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RESEARCH ARTICLE

# Testing the information centre hypothesis in a multilevel society

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## Abstract

1. In various animal species conspecifics aggregate at sleeping sites. Such aggregations can act as information centres where individuals acquire up-to-date knowledge about their environment. In some species, communal sleeping sites comprise individuals from multiple groups, where each group maintains stable membership over time.
2. We used GPS tracking to simultaneously record group movement in a population of wild vulturine guineafowl (*Acryllium vulturinum*) to investigate whether communal sleeping sites can facilitate the transfer of information among individuals across distinct groups. These birds live in large and stable groups that move both together and apart, often forming communal roosts containing up to five groups.
3. We first test whether roosts provide the opportunity for individuals to acquire information from members of other groups by examining the spatial organization at roosts. The GPS data reveal that groups intermix, thereby providing an opportunity for individuals to acquire out-group information.
4. We next conduct a field experiment to test whether naïve groups can locate novel food patches when co-roosting with knowledgeable groups. We find that co-roosting substantially increases the chances for the members of a naïve group to discover a patch known to individuals from other groups at the shared roost. Further, we find that the discovery of food patches by naïve groups subsequently shapes their space use and inter-group associations. We also draw on our long-term tracking to provide examples that demonstrate natural cases where communal roosting has preceded large-scale multi-group collective movements that extend into areas beyond the groups' normal ranges.
5. Our findings support the extension of the information centre hypothesis to communal sleeping sites that consist of distinct social groups.

**KEYWORDS**
communal roosting, GPS-tracking, information centre hypothesis, multilevel sociality, vulturine guineafowl

## 1 | INTRODUCTION

Across a wide range of social species, individuals aggregate with conspecifics at sleeping sites (Beauchamp, 1999; Fischer et al., 2017; Gager, 2019; Henriquez et al., 2021; Loretto et al., 2017; Snyder-Mackler et al., 2012; Still et al., 1986). Individuals at these sites can each have different information about the environment, including the location of resources such as food, water or shelter, as well as information on predation risk, travel companions and potential mates (Bijleveld et al., 2010). For example, experimental work using colour-coded plastic beads has shown that ravens can localize specific food resources that their communal roosting associates have discovered before (Wright et al., 2003). Thus, sleeping sites provide the opportunity for individuals to acquire information—a phenomenon now referred to as the information centre hypothesis (Harel et al., 2017; Kohles et al., 2022; Ward & Zahavi, 1973). By facilitating information flow, these sites can play a pivotal role in facilitating coordinated action, such as by shaping where animals move, what resources they encounter, and the contact that they have with other individuals (Cantor et al., 2021).

Species forming communal sleeping sites vary in their social organization (Grueter et al., 2020). While they most commonly occur in species where individuals move alone during the day or with different individuals each day (fission-fusion dynamics; Aureli et al., 2008), they can also occur in species that live in stable social groups and in such cases communal sleeping sites consist of aggregations of multiple such groups. These distinct groups maintain stable membership with group members moving cohesively throughout the day. In addition, they do not maintain territories, meaning that different groups can use the same space, and move together with other groups. Perhaps the best-known cases are primate species, such as guinea and hamadryas baboons, as well as geladas (Fischer et al., 2017; Henriquez et al., 2021; Snyder-Mackler et al., 2012). The consistent patterns of fission-fusion among groups in these species generate so-called multilevel societies (Grueter et al., 2020; Papageorgiou & Farine, 2021). While information transmission among individuals has been observed in communal roosts (Bijleveld et al., 2010; Harel et al., 2017; Ward & Zahavi, 1973; Wright et al., 2003), a key question (Gager, 2019) is whether this process can also act in sleeping sites comprised of distinct social groups (Figure 1).

Social structure, and more specifically the stability of group membership, impact the information about the environment that each individual has access to (Aplin et al., 2012). In species that express more open social networks, such as common ravens (*Corvus corax*; Loretto et al., 2017), or where the members of a group can move independently, such as in the fission-fusion groups of spotted hyenas (*Crocuta crocuta*; Gersick et al., 2015), each individual has the possibility of acquiring different information about their environment. This contrasts with animals that form stable, cohesive social groups. In stable groups, individuals largely experience the same (or very similar) environments as all other group members, meaning that their experiences are highly correlated (Kao & Couzin, 2014). As a result, the pool of information across all members of the same group should be more limited than among a temporarily forming group of the same size in a more open society. This further means that the greatest variation in

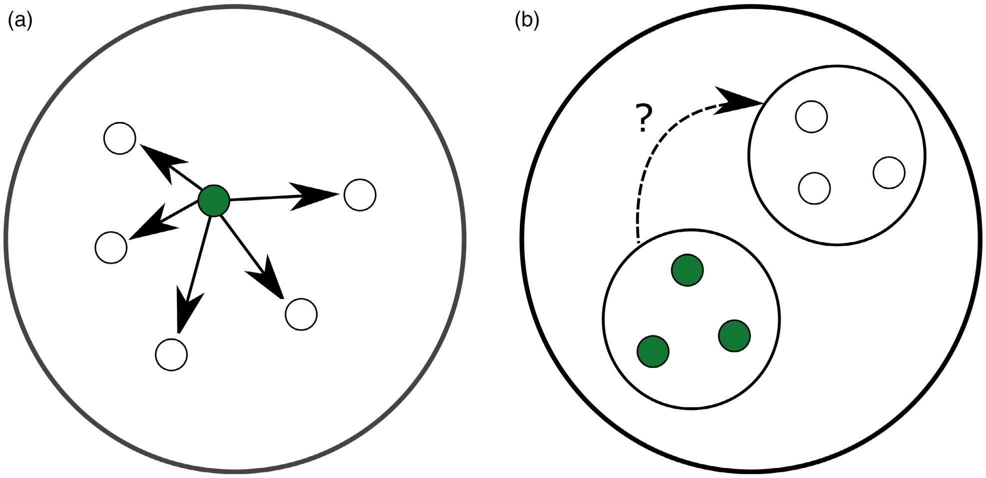

FIGURE 1 (a) Observed and (b) hypothesised patterns of information transmission in communal roosts. (a) Communal roosts (largest circles) often consist of individuals (small circles) that exhibit fission-fusion dynamics, whereby individuals move independently or in small groups with different membership each day. In such roosts, uninformed individuals (small open circles) can acquire information (arrows) from informed (filled green circles) co-roosting conspecifics (e.g. Marzluff et al., 1996). (b) Communal roosts can also be the aggregation of individuals from multiple social groups (intermediate circles), where the members of each group move cohesively with the same conspecifics each day. Whether information can transmit among groups (dashed arrow) in such roosts remains unknown.

information state will occur among groups. Individuals in multilevel societies should, therefore, benefit from access to out-group information during inter-group associations, such as at communal roosts.

In this study, we test whether information about new food resources can transmit among groups of vulturine guineafowl. Vulturine guineafowl live in large, stable social groups that vary in size from 13 to 65 or more individuals (Papageorgiou & Farine, 2020a). Group membership is maintained over months and years (Ogino et al., 2023) and group members move very cohesively during the day (Papageorgiou et al., 2019). Vulturine guineafowl usually feed on dispersed seeds and grasses (Madge & McGowan, 2002), but they also feed on clumped and unpredictable resources such as insect-rich elephant dung (Papageorgiou & Farine, 2020b). Groups are not territorial, and often move with other groups, exhibiting preferences for certain groups (Papageorgiou et al., 2019). These associations are also often expressed at shared communal roosts, which can contain the members from two to five different groups, even if each group has a distinctly different home range (Papageorgiou et al., 2019). Communal roosts are generally located in areas of dense acacia trees next to glades [i.e. open areas rich in nutrients (Young et al., 1995) where guineafowl typically forage]. Because of their large body size, and because each tree can only hold a few birds (Figure 2a), group members generally spread out over a much larger area at night time than they do during the day and potentially intermix spatially with members of other groups, which could facilitate the transmission of information among them. Roosts do not seem to constitute a limited resource for vulturine guineafowl, as groups have been observed using many different roosting locations since the start of our field study (2016) and can change roosting locations with some regularity.

At present, it remains unclear what benefits communal roosting provides to group members. The fact that vulturine guineafowl from one group distribute themselves across the tops of several neighbouring roost trees (Figure 2), implies that they are unlikely to gain thermoregulatory benefits (Beauchamp, 1999). Individuals may benefit from reduced predation risk due to enhanced predation detection (Powell, 1974) or dilution effects (Foster & Treherne, 1981). However, the already large group sizes of vulturine guineafowl (Papageorgiou & Farine, 2020a) that allows them to cope with the high intensity of the diurnal predation they face raises the question about whether it would still be necessary to further increase this size (by merging with other groups) to cope with night time predation risk. Regardless of the main driver of communal roosting, group members could still benefit from information available at communal roosts.

To test whether the information centre hypothesis can operate at a group-to-group level, we first studied how the members from different groups are spatially organized within a roost. If groups mix, then this could potentially facilitate information transfer. Second, we conducted a replicated food patch discovery experiment to test the potential for information transmission among groups within the same communal roost. In each replicate, we created an artificial food patch within the recent range of one group (Target Group 1; TG1) but outside the recent range of another group (Target Group 2; TG2) and asked if this second group from the same communal roost would subsequently move outside its recent range to discover the food patch. We predicted that if information is transmitted between communally roosting groups, then TG2 would discover the food patch only after co-roosting with TG1 and if TG1 had discovered the patch previously. Finally, we illustrate the generality of our findings by reporting on two of the many natural cases of potential information transmission that we have observed after groups roost communally. In both these cases, two or more groups roosted communally and subsequently travelled together to areas where one of the groups had been recently, but where the other group(s) from the same roost had not visited, based on long-term GPS tracking.

## 2 | MATERIALS AND METHODS

### 2.1 | GPS data collection

We have been studying a population of vulturine guineafowl since 2016. Our population contains on average 20 groups that reside in the southern part of the Mpala Research Conservancy (MRC)

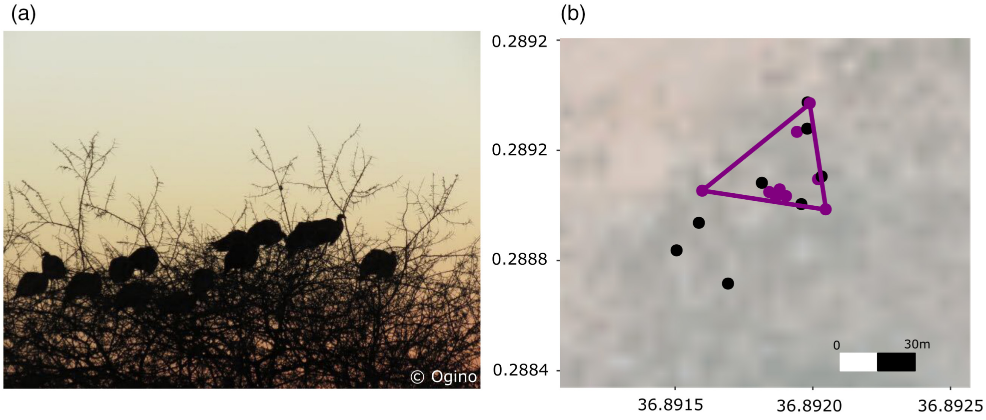

FIGURE 2 Spatial organization on communal roosts. (a) Vulturine guineafowl roost together on acacia trees and (b) members of one group (purple) mix up with members of other groups (black) on the roost.

in Laikipia, Kenya. As part of this long-term study on the movement behaviour of vulturine guineafowl, we have been fitting GPS tags (15 g Bird Solar, e-obs Digital Telemetry, Grünwald, Germany), which together with the harness (25 g) weigh less than 2% of the smallest individuals' body weight in our study population. Therefore, our GPS-tagging respects the strictest animal welfare guidelines (Portugal & White, 2021). GPS tags were programmed to collect data from 06:00 to 19:00 (representing dawn until dusk) and here we use data from April 2018 to April 2022 (see details below).

Each group in our study area had between one and six individuals fitted with a GPS tag, which we call 'group representatives' hereafter. These individuals are randomly selected adults (Papageorgiou & Farine, 2020a), either males that stay in their natal group, or females, after having dispersed from their natal group and settled in another group for life (Klarevas-Irby et al., 2021). Previous data, together with field observations, have shown that guineafowl groups generally move as single entities, especially during non-breeding seasons (when we ran this study), meaning that each adult group member can act as a representative of the movements of its group (Papageorgiou et al., 2019; Papageorgiou, Nyaguthii, et al., 2024).

Group-representative tags were programmed to record data at high-resolution (1 Hz; 1 position per second) when the batteries were fully charged, and a burst of 10 points every 5 min when the batteries were not fully charged, allowing us to monitor group movements in the frame of our long-term study (He et al., 2023; Papageorgiou et al., 2021). As part of other studies (Musciotto et al., 2022; Papageorgiou, Nyaguthii, et al., 2024), in four groups we fitted between 50% and 100% of group members with a GPS tag, and call these groups 'high-coverage' hereafter. Tags on these high-coverage groups were programmed to collect 1 Hz data every fourth day (outside of breeding seasons) to allow them to fully recharge over 3 days before starting a full day of operation. Here, we mainly use the roosting data of these high-coverage groups to investigate the within-roost spatial distribution of individuals. High-coverage groups also had one to two tags (depending on the group size) that were programmed using the group-representative settings. We specify in the following sections for which questions we used data just from group representatives and when we used data from high-coverage groups. See Papageorgiou et al. (2019, 2021) for how we assign individuals to groups, for more details on trapping the birds, tag deployment, programming, and data storage, and He et al. (2023) for further details on the design of the GPS sampling and on the questions our data collection was designed to answer.

## 2.2 | Spatial overlap between groups at communal roosts

We used data from a total of 190 birds fitted with GPS tags between 1 April 2018 and 1 July 2021. To get the exact location of the roosting site for each bird we used the tenth location of the second burst of the day (06:05:10) as our GPS tags tend to perform with higher accuracy after recording a few initial positions following a prolonged period of inactivity during the night. Note that the distance moved from previous evening's final timestamp (18:55:10) to the following morning (median distance moved = 4.30 m, see distribution in Figure S1) is equivalent to the absolute GPS error in spatial position for these tags (He et al., 2023), suggesting that the roosting location was accurately determined.

We then quantified how individuals position themselves on the roost relative to other groups. Focusing on one high-coverage group at a time, we first chose a threshold below which two individuals would be regarded as roosting together. Plotting the distribution of pairwise distances on the roosting sites between all tagged group members suggested that a threshold of 200 m (see Figure S2) always captured the largest between-individual distance among members of the same high-coverage group.

We next quantified the spatial overlap among groups within the same communal roost. For this analysis, we used data from 557 nights of data from 72 members of four high-coverage groups and data from 79 individuals that were tagged as group representatives. We started by computing a Minimum Convex Polygon (herein MCP) of each roost position on a given night for each high-coverage group (Figure 2b). We computed both the 50% and the 95% MCPs, as the 50% represented the core of the roosting site and the 95% also included the peripheral locations. We then calculated the binomial probability of an individual, which was not a member of the focal high-coverage group but was determined to be at the same roost (using the 200 m threshold), being detected inside the 50% and 95% MCPs of the focal high-coverage group on that same night. We calculated confidence intervals of this probability using the function *binconf* in the R package *Hmisc* (Brown et al., 2001; Harrell, 2021), which allows us to examine if the probability of an individual to be within the roosting range of another group, for a given night, differs significantly from zero.

## 2.3 | Food patch discovery experiments

To test if groups acquire information about the environment from other groups at communal roosts, we created artificial food patches close to communal roosts within the movement area of one group (Target Group 1, TG1) but not of another (Target Group 2, TG2). To choose TG1 and TG2, we plotted the daily ranges of the group representatives within our study population and identified groups that frequently roosted communally. The two target groups varied across the different experimental trials (see details on Table S1). Food patches were fixed in place for each experimental trial and consisted of a controlled amount of mixed millet seed (9 g per individual of TG1, spread over 1 m diameter that allows initial access to all group members as in Papageorgiou & Farine, 2020b). Food patches were replenished every morning, before dawn, on the days that the experimental trial was running (Table S1).

We selected the location of food patches by plotting the daily ranges of each group representative each day. Specifically, we looked for places that TG1 had frequently used (i.e. was found there every day or every couple of days) during the 15 days prior to the start of the food patch experiment but where TG2, which was often roosting together with TG1, had not been detected during that period. We also made sure that the location was accessible by car and deemed safe to work at pre-dawn. Food patches were between 80 and 490 m from the edge of the target roost. To exclude the scenario of local enhancement (Buckley, 1997), we also ensured that the food patch locations were not visible from the site where the groups were roosting.

While all groups contained at least one representative GPS tag, we also placed camera traps (StealthCam P12, 6.0 MP) to confirm (where possible) the presence of specific groups on the food patch and the timing of its arrival using colour bands fitted to each individual. On some mornings, observers were present at the food patch to observe if groups arrive at the same time or separately, but no systematic information was collected as these observations were conducted in between other field tasks.

## 2.4 | Quantifying the null expectation of discovery rates

To estimate the rate at which we would expect groups to discover patches in the absence of social information at roosts, we constructed a null model using our long-term GPS data. Specifically, for each experimental trial that is included in the final analysis, we calculated the pairwise distances on the morning roost between all group representatives involved in our broader study, from which we could extract information about groups that roosted together the night before the baiting started for a specific pair of groups (i.e. the current TG1 and TG2). We defined communal roosts using the same threshold as above (i.e. a dyad of group representatives had to be within 200 m to be considered as co-roosting). From these, we excluded the focal groups as well as any group that was roosting with TG1 and TG2 of the respective trials. If more than two groups were roosting together, we randomly picked the dyad with the smallest metal ring numbers.

For each dyad of null groups, we first selected one group to be TG1 (using the group with the smallest identification number in its metal ring). Next, we plotted the daily tracks of the null TG1 and TG2, for the last 15 days prior to the initiation of the patch for our actual target groups and defined a null patch at a location that followed the same procedure that we used for our true patches (e.g. it was within the recent range of the null TG1 and outside that of the null TG2, in an accessible area). Finally, for the 60 days after the 'initiation' of the null patch, we calculated how many days would take for the groups to 'discover' the null patch, which we defined as moving within 30 m of the patch. This threshold is based on our previous work showing that individuals from the same group are found within 30 m from each other at 95% of the time during daytime (Papageorgiou et al., 2019; Papageorgiou, Nyaguthii, et al., 2024).

## 2.5 | Consequences of patch discovery on subsequent group ranging behaviour and social associations

We explored whether the discovery of the patch by TG2, following the discovery by TG1, resulted in changes in space use by TG2 and social contacts between TG1 and TG2. Specifically, we quantified the increase in the use of the area surrounding the food patch by TG2 after discovering the patch (and how this relates to TG1) by comparing each group's space use for 14 days before starting the food patch and for the 14 days after the end of the trial. For each date and time when the tags of group representatives collected data, we tested whether the GPS position was within 50 m from the food patch (see Table S1 for details of the individuals used across each trial).

To test whether the use of the space near the new food patch increased following discovery, we ran a generalized linear mixed effects model (GLMM) with a binomial family for each of the two groups (one model for TG1 and one model for TG2, because each was a separate discovery event). The response variable was the frequency of times a group representative tag was detected within 50 m of the food patch, capturing its surroundings, in each of the experimental trial phases. We included experimental trial phase (categorical variable: before discovering the food patch, during using the patch, and post presence of the food patch) as predictor variable. A unique code for each experimental replicate was set as a random effect. Because individuals were always in the same group, the high correlation among group members prevented us from running this analysis at the individual level. Finally, data are highly standardized across each day as tags collect data synchronously every 5 min from morning to evening.

To test the effect of food discovery by TG2 on the associations between groups, we first estimated the distance between the group representatives of each experimental trial's TG1 and TG2, at 5-min intervals. We considered data after 9 AM to exclude the periods when the groups visited the food patch together (which was typically before 7:15 AM) and we defined the following experimental trial phases: (a) during the 3 days before TG2 discovered the patch, (b) up to 3 days during which both groups had discovered the food patch and (c) during the first 3 days after the food patch discontinued. We characterized as associating groups which were in close proximity to each other by using a threshold (28.67 m), as defined in Papageorgiou et al. (2019). This threshold is calculated based on the distribution of pairwise distances of all group members of one group that were simultaneously tracked with GPS devices. We then ran a GLMM with a binomial family. The response variable was the frequency of times two groups were associating versus not, in each of three experimental trial phases. We included as predictor variable the experimental trial phase, defined as in the previous paragraph.

A unique code for each experimental replicate was set as a random effect.

### 2.6 | Potential natural information transmission between groups at communal roosts

We present GPS-tracking data that capture two natural examples of likely information transmission taking place at a communal roost. These events are representative of the many that the research team have noted from field observations. Events (including these presented here) involve two or more co-roosting groups before making large movements together away from at least one group's recent range. Here, we first present an example where two groups that roosted together subsequently moved together outside of the area in which one group has ever been known to move since the start of our study (in 2016) but where the other group moved to regularly. In the second example, which took place during a period of severe drought, three groups that roosted together moved first into an area often used by one group during dry seasons (see Papageorgiou et al., 2021), and then all temporarily moved beyond the boundaries of that area into an area that is completely outside the normal range of vulturine guineafowl. We calculated home ranges using Auto-correlated Kernel Density Estimation (Calabrese et al., 2016).

## 3 | RESULTS

### 3.1 | Spatial overlap between groups at communal roosts

We analysed data from a total of 190 birds fitted with GPS tags. That number includes 91 individuals from four high-coverage groups and 99 group representatives of non-high-coverage groups. From the 1181 days during which these birds were tracked, high-coverage groups co-roosted with other groups on 557 different nights (774 different combinations of groups and nights). These data showed that individuals from different groups regularly overlap in space while roosting. Specifically, we found that the probability of an individual from a group that is at the same roost as a high-coverage group to be located inside the MCP of the latter was 0.23 (CI: 0.23–0.25) for the 95% MCP and 0.07 (CI: 0.07–0.08) for the 50% MCP, with both probabilities being significantly greater than 0.

### 3.2 | Food patch discovery experiments

We created 17 artificial food patches in total, each targeting a unique pair of groups. Table S1 contains detailed outcomes of each trial and for which groups participated. In four trials no group discovered the food patch, in three trials another non-focal group discovered the food patch first, and in one trial TG2 first discovered a food patch unrelated to our experiment. Of the nine trials in which TG2 discovered the food patch after TG1, in one trial TG2 temporarily shifted its range to a completely different area after the start of the experiment and subsequently discovered the food patch on its way back to the area before roosting with TG1. Thus, in eight out of nine trials in which TG2 discovered the experimental patch, it did so after roosting with TG1 (see Figure 3 for an example) and was at the food patch at the same time when TG1 was also there. GPS data and camera traps confirm that after TG1 discovered the food patch and at least until the day that TG2 also discovered it, TG1 was visiting the food patch each of those mornings. We subsequently analysed data from these eight successful trials when characterizing the consequences of patch discovery. It is worth to note that while TG1 and TG2 often roosted together, this was not always the case prior and during when the experimental trials ran. Specifically, TG1 and TG2 roosted together in 34.52% of the nights in the 14 days prior to establishing experimental food patches (this percentage regards the eight trials used for GPS analyses). However, in each of these eight trials, TG1 and TG2 roosted together (i.e. within 200 meters from each other) the night prior the discovery of the food patch by TG2, but TG2 did not always discover the patch immediately after it began sharing a roost with TG1 (on average 1–2 days).

In true patch results, TG1 took on average 0.63 days (range = 0–2, SD = 0.74) to discover the food patch. TG2 subsequently discovered the food patch on average 3.5 days (range = 1–9, SD = 2.56) after TG1 had discovered it. More specifically, TG2's discovery occurred 1.75 days (range = 1–4, SD = 1.65) after TG1 and TG2 roosted together for the first time since TG1 initially discovered the patch. They continued roosting together thereafter, including at least the night before TG2 discovered the patch. Groups typically visited the food patch as first activity in the morning (before 7 AM), and at three out of the eight trials that we used for GPS data analyses where we could opportunistically observe arrivals (in person or from camera traps), we observed groups arriving with members intermixed. In the remaining five trials, we are uncertain whether the groups arrived intermixed or separately. This uncertainty arose because it was either too dark for the camera traps to capture the colour band combinations, or they were not operational due to low battery voltage, or no observers were present. Unfortunately, the resolution (both temporal resolution and the coverage, see He et al., 2023) of the GPS data and the frequency of the images captured by camera traps did not allow us to differentiate the arrival times at the patch between the members of the different groups, and hence to determine which individuals led the way. In Figure S3, we show the distances of TG1—TG2 as well as the distances of TG1—food patch and TG2—food patch, at 06:05:10, for each day of the eight experimental trials, from which we can infer which mornings TG1 and TG2 roosted together and were close to the food patch, in each of the mornings of the experimental trials.

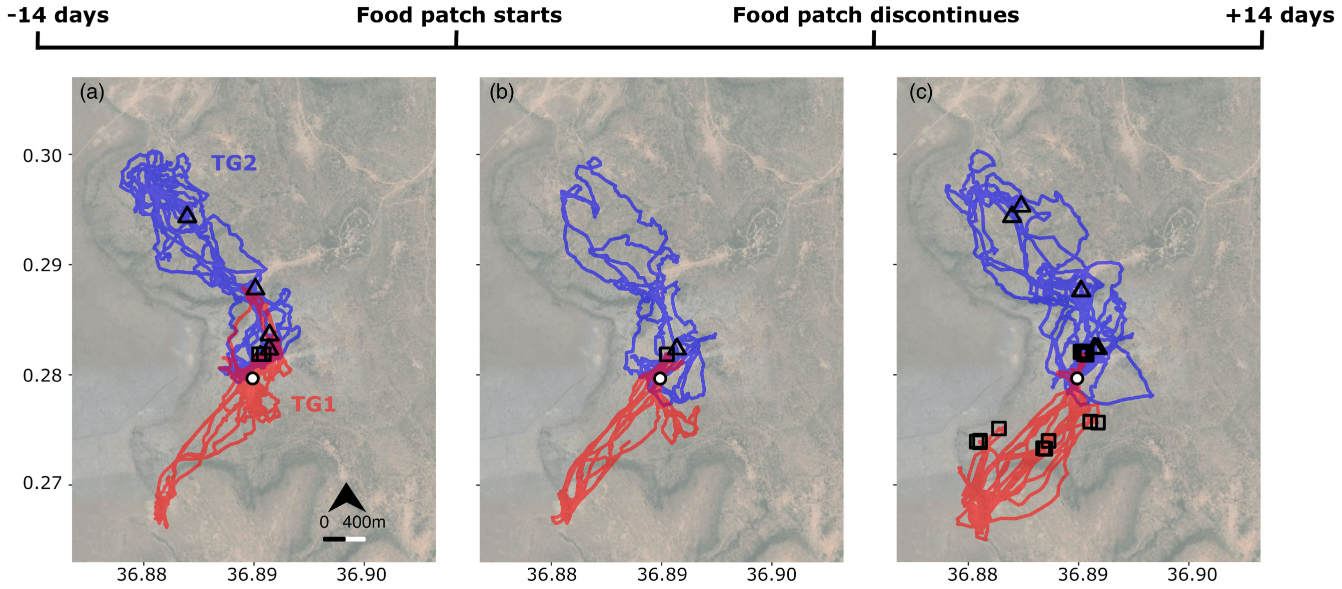

FIGURE 3 Example of information transmission experiment between two groups that roost communally (one group representative from TG1 and one from TG2 are shown here). (a) The daily paths of TG1 are shown in red and the daily paths of TG2 are shown in blue for the 14 days before we started an artificial food patch (white circle). The food patch was within the recent range of TG1 but outside that of TG2 during this period and on average 200 m from a site where the two target groups often roosted communally (roosting sites for TG1 and TG2 are represented by squares and triangles, respectively). (b) After starting the food patch, both TG1 and TG2 visited the food patch, with TG1 discovering it first and being joined by TG2 within 1–4 days after the latter roosted communally with TG1. In this panel only the roosting location of the TG1 representative (square) and the TG2 representative (triangle) on the night prior to the discovery of the food patch by TG2 are shown. As a result of following TG1 to the food patch, TG2 extended their recent movement range. (c) After the food patch was discontinued, both TG1 and TG2 continued to overlap in the area where TG2 had extended its range.

### 3.3 | Quantifying the null expectation of discovery rates

In 19 out of the 20 null patch trials TG1 'discovered' the null patch. In one of the null trials neither of the groups 'discovered' the patch. In eight of the remaining 19 null trials, only TG1 'discovered' the null patch. In the 11 cases where both null groups, TG1 and TG2, 'discovered' the null patch, TG2 was significantly slower at 'discovering' it compared to the true trials (Figure 4, Table S2).

### 3.4 | Consequences of patch discovery on subsequent group ranging behaviour and social associations

In each trial, TG2 significantly increased the use of the area around the food patch (circle centred on the food patch with a 50 m diameter) during the period when food was provided (Figure 5, Table S4), but decreased it after the food patch was discontinued, indicating that food patch discovery introduced TG2 to a new habitat. This pattern was mirrored by TG1 in each trial (Figure 5, Table S3). We also found that for each trial and while considering data after 9 AM (to exclude the periods when the groups visited the food patch together), TG1 and TG2 associations increased during the period when both groups were using the food patch (Figure 6b, Table S5), with associations being maintained after the food patch was discontinued.

### 3.5 | Potential natural information transmission between groups at communal roosts

The potential for information transfer through communal roosting is evident from two examples of natural cases. In case one (Figure 7a), within 1 day, a group moved into a new area more than 2.5 km outside its normal range—where it had never been recorded since the beginning of our study in 2016—together with another group from the same roost that moved there regularly. Note that both groups remained cohesive for the entire day of movement. In the second case (Figure 7b), three groups that roosted together moved to an area that only one of the groups had used during the previous year, and then moved beyond this over 4 days into an area more than 9 km away from the normal range of the naïve groups. In this case, none of the three groups were known to use this area previously (in fact, the groups temporarily moved outside of the current known species range of vulturine guineafowl). The three groups moved as a single entity until they returned to their normal home ranges. While we demonstrate two exemplary cases, these types of movements commonly occur in our population.

## 4 | DISCUSSION

We presented experimental and observational evidence that communal roosting reduces the latency for social groups to discover new

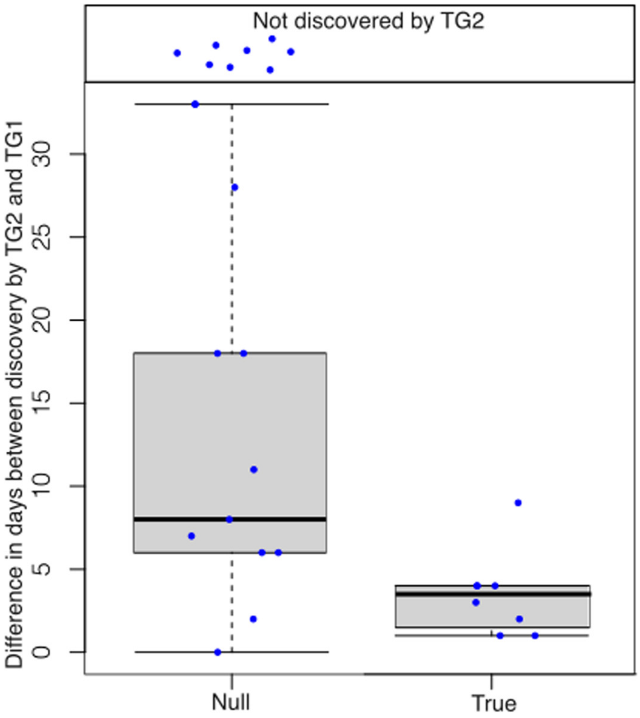

FIGURE 4 In true experimental trials TG2 discovered the food patch sooner than in null trials. For each experimental trial, we extracted pairs of groups that were roosting together. For each such communally roosting dyad we picked a group to represent TG1 and one for TG2 (see Section 2.4 for details), selected a patch following the same rules as our true experimental patches, and calculated the first time that TG1 and TG2 were found in close proximity (within 30 m) to the null patch. In eight of the null patch cases TG1 'discovered' the patch but TG2 didn't. This never happen in true experimental trials were TG2 always discovered the food patch if TG1 did. For a statistical comparison see Table S2.

resources. First, we showed that there is significant spatial overlap between members of different groups at communal roosts, which might facilitate inter-group information transmission. Second, we showed that when roosting together with a group that had knowledge of a food resource, a naïve group could rapidly discover this resource even when the resource was outside of its recent range. Groups also decreased their inter-group distances (increasing the potential for social interactions) and expanded their use of the area around the food patch (increasing their use of recently unused habitat). Finally, we use long-term tracking data to draw examples from natural cases of groups moving into new areas from a communal roost. Together, our findings suggest that group-to-group information transmission is likely to commonly occur at communal roosts.

Following individuals from other groups from the communal roost is likely to provide the opportunity for the members of naïve groups to explore areas in which they have not been recently and thus increase the chances to encounter vital resources. Such group merges are potentially beneficial for knowledgeable groups as well, for example by providing safety in numbers (Powell, 1974). If both groups benefit mutually, or even if one of the participating groups benefits and the other doesn't displace them, then this could lead to continued associations. From our experimental trials, we found that this was sometimes the case, resulting in a bimodality in the inter-group distances after the patches were removed (Figure 6c) that was not present before (Figure 6a,b). Such events might be indicating a feedback between social information spread and social network structure (sensu Cantor et al., 2021; Kulahci & Quinn, 2019).

While we found support for the hypothesis that groups can benefit from the information that other groups have in communal roosts by moving into new areas and encountering new resources, we could not determine the exact mechanism by which this information was transmitted. A recent review, focussed on bats, highlighted that this is a general gap, stating that '...firm evidence that bats follow knowledgeable individuals from the colony to food patches in the wild is still lacking' (Gager, 2019). Thus, while there is a growing body of evidence that information does transmit between individuals (and now groups; Boyd et al., 2016), the mechanisms of transmission remain unclear. One hypothesis is that naïve individuals observe distinct movement cues associated with being knowledgeable, as has been demonstrated in studies of leadership when groups make collective decisions (Couzin et al., 2005). For example, olive baboons are more likely to follow an initiator when the initiator moves in a more directed manner at a medium to high speed (Strandburg-Peshkin et al., 2017). Observations in chacma baboons, focussed on movements, found that individuals walk faster and in a more directed manner when moving towards known food resources (i.e. fruiting fig trees; Noser & Byrne, 2010). However, the data to test this hypothesis in the context of the information centre hypothesis is challenging to acquire.

In our study on vulturine guineafowl, the members of naïve groups could have acquired information from the movement cues expressed by individuals of knowledgeable groups as they departed the roost. To test whether individuals express different movement characteristics when leaving roosts and moving towards known, high quality food patches, we conducted a post hoc analysis (see Supporting Information Section 1 and Figure S5). Specifically, we examined the movement cue hypothesis using high-resolution GPS-tracking data from one high-coverage group, which was heading to a morning experimental food patch almost every morning. We collected this dataset during a previous experiment in which GPS tags were programmed to work at high resolution from dawn. This analysis shows that when departing a roost for a rich food patch, individuals move in a faster and more directed manner than on days when they visit natural patches. While we did not have data from two high-coverage groups—one informed and one uninformed—departing from the same communal roost, it is reasonable to hypothesize that individuals from other groups could perceive these differences in movement as cues indicating that individuals have information about a specific resource. Further, we also know that knowledgeable individual bats (Hügel et al., 2017) and birds (Brown et al., 1991; Hillemann et al., 2019) can recruit others using vocal signals, which can play an important role in maintaining group cohesion. As vulturine guineafowl are also highly vocal, it is also possible that calls directed to group

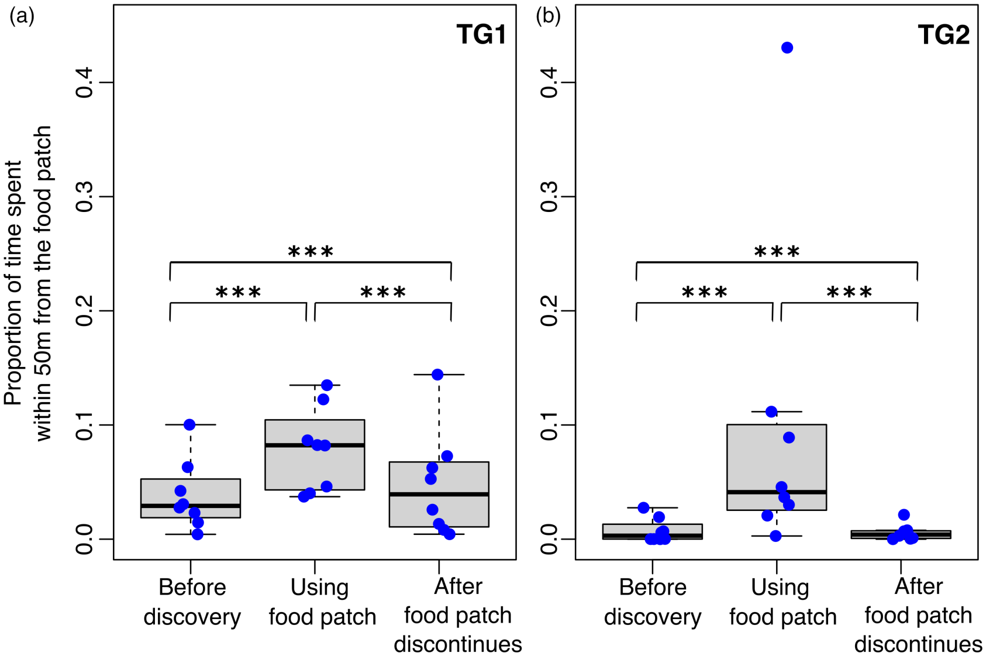

**FIGURE 5** Both TG1 (a) and TG2 (b) increased the time spent near the food patch after discovering the food patch and decreased their presence near the food patch after it was discontinued. GLMM summaries are presented in Tables S3 and S4. Each blue point represents the data of a group representative from (a) TG1 and (b) TG2 in each of the eight experimental trials used in the analyses (see metadata in Table S1). Three asterisks correspond to $p$ values less than 0.001.

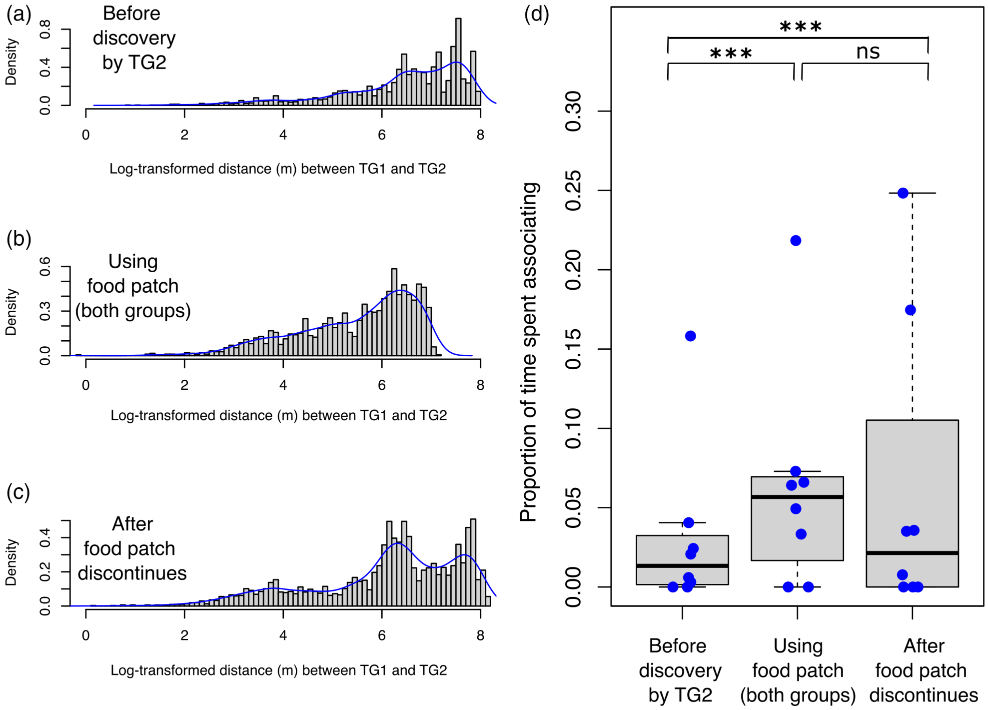

**FIGURE 6** TG1 and TG2 spent more time associating during the period that they both exploited the food patch. (a–c) The distribution of the log-transformed distance in meters between TG1 and TG2, across all eight experimental trials, (a) during the 3 days prior to TG2 discovering the food patch, (b) during the period that they were exploiting the food patch, and (c) during the first 3 days after the food patch discontinued. The blue lines represent an estimated kernel density for each plot. (d) TG1 and TG2 significantly increased the time they spent associating while they were both using the food patch than before TG2 discovered it, with some of these associations being maintained after the food patch was discontinued. To avoid the confounding effects of the groups moving to the patch together, we limited these visualizations (a–c) and analyses (d) to the GPS data collected after 9 AM. In (d), blue points represent the proportion of time TG1 and TG2 spent associating in each of the eight experimental trials used in the analyses (see metadata in Table S1). Three asterisks correspond to $p$ values less than 0.001 and 'ns' correspond to non-significant $p$ values, more than 0.05 (see Table S5 for full results).

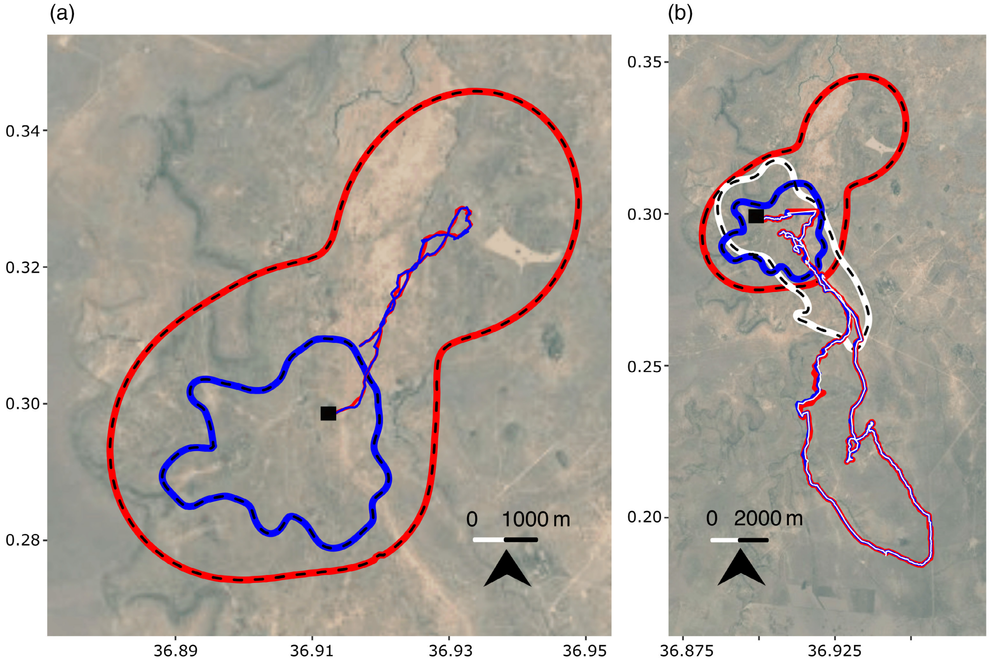

**FIGURE 7** Naturalistic examples on potential information transmission between groups that roost communally. (a) the home ranges from 1 year (12 March 2021–11 March 2022) for two groups that roosted together and subsequently (on 12 March 2022) moved together into an area that only the one group (red) had previously been known to use. (b) The home ranges from 1 year (28 April 2021–23 April 2022) prior to 4 days (24 April 2022–27 April 2022) of joint movements by the three groups, initially starting in an area used previously by only one of the three groups (white). The dashed, coloured polygons represent the 99% home range of each group. The tracks represent the movement of the groups on the day(s) when they travelled outside of the range of at least one participating groups. Track lines width differs for visualization purposes. Black squares indicate the communal roosting sites prior to the first day of joint movement. Figure S4 shows the tracks including all GPS-tagged members of these groups.

members act as public information that is available to neighbouring groups (i.e. inadvertent social information via eavesdropping; Bijleveld et al., 2010).

While our findings support the potential for group-to-group information transmission at communal roosts, it is important to note that this does not necessarily imply information transmission as the primary evolutionary driver of communal roosting. Communal roosts may have evolved for various reasons, with the exchange of information offering an additional, significant benefit (Harel et al., 2017). Communal roosting offers not only some of the benefits mentioned earlier, such as antipredator and thermoregulatory advantages, but also provides breeding and dispersal opportunities (Dwyer et al., 2018; Toth et al., 2015). While evidence is growing that living in multilevel societies, including some of those that share sleeping sites, can benefit individuals through access to public goods (Camerlenghi et al., 2023; Samuni & Surbeck, 2023), revealing the ultimate drivers of behaviours that can only be observed under natural conditions generally requires understanding the long-term consequences associated with their expression (see Cantor et al., 2023 for an example). Thus, long-term studies are essential for placing the results of fine-scale observations, such as in our experimental trials, into a broader context necessary to reveal where the benefits are most strongly expressed (Sheldon et al., 2022). This could, for example, involve linking rates of communal roosting to environmental predictors (e.g. drought or predation pressure), and identifying how within-population variation in survival during key periods correspond with variation in the expression of communal roosting among individuals or groups. Given that the importance of information transmission depends on resource ephemerality and distribution (Kohles et al., 2022), the importance of roosts acting as information centres will depend on how much vulturine guineafowl depend on ephemeral resources, and under what circumstances. For instance, during wet seasons, seeds and grass are widely abundant, and thus, ephemeral and patchy resources might not be a crucial component of their diet. Conversely, during droughts when grass and seeds are scarce, guineafowl groups might rely on the information from neighbouring groups to locate water and specific areas rich in food.

By using a combination of experiments with long-term GPS tracking, we have shed new light on the potential for information transmission to occur between groups that roost communally, and on some of the consequences that this has on inter-group dynamics. Our work illustrates a new dimension of the information centre hypothesis (Ward & Zahavi, 1973), whereby the members of stable social groups might be able to overcome the limitations related to acquiring new information (caused by cohesion limiting the diversity of information acquired among group members) by following other groups to discover new areas and resources. Studies in other multilevel societies, in both mammals (VanderWaal et al., 2014; Whitehead et al., 2012; Wittemyer et al., 2005) and birds

(Camerlenghi et al., 2022; Papageorgiou & Farine, 2021), could explore the potential processes of information transmission between stable social units, as well as their impact on fitness and survival (Foley et al., 2008). This can be achieved by conducting food discovery experiments, widely popular so far in studies of information transmission in birds (Beck et al., 2024; Marzluff et al., 1996; Wright et al., 2003), but also by looking at other sources of information, such as information about risk.

## AUTHOR CONTRIBUTIONS

Danai Papageorgiou, Gabriella Gall and Damien R. Farine conceived the study; Danai Papageorgiou and Damien R. Farine designed the study, Danai Papageorgiou, Wismer Cherono and Brendah Nyaguthii collected the data; Danai Papageorgiou performed the analyses; Damien R. Farine supervised all aspects of the study, Danai Papageorgiou wrote a first draft and all authors contributed to revisions.

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## CONFLICT OF INTEREST STATEMENT

We declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The code to run the analysis and conduct the statistics is available on Figshare https://doi.org/10.6084/m9.figshare.25153304.v1 (Papageorgiou, Cherono, et al., 2024 ). All raw GPS data used in this study are stored on Movebank under the study name Avulturinum_Farine: https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study475851705.

## ETHICAL APPROVAL

The Vulturine Guineafowl Research Project is conducted in collaboration with the National Museums of Kenya and under a Prior Informed Consent and Mutually Agreed Terms agreements with the Kenyan Wildlife Service. Permits for conducting research, capturing birds and marking birds were issued by the Kenyan Wildlife Service (KWS-0016-01-21), the Kenyan National Commission for Science, Technology and Innovation (NACOSTI/P/16/3706/6465), and the National Environmental Management Authority (NEMA Access Permit NEMA/AGR/68/2017). The project was also reviewed and approved by the Ethikrat committee of the Max Planck Society.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1.** Metadata summary of the information transmission experiment for each experimental trial.

**Table S2.** Results of the GLM, with binomial family, on the difference of the number of days between TG2 and TG1 on the discovery of the patch as a function of whether the patch was true or null.

**Table S3.** Results of the GLMM, with binomial family, on the probability of TG1 to be using the food patch area (50 m diameter centred on the food patch) as a function of the Experimental Stage (before, during and after baiting the food patch).

**Table S4.** Results of the GLMM on the probability of TG2 to be using the food patch area (50 m diameter centred on the food patch) as a function of the Experimental Stage (before, during and after baiting the food patch).

**Table S5.** Results of the GLMM on the probability of TG1 and TG2 to associate after 9 AM, as a function of the Experimental Stage.

**Table S6.** Results of the LMM for path directedness as a function of whether or not a focal individual visited the food patch on a given day.

**Table S7.** Results of the LMM for speed as a function of whether or not the focal individual visited the food patch on a given day.

**Figure S1.** Distributions of the distances individuals moved on their roosts between the evening (18:55:10) and the following morning's roosting site location (06:05:10). Individuals moved, at most, very little within their roost on a given night.

**Figure S2.** The distributions of pairwise distances between dyads of vulturine guineafowl at their nightly roosts.

**Figure S3.** Raw data for each of the experimental trials on the distances (in meters) between: TG1—TG2 (black line), TG1—food patch (red line), TG2—food patch (blue line), for each of the 14 days before TG2 discovered the food patch and for each of the 14 days after, at 06:05:10 AM, when birds are supposed to still be roosting.

**Figure S4.** The naturalistic example of Figure 7b in more detail.

**Figure S5.** Group members exhibited higher path directedness and speed (m/s) on days that they visited the patch (1) relative to days that they did not visit the food patch (0).

**Section S1.** Path directedness and speed might be functioning as cues for TG2 to follow TG1 to a food patch.

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