Crested Guineafowl and samango monkey associations

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Associations between animals of different species have been observed for a large variety of taxa. These polyspecific groups are thought to provide advantages for at least one of the species involved, especially foraging benefits or reduced predation risk. In the case of primate-bird associations, both foraging benefits and reduced predation risk have been suggested. We investigated whether flocks of Crested Guineafowl (Guttera edouardi) join groups of samango monkeys (Cercopithecus albogularis schwarzi) and examined benefits to the birds. Using behavioural data, we tested (1) whether Crested Guineafowl associate with samango monkeys for a longer period of time than can be expected by chance, using a movement simulation model, and (2) whether Crested Guineafowl show differences in foraging and predation risk behaviour and habitat selection in relation to vegetation cover in the presence of samango monkeys. Observations were done in the Soutpansberg Mountain Range, South Africa. We found that (1) Crested Guineafowl join samango monkeys for a longer period of time than expected by chance, and (2) Crested Guineafowl show significantly less sentinel behaviour with samango monkeys present. These findings suggest that the birds experience reduced predation risk in the presence of the monkeys. Our study is the first to report association between Crested Guineafowl and samango monkeys and contributes to understanding why birds and primates associate.

Keywords: mixed-species associations, movement simulation model, predation risk, sentinel animals

Introduction

Polyspecific associations (or mixed-species groups) have been shown to occur in many species (e.g. Morse 1970; Noé and Bshary 1997; Ward et al. 2002; Buzzard 2010; Harrison and Whitehouse 2011; Makenbach et al. 2013; Schmitt et al. 2016). While such associations may temporarily form by chance, they are often non-random and can persist over long periods of time up to 7 hours/day (Siegel et al. 1989; Hauagassen and Peres 2009; Heymann and Hsia 2015). Polyspecific groups are thought to provide advantages for at least one of the associating species, especially foraging benefits and reduced predation risk (Stensland et al. 2003; Heymann and Hsia 2015; van Langevelde et al. 2022). Foraging benefits include increased availability of food items (Rasa 1983; Barnett and Shaw 2014), detection of food sources (Cords 1987), protection of food patches (Garber 1988), and lower vigilance rates allowing individuals to spend a higher proportion of time on foraging (Sullivan 1984; Ridley et al. 2014). An individual can have a lower chance of being preyed upon when in a polyspecific group due to dilution when the group size is large (Turner and Pitcher 1986), including individuals in the inner part of the group, Hamilton (1971), predator confusion (Landau and Terborgh 1986), increased predator detection when the participating species have complementary sensory abilities (Bshary and Noé 1997; Heymann and Buchanan-Smith 2000), predator deterrence (Zuberbühler et al. 1999), predator mobbing (Struhsaker 1981), or predator preference for individuals of the other species (Fitzgibbon 1990). Increased predator detection is often caused by eavesdropping on the warning call of the other species (Rainey et al. 2004; Magrath et al. 2015). In polyspecific groups, the other species could provide extra information about the environment, but without increasing competition for resources as in single-species groups (Goodale et al. 2010). It is often unknown whether polyspecific groups are established to reduce predation risk or increase foraging benefits, or both (Bohlin and Johnsson 2004).

Regular reports have been made on associations of primates with non-primates (Heymann and Hsia 2015). Primates are highly social animals which forage in groups (Mitani et al. 2012), while their foraging behaviour is often considered “wasteful” as food items frequently drop on the ground below the group (Howe 1980; Richard 1985). This wasteful behaviour potentially makes associating with primates beneficial for non-primates, as the latter may feed on these dropped food items. Yet, the stability and consistency of these associations seem to be less than primate-primate associations (Heymann and Hsia 2015). The majority of observed associations of primates with non-primates involve birds (Heymann and Hsia 2015). However, most reports of primate-bird associations are
anecdotal or merely report on the percentage of time in
association (e.g. Hill 1974; Siegel et al. 1989; Peres 1992;
Seavy et al. 2001), rather than unravelling the mechanisms
behind the association (Barnett and Shaw 2014; Heymann
and Hsia 2015). Only a few studies have shown foraging
benefits or reduced predation risk for birds in a primate-
bird association (e.g. Ruggiero and Eves 1998; Barnett and
Shaw 2014).

The presumed mechanisms behind the foraging benefits
clearly differ between insectivorous and herbivorous birds:
the former can mostly benefit by catching prey flushed by
foraging primates, while the latter mainly take advantage
of the food items dropped by foraging primates (Dean and
MacDonald 1981).

In many primate–non-primate associations, the non-
primate approaches and follows the primate (Heymann
and Hsia 2015). Our study aims to investigate if and why flocks
of Crested Guineafowl (Guttera edouardi) associate with
groups of samango monkeys (Cercopithecus albogularis
schwarzi). Both species share largely the same predators:
leopards (Panthera pardus), eagles (e.g. Stephanoaetus
coronatus, Aquila verreauxii), baboons (Papio ursinus)
and pythons (Python sebae) (Coleman and Hill 2014),
which could form the basis for an antipredator warning
call relationship, as has already been observed between
Crested Guineafowl and vervet monkeys (Chlorocebus
pygerythrus) (Hill 1974; Dean and MacDonald 1981).

Furthermore, the partly herbivorous Crested Guineafowl
could benefit from fruits and leaves dropped by the
highly frugivorous samango monkeys (Hill 1974; Lawes
et al. 1990; Seufert et al. 2010; Linden et al. 2015), eat
undigested seeds out of the monkeys’ faeces (Hill 1974),
or capture insects flushed by the monkeys (Fontaine 1980;
Ruggiero and Eves 1998; Barnett and Shaw 2014).

We tested whether (1) Crested Guineafowl associate with
samango monkeys for a longer time than can be expected
by chance. If this were not the case, it does not necessarily
mean that this association has no biological significance
(Whitesides 1989). Therefore, we also tested whether (2)
Crested Guineafowl spend more time foraging, less time
vigilant and sentinel (i.e. individuals in upright position
scanning for predators [Bednekoff 2015]), or more time in
riskier patches (i.e. patches with less vegetation cover) in
the presence of the samango monkeys.

Methods

Study area
The study was conducted at Lajuma Research Centre in
the western part of the Soutpansberg Mountain Range in
north-eastern South Africa (23°02′ S, 29°26′ E). Lajuma is
a privately-owned property of 4.3 km² with a strong altitudinal
gradient, which facilitates a variety of vegetation types,
ranging from montane grassland to thickets and forests.
The climate in the area can roughly be divided into a warm, wet
season (September to March) and a cool, dry season (April
to August), with an average annual rainfall of approximately
730 mm (Mourik et al. 2007; van Langevelde et al. 2014).

The area is home to all five South African primate species:
samango monkey, vervet monkey, chacma baboon,
thick-tailed greater galago (Otolemur crassicaudatus), and
southern lesser galago (Galago moholi). Furthermore,
Lajuma supports predators like leopard, brown hyena
(Parahyaena brunnea), several species of mongoose
(Herpestidae), honey badger (Mellivora capensis),
African civet (Civetecis civetta), rusty-spotted genet
(Genetula maculata), and also large raptors like Crowned
Eagle (Stephanoaetus coronatus) and Verreaux’s Eagle
(Aquila verreauxii). Samango monkeys are medium-
sized, diurnal, mainly arboreal, and frugivorous guenons
which live in groups ranging from 4 to 65 individuals (see
references in Coleman and Hill 2014; Linden et al. 2015).
They produce acoustically distinct alarm calls for different
predators (Papworth et al. 2008). Both Crested Guineafowl
and samango monkeys are forest-dwelling species showing
a fragmented distribution throughout South Africa (Hockey
et al. 2005; Linden et al. 2016). On Lajuma, the occurrence
of both species is associated with the presence of patches
of mistbelt forest; an indigenous, high canopy, evergreen
and rare forest type (Von Maltitz et al. 2003; Geldenhuys
and Mucina 2006). Crested Guineafowl forage on the ground
where they search for fruits, seeds, leaves, and soft shoots
and stems, as well as small spiders and insects (Hockey
et al. 2005). In the non-breeding season, which coincides
with the dry season (April to August), the birds form flocks
ranging from 10 to 30 individuals (Lawes et al. 2006). On
Lajuma, Crested Guineafowl live in several flocks, which
show fission-fusion dynamics where the size of the flock
changes due to splitting (while foraging or during breeding
season) and reformation (Linden, unpublished data), and the
samango monkeys occur in two big groups ranging
from 30 to 70 individuals (Parker et al. 2020). Both Crested
Guineafowl and samango monkeys on Lajuma are free
ranging but well habituated to human observers as a result
of ongoing behavioural research.

Movement simulation model
To test hypothesis (1), we developed a movement
simulation model in R (R Core Team 2021) to explore
whether the observed time that Crested Guineafowl and
samango monkeys associated was longer than would be
expected by chance. For that purpose, we used GPS data
of movement tracks of both species to extract the distances
(in m) between two consecutive GPS fixes (referred to as
step lengths) and the turning angles (in radians) with
which the next GPS fix deviated from forward movement
(with interval (-π, π) and 0 radians as forward movement;
de Knecht et al. 2007). Additionally, we calculated the
length and width of the area where Crested Guineafowl
occurred (Table 1), and assumed this to be the home
range of a Crested Guineafowl flock (89.3 ha). As one
samango monkey group was mainly outside the Crested
Guineafowl home range, we merely included the other
group in our analyses. Although the samango monkey
home range may be slightly smaller (54.7 ha; Coleman and
Hill 2014), we assumed that its home range was equal to
and completely overlapping the home range of the Crested
Guineafowl, as we could not make an accurate estimate of
the size of the home range of the samango monkeys and
its relative position to the Crested Guineafowl home range.
We changed the size of the home range of the samango
monkeys in the simulations and found that slightly different
sizes did not have a qualitative impact on the outcome of the model. Based on our field observations, we also estimated the length and width of the area where both species spent the night (referred to as sleeping range). This sleeping range is smaller than the home range as it excludes parts of the home range with small trees and shrubs, Senegalia (Acacia) woodland adjacent to the mistbelt forest, that are unsuitable for sleeping. Apart from that, the home range was assumed to be homogeneous habitat, i.e. we assumed that the groups had equal preference for every part of the range.

The Crested Guineafowl movement paths were collected while following the flocks for behavioural data collection (see Behavioural analysis) during a three-month period from the beginning of June until the end of August 2017, using a GPS which recorded the location of the flocks every 10 minutes. The Crested Guineafowl follow distance (observer to animal) was 5 to 10 m on average. For both species we also collected data on the group spread, i.e. the distance between the two individuals furthest away from each other, from which we calculated the average radius of the Crested Guineafowl flocks (referred to as 'RadiusGF') and the samango monkeys (referred to as 'RadiusSM') (Table 1). Samango monkey movement paths were provided by the Primate & Predator Project based at Lajuma, which were collected in July 2017 by following one samango group from dawn to dusk and recording their location every 20 minutes. For that reason, the step lengths and turning angles of the Crested Guineafowl movements were resampled based on similar 20-minute intervals.

We included a parameter in the model which we called ‘attraction distance’ (referred to as ‘AD’), defined as the distance from which one of the species is attracted towards the other. This AD represented the strength of the attraction. A value of AD = 0 thus simulated the situation where none of the species actively tried to join the other. We varied the value of AD and performed 100 simulations (see details on simulations below) per value (we increased AD from 0 to 1500 m with steps of 1 m) and compared per AD the average simulated distance between the groups of the two species to our observed distances, to test what value of AD resembles the actual attraction between both species. In case both species do not associate longer than can be expected by chance (hypothesis 1), we would expect no significant differences between our simulation and our observations at AD = 0. All parameter settings are given in Table 1.

We simulated two points moving within the home range area, representing a Crested Guineafowl flock and the samango monkey group. Each time step in the model represented 20 minutes in reality. Each simulation lasted 856 time steps, consisting of 25 days with each having 33 to 36 time steps. The number of time steps per day corresponds with the number of 20-minute time steps observed during each of the 25 days of following the Crested Guineafowl (see Behavioural analysis), thus allowing us to compare the results of our simulation with our field observations.

For the first time step of each day in the simulation, a starting point somewhere within the sleeping range was randomly assigned for the Crested Guineafowl flock and the samango monkey group. Every following time step, the new location of each of the groups was determined by:

\[ x_t = x_{t-1} + dx \\
\]

\[ y_t = y_{t-1} + dy \\
\]

where, the step length for each species was randomly drawn from their respective distributions of observed step lengths. The value of \( \alpha \) depended on several conditions. If the group moved outside of its home range, then \( \alpha \) was defined as the direction back into the home range. If more than 85% of the day had passed (referred to as ‘RT’, Table 1), then \( \alpha \) became the direction towards the sleeping range. For every time step, the distance between the two groups was calculated by:

\[ \text{Distance} = \sqrt{(x_{GF} - x_{SM})^2 + (y_{GF} - y_{SM})^2} - \text{RadiusGF} - \text{RadiusSM} \]

with the x- and y-coordinates of the Crested Guineafowl (referred to as 'xGF' and 'yGF') and the samango monkeys

Table 1: List of parameters, their interpretation, value and units used in our movement simulation model

| Parameter       | Interpretation                                      | Value | Unit  |
|-----------------|------------------------------------------------------|-------|-------|
| D               | Number of days for the simulation                   | 25    | d     |
| N               | Number of time steps per day                        | 33–36 | d⁻¹   |
| AD              | Distance between Crested Guineafowl and samango monkeys from which Crested Guineafowl start moving towards the samango monkeys | 0–1500 | m     |
| RT              | Proportion of the day progress (N) at which both return to sleeping range | 0.85  |       |
| RadiusGF        | Average radius of guineafowl flock                  | 8.2   | m     |
| RadiusSM        | Average radius of samango monkey group              | 29.6  | m     |
| Homerange_length| Length of home range of both groups                 | 1514  | m     |
| Homerange_width | Width of home range of both groups                  | 590   | m     |
| Sleepingrange_length| Length of sleeping range of both groups         | 681   | m     |
| Sleepingrange_width| Width of sleeping range of both groups         | 344   | m     |

- GF: Crested Guineafowl
- SM: Samango monkeys
- D: Distance
- N: Number of steps
- AD: Attraction distance
- RT: Proportion of the day
- RadiusGF: Average radius of Crested Guineafowl flock
- RadiusSM: Average radius of Samango monkey group
- Home: Home range
- Sleep: Sleeping range
- x: X-coordinate
- y: Y-coordinate
- N: Days
- dx: Step length in x-direction
- dy: Step length in y-direction
- \( \alpha \): Turning angle
- \( \text{Distance} \): Distance between groups
- \( x_{GF} \): X-coordinate of Crested Guineafowl
- \( y_{GF} \): Y-coordinate of Crested Guineafowl
- \( x_{SM} \): X-coordinate of Samango monkeys
- \( y_{SM} \): Y-coordinate of Samango monkeys
- \( \text{RadiusGF} \): Average radius of Crested Guineafowl
- \( \text{RadiusSM} \): Average radius of Samango monkey group
- \( \text{Radius} \): Average radius of home range
- \( \text{Sleeping range} \): Average width of sleeping range
- \( \text{Homerange} \): Average length of home range
- \( \text{Homerange} \): Average width of home range
- \( \text{Sleeping range} \): Average width of sleeping range
- \( \text{Homerange} \): Average length of sleeping range
- \( \text{Homerange} \): Average width of home range

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Leemans, Linden and van Langevelde

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Number of days for the simulation: 25 days
Number of time steps per day: 33–36 steps per day
Distance: 0–1500 m with steps of 1 m
Proportion of the day: 0.85
Average radius of guineafowl flock: 8.2 m
Average radius of samango monkey group: 29.6 m
Length of home range of both groups: 1514 m
Width of home range of both groups: 590 m
Length of sleeping range of both groups: 681 m
Width of sleeping range of both groups: 344 m
Radius of the Crested Guineafowl flocks (referred to as ‘RadiusGF’) and the samango monkey group (referred to as ‘RadiusSM’) (Table 1). Samango monkey movement paths were provided by the Primate & Predator Project based at Lajuma, which were collected in July 2017 by following one samango group from dawn to dusk and recording their location every 20 minutes. For that reason, the step lengths and turning angles of the Crested Guineafowl movements were resampled based on similar 20-minute intervals.

We included a parameter in the model which we called ‘attraction distance’ (referred to as ‘AD’), defined as the distance from which one of the species is attracted towards the other. This AD represented the strength of the attraction. A value of AD = 0 thus simulated the situation where none of the species actively tried to join the other. We varied the value of AD and performed 100 simulations (see details on simulations below) per value (we increased AD from 0 to 1 500 m with steps of 1 m) and compared per AD the average simulated distance between the groups of the two species to our observed distances, to test what value of AD resembles the actual attraction between both species. In case both species do not associate longer than can be expected by chance (hypothesis 1), we would expect no significant differences between our simulation and our observations at AD = 0. All parameter settings are given in Table 1.

We simulated two points moving within the home range area, representing a Crested Guineafowl flock and the samango monkey group. Each time step in the model represented 20 minutes in reality. Each simulation lasted 856 time steps, consisting of 25 days with each having 33 to 36 time steps. The number of time steps per day corresponds with the number of 20-minute time steps observed during each of the 25 days of following the Crested Guineafowl (see Behavioural analysis), thus allowing us to compare the results of our simulation with our field observations.

For the first time step of each day in the simulation, a starting point somewhere within the sleeping range was randomly assigned for the Crested Guineafowl flock and the samango monkey group. Every following time step, the new location of each of the groups was determined by:

\[ x_t = x_{t-1} + dx \]
\[ y_t = y_{t-1} + dy \]

with:

\[ dx = \sin(\alpha) \times \text{step length} \]
\[ dy = \cos(\alpha) \times \text{step length} \]

where, the step length for each species was randomly drawn from their respective distributions of observed step lengths. The value of \( \alpha \) depended on several conditions. If the group moved outside of its home range, then \( \alpha \) was defined as the direction back into the home range. If more than 85% of the day had passed (referred to as ‘RT’, Table 1), then \( \alpha \) became the direction towards the sleeping range. For every time step, the distance between the two groups was calculated by:

\[ \text{Distance} = \sqrt{(x_{GF} - x_{SM})^2 + (y_{GF} - y_{SM})^2} - \text{RadiusGF} - \text{RadiusSM} \]

with the x- and y-coordinates of the Crested Guineafowl (referred to as ‘xGF’ and ‘yGF’) and the samango monkeys
(referred to as ‘SM’ and ‘SM’). If the distance between both groups was smaller than AD, then α of the Crested Guineafowl flock was defined as the direction towards the samango monkey group (note that we equally likely could have chosen to set α of the samango monkey as the direction towards the Crested Guineafowl instead of vice versa, as we did not have any data on who might initiate the association). When the distance was zero, then the α of the Crested Guineafowl flock became equal to the α of the samango monkey group, thus simulating that the Crested Guineafowl were following the samango monkeys. However, both groups could still split up by having different step lengths. In every other situation, α for each of the species was randomly selected from the respective distributions of the observed turning angles.

**Behavioural analysis**

While GPS fixes were recorded, behavioural data of the flocks of habituated Crested Guineafowl were collected. Crested Guineafowl flocks were followed and observed from dawn to dusk (typically from 6:30 am to 5:30 pm) for 25 days, corresponding to a total of 279 hours of observation. As the Crested Guineafowl were displaying fission-fusion dynamics and individual birds were not recognisable, we were not able to constantly follow the same subset of individuals (i.e. subgroup) of the overall flock. Therefore, we chose to follow the subgroup first encountered. On consecutive days of following we followed the same subgroup, as we knew in which tree they roosted. In total 1701 behavioural observations were done using an instantaneous scan sampling technique (Altmann 1974). At 10-minute intervals, the behaviour of at least 15 individuals was sampled. If we did not manage to sample 15 individuals in 3 minutes, we ceased sampling. Individuals for sampling were picked in the order in which they were seen, usually starting from either the left or right side of the flock, to minimise the risk of sampling the same individual twice.

We further estimated per 10-minute interval the distance between the nearest two individuals of the Crested Guineafowl flock and the samango monkey group as ‘0 m’, ‘0–50 m’, or ‘>50 m’ (at further distances an accurate estimate was not possible), the flock size of the Crested Guineafowl, canopy cover of the trees at that location (as percentage of total cover), horizontal cover of the vegetation in four directions (defined as the average distance to the nearest object that provided cover, e.g. tree, rock, dead tree trunk, in five categories: ‘0–1 m’, ‘1–4 m’, ‘4–6 m’, ‘6–10 m’, ‘>10 m’), forest or thicket (defined by average stem diameter >10 cm or not), rocky or not rocky (defined by cover of >50% rocks or not), and average canopy height as ‘0–5 m’, ‘5–10 m’, or ‘>10 m’.

To test hypothesis 2, we tested for differences in the proportion of Crested Guineafowl exhibiting certain behaviours with a Generalised Linear Mixed Model (GLMM) using the glmer function of the ‘lme4’-package in R, with a binomial distribution and the number of sampled individuals set as the upper limit of the binomial structure (Bates et al. 2015). We used five different behaviours as dependent variable to test for the foraging benefits and reduced predation risk (Table 2). Our fixed factor in the GLMM was association distance between both species (in three classes, see above), with covariates canopy cover and horizontal cover, and random factors habitat, canopy height, time of day, and flock size as subject, as we assumed that flocks of different sizes behaved differently. The analysis was followed by the Tukey-Kramer post hoc test (using the ‘multcomp’ package in R (Hothorn et al. 2008). Furthermore, we tested for differences in vegetation cover between different association distances using the lmer function of the ‘lme4’-package (Bates et al. 2015). For this, we used the same variables as described above, except that we used either canopy cover or horizontal cover as dependent variable. This analysis was also followed by the Tukey-Kramer post hoc test. We dropped all insignificant fixed variables from the model in turn to get a parsimonious model with most explanatory power.

**Results**

Our model showed that the average distance between Crested Guineafowl flocks and samango monkey groups decreased with an increasing attraction distance. In the field, we observed Crested Guineafowl in the presence of samango monkeys 12.3% of time, while another 9.8% of time both species were within 50 m of each other (Table 3). Our simulation showed that if no group was attracted towards the other (i.e. with attraction distance AD = 0), they would by chance encounter each other on average 1.8% of the time, with an additional 4.6% of time spent within 50 m of each other, which is significantly

**Table 2:** Definition of the five behaviours used as dependent variables in the GLMM to test for the foraging benefits and reduced predation risk

| Behaviour    | Definition                                                                 |
|--------------|---------------------------------------------------------------------------|
| Feeding      | Individual feeds on identified food source and ingestion is observed.     |
| Foraging     | Individual moves at a slow pace with head beneath shoulder level looking for food, beak points to the ground. |
| Pecking      | Individual repeatedly strikes the ground with its beak, simultaneously looking for and eating small food items. |
| Sentinel     | Individual looks out for predators for a period of more than 3 s in an upright position, either on the ground or on higher surface. |
| Vigilance    | Individual stops what it is doing and looks up for short moment.          |

**Table 3:** Comparison of observed and simulated occurrences of Crested Guineafowl at three distance categories from samango monkeys (N = 856). Simulated numbers are the average of 100 simulations without attraction (AD = 0)

| Distance | Observed | Percentage | Number | Percentage |
|----------|----------|------------|--------|------------|
| 0 m      | 105      | 12.3       | 15.77  | 1.8        |
| 0–50 m   | 84       | 9.8        | 39.09  | 4.6        |
| >50 m    | 667      | 77.9       | 801.14 | 93.6       |
less than observed in the field: \( \chi^2 (df = 2, N = 856) = 1174.0, p < 0.001 \) (Table 3). At attraction distances ranging from roughly 80 to 190 m, we simulated the same encounter percentages as observed in the field. A sensitivity analysis showed that none of the parameters are of dominant influence on our results, i.e. every change of 10% in a parameter value lead to less than 10% change in the average distance between both groups (Appendix 1).

In our behavioural analysis, we found that pecking was the most recorded behaviour, with on average 55% of the individuals in a flock showing this behaviour. However, we found no significant differences in the proportion of pecking Crested Guineafowl between the different distance categories to samango monkeys (model 5 in Table 4). Likewise, we found no significant effect of the presence of samango monkeys on the vigilance and feeding behaviour of Crested Guineafowl (model 1 and 3). However, we found a significantly larger proportion of Crested Guineafowl as sentinel and also a significantly larger proportion of Crested Guineafowl showing foraging behaviour when no samango monkeys were around, compared to when they were in association with the samango monkeys (model 2 and 4).

The odds of being sentinel were 1.63 times larger without monkeys, corresponding with an increase in probability of being sentinel of 59% (Figure 1a-d). Likewise, Crested Guineafowl were 19% more likely to show foraging behaviour without the monkeys (odds ratio of 1.22). No significant difference in canopy cover with and without samango monkeys was found, i.e. Crested Guineafowl did not spend more time in patches with a lower canopy cover when monkeys were present (model 6). However, when in association, Crested Guineafowl spent significantly more time in patches with a higher average horizontal vegetation cover (model 7; Cohen’s d = 0.89).

Discussion

Our results suggested that Crested Guineafowl associate with samango monkeys more than expected by chance alone. Testing for randomness is rarely done as it requires movement patterns of both species (Hutchinson and Waser 2007), which we had available for our study. If both species were not attracted towards one another, they would encounter each other on average 1.8% of time, with an additional 4.6% of time spent within 50 m of each other (Table 3). We observed reasonably higher percentages of 12.3% and 9.8%, respectively, which indicates that at least one species is following the other.

As is hypothesised (Waser 1982), one could also observe higher encounter rates when both species are attracted towards common resources. In the case of Crested Guineafowl and samango monkeys, common resources could potentially entail sleeping trees, fruiting trees, seed sources, water sources, and patches with high vegetation cover. In our model, however, we have accounted for attraction towards the same sleeping trees by defining the sleeping range where both groups start the day and return to at the end of the day. Whilst fruiting trees could be all over the area (Linden et al. 2015), we observed Crested Guineafowl eating fruits just twice in 279 hours of observation. Also, we observed that Crested Guineafowl did not seem to spend more time foraging underneath certain trees than others. These observations suggest that, at least during our study period in the dry season, no single food patch, including fruiting trees, seemed to attract them more than another, and this is possibly because fruits and seeds are very scarce in this period. Water sources, on the contrary, are more likely to attract both Crested Guineafowl and samango monkey in the dry season. However, as water availability is fairly equally distributed over the home range due to the presence of small streams, we expect that water sources have not significantly increased the encounter rate between Crested Guineafowl and samango monkeys. Furthermore, their home range has continuous vegetation cover (with varying canopy height), as it consists of mistbelt forest and adjacent Senegalia (Acacia) woodland, and it is thus unlikely that both species avoid any of these areas in their home range. Therefore, it is not likely that vegetation cover had a large effect on the observed time of association. Additionally, we did not observe associations between Crested Guineafowl and samango monkeys for some days, whereas both species were in association non-stop for hours in a row on other days. It is unlikely that such a pattern occurs when both species are merely encountering each other by attraction to common resources. Although it is difficult to completely rule out the possibility that both species are attracted towards some common resource, we are confident to conclude that our model suggests that Crested Guineafowl and samango monkeys have a tendency to associate, which supports our first hypothesis.

Studies on primate–bird associations so far only showed an increased availability of food items as potential foraging benefit for the birds (Ruggiero and Eves 1998; Barnett and Shaw 2014). While these studies featured birds feeding mainly on insects and arthropods flushed by primates, the omnivorous Crested Guineafowl in our study could additionally benefit from fruits dropped by monkeys and seeds in the monkeys’ faeces (Hill 1974; Siegel et al. 1989; Seufert et al. 2010). On several occasions, we observed Crested Guineafowl chasing flushed insects and eating seeds out of samango faeces. However, we did not find a significant increase in feeding behaviour of Crested Guineafowl when in association. One reason could be that Crested Guineafowl simply might not change their frequency of food ingestion in the presence of samango monkeys, as insects are also flushed by conspecifics, and suitable monkey faeces can also be found without monkeys nearby. Yet, another possibility is that Crested Guineafowl change their feeding sources when in association, but not increase their actual time showing feeding behaviour. This would not lead to significant changes in feeding behaviour in our study but would still mean that Crested Guineafowl may gain benefits from samango monkeys. A further study which consistently records which food sources are ingested by Crested Guineafowl could bring clarification.

Another potential foraging benefit of polyspecific associations is a decrease in vigilance, thus allowing higher foraging rates (Sullivan 1984). We found no evidence that this benefit applies to our study. Crested Guineafowl were not significantly less vigilant in the presence of monkeys, and we did not find higher feeding, foraging or pecking rates with the monkeys. On the contrary, we found significantly
Table 4. Summary of the results of the (generalised) linear mixed models for the effect of distance between Crested Guineafowl and samango monkeys on several response variables: vigilance, sentinel, feeding, foraging, pecking, and canopy cover and horizontal cover. For each fixed factor, Z-values, p-values and effect sizes are given, with (*) indicating odds ratio, (**) indicating Cohen’s d effect size, and (***) indicating standardised coefficients, and 95% confidence intervals between brackets. Random variables habitat, canopy height, time of day, and subject are tested through a likelihood-ratio test between the models with and without the random variable, and reported by its Chi-square-value and p-value. Bold indicates statistical significance with p < 0.05. For every model, its type and distribution is stated. Dash (-) means that the corresponding variable was not used in the model. Every model has N = 1701, consisting of N = 210 for ‘0 m’, N = 157 for ‘0–50 m’ and N = 1334 for > 50 m’ (corresponding with the number of observations in each distance category).

| Model number | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|--------------|---|---|---|---|---|---|---|
| Independent variables | Statistics | Vigilance | Sentinel | Feeding | Foraging | Pecking | Canopy cover | Horizontal cover |
| Distance      | 0 m     | (Intercept) | – | – | – | – | – | – |
|               | 0–50 m  | 0.20 | 0.29 | 0.18 | 0.09 | 0.64 | 1 | 0.11 |
|               | Effect size | 0.85* | 1.19* | 0.75* | 1.12* | 0.98* | 0.01** | 0.05** |
|               | Z       | -1.29 | 1.06 | -1.35 | 1.71 | -0.47 | -0.22 | -2.17* |
|               | p       | 0.20 | 0.91 | 0.91 | < 0.001 | < 0.001 | 0.82 | < 0.001 |
|               | *       | 0.66,1.09 | (0.86,1.66) | (0.49,1.14) | (0.99,1.25) | (0.88,1.08) | (-0.20,0.22) | (-0.10,0.25) |
|               | > 50 m  | p       | 0.11 | < 0.001 | 0.91 | < 0.001 | 0.82 | < 0.001 |
|               | Effect size | 0.87* | 1.62* | 0.98* | 1.22* | 1.01* | 0.01** | 0.03** |
|               | Z       | -1.60 | 3.91 | -0.11 | 4.07 | 0.23 | 1.13 | -4.07* |
|               | p       | 0.11 | < 0.001 | 0.91 | < 0.001 | 0.82 | < 0.001 |
|               | *       | 0.73,1.03 | (1.28,2.10) | (0.75,1.32) | (1.12,1.33) | (0.94,1.09) | (-0.10,0.16) | (-0.10,0.18) |
| Canopy cover  | Z       | -5.52 | -3.18 | -7.45 | -9.62 | – | – | -5.35 |
|               | p       | < 0.001 | 0.002 | < 0.001 | – | < 0.001 | < 0.001 |
|               | *       | (0.81,0.91) | (0.85,0.96) | (0.73,0.83) | – | (1.10,1.15) | – |
|               | Z       | -0.87 | -4.49 | – | 6.12 | 13.58 | -6.92 | – |
|               | p       | 0.39 | < 0.001 | – | < 0.001 | < 0.001 | < 0.001 | – |
|               | *       | (0.86,1.06) | (0.68,0.96) | (1.12,1.24) | (1.28,1.40) | – | (0.23,0.13) |
| Habitat       | Chi-square | 4.68 | 10.89 | – | 6.98 | 142.65 | 2.43 | 116.14 |
|               | p       | 0.03 | < 0.001 | – | 0.008 | < 0.001 | 0.12 | < 0.001 |
| Canopy height | Chi-square | – | – | 21.60 | 49.95 | 130.82 | – | 52.37 |
|               | p       | – | – | < 0.001 | < 0.001 | < 0.001 | – | < 0.001 |
| Time of day   | Chi-square | 22.64 | 59.44 | – | 21.29 | 306.57 | – | 9.44 |
|               | p       | – | – | < 0.001 | < 0.001 | < 0.001 | – | < 0.001 |
| Subject       | Chi-square | 0.04 | 20.98 | 60.81 | 67.57 | 144.33 | 14.93 | 58.01 |
|               | p       | 1 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | 0.002 | < 0.001 |
| Type          | GLMM | GLMM | GLMM | GLMM | GLMM | LMM | LMM |
| Distribution  | Binomial | Binomial | Binomial | Binomial | Binomial | Gaussian | Gaussian |

* Lower value of horizontal cover corresponds to a higher actual horizontal cover (see text for explanation).
higher proportions of foraging Crested Guineafowl without
monkeys. This result may suggest that Crested Guineafowl
spend more time searching for food (i.e. foraging) when
they are without monkeys. However, we found a significant
decrease in sentinel behaviour with samango monkeys
present, which indicates that Crested Guineafowl may
rely on samango monkeys as lookouts so allowing them
to act less frequently as sentinels. This decrease in
sentinel behaviour suggests that Crested Guineafowl may
experience a reduced predation risk when in association with
samango monkeys, which supports our second hypothesis.

During the behavioural observations of Crested Guineafowl,
we observed multiple times that the birds responded to
the alarm calls of nearby samango monkeys. Preliminary
results of an experiment in which we tested whether Crested
Guineafowl respond to the alarm call of samango monkey
indicate that Crested Guineafowl become significantly more
vigilant after playing a samango alarm call, than after playing
control bird calls (Leemans, unpublished data). Although this
experiment only entailed the use of an alarm call recording
of one individual male samango, it suggests that Crested
Guineafowl might eavesdrop on samango alarm calls.

A response of Crested Guineafowl to alarm calls of
samango monkeys would not be surprising given that both
species largely share the same predators. The Crested
Guineafowl could make use of the complementary abilities
of samango monkeys in detecting predators such as
eagles, leopards and snakes, as the monkeys have better
views over the area high in the tree canopy. For example,
at Lajuma, resident pairs of Crowned Eagle and Verreaux’s
Eagle regularly patrol the air above the Crested Guineafowl
home range, which increases the importance of enhanced
predator detection. Associating with samango monkeys
could be a way for Crested Guineafowl to achieve this. If
that would be true, the Guineafowl-samango association
is analogous to several primate-primate associations, as
predation risk from eagles is often considered to be the
main driver of polyspecific associations between primates
(Bshary and Noé 1997).

Figure 1. Predicted chances of Crested Guineafowl performing (a) vigilance, (b) sentinel, (c) feeding, or (d) foraging behaviour for the
different distances between Crested Guineafowl and samango monkeys. Error-bars indicate standard errors. Letters indicate differences
between the distance categories.
Our study is the first to report on the polyspecific association between Crested Guineafowl and samango monkeys. This association occurs for a longer time than expected by random movement. Furthermore, we suggest that this primate-bird association is occurring because of reduced predation risk. As both Crested Guineafowl and samango monkey are social species, they both could potentially be ‘leading’ the association (Sridhar et al. 2009; Goodale and Beauchamp 2010). Therefore, further research is needed on which species might initiate the association and the potential benefits of this association for samango monkeys, for example if Crested Guineafowl indeed respond to the alarm calls of samango monkeys. With this study, we contribute to understanding the mechanisms behind primate-bird associations, to shed further light on the driving forces behind these frequently observed phenomena.

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Appendix 1: Results of the sensitivity analysis of the simulation model. Change in the average distance between Crested Guineafowl and samango monkey compared to the simulation with default parameter values (Table 1). Average distances were calculated over all attraction distances from 0 to 700 m by steps of 5 m, with 1000 simulations per attraction distance. The value of each parameter was either decreased by 10% or increased by 10%, while other parameter values remained constant. An exception was ‘sleep location’, for which we randomised the location of the sleeping range within the home range in each simulation.

| Parameter        | 10% decrease | 10% increase | Randomised |
|------------------|--------------|--------------|------------|
| RT               | −2.2%        | 0.6%         |            |
| RadiusGF         | 0.3%         | −1.0%        |            |
| RadiusSM         | 2.0%         | −3.1%        |            |
| Home range       | −1.4%        | 0.6%         |            |
| Sleep range      | −5.4%        | 5.1%         |            |
| Sleep location   |              | −0.5%        |            |