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Activity Budget and Sociality of the Northern Lesser Galago, *Galago senegalensis*

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Abstract

Complex sociality in primates often is argued to have evolved after the appearance of diurnal activity. Studying the behaviour of nocturnal primates is fundamental to understanding the evolutionary origins of primate behaviour and ecology, yet much less is known about the nature of sociality in nocturnal primate species than their diurnal counterparts. We investigated group size, communication, and social interactions in free-ranging, Northern lesser galagos (*Galago senegalensis*) and present an activity budget and assessment of temporal variation in their behaviour. We collected continuous behavioural data using focal follows at three different stages of the night from individuals at Kwakuchinja, Northern Tanzania. We also collected group size data from Northern lesser galagos at Fongoli, Southeastern Senegal, and Lollidaiga Hills Ranch, Central Kenya. We categorised behaviours and, where sample sizes permitted, used Kruskal–Wallis tests to compare the durations of observed behaviours between the morning (pre-dawn), evening (from dusk), and later in the night. We analysed 140 focal follows (31.4 h of continuous behavioural data) and found that the proportion of time spent foraging, inactive, in locomotion, in self-maintenance, and vigilant, varied across the three stages of the night; galagos spent a great deal of their time inactive in the morning and foraging was more prevalent in the evening. Group size at Kwakuchinja was significantly larger than at Fongoli or LHR. Galagos were in groups of two or more in the majority of encounters at Kwakuchinja (55%; $N=76$), rather than alone, but spent most of their nighttime activity alone at Fongoli (79%; $N=185$) and LHR (80%; $N=142$). Overall vocalisation rates were higher in the morning than other times throughout the night, although contact calls were relatively more frequent in the evening than other times. We recorded both affiliative and agonistic social interactions, but these contributed almost nothing to the overall activity budget. Our preliminary investigation into the social structure of Northern lesser galagos suggests that there are population differences in sociality and that overall, they connect more through vocalisations than through direct social interactions, thereby avoiding some of the potential costs

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associated with group-living. This variation in social organization suggests that we have more to learn about the drivers of sociality in nocturnal primates and the nature of their social structure.

Keywords Behavioural ecology · Bushbaby · Consolation behaviour · Galagidae · Strepsirrhine

Introduction

Primates exhibit a range of social systems and structures with considerable inter- and intraspecific variation. Predation risk (van Schaik, 1983) and food availability and distribution (Chapman *et al.*, 2015; Wrangham, 1980) are commonly considered major drivers of group-living (Port *et al.*, 2020), with additional benefits incurred through social support (Alberts, 2019) and thermoregulation (McFarland *et al.*, 2015).

The co-evolution of the change from nocturnal to diurnal activity and solitary to group living in primates (Shultz *et al.*, 2011) supports the idea that gregariousness is a response to increased predation risk during the day. Whilst no one extant species is likely to be a perfect model for our earliest primate ancestors, studying nocturnal primate behaviour can contribute to understanding the ecological drivers of sociality and activity patterns of our earliest primate ancestors, which also were likely small (Soligo & Martin, 2006) and nocturnal (Ross *et al.*, 2007).

Quantifying group size may be the easiest way to measure animal sociality (Reizig *et al.*, 2008), but observations of social behaviour, including conspecific interactions and sleeping associations, enhance our understanding of social relationships within a species (Clark, 1985; Kutsukake, 2009; Poindexter & Nekaris, 2020). Primate social complexity increased over evolutionary time (Opie *et al.*, 2012), but recent studies support the view that social complexity is not limited to highly gregarious, diurnal primate species (Müller & Thalmann, 2000), and although many nocturnal primates do not forage in groups, they maintain social networks during the night through both vocal and olfactory communication (Clark, 1985; Poindexter & Nekaris, 2020).

Activity budgets indirectly measure how primates meet their energetic requirements and are expected to reflect both the ecological environment (e.g., food distribution and quality) and individual characteristics (e.g., age, sex, and reproductive state/condition). Individuals trade-off the demands of foraging, resting, and other daily requirements, leaving the remaining time available for maintaining social relationships (Dunbar *et al.*, 2009). Studying activity budgets can help to identify the underlying mechanisms of relationships between environmental variables and population-level outcomes, such as group size and distribution (Dunbar *et al.*, 2019). Activity budgets can be affected by climatic conditions (Majolo *et al.*, 2013), food availability (Zhou *et al.*, 2007), and anthropogenic disturbance (Scheun *et al.*, 2015, 2019). Temporal variation in activity budgets can occur daily (Naher *et al.*, 2022) or seasonally (Dagosto, 1995; Guo *et al.*, 2007; Gursky, 2000; Zhou *et al.*, 2007).

Researching nocturnal primate sociality is particularly problematic owing to difficulties moving around study areas at night and because behaviours are difficult to perceive in low light levels. Furthermore, many interactions occur via auditory or olfactory signals, which can be challenging to measure (Sterling *et al.*, 2000). These challenges of nocturnal research, along with the widespread use of group size as a proxy for sociality, mean it is not surprising that many researchers do not consider galagids to be highly social compared with other primate groups (Shultz *et al.*, 2011). A review of the social organisation of strepsirrhine primates (suborder Strepsirrhini) revealed that only 7% of species are exclusively solitary living, with an additional 34.9% sometimes solitary living (Agnani *et al.*, 2018). However, Agnani *et al.* (2018) found data on only 43 of 132 species, with no information on social organisation for the other 89, and data on those species is needed for a greater representation of the group's sociality.

Historically, relatively few activity budgets have been published for nocturnal primates (Nekaris & Bearder, 2011). Despite some valuable recent additions to our knowledge of this area (including Al-Razi *et al.*, 2020; Reinhardt *et al.*, 2016; Romdhoni *et al.*, 2022; Scheun *et al.*, 2015), there are still little data compared with diurnal species making this a substantial hurdle in understanding how these animals cope with and respond to changes in their environment (Marshall *et al.*, 2012; Ortega-Ballesteros *et al.*, 2022). For example, activity budgets for galagids are scarce (Nekaris & Bearder, 2011), but the limited available data from long-term studies suggest that there is inter- and intraspecific variation in activity. For example, small-eared greater galagos (*Otolemur garnettii*) spend most of their time (52.3%) traveling, and whilst some populations of Southern lesser galagos (*Galago moholi*) spend a large proportion (63.9%) of their time foraging (see Nekaris & Bearder, 2011 for review and original sources of data), others show much lower levels of foraging activity (Scheun *et al.*, 2015).

The reasons for the variation are not known but may be due to differences in habitat quality (Ménard *et al.*, 2013) and body size (Prates & Bicca-Marques, 2008). Recent studies on slow lorises (*Nycticebus* spp.) suggest that humidity and temperature affect activity budgets (Reinhardt *et al.*, 2016; Rhomdhoni *et al.*, 2022), either directly through changes in energy requirements or indirectly through changes to food availability and distribution. Intraspecific variation in Southern lesser galago activity budgets also is attributed to differences in food availability (Scheun *et al.*, 2015). Individuals living in urban areas with high anthropogenic disturbance were observed in larger groups, and spent less time moving and more time engaging in social interactions compared with rural individuals (Scheun *et al.*, 2015, 2019), most likely due to the former's use of provisioned food.

Many species of galagid sleep communally during the day, with groupings of up to nine individuals recorded in Eastern dwarf galagos (*Paragalago* spp.) and ten individuals in Demidoff's dwarf galagos (*Galagoides demidovii*: Svensson *et al.*, 2018). Researchers have observed grouping when galagids are active, with some individuals spending a large proportion of their time with others. For example, Northern lesser galagos (*Galago senegalensis*) in The Gambia were in groups of at least two in 60% of encounters (Svensson & Bearder, 2013), and one female thick-tailed greater galago (*Otolemur crassicaudatus*)

spent approximately 50% of observed time with others (Harcourt, 1980; Nash & Harcourt, 1986). Rather than solitary animals, some researchers prefer the term “solitary foragers” (Bearder, 1987; Müller, 1999) for galagids, because they may not forage in groups but likely remain connected to social networks through vocal and olfactory communication during the night. With so few studies on wild galagids ($N=65$ or 30.8% of galagid studies identified by Ellison *et al.*, 2021), a broader picture beyond observable groupings is needed to understand their sociality.

Galagids use a mixture of visual, olfactory, and auditory signals when recognising or assessing unfamiliar conspecifics and for communication (Bearder & Doyle, 1974; Nekaris & Bearder, 2011). They have an extensive vocal repertoire, which they use to maintain contact with others, keep distance from rivals to reduce conflict, and for defence, either by alarm calling or group mobbing of potential predators (Bearder, 1999; Bearder *et al.*, 2003; Becker *et al.*, 2003a, b; Bettridge *et al.*, 2019; Nash & Harcourt, 1986; Nekaris & Bearder, 2011; Zimmermann, 1985, 1989). Olfactory communication is important for marking territories and assessing the sex and age of conspecifics (Newell, 1971; Bearder & Doyle, 1974; Charles-Dominique, 1977; Katsir & Crewe, 1980; Clark, 1982a; Clark, 1982b), which is the case for many nocturnal strepsirrhines (Drea *et al.*, 2019).

In addition to varied modes of communication, researchers have observed galagids closely interacting with each other. Captive, thick-tailed greater galagos and both captive and free-ranging Southern lesser galagos are bonded by affiliative social interactions, such as allogrooming (Bearder & Doyle, 1974; Clark, 1985; Ehrlich, 1977) and social play (Clark, 1985; Ehrlich, 1977; Newell, 1971). Both behaviours strengthen bonds between individuals, and allogrooming potentially reduces disease transmitted by ectoparasites (Clark, 1985). Social interactions accounted for 14–30% of nighttime observations on wild Southern lesser galagos, and some individuals followed others for several hours (Bearder & Doyle, 1974; Bearder *et al.*, 2002).

Due to its wide distribution across a variety of habitats, the Northern lesser galago provides an excellent model species in which to investigate the behaviour and ecology of, and potential threats to, African nocturnal primates. There are four recognised subspecies of Northern lesser galago (also known as the “Senegal galago”): *G. s. senegalensis*, *G. s. braccatus*, *G. s. dunni*, and *G. s. soti-kae* (see Svensson *et al.*, 2019 for geographic separation and phenotypic differences). The social behaviour of Northern lesser galagos has not been studied in detail in the wild, but in The Gambia they spend the majority of their time with conspecifics rather than alone (Svensson & Bearder, 2013). There is very little basic information on the behaviour and ecology of Northern lesser galagos, and factors that may contribute to galago activity are poorly understood. Our purpose was to assess temporal variation in activity by establishing their activity budget and to investigate sociality by using group size as a quantitative measure of sociality (Reiczigel *et al.*, 2008), alongside observations of vocal and olfactory communication and social interactions.

Methods

Study Sites

We collected data from three populations: Fongoli, Senegal; Lolldaiga Hills Ranch, Kenya; and Kwakuchinja, Tanzania (Fig. 1a-c).

We collected data over 8 weeks from July to August 2016 and over 3 weeks in July 2017 at Kwakuchinja, Northern Tanzania. Kwakuchinja is a 9.2 km² area, ranging between 962–977 m in altitude within the Kwakuchinja wildlife corridor (“Kwakuchinja” hereafter), located in the Babati District of Northern Tanzania, between Lake Manyara and Tarangire National Parks (Fig. 1c). The subspecies *G. s. sotikae* is present at Kwakuchinja and other primates regularly seen are vervet monkeys (*Chlorocebus pygerythrus*) and olive baboons (*Papio anubis*). The habitat in the study area is mainly woodland dominated by *Vachellia* and *Commiphora* species, with scattered Baobab (*Adansonia digitata*) and palm (*Hyphaene* and *Borassus* spp.) trees.

We also obtained group size data from Fongoli, Southeastern Senegal between March and May 2018 and Lolldaiga Hills Ranch (LHR), Central Kenya in June and July 2018 (Fig. 1). The subspecies present at Fongoli is *G. s. senegalensis*;

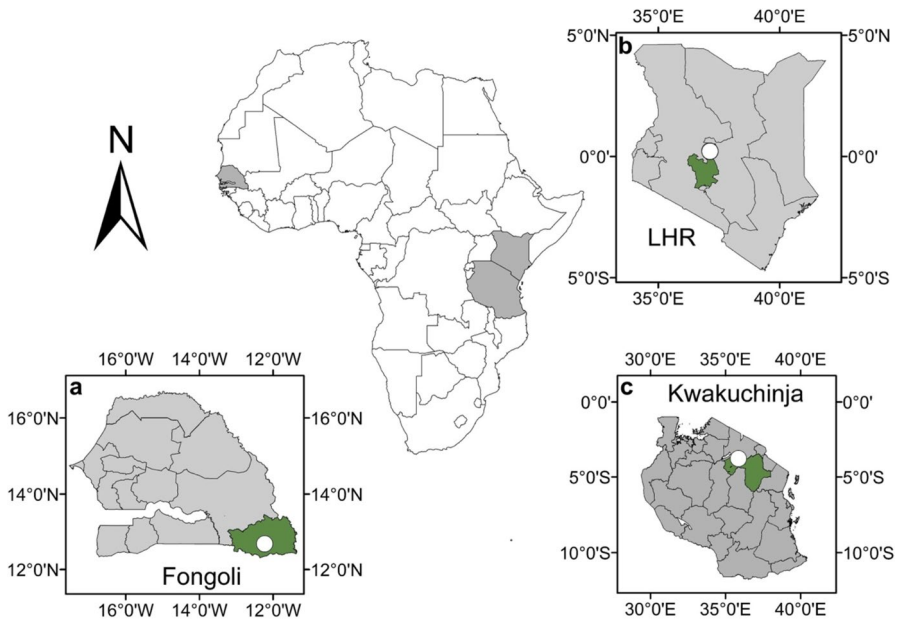


Fig. 1 Study sites of Northern lesser galagos. Green areas are the Kedougou region of Senegal (a), Central province of Kenya (b), and Manyara region of Tanzania (c). White circles indicate the locations of the study sites. ArcGIS® software by Esri was used to create map. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. . Copyright © Esri. All rights reserved. For more information about Esri® software, please visit <http://www.esri.com>

other primates at the site are Western chimpanzees (*Pan troglodytes verus*), green monkeys (*Chlorocebus sabaeus*), patas monkeys (*Erythrocebus patas*), and Guinea baboons (*Papio papio*). Fongoli is situated outside of nationally protected park areas in the Kedougou region of Southeastern Senegal. The Fongoli study site (Fig. 1a) is an area covering more than 81.5 km², where topography ranges from 75–203 m in altitude, and the habitat is mainly primarily woodland, plateau/open grassland, and bamboo woodland, with some agricultural fields and gallery forests (Lindshield *et al.*, 2019; Pruetz, 2006).

Lolldaiga Hills Ranch is a livestock ranch and wildlife conservancy in Central Kenya (Fig. 1b). The subspecies there is *G. s. braccatus*, and the site also is habituated by vervet monkeys and olive baboons. The ranch is 200.1 km², ranges from 1737–2265 m in altitude, and is composed of woodland, bushland, and other habitat types, including forest and savannah. We called the habitat “bushland” when there was the same density of trees and bushes as in woodland habitat, but the majority were < 2 m in height, as opposed to ≥ 2 m in woodland. Many woodland and bushland areas used by galagids were dominated by whistling thorn (*Vachellia drepanolobium*) and some by other species, such as fever trees (*V. xanthophloea*). We conducted our study during the dry season at all three sites.

Data Collection

Group Size

At Kwakuchinja, we collected group size data when carrying out focal follows on foot. We located Northern lesser galagos by using handheld LEDlenser p7.2 torches fitted with red filters (Finley, 1959) and then followed the first individual that we saw for as long as we could. We recorded group size as the focal individual plus the number of other individuals within 20 m if they remained together for more than 50% of the focal follow. Twenty meters is comparable to the distance used when determining association behaviour in pair-living nocturnal primates (Dröscher & Kappeler, 2013 and refs therein). At Fongoli and LHR, we collected group size data during line transect surveys as part of a separate study on Northern lesser galago spatial distribution. We conducted line transect surveys between 19:00 and 23:00 h, on foot and by motorbike at Fongoli and by car in LHR using handheld LEDlenser p7.2 torches. When on foot, we walked at a pace of approximately 2–5 km/hr and searched for galagos scanning all strata from the ground to the top of the tree. When surveying by motorbike, we travelled at approximately 5–10 km/hr with one observer searching with a torch from the passenger seat. At LHR, we surveyed by using a car, driving slowly (5–10 km/hr) along each transect with one observer searching with a torch from each side of the vehicle. When we spotted a galago, we recorded the number of galagos seen and estimated the distance between ourselves and the galago(s). We considered individuals within 20 m of each other to be in the same group.

Activity Budget

At Kwakuchinja only, we conducted focal follows by using handheld LEDlenser p7.2 torches fitted with red filters and collected behavioural data using continuous sampling of focal individuals (Altmann, 1974) at three different stages of the night. Each “evening” (from dusk: 18:30–20:00 h), we visited one known sleeping site to observe the waking behaviour of focal individuals and then followed them for as long as possible. Later in the night (“night” hereafter; 20:30–22:30 h) and in the “morning” (predawn: 05:30–07:00 h), we located and observed galagos across the study site and followed each galago for as long as we could. During morning follows, we aimed to stay with them until they returned to their sleeping sites. We were unable to collect behavioural data throughout the other hours of the night due to logistical difficulties. We split the study area into five grid areas (Ellison *et al.*, 2019) and visited different areas each night to ensure an even sampling effort of the area. Focal follows began when we first spotted a Northern lesser galago and were able to observe their behaviour. We recorded behaviours continuously, visually estimating the distance to any other individuals within 20 m of the focal individual *ad hoc*. Due to the visual restrictions of night work, we recorded all behavioural data via Dictaphone to allow us free hands for torches and navigation.

During the focal follows at Kwakuchinja, we collected behavioural data until the individual was out of sight or had “settled in” to their sleeping position during a morning follow. If the focal individual was out of sight for more than 10 min, we searched for a new focal individual. If the focal individual was in a group and we lost clarity of which one we were focussing on, we chose a new individual from the same group to observe (this could have been the same individual as before). We were not able to collect such detailed behavioural data at Fongoli and LHR due to time constraints and safety restrictions.

The behavioural categories used to record state behaviours can be found in the ethogram (Table I). We predetermined all behaviours by using a short pilot study, except antipredator behaviour (freeze) and social: agonistic (chase and stare), which were not seen until the data collection period. We extended the “vertical clinging and leaping” behaviour described by Napier and Walker (1967) to record different types of saltatory locomotion: “leaps” (within the same tree); “canopy-leaps” (from the canopy of one tree to another); “trunk-leaps” (from the trunk of one tree to another); and “ground-leaps” (across the ground or to a tree from the ground). We recorded the form of locomotion observed, generating counts of event behaviours; this enabled quantification of within tree, between tree, or across the ground locomotion. We also recorded the total bout duration of each type of locomotion.

Vocalisations

We quantified vocalisations by counting instances of audible calls. We classed calls made within 5 s of each other as part of the same “bout.” We analysed vocalisations separately to the activity budgets and recorded all vocalisations heard during

Table 1 Ethogram of behaviours observed in the Northern lesser galago at Kwakuchinja, Tanzania, in June–July of 2016 and 2017

Behaviour category	Behaviour	Description
Antipredator	Freeze	No movement or vocalisations produced for a > 10 s) when near a potential predator (e.g., African civet; <i>Civettictis civetta</i>)
Foraging	Arthropods	Catching insects by leaping, or crawling, and grabbing them. Prey often taken by hand and sometimes by the mouth. Face close to branch with occasional licking was also classed as foraging arthropods, as visibility was sometimes compromised because of low light levels
	Tree exudates (gum)	Licking and eating gum that exudes from tree bark using tooth comb on lower jaw (Bearder & Martin, 1980; Burrows & Smith, 2005)
Inactive	Still	Eyes open in either a standing or sitting position, no movement (the observer has no knowledge of a nearby potential predator)
Locomotion	Crawl	Quadrupedal movement through a tree or on the ground with a minimum of two limbs touching the substrate at any one time
	Leap	Bipedal movement within one tree. Arms held upwards or out in front of individual
	Canopy-leap	Bipedal movement from one tree canopy to another tree without touching the ground
	Ground-leap	Bipedal movement across the ground or to a tree from the ground
	Trunk-leap	Bipedal movement from one tree trunk to another tree without touching the ground
Olfaction	Scent mark	Lowering hindquarters and releasing a few drops of urine (drops not always observed due to visibility) often as individual wriggles forward
	Urine wash	Depositing drops of urine (drops not always observed due to visibility) on to the hands and feet, and then rubbing them together
Self-maintenance	Scratch	Scratching self, often but not always using the back leg
	Self-groom	Using tongue, tooth comb, and grooming claw to clean own fur
	Stretch	Extending at least one limb out from the body
Sleeping	Sleep	No movement and eyes closed
Social: agonistic	Chase	Traveling in the direction of another individual very fast with the other moving away, preceded by a stare
	Stare	Looking directly at another individual face on, on all four limbs, before a chase

Table 1 (continued)

Behaviour category	Behaviour	Description
Social: affiliative	Allogroom	Using tongue, toothcomb, and grooming claw to clean a conspecific's fur. May be directed or received
	Play	Tumbling over others, grabbing others, pulling and pushing others
	Scan environment	Moving head around to check different directions, sometimes assisted by head-cocking (rotating of head in response to novel object; Rogers <i>et al.</i> , 1993)
Vocalisation	Watch observer	Looking towards ≥ 1 observer for more than two s, often assisted by head-cocking
	Honk	Creating an advertising call consisting of a single, low pitched note uttered persistently at a regular tempo (Svensson <i>et al.</i> , 2019)
	"Other" call	Creating a call that differs from a honk

WWFocal follows (not just those of the focal individual, as it was difficult to determine which galago was vocalising). We classed vocalisations as “honks” (Svensson *et al.*, 2019) or “other vocalisations” for any Northern lesser galago vocalisation other than a honk. We split the calls this way, because honks are loud calls that are easily distinguishable from other calls and are considered the main advertising call of the species (Zimmermann, 1985; Svensson & Bearder, 2013) and therefore have a clear social function. Other vocalisations are quieter and harder to distinguish with the limited recording equipment that we had (dictaphone) and include calls that may be triggered by events, such as predator presence, as well as direct interactions with other galagos.

Statistical Analysis

For all data, we used Shapiro–Wilk tests to determine normality. No data were normal (all $P < 0.001$), so we present median and interquartile range (IQR) and used Kruskal–Wallis tests to assess significant differences between ranks of the variables of interest. For any significant results, we used Dunn’s tests for multiple comparisons, which retains the rank sums from the Kruskal–Wallis test (Dunn, 1964) to compare the ranks. All statistical tests were conducted in R version 4.0.5 (R Development Core Team, 2021).

Group Size

We tested for significant differences in the ranks of group size (the first group size recorded at each encounter) across: 1) the three populations; and 2) the three time periods (evening/night/morning) at Kwakuchinja.

Activity Budget

We included all focal follows in the overall activity budget for the evening, night, morning, and total. For additional analysis, we only included focal follows with a duration of ≥ 30 s. Because encounter rates and focal data were not evenly distributed across the three periods, for each focal follow, we combined the duration of behaviours in each category of the ethogram and converted them into a proportion of time spent exhibiting behaviours in each category (not including “sleep” or “out of sight”) to account for the variation in follow/sample duration. We kept “watch observer” in the “vigilance” behaviour category for analysis, because we could not be sure that they were not just looking in our direction rather than at us. We assessed significant differences in the ranks of activity across the three periods of the night.

Locomotion

To investigate the types of movements used at different stages of the night, we totalled the number of times each individual exhibited each form of locomotion

(Table 1). Because of the different lengths of the focal follows, we calculated the proportion of recorded movements for each individual followed for ≥ 30 s and tested for significant differences in the ranks of the types of locomotion across the three periods of the night.

Vocalisations

We plotted the total frequency of bouts of vocalisations (honks and other) heard every half hour during the three sampling periods. The three time periods were not sampled for equal durations, so we also calculated the calling rate for each time period. To do this, we combined all bouts of honks and other vocalisations for each time period and divided this by the total duration of focal follows, including “sleep” and “out of sight,” for each time period. We did not exclude the time the focal galago spent sleeping or out of sight, because we recorded all Northern lesser galago vocalisations heard during focal follows.

Ethical Note

We only used noninvasive methods in this study and remained at least 5 m from the galagos at all times. This research was approved by the Manchester Metropolitan University Ethics Committee, and the research complied with the International Primatological Society’s Code of best practice for field primatology. In Tanzania, we collected data under COSTECH permit no. 2017–300-NA-2017–192 with approval from the Tanzania Wildlife Research Institute (TAWIRI) and Tanzania Immigration (Class C Residency Permit No. RPC1091195). In Senegal, we collected data in collaboration with Dr Jill Pruetz via the Department of Water, Soils, and Forestry in Senegal and in Kenya under NACOSTI permit no. NACOSTI/P/18/77774/22760 with support from the National Museums of Kenya. We adhered to the legal requirements of Tanzania, Senegal, and Kenya at all times.

Results

Group Size

We recorded active Northern lesser galagos in groups of 1–5 individuals at Kwakuchinja (median = 2; IQR = 1–2) and Fongoli (median = 1; IQR = 1–1) and in groups of 1–3 individuals at LHR (median = 1; IQR = 1–1). There was a significant difference in the ranks of group size between the three populations (Kruskal–Wallis test: $H=63.75$, $df=2$, $P<0.001$; Fig. 2). Group size was significantly greater at Kwakuchinja compared with LHR (Dunn’s post hoc tests $z=7.04$, $P<0.001$) and Fongoli ($z=-7.22$, $P<0.001$), and there was no significant difference between the ranks of group size between LHR and Fongoli ($z=0.23$, $P=0.409$). There was no significant difference between the ranks of group size across the three time periods

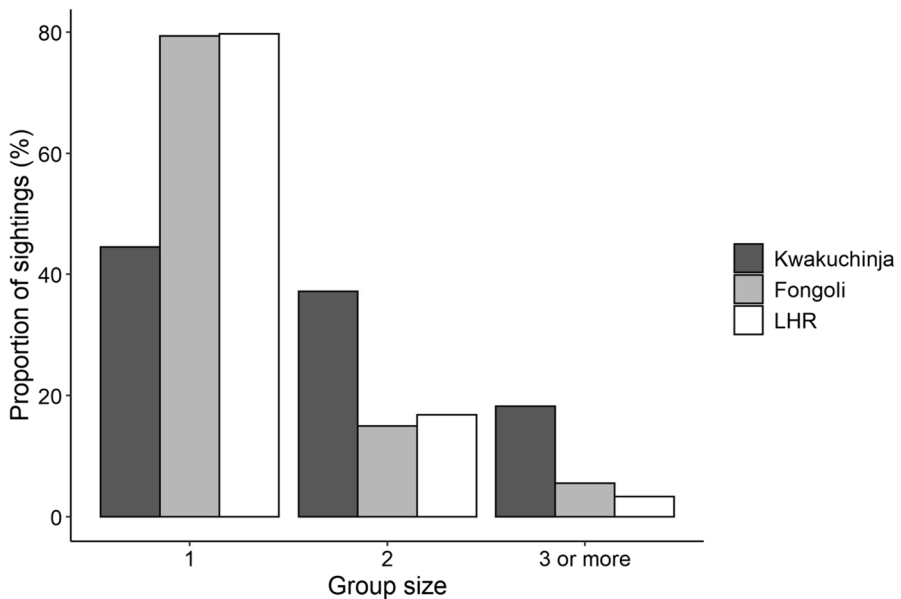


Fig. 2 Group size of active Northern lesser galagos at Kwakuchinja, Tanzania (July–August 2016 and July 2017), Fongoli in Senegal (March–May 2018), and Lolldaiga Hills Ranch (LHR) in Kenya (June–July 2018).

at Kwakuchinja (Kruskal–Wallis test: $H=3.51$, $df=2$, $P=0.173$; morning: 2 ± 1 individuals; evening: 2 ± 1 individuals; night: 2 ± 1 individuals).

Activity Budget

In total, we carried out 180 focal follows at Kwakuchinja. Of these, 140 had a duration ≥ 30 s (median = 6.4 min; IQR = 2.1–19.1 min; 31.4 h of continuous behavioural observations in total) and therefore were included in the analysis.

The most common behaviours Northern lesser galagos exhibited were: vigilance (median 38%; IQR 8–57%); inactive (median 20%; IQR 4–36%); and locomotion (median 16%; IQR 6–32%); Figs. 3, 4; Table II). Of the vigilance behaviours, the majority were “scan environment” (median 26%; IQR 4–49%) rather than “watch observer” (median 0.0%; IQR 0.0–6%).

Galagos spent significantly more time inactive in the morning than the evening (Table II: Dunn’s post hoc test: $z=-4.09$, $P<0.001$) or the night ($z=4.60$, $P<0.001$). They foraged significantly more in the evening compared with the morning ($z=4.42$, $P<0.001$) or night ($z=2.51$, $P=0.006$) and significantly more in the night than the morning ($z=-2.33$, $P=0.010$). Galagos locomoted significantly more in the night than the morning ($z=-2.00$, $P=0.023$) and the evening ($z=-3.79$, $P<0.001$). Galagos spent significantly more time showing self-maintenance behaviours in the evening than the morning ($z=4.71$, $P<0.001$) or

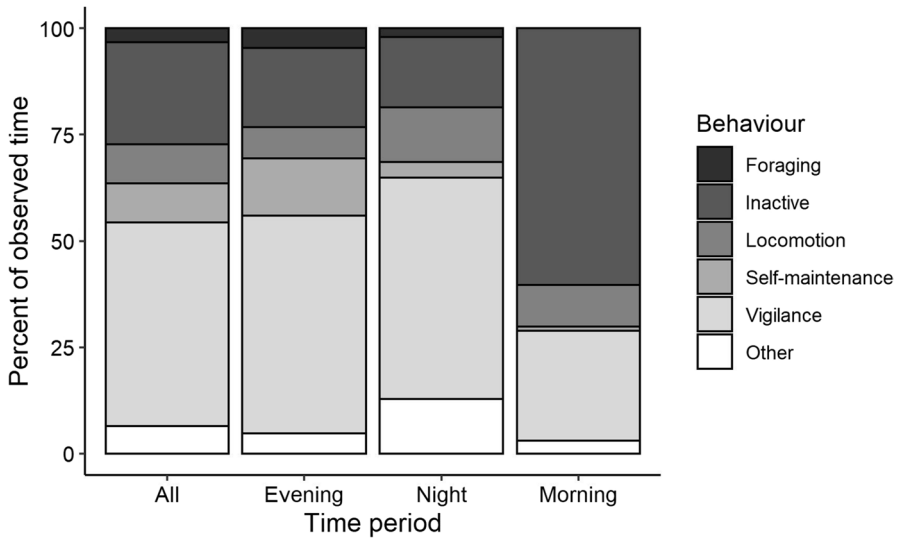


Fig. 3 The percentage of observed time Northern lesser galagos at Kwakuchinja, Tanzania, was observed in each behaviour category in July–August 2016 and July 2017. “All” shows the mean across the three time periods. The category “other” contains all other behaviours (antipredator; social: affiliative; social: agonistic; territorial; and unknown). Time spent sleeping or out of sight was not included

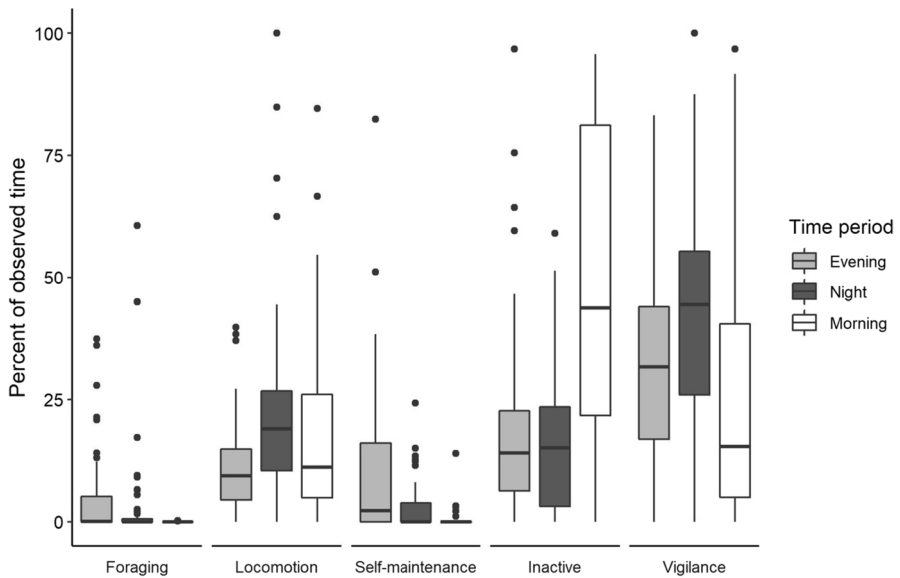


Fig. 4 Differences in median and IQR of percent of observed time Northern lesser galagos spent showing each of the above behaviours in the morning, evening, and night in June–July 2016 and July 2017 in Kwakuchinja, Tanzania. The black dots represent outliers, which remained in the analysis, and the whiskers represent $1.5 \times \text{IQR}$

Table II Summary of the percent time (%) Northern lesser galagos spent in each type of activity, and the percent (%) of observed movements that were each type of locomotion, when not sleeping at Kwakuchinja, Tanzania, in June–July 2016 and July 2017

Behaviour	Evening			Night			Morning			H	P
	Median	IQR	Range	Median	IQR	Range	Median	IQR	range		
<i>Activity</i>											
Antipredator	0.0	0.0–0.0	0.0–0.0	0.0	0.0–0.0	0.0–21.1	0.0	0.0–0.0	0.0–0.0	NA	NA
Foraging	0.0	0.0–5.3	0.0–37.4	0.0	0.0–0.7	0.0–60.6	0.0	0.0–0.0	0.0–0.2	19.67	<0.001***
Inactive	14.0	6.2–23.0	0.0–96.8	15.1	2.8–24.4	0.0–59.1	43.7	21.0–82.4	0.0–95.7	23.94	<0.001***
Locomotion	9.4	4.3–15.1	0.0–39.8	19.0	10.3–27.3	0.0–100.0	11.1	4.3–26.4	0.0–84.6	14.6	<0.001***
Olfaction	0.0	0.0–0.0	0.0–3.8	0.0	0.0–0.0	0.0–12.9	0.0	0.0–0.0	0.0–6.7	NA	NA
Self-maintenance	2.2	0.0–16.1	0.0–82.4	0.0	0.0–4.1	0.0–24.2	0.0	0.0–0.0	0.0–14.0	22.55	<0.001***
Social: agonistic	0.0	0.0–0.0	0.0–0.0	0.0	0.0–0.0	0.0–12.3	0.0	0.0–0.0	0.0–0.0	NA	NA
Social: affiliative	0.0	0.0–0.0	0.0–24.4	0.0	0.0–0.0	0.0–17.7	0.0	0.0–0.0	0.0–27.4	NA	NA
Vigilance	50.9	36.5–65.0	2.1–86.1	47.3	33.3–57.1	0.0–100.0	16.4	5.4–53.1	0.0–100.0	13.32	0.001**
Unknown	0.0	0.0–0.8	0.0–26.6	0.0	0.0–7.1	0.0–90.0	0.0	0.0–0.0	0.0–16.4	NA	NA
<i>Locomotion type</i>											
Canopy-leap	5.0	2.0–10.0	0.0–30.4	0.0	0.0–2.5	0.0–21.2	5.2	0.0–10.8	0.0–38.1	15.08	<0.001***
Crawl	24.6	19.4–34.5	8.3–100.0	27.0	18.2–35.3	0.0–80.0	25.0	14.3–40.0	0.0–100.0	0.01	0.993
Ground-leap	0.0	0.0–1.2	0.0–36.0	0.0	0.0–0.0	0.0–18.8	0.0	0.0–0.0	0.0–83.3	5.93	0.052
Leap	63.5	46.8–69.0	0.0–91.7	70.0	60.4–76.9	20.0–100.0	61.9	40.0–72.7	0.0–100.0	8.01	0.018*
Trunk-leap	0.0	0.0–0.9	0.0–17.2	0.0	0.0–0.0	0.0–11.8	0.0	0.0–0.0	0.0–2.6	4.23	0.121

IQR interquartile range, *H* Kruskal–Wallis test statistic, (2 degrees of freedom) between the ranks of behaviour for each time period. *Significant at the 0.05 level; **Significant at the 0.01 level; ***Significant at the 0.001 level.

night ($z=2.87$, $P=0.002$), and significantly more in the night than the morning ($z=-2.30$, $P=0.011$). Galagos were significantly less vigilant in the morning compared with the evening ($z=3.54$, $P<0.001$) and night ($z=-2.82$, $P=0.002$).

Locomotion

Northern lesser galagos leapt (within tree) and crawled more than any other type of locomotion (Table II). The use of some types of locomotion in the night varied from that used during the morning and evening (Table II). Galagos moved between trees (canopy-leapt) significantly less in the night than the morning ($z=2.65$, $P=0.004$) or evening ($z=3.72$, $P<0.001$) but they moved within-tree (leapt) significantly more in the night than the morning ($z=-2.46$, $P=0.007$) and evening ($z=-2.34$, $P=0.010$).

Vocalisations

We recorded a total of 21 honk bouts, ranging in length from one to 53 individual honks (median 10; IQR 4–21); we recorded 32 instances of other vocalisations (Fig. 5). Both overall (4.2/hr) and honk (0.9/hr) calling rate are higher in the morning than the other two periods (Table III), but we did not have enough data to test this statistically. The ratio of honk bouts to other calls differs between time periods, with relatively more honks in the evening than in the night or morning.

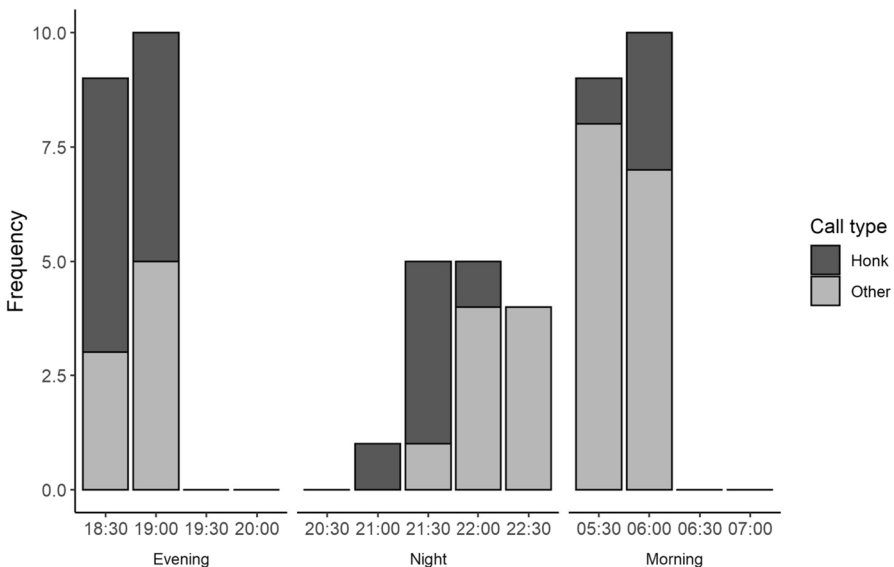


Fig. 5 Total frequency of bouts of honks and bouts of other calls made by Northern lesser galagos each half-hour (e.g., “18:30”=18:30–18:59) at Kwakuchinja, Tanzania in June–August 2016 and July 2017. We did not collect any data between the hours of 20:00–20:30 and 22:30–05:00 or during the day (07:00–18:30). The three time periods were not sampled equally.

Table III Summary of Northern lesser galago vocalisations recorded at Kwakachinja, Tanzania, in June–August 2016 and July 2017, over a total of 31.4 h of data collection

	Evening	Night	Morning
Honk bouts (rate/hr)	0.6	0.6	0.9
Other calls (rate/hr)	0.5	0.9	3.3
Overall rate (calls/hr)	1.1	2.0	4.2
Ratio honks to other	1.4:1	0.7:1	0.3:1

Qualitative Observations

We observed one form of affiliative behaviour that strongly resembles consolation, or post-conflict third party affiliation behaviour, i.e., an empathy-driven act by the consoler following an aggressive or stressful encounter with a different individual (de Waal & van Roosmalen, 1979; Preston & de Waal, 2002). The observation happened on 12 July 2017 during a waxing crescent moon and usual temperature of around 18 °C for the time of the night. At 22:30 h, we were following one individual who was moving and foraging with two others. The focal individual moved a few metres away from the other two and began leaping within a bush close to the ground. An African civet (*Civettictis civetta*) appeared approximately 4 m away and stopped. It sat upright and looked in the direction of the galago. The galago crawled for 20 s and then froze still with one arm close to the body and the other stretched out on the branch for 2 min 34 s. The civet then moved off and out of sight, and the galago then leapt in the other direction, back to where the other two individuals were seen. After 1 min and 44 s, the galago began producing frequent “attention or alarm” calls (“tjong”: Zimmermann, 1989; Anderson *et al.*, 2000; Schneiderová *et al.*, 2016) every few seconds. Around 2 min after the vocalisations started, the galago defecated a loose stool. The vocalisations continued intermittently, and 12 min later, another individual was spotted near the focal individual. Just over 1 min later, a third individual was spotted within a few metres of the other two, and 3 min later, the vocalisations stopped. The three individuals engaged in reciprocal allogrooming with each other on and off over a period of 2 min 30 s. It was not possible to determine the focal individual after that, but two galagos moved off together around 1 min later.

Discussion

Activity Budget

The activity budget for free-ranging Northern lesser galagos we present shows that their activity varied across the night, similar to the slender loris (*Loris lydekkerianus*: Nekaris, 2001). In the evening, when galagos woke, they spent a large proportion of their time on self-maintenance, canopy-leaping between trees, foraging, and being vigilant. Later in the night, galagos moved more within trees than between

them and spent a large proportion of their time foraging, vigilant, and on self-maintenance. In the morning, they spent time canopy-leaping back to their sleeping sites and were inactive for a large proportion of time when “settled” in their sleeping sites.

Northern lesser galagos, along with some other species of galagid, are known for their characteristic saltatory (leaping) locomotion (Aerts, 1998; Crompton & Sellers, 2007; Crompton *et al.*, 1993; Huq *et al.*, 2015, 2018; Napier & Walker, 1967; Nekaris & Bearder, 2011; Sellers, 1996; Shapiro, 2007). By categorising their leaping locomotion into leaps (within one tree), trunk-leaps (from the trunk of one tree to a new tree), ground-leaps (across the ground or to a tree from the ground), and canopy-leaps (from one tree canopy to a new tree), we were able to learn more about how galagos move through their environment. Overall, locomotion was more prevalent at night than morning or evening. Specifically, galagos leapt within trees significantly more at night than in the morning or evening, possibly because they were foraging in trees. Canopy-leaping between trees was significantly more prevalent in the morning and evening than the night, likely because galagos were moving swiftly to and from their sleeping sites. We observed galagos canopy-leaping between trees more than 6 m apart on several occasions, making them very difficult to follow and supporting the idea that leaping evolved for predator avoidance (Crompton & Sellers, 2007). Galagos ground-leapt between structures (most often a tree or bush) over short distances and spent very little time on the floor.

Foraging behaviour has been a focus of a number of studies on galagids (Bearder & Martin, 1980; Butynski & de Jong, 2004; Clark, 1985; Harcourt, 1986; Nash & Whitten, 1989; Scheun *et al.*, 2014). At Kwakuchinja, the most important time for Northern lesser galagos to forage was the evening, soon after leaving sleeping sites. Unfortunately, we did not collect enough data to study their diet in detail, but we observed them eating tree exudates, or “gum” (Bearder & Martin, 1980; Butynski & de Jong, 2004; Clark, 1985; Génin *et al.*, 2016; Nash & Whitten, 1989; Nekaris & Bearder, 2011; Scheun *et al.*, 2014; Svensson & Bearder, 2013), and arthropods (Butynski & de Jong, 2004; Clark, 1985; Génin *et al.*, 2016; Nash & Whitten, 1989; Nekaris & Bearder, 2011; Scheun *et al.*, 2014; Svensson & Bearder, 2013). On some occasions, individuals used our torchlight to their advantage and caught flying insects attracted to the beam of the light. Unlike some other species (Nekaris & Bearder, 2011; Scheun *et al.*, 2014) and a population of Northern lesser galagos in The Gambia (Svensson & Bearder, 2013), we did not observe galagos eating fruit (Nash & Whitten, 1989). However, our study was limited to the dry season (June to August), and their diet may change throughout the year (Harcourt, 1986) perhaps with the addition of available fruit.

Vigilance behaviours are of great importance to Northern lesser galagos, comprising a large proportion of the activity budgets in our study. They were less vigilant during the morning observations compared with the evening and night, but they spent more time inactive (no movement but eyes open) in the morning, usually before sleeping. This may indicate that, at Kwakachinja, galagos feel secure when in their sleeping sites in the morning but remain alert for a short while before sleep. Although we do not have data on galagos at their sleeping sites at LHR or Fongoli, it is likely that those populations also stay vigilant for some time before sleeping,

especially at Fongoli where the risk of predation at sleeping sites is so high (Pruetz *et al.*, 2015). We know very little about galagid predation, but potential predators of Northern lesser galagos are aerial (e.g., birds of prey, such as African wood owls, *Strix woodfordii*: Rosti *et al.*, 2020), terrestrial (e.g., small carnivores, such as caracals, *Caracal caracal*: Cuzzo *et al.*, 2021), and other primates: Butynski, 1982), and scansorial animals (e.g., snakes: Burnham *et al.*, 2012). Because predators approach from above, below, and within trees, it is understandable why galagids spend so long being vigilant and, in particular, scanning the environment. Although we remained at least 5 m away from our focal animal at all times, our presence may have increased the time galagids spent being vigilant, but the majority of vigilance behaviours were “scan environment” rather than looking directly at us.

Self-maintenance behaviours increase the well-being of the individual and keep the body in a good condition (Bolhuis & Giraldeau, 2005). In our study, these included self-grooming, stretching, and scratching. We observed the majority of these behaviours in the evening, shortly after galagos woke but before they left their sleeping sites. Although galagos spent a significantly greater proportion of time on self-maintenance during the evening than the morning or night, they also spent significantly less time on self-maintenance in the morning than the night. As previously mentioned, the priority for galagos in the hour before dawn appeared to be to return to their sleeping sites and to settle down to sleep, not for self-maintenance or any other behaviour.

Galagid Sociality

Characterising animal sociality is most easily done by quantifying group size (Reiczigel *et al.*, 2008). We therefore used group size as one measure of sociality. Average group sizes were similar to other populations of species of *Galago* (Poindexter & Nekaris, 2020). Group size was significantly greater at Kwakuchinja (and did not vary across the night) than at Fongoli and LHR, where the majority of observations were of lone individuals.

There are several potential factors affecting group size (Clutton-Brock & Harvey, 1977). One possibility is that the distribution of resources, such as tree gum at Kwakuchinja, might encourage grouping. Small-eared greater galagos, whose diet contains a greater arthropod component than thick-tailed greater galagos, are less often observed in groups, possibly due to insect foraging being more of a solitary activity (Nash & Harcourt, 1986). Alternatively, food resources could be more abundant at Kwakuchinja and encourage grouping; the availability of resources to urban Southern lesser galagos was positively associated with social group formation (Scheun *et al.*, 2019). The fact that this study population spent very little of their time foraging would support the idea that food resources are abundant here; however, without detailed data on the diet composition or resource distribution, we are unable to determine which factor(s) are driving this behaviour in this population.

Our methods for collecting group size data could have influenced the results. At Fongoli and LHR, we relied on transects rather than focal follows to collect group size data and therefore were not in as close proximity to galagos as we

were in Kwakuchinja. This could have affected our ability to detect other galagos within 20 m of the one spotted. It also is possible that although vehicle noise is not uncommon at both Fongoli and LHR, galagos moved away when hearing our vehicle approaching. However, motorbikes also are fairly common at Kwakuchinja, and although we did not use them for this research, we did not notice galagos moving away from any passing motorbikes.

Vocalisations are an important social behaviour in galagids, with many using calls to keep or regain contact with others (Bearder *et al.*, 2003; Becker *et al.*, 2003a, b; Zimmermann, 1985). Our data show that Northern lesser galagos called at a higher rate in the morning than at any other time and that both honks and other calls increase during this time. The increase in honks (otherwise known as loud calls) supports findings from Northern lesser galagos in Senegal (Schneiderová *et al.*, 2020) and from small-eared greater galagos in Tanzania and Kenya (Bettridge *et al.*, 2019), which both showed a peak in loud calls in the period before sunrise. Loud calls are thought to be used for territorial spacing and long-distance communication (Bearder *et al.*, 2003). Their increased use in the morning has been suggested to indicate that they could play a role in coordinating social cohesion when returning to sleeping sites (Bettridge *et al.*, 2019; Schneiderová *et al.*, 2020). Their use throughout the night (although at a lower rate) suggests that their function is broader than only to coordinate sleeping groups. The nighttime calls may be used to keep contact with others while feeding separately and/or for maintaining adult-infant contact (Bearder *et al.*, 2003). In the evening, galagos often were already with others and usually moved off in the same direction and may not have needed to call to keep contact during that time. We also found a considerable difference in the length of honk bouts, and this might be related to their use across a range of situations. Future focal follows could be enhanced by using good-quality, audio-recording equipment to allow better identification and bioacoustics analysis of calls as well as the behavioural context in which they are given.

In addition to vocalisations, olfactory communication is common in nocturnal strepsirrhines and allows communication without being in close proximity (Drea *et al.*, 2019; Nekaris & Bearder, 2011). We observed scent-marking and urine-washing at each stage of the night, consistent with, but less frequently than, Allen's galagos (*Sciurocheirus alleni*) in Gabon (Charles-Dominique, 1977). Although scent-marking and urine-washing behaviours were not regularly observed in this study, the chemicals would likely persist allowing information to be conveyed to others over time. The ability to connect to other individuals through olfactory signals may be extremely important in Northern lesser galago sociality but is very difficult to measure.

Although agonistic encounters are fairly common in studies on captive galagids (e.g., thick-tailed greater galagos: Newell, 1971; Roberts, 1971), we saw few such encounters and this is consistent with research on other free-ranging populations (e.g., Southern lesser galagos: Bearder & Doyle, 1974). The reasons for the agonistic encounters are unknown but could have been due to competition for resources (Scheun *et al.*, 2015). The majority of social interactions recorded were affiliative, and although they only comprised a small proportion of the total time budgets, we observed play and allogrooming on many occasions involving both adults and

infants, mostly when at sleeping sites (Nekaris & Bearder, 2011). To the best of our knowledge, these behaviours have not been recorded in wild Northern lesser galagos before but have been seen in captive populations during early development (Nash, 2003; Zimmermann, 1989). Play and allogrooming also have been observed in free-ranging populations of Southern lesser galagos (Bearder & Doyle, 1974) and thick-tailed greater galagos (Clark, 1985) but were not specifically recorded at sleeping sites.

In addition to the above social behaviours, we recorded one observation that resembled consolation behaviour. The behaviour observed was in response to an encounter with a potential predator (an African civet). The individual seemed extremely distressed, producing frequent “attention/alarm” calls (“tjong”: Zimmermann, 1989; Anderson *et al.*, 2000; Schneiderová *et al.*, 2016), and an uninvolved galago appeared and groomed the victim until the vocalisations stopped. Consolation is a very complex behaviour once thought to be unique to apes (Preston & de Waal, 2002). It has more recently been observed in other primates in captivity (e.g., stumptailed macaques, *Macaca arctoides*: Palagi *et al.*, 2004; Hamadryas baboons, *Papio hamadryas*: Butovskaya *et al.*, 2015), corvids (Seed *et al.*, 2007; Fraser & Bugnyar, 2010), and canids (Cools *et al.*, 2008). Consolation behaviour reduces stress in chimpanzees (Fraser *et al.*, 2008), and observations over time revealed that a higher tendency for chimpanzees to show this behaviour predicts better social integration (Webb *et al.*, 2017). More observations are needed to determine how common the behaviour is, but our observation may indicate that galagids interact socially in a highly developed way.

Galagos were not always close to others during their active hours. However, group size alone should not define the social complexity of these animals (Clark, 1985; Poindexter & Nekaris, 2020). Our study supports the possibility that galagids are connected through networks of vocal and olfactory communication and benefit from mostly affiliative social interactions, whilst avoiding some of the potential costs associated with group living, such as competition for resources and being detected by predators more easily (Clark, 1985).

Future Research and Conclusion

Studying nocturnal primate behaviour is challenging due to low light levels and the arboreal nature of the animals, and continuously observing behaviour is particularly difficult. It is understandable that behavioural studies on in situ populations of nocturnal primates often use instantaneous sampling (Bearder *et al.*, 2006; Nekaris, 2001, 2003; Pullen *et al.*, 2000; Starr *et al.*, 2012). Continuous observations of nocturnal primates may be more feasible in captivity (Fuller *et al.*, 2016), but successfully conducted continuous focal follows on wild nocturnal primates (sportive lemurs, *Lepilemur* spp.: Rasoloharijaona *et al.*, 2006) are important in providing greater understanding of how these animals spend their time.

Our study is limited in that we were not able to follow galagos for a longer period of time or compare between the different seasons (Diete *et al.*, 2017). We also did not collect data between 22:30–05:00 h, and it is possible that we missed social

behaviours during this time. If feasible, future research on galagid activity should take all hours of darkness into account. Similarly, we recommend collecting auditory data in equal detail in further behavioural studies. The influence of the level of moonlight on Northern lesser galago behaviour would be another important future avenue of study, as moonlight is associated with foraging activity in Mysore slender lorises (*Loris lydekkerianus lydekkerianus*), travel speed and night range length of male Southern lesser galagos (Bearder *et al.*, 2002), and foraging behaviour and predator avoidance in spectral tarsiers (*Tarsius spectrum*: Gursky, 2003).

Nocturnal primates are a socially diverse group of animals with interspecific variation in behaviour and ecology. We presented temporal variation in the activity of wild Northern lesser galagos and observed behaviours not yet documented in this species in the wild, such as play, allogrooming, antipredator, and territorial behaviour. The social interactions and different types of communication noted are crucial for understanding Northern lesser galago sociality and with more data could reveal the extent to which they are connected by networks. These results add to our understanding of Northern lesser galago activity and can form a basis for comparative studies to aid understanding of extant nocturnal primates more broadly, as well as how some of the earliest primate species may have lived.

Data Availability The datasets analysed during the current study available from the first author on reasonable request. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

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