and in association over all target groups and over all associated monkey species. To control for biases in encounter rate due to group size with larger groups potentially being easier to detect and to locate, we first calculated Pearson correlation coefficients between group size and the number of encounters. We subsequently computed association indices for specific, associated monkey species by dividing the number of associated encounters for a particular species by the number of total encounters with *C. nictitans*. We investigated the impact of rainfall as potential indication for resource availability on the formation of associations by comparing associations indices during the observed main dry season with all other months for each of the associated species observed using two-sided Wilcoxon signed-rank tests (level of significance $\alpha=0.05$). We then analyzed a potential interactive effect of season and *C. nictitans* group size on association patterns using Pearson correlation coefficients and a Bonferroni correction for multiple hypothesis testing with an adjusted α level of 0.025. To elucidate species-specific differences, we calculated Pearson correlation coefficients between *C. nictitans* group size and association indices for each associated species. To control for multiple hypothesis testing, we applied a Bonferroni correction and adjusted the α level to 0.01.

Results

Each *C. nictitans* group was sampled 11–44 times throughout the study period, resulting in 660 group encounters. Group size and numbers of encounters were not strongly correlated, thus confirming that there was no statistically significant bias towards sampling larger groups more frequently ($R=-0.34$, $p=0.099$, S2), although the trend found merits further evaluation of possible biases. Overall, in 32.7% of cases, *C. nictitans* groups were encountered alone, contrasting 67.3% of all observations in which a target group was associated with at least one other monkey species (Table 1). The likelihood of being in association varied between groups with inter-group variation ranging from 58 to 81% that single groups were encountered with another monkey species. Such inter-group differences, however, were not generally due across seasons to group size ($R=0.34$, $p=0.125$). *C. nictitans* groups were most often seen with *L. albigena*, followed by *C. pogonias* and *C. cephus* (Fig. 1).

To investigate overall seasonal effects on the occurrence of heterospecific associations, we first compared the reported main dry season for this area with observed rainfall for the duration of data collection and identified 4 major dry seasons with less than 50 mm rainfall/month (February and March 2019, October 2019–April 2020, November 2020–February 2021, January & February 2022). Second, we compared associations indices between identified major dry seasons and the rest of the year over all groups, which did not systematically differ for any associated species (Table 2). Hence, the occurrence of associations on a species level did not vary with season and the likelihood to encounter *C. nictitans* in association was the same for the dry season and the rest of the year.

To unravel a potential interaction between season and group size, we analysed intra-specific variation in association patterns as a function of *C. nictitans* group size separately for main dry seasons and the rest of the year. Larger *C. nictitans* groups were more likely to be found in association than smaller groups in the major dry season ($R=0.64$, $p<0.001$) but not during the rest of the year ($R=0.29$,

Table 1 Percentages of cases in which *C. nictitans* groups were encountered alone (0) or in association with one to 5 other monkey species

	No. species in association	No. total encounters	%
0		216	32.7
1		227	34.4
2		160	24.2
3		44	6.7
4		10	1.5
5		3	0.5
total		660	100

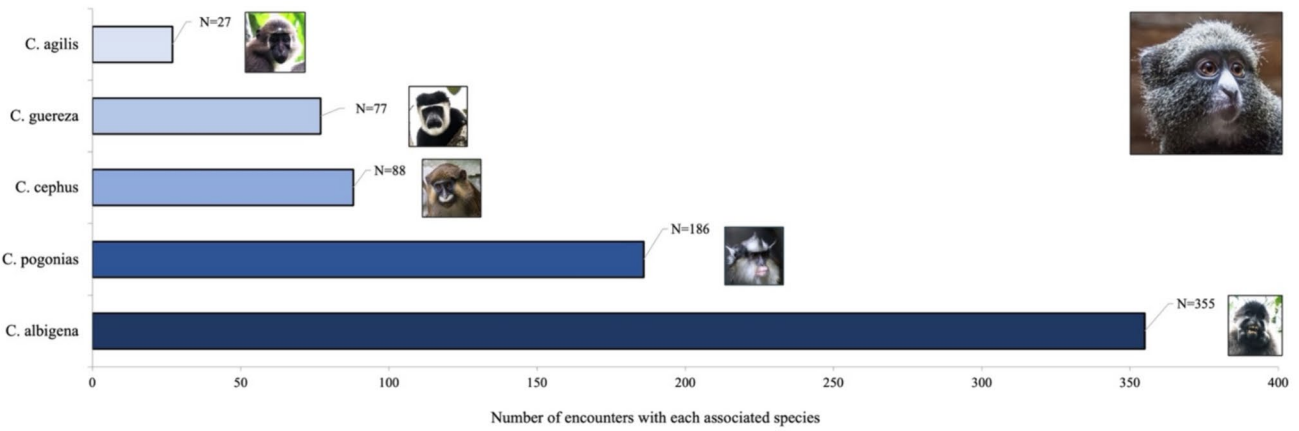


Fig. 1 Number of *C. nictitans* group encounters in association with each monkey species. Please note that the sum of observed associations across all species exceeds the total of $N=660$ group encounters

as one group could have been associated with more than one species. Pictures: © Scott Ramsay/WCS

Table 2 Wilcoxon test results for the seasonal comparison of association indices for each species associated with *C. nictitans*

Associated species	Mean ass. index wet season	Mean ass. index dry season	W	P-value
<i>C. nictitans</i> – <i>L. albigena</i>	0.52	0.56	167	0.58
<i>C. nictitans</i> – <i>C. pogonias</i>	0.33	0.23	169	0.69
<i>C. nictitans</i> – <i>C. cephus</i>	0.15	0.24	180	0.45
<i>C. nictitans</i> – <i>C. agilis</i>	0.05	0.09	133	0.43
<i>C. nictitans</i> – <i>C. guereza</i>	0.04	0.11	127	0.35

$p=0.17$; Fig. 2). This group size effect was predominantly expressed in association with *L. albigena* ($R=0.09$, $p<0.001$) and *C. pogonias* ($R=0.45$, $p=0.025$), although the latter was statistically not significant after Bonferroni correction. The effect of group size on association formation with *C. cephus*, *C. agilis*, and *C. guereza* was considerably weaker (Fig. 3).

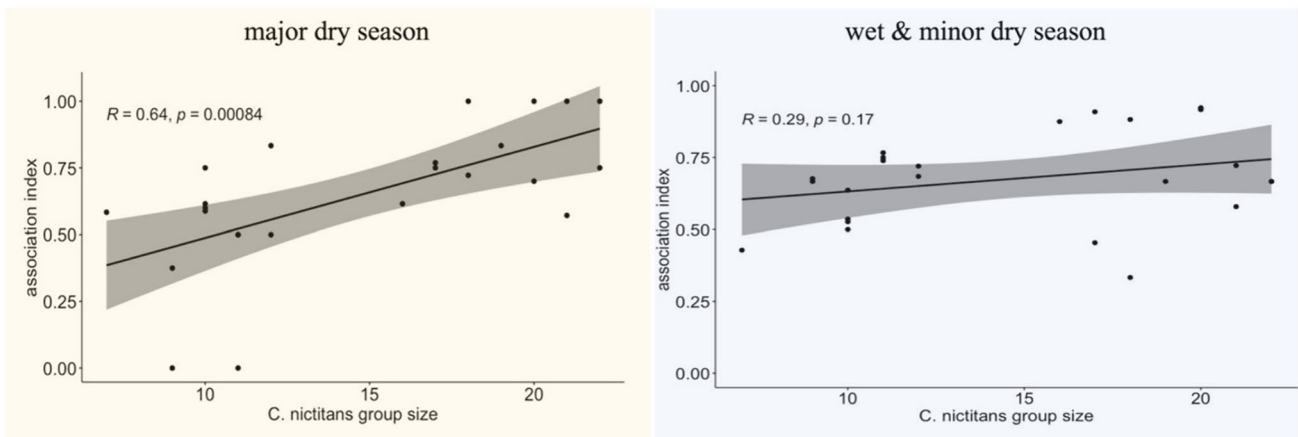


Fig. 2 Correlation between *C. nictitans* group size and association index over all 24 groups during the major dry season (left) and the rest of the year (right) including 95% confidence intervals in grey

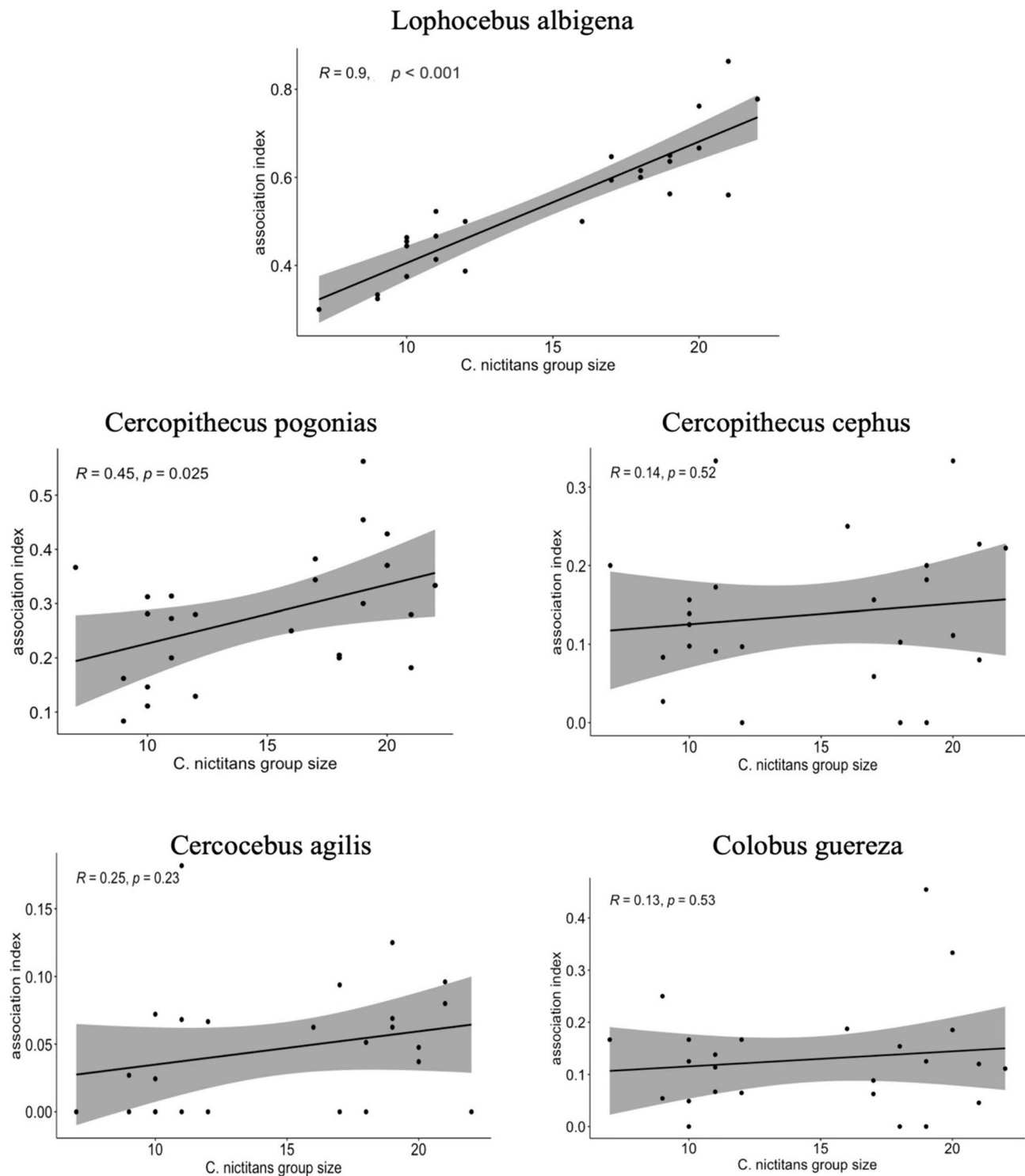


Fig. 3 Correlation between *C. nictitans* group size and association index for each associated monkey species

Discussion

We are confident to claim that we have convincingly provided a first summary of the nature of associations between

C. nictitans and other monkey species in the Nouabalé-Ndoki National Park (NNNP) of the Republic of Congo. The present findings provide important first insights in the social organization of *C. nictitans* in the area beyond their own

species and represent the most detailed and extensive heterospecific association observations of guenons in the Ndoki forests yet compiled. Results presented here emphasize that heterospecific associations are common forest phenomena in the Nouabalé-Ndoki National Park, thus extending previous, seminal research on interspecific interactions between ape species (Kuroda 1992) to monkeys, and advising future research on the effect of group size and seasonality in Nouabalé-Ndoki primate communities.

In two-thirds of all encounters, we found *C. nictitans* groups in association with at least one other primate species, which is in line with previous reports for this species in Cameroon (Mitani 1991) and in Gabon (Gautier-Hion et al. 1983). Primate species most frequently found in association were *L. albigena*, *C. pogonias* and *C. cephus*. *L. albigena*, *C. pogonias* and *C. nictitans* greatly overlap in spatial forest strata use while *C. cephus* usually occupies lower strata (Gabon, Gautier-Hion 1980). Diet overlap was reported high for all four species in Gabon with a strong preference for fruits and seeds, although *C. nictitans* has been reported to show higher foraging flexibility than the other three species (Gautier-Hion, 1980). Agonistic interactions at food patches or the monopolization thereof by any of the species is rare (Ivory Coast: Eckardt and Zuberbühler 2004; study population: personal observation). *C. agilis* and *C. guereza* were encountered less frequently together with *C. nictitans*. Low association rates are likely due to different preferences in diet and habitat use. *C. agilis* usually use lower canopy levels, spending 12–22% of their time on the ground (Gabon, study population: Quris 1975; Shah 2003) and have a strong preference for fruits and seeds (Central African Republic, study population: Shah 2003). The spatial habitat use of *C. guereza* is similar to *C. agilis*, although they are mainly folivorous with a bias towards young leaves (Uganda: Harris and Chapman 2007). Hence, *C. nictitans* was encountered predominantly with species that are supposed to elicit high levels of food resource competition based on described ecological niches from other study populations, which questions the formation of associations to gain foraging benefits. We found no seasonal variation of association indices for any of the sympatric primate species. *C. nictitans* may thus either switch food resources during times when fruits are scarce or feeding benefits through other species are either the same across seasons or less relevant. We encountered larger *C. nictitans* groups more often in association during the major dry season than smaller groups. This effect could be the result of two potential scenarios. First, smaller groups may avoid being in association when resources are scarce. Second, larger groups might be actively preferred by other species. Surprisingly, we only found an effect of group size during the major dry season and not, as initially predicted, throughout the year. This might indicate that either predation pressure and/or primates' vulnerability to predation varies

across seasons. Some information about predation is available from other sites that might support this assumption. Specifically, crowned eagles are amongst the fiercest predators for forest guenons including *C. nictitans* (Struhsaker and Leakey 1990; Mitani et al. 2001; Shultz et al. 2004). High predation pressure by crowned eagles is further supported by high degrees of anti-predator responses related to eagle presence including our study population (Arnold and Zuberbühler 2006; N'zoulou Kiminou et al. 2022). Eagles in Uganda have been reported to hatch in November and adult eagles increase their hunting effort to feed the nestling during subsequent months (Seike 2022). A second increase in hunting usually occurs in the late nestling phase from January to approximately March when also the female leaves the nest to contribute to prey delivery (Seike 2022). These periods of increased predation pressure fall in the major dry season of our study area. Hence, increasing heterospecific group size could simultaneously increase dilution and safety in numbers effects, the number of individuals who could be vigilant, and the availability of collaboration partners for joint mobbing activities during attacks. A joint mobbing event was previously reported for a male *C. nictitans* and a male *C. albigena* in Gabon (Gautier-Hion and Tutin 1988), although such anecdotal report warrants more systematic investigation of predator-prey relationships and especially the seasonality thereof. This line of argument is further supported by species-specific differences in the likelihood to be associated with larger *C. nictitans* groups. Strong effects of groups size were only found in *L. albigena* and *C. pogonias*—the two species with whom *C. nictitans* occupies upper forest strata. Both species are likely mobbing partners and valuable early warning collaborators once eagles approach from above. Our results suggest that especially *L. albigena* and *C. pogonias* follow *C. nictitans*, with a preference for bigger *C. nictitans* groups that provide more antipredation benefits to them than smaller groups during periods of increased vulnerability. In another population, *C. nictitans* and *C. pogonias* share similar birth seasons from December to April and November to April, respectively (Butynski 1988). This period of increased vulnerability and the need of enhanced protection falls in the major dry season of our study population. It provides promising ground for future studies to identify birth seasons across populations in our study area to investigate the possibility that heterospecific associations are promoted by benefits from increase antipredation defence in larger groups. An alternative explanation that refers to foraging benefits might be that either larger groups of *C. nictitans*, or *L. albigena* as mainly seed consumers, increase the amount of flushed prey and thus insect consumption for associated species in lower strata. This argumentation leads to the interesting opportunity that *C. nictitans* does not gain any benefits from associating but is rather used by other species to obtain either predation-related or feeding benefits.

Caution is warranted in the interpretation of the current results and simultaneously provides promising ground for future studies. Correlations might be due to a yet unknown factor instead of direct causal relationships between group size and species-specific associations. Systematic assessments of food item consumption, resource switching, species-specific abundance data, and the effect of group size effects and body size effects (S4) of other species than *C. nictitans* might help to further elucidate the interaction of different social factors and foraging strategies in associated primate species. Second, observations of seasonal variation in predator–prey interactions and the confirmation of birth seasons for our study site could further unravel behavioural adaptations in primate communities, in particular hetero-specific associations. Third, systematic assessments of the initiation and the maintenance of associations remains a promising topic for future studies to clarify whether there are species-specific biases in benefits from and seeking heterospecific associations. Forth, detailed assessments of variation in plant species diversity in different home ranges could shed light on the impact of habitat structure on association patterns.

The present results also emphasize the importance of a polyspecific approach to primate conservation strategies. First, our results suggest that especially during major dry seasons, heterospecific troops are likely composed of more individuals than during the rest of the year and thus more conspicuous and easier to detect for e.g., poachers. Increased monitoring and patrolling efforts by eco-guards could help to compensate the increased vulnerability of primate communities during this period. During such direct anti-poaching efforts, further assessments of seasonal variation in troop size either by direct observations or by remote recordings are highly promising to complement and extend present results across a broader landscape within the Nouabalé-Ndoki National Park and its periphery. Second, species like *L. albigena* that are already IUCN classified as “vulnerable” can be additionally protected and probably stabilized on a population level by conservation strategies that also address species with a lower conservation status like e.g., *C. nictitans*. This would strengthen species-specific conservation efforts by conserving evolutionary benefits from antipredation strategies through heterospecific aggregations.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10329-024-01153-5>.

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Author contributions Frédéric Mehon and Claudia Stephan contributed to the study conception and design. Data collection was performed by Daniel N’zoulou Kiminou and Frédéric Mehon. Data analysis was performed by Claudia Stephan with contribution from Frédéric Mehon. The first draft of the manuscript was written by Claudia Stephan and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability Data presented here are available upon request from the corresponding author.

Declarations

Conflict of interest The authors declare that they do not have any competing interests. The research presented here utilizes data from the Mbeli Bai Study of the Wildlife Conservation Society (WCS)—Congo Program. The views expressed here are those of the authors and do not necessarily represent the views of WCS. Any errors are attributable to the authors.

Ethical approval We express our gratitude to the Ministère de l’Economie Forestière, the Agence Congolaise de la Faune et des Aires Protégées (ACFAP), and to the Institut en Recherche Forestière within the Ministère de la Recherche Scientifique et de l’Innovation Technologique for permission to work in the Nouabalé-Ndoki National Park (research permit no. 270/2020; 001/2021). All observational methods applied here also adhere to the ethics guidelines of the Association for the Study of Animal Behaviour (ASAB).

References

- Arnold K, Zuberbühler K (2006) The alarm calling behavior of adult male putty-nosed monkeys (*Cercopithecus nictitans martini*). *Anim Behav* 72:643–653
- Beauchamp G, Cabana G (1990) Group size variability in primates. *Primates* 31:171–182
- Beaudrot L, Palmer MS, Anderson TM, Packer C (2020) Mixed-species groups of Serengeti grazers: a test of the stress gradient hypothesis. *Ecology* 101:e03163
- Bitty EA, McGraw WS (2007) Locomotion and habitat use of Stampflii’s putty-nosed monkey (*Cercopithecus nictitans stampflii*) in the Tai National Park. *Ivory Coast Am J Phys Anthropol* 134(3):383–391
- Brncic T (2018) Ndoki-Likouala large mammal survey. Nouabalé-Ndoki Foundation.
- Bshary R, Noë R (1997) Red colobus and Diana monkeys provide mutual protection against predators. *Anim Behav* 54:1461–1474
- Butynski TM (1988) Guenon birth seasons and correlates with rainfall and food. In: Gautier-Hion A, Bourlière F, Gautier J-P, Kingdon J (eds) *A primate radiation: evolutionary biology of the african guenons*. Cambridge University Press, New York, pp 284–322
- Buzzard PJ (2010) Polyspecific associations of *Cercopithecus campbelli* and *C. petaurista* with *C. diana*: what are the costs and benefits? *Primates* 51:307–314
- Buzzard P, Eckardt W (2007) Social systems of the Tai Guenons (*Cercopithecus spp.*). In S. McGraw, K. Zuberbühler, & R. Noe (Eds.),

- Monkeys of the Tai Forest: An African Monkey Community* (pp. 51–71). Cambridge: Cambridge University Press.
- Coelho AM (1974) Socio-bioenergetics and sexual dimorphism in primates. *Primates* 15:263–269
- Cords M (1987) Mixed species associations of Cercopithecus monkeys in the Kakamega Forest. *Univ Calif Publ Zool* 117:1–109
- Cords M (1990) Mixed-species association of East African guenons: general patterns or specific examples? *Am J Primatol* 21:101–114
- Delm MM (1990) Vigilance for predators: detection and dilution effects. *Behav Ecol Sociobiol* 26:337–342
- Eckardt W, Zuberbühler K (2004) Cooperation and competition in two forest monkeys. *Behav Ecol* 15(3):400–411
- FitzGibbon CD (1990) Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Anim Behav* 39:1116–1126
- Gautier-Hion A (1980) Seasonal variations of diet related to species and sex in a community of Cercopithecus monkeys. *J Anim Ecol* 49(1):237–269
- Gautier-Hion A, Tutin CEG (1988) Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Fol Primatol* 51:149–151
- Gautier-Hion A, Quris R, Gautier JP (1983) Monospecific vs polyspecific life: a comparative study of foraging and antipredatory tactics in a community of Cercopithecus monkeys. *Behav Ecol and Sociobiol* 12:325–335
- Greenberg R (2000) Birds of many feathers: the formation and structure of mixed-species flocks of forest birds. In: Boinski S, Garber P (eds) *On the move: how and why animals travel in groups*. University of Chicago Press, Chicago, pp 521–558
- Harris DJ (2002) *The Vascular Plants of the Dzanga-Sangha Reserve*. Central African Republic, Meise, Belgium, National Botanic Garden (Belgium)
- Harris TR, Chapman CA (2007) Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates* 48:208–221
- Heymann EW, Buchanan-Smith HM (2000) The behavioural ecology of mixed-species troops of callitrichine primates. *Biol Rev* 75:169–190
- Isbell LA (2004) Is there no place like home? Ecological bases of female dispersal and philopatry and their consequences for the affiliation of kin groups. In: Chapais B, Berman C (eds) *Kinship and Behavior in Primates*. Oxford University Press, New York, pp 71–108
- Kenward RE (1978) Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *J Anim Ecol* 47(2):449–460
- Kingdon J (2015) *The Kingdon field guide to African mammals*. Bloomsbury Publishing
- Kuroda S (1992) Ecological interspecies relationships between gorillas and chimpanzees in the Ndoki-Nouabale reserve, northern Congo. In N. Itoigawa, Y. Sugiyama, G. P. Sackett & R. K. R. Thompson (Eds.), *Topics in Primatology*, Vol. 2: Behavior, Ecology, and Conservation. Tokyo: University of Tokyo Press.
- Lambert JE (2002) Resource switching in guenons: A community analysis of dietary flexibility. In: Glenn M, Cords M (eds) *The Guenons: Diversity and Adaptation in African Monkeys*. Kluwer Academic Press, New York, pp 303–317
- Maisels F, Blake S, Fay M, Mobolambi G, Yako V (2006) A note on the distribution of Allen's swamp monkey, *Allenopithecus nigro-viridis*, in Northwestern Congo. *Primate Conserv* 21:93–95
- McGraw WS, Zuberbühler K (2008) Socioecology, predation, and cognition in a community of West African monkeys. *Evol Anthropol* 17:254–266
- Mehon FG, Stephan C (2021) Female putty-nosed monkeys (*Cercopithecus nictitans*) vocally recruit males for predator defence. *R Soc Open Sci* 8:202135
- Mitani M (1991) Niche overlap and polyspecific associations among sympatric cercopithecids in the Campo Animal Reserve, southwestern Cameroon. *Primates* 32:137–151
- Mitani M (1992) Preliminary results of the studies on wild western lowland gorillas and other sympatric diurnal primates in the Ndoki Forest, Northern Congo. In: Itoigawa N, Sugiyama Y, Sackett GP, Thompson RKR (eds) *Topics in Primatology Behavior, Ecology and Conservation*. University of Tokyo Press, Tokyo, pp 215–225
- Mitani JC, Sanders WJ, Lwanga JS, Windfelder TL (2001) Predatory behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale national park, Uganda. *Behav Ecol Sociobiol* 49:187–195
- Mugambi KG, Butynski TM, Suleman MA, Ottichilo W (1997) The vanishing De Brazza's monkey (*Cercopithecus neglectus*) in Kenya. *Int J Primatol* 18:995–1004
- N'zoulou Kiminou D, Mehon FG, Stephan C, (2022) Vocal recognition of alarm calls in wild putty-nosed monkeys (*Cercopithecus nictitans*). *Anim Behav* 190:199–208
- Noë R, Bshary R (1997) The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. *Proc Roy Soc Lond b: Biol* 264:253–259
- Oates JF (2011) *Primates of West Africa*. Conservation International.
- Patterson SK, Sandel AA, Miller JA, Mitani JC (2014) Data quality and the comparative method: the case of primate group size. *Int J Primatol* 35:990–1003
- Peres CA (1992) Consequences of joint territoriality in a mixed species group of tamarin monkeys. *Behaviour* 123:220–246
- Powell GVN (1985) Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. In: Buckley PA, Foster MS, Morton ES, Ridgely RS, Buckley FG (eds) *Ornithological Monographs*. JSTOR, pp 713–732
- Quérouil S, Silva MA, Cascao I, Magalhaes S, Seabra MI, Machete MA, Santos RS (2008) Why do dolphins form mixed-species associations in the Azores? *Ethology* 114:1183–1194
- Quris R (1975) *Ecologie et organisation sociale de Cercocebus galeritus agilis dans le nord-est du Gabon*. *Terre Vie* 20:337–398
- Schradin C, Vonk J, Shackelford T (2019) Confusion effect. In: Vonk J, Shackelford T (eds) *Encyclopedia of animal cognition and behaviour*. Springer, pp 375–376
- Seike T (2022) Frequent predation on primates by crowned eagles (*Stephanoaetus coronatus*) in Mahale Mountains National Park, Tanzania. *Primates* 63:327–333
- Shah NF (2003) *Foraging strategies in two sympatric mangabey species (Cercocebus agilis and Lophocebus albigena)*. PhD thesis. State University of New York at Stony Brook.
- Shultz S, Noë R, McGraw WS, Dunbar RIM (2004) A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proc R Soc B* 271:725–732
- Sridhar H, Beauchamp G, Shanker K (2009) Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim Behav* 78:337–347
- Strier KB, Lee PC, Ives AR (2014) Behavioral flexibility and the evolution of primate social states. *PLoS ONE* 9:e114099
- Struhsaker TT (1981) Polyspecific associations among tropical rain-forest primates. *Z Tierpsychol* 57:268–304
- Struhsaker TT (2000) Variation in adult sex ratios of red colobus monkey social groups: implications for interspecific comparisons. In: Kappeler PM (ed) *Primate Males*. Cambridge University Press, Cambridge, pp 108–119
- Struhsaker TT, Leakey M (1990) Prey selectivity by crowned hawk eagles on monkeys in the Kibale forest, Uganda. *Behav Ecol Sociobiol* 26:435–443
- Syme J, Kiszka JJ, Parra GJ (2021) Dynamics of cetacean mixed-species groups: a review and conceptual framework for assessing their functional significance. *Front Mar Sci* 8:678173

- van Schaik CP (1983) Why are diurnal primates living in groups? *Behaviour* 87:120–144
- Waser PM (1980) Polyspecific associations of *Cercocebus albigena*: geographic variation and ecological correlates. *Folia Primatol* 33:57–76
- Whitesides GH (1989) Interspecific associations of Diana monkeys, *Cercopithecus diana*, in Sierra Leone, West Africa: biological significance or chance? *Anim Behav* 37:760–776
- Wolters S, Zuberbühler K (2003) Mixed-species associations of Diana and Campbell's monkeys: the costs and benefits of a forest phenomenon. *Behaviour* 40:371–385
- Zeeve SR (1991) Behavior and ecology of primates in the Lomako Forest, Zaire [PhD thesis]. State University of New York, Stony Brook.

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