Behaviour and ecology of the Northern lesser galago (*Galago senegalensis*)

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Abstract

Galagids (family: Galagidae; suborder: Strepsirrhini) are small nocturnal primates distributed across sub-Saharan Africa. Knowledge on their behaviour and ecology is important for understanding our early primate ancestors, who were also most likely small and nocturnal. Data on the behaviour and ecology of many galagid species is lacking but urgently needed for their effective conservation in the face of anthropogenic threats. The Northern lesser galago (*Galago senegalensis*) is the most widely distributed of all the galagids, occupying a range of habitats, and is therefore a particularly suitable model species for the study of the behaviour and ecology of galagids.

I researched Northern lesser galagos from January 2016 to January 2022. For my thesis I had the following aims: highlight taxonomic and geographic biases in the study of all galagids; investigate Northern lesser galago activity and social behaviour; determine factors that contribute to Northern lesser galago sleeping ecology; assess the response of Northern lesser galagos to systematic predation from Western chimpanzees (*Pan troglodytes verus*); and create a non-invasive method to retrieve DNA from wild galagids. I used a range of methods for data collection: systematic search of the literature, continuous behavioural observations, vegetation surveys, line transect surveys, and non-invasive sampling; and analysis: hypothesis testing, negative binomial regression, logistic regression, text mining, random forest classification analysis, distance sampling, density surface modelling, and DNA extraction and amplification.

My systematic review in Chapter 2 revealed that, between 1971 and 2020, most research was on larger-bodied species and those with larger geographic ranges, and study sites were in cooler and more accessible areas. The behavioural study in Chapter 3 found that, at Kwakuchinja in Tanzania, Northern lesser galago behaviour varied across different periods of the night, with foraging being most prevalent in the evening (post-dusk). The use of both vocal and olfactory social communication, observations of complex social behaviours, and galagos at Kwakuchinja being in groups in the majority of observations, suggests that Northern lesser galagos may have a higher degree of sociality than previously thought. The study of Northern lesser galago sleeping ecology at Kwakuchinja in Chapter 4 revealed that sleeping sites allow galagids to remain hidden but able to escape easily from opportunistic predators, especially aerial predators, and remain cool when sleeping during the day. Chapter 5 found that, at Fongoli in Senegal, Northern lesser galagos sleep inside trees with several escape routes from chimpanzees, which systematically hunt them at their sleeping sites. When active, galagos at Fongoli avoid areas frequently used by chimpanzees. Finally, Chapter 6 describes a novel non-invasive technique that can be used to obtain samples from galagids for genetic analysis.

This thesis contributes significantly to the understanding of Northern lesser galago behaviour and ecology, revealing how they respond to the different pressures acting on populations across their range. The knowledge on Northern lesser galago microhabitat requirements and activity will be invaluable in future behavioural research and for implementing effective conservation strategies. For the study of all galagids, the review acts as a guide to ensure that future research addresses the uneven representation of species and study sites. The novel non-invasive genetic sampling method presents a way to study the genetics of galagids and other nocturnal, arboreal or cryptic animals, with a plethora of applications.

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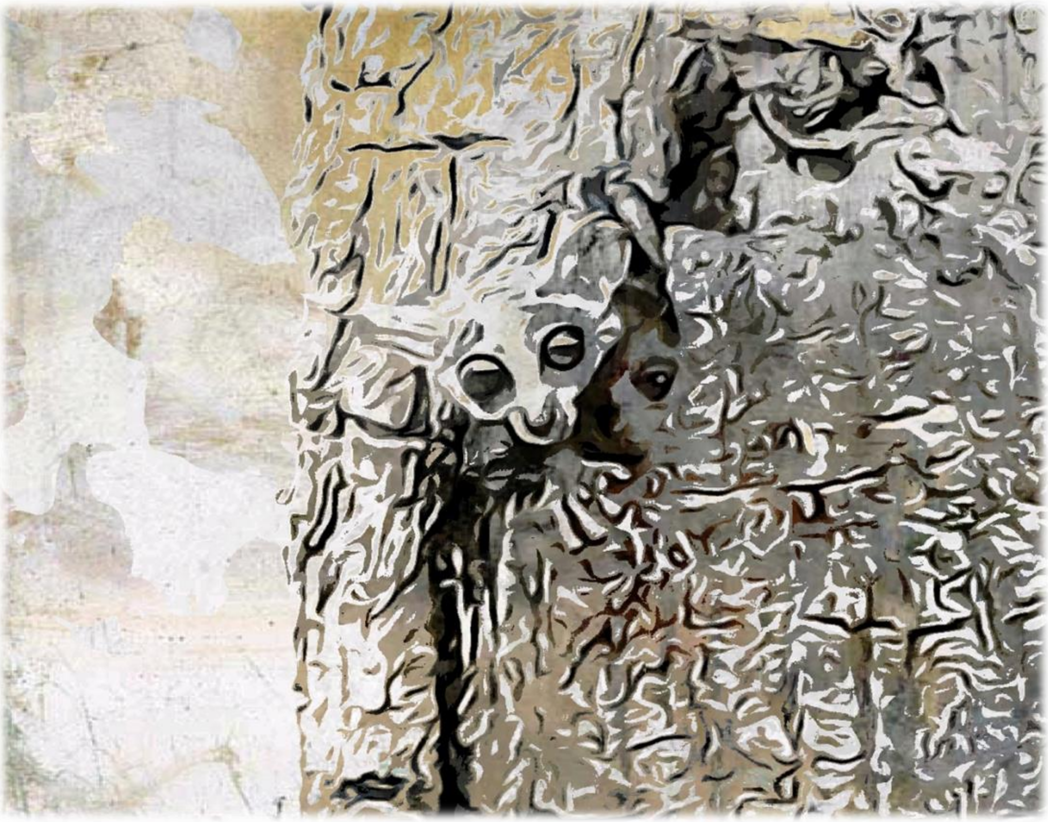
Chapter 1. Introduction



Galagids, or ‘bushbabies’, (family: Galagidae, or ‘Galaginae’; suborder: Strepsirrhini) are small, arboreal, nocturnal primates distributed throughout sub-Saharan Africa. The study of galagid behaviour and ecology can provide insights into the evolution of primates and contribute to understanding our earliest primate ancestors, which, like galagids, were likely small (Soligo and Martin, 2006) and nocturnal (Ross et al., 2007). The current knowledge on the behaviour and ecology of each species of galagid is either incomplete or non-existent, but where comparisons are possible there is huge interspecific variation (Bearder et al., 2003; Nekaris and Bearder, 2011). A recent review found that the Galagidae family is the primate family with the lowest percent of species threatened with extinction, but predicted that they will follow a similar pattern to Malagasy lemurs, where species once thought to be widespread were revealed to be highly threatened (Estrada et al., 2017). Addressing gaps in the literature on galagid behaviour and ecology, and understanding the requirements of each species, is critical to their effective conservation.

1.1 Taxonomy and evolution

Traditionally, galagids were classified by the analysis of museum specimens, which largely involved comparing the morphology of each species (Bearder, 1999). This often led to several species being misclassified as one, until differences in vocalisations and other elements of behaviour became apparent from field studies (e.g.: Honess, 1996; Ambrose, 2003) and subsequent taxonomic revisions were made (Grubb et al., 2003). I follow the taxonomy of Svensson et al. (2018), who, in addition to the species recognised by Nekaris (2013), used the genus name ‘*Paragalago*’ for the eastern clade of dwarf galagids (Masters et al., 2017), and included *Sciurocheirus makandensis* (Svensson et al., 2020) and the recently described *Galagoides kumbirensis* (Svensson et al., 2017). Consistent with Svensson et al. (2018), I hereafter use the abbreviation ‘*G.*’ for the genus *Galago* and ‘*Gd.*’ for *Galagoides* to avoid confusion. I therefore recognise the following 20 extant species of galagid: Southern needle-clawed galago, *Euoticus elegantulus*; Northern needle-clawed galago, *E. pallidus*; Somali lesser galago, *Galago gallarum*; Spectacled lesser galago, *G. matschiei*; Southern lesser galago, *G. moholi*; Northern lesser galago, *G. senegalensis*; Demidoff’s dwarf galago, *Galagoides* *demidovii*; Angola dwarf galago, *Gd*. *kumbirensis*; Thomas's dwarf galago, *Gd*. *thomasi*; large-eared greater galago, *Otolemur crassicaudatus*; small-eared greater galago, *O*. *garnettii*; Kenya coast galago, *Paragalago cocos*; Mozambique dwarf galago, *P*. *granti*; Mountain dwarf galago, *P*. *orinus*; Rondo dwarf galago, *P*. *rondoensis*; Zanzibar dwarf galago, *P*. *zanzibaricus*; Allen's galago, *Sciurocheirus alleni*; Cross River galago, *S*. *cameronensis*; Gabon squirrel galago, *S*. *gabonensis;* and Makandé squirrel galago, *S. makandensis*.

Throughout this thesis I refer to 'galagid' or 'galagids' for individual(s) of any species within the Galagidae (or 'Galaginae') family, and 'galago' or 'galagos' for individual(s) of a particular species.

1.2 Activity and social behaviour

Galagids are nocturnal animals that generally leave their sleeping sites after sunset to return before sunrise (Bearder et al., 2003; Nekaris and Bearder, 2011). Detailed behavioural studies are unavailable for many species and ethograms used to study behaviour are often broad to allow application to multiple species (e.g. Fuller et al., 2016). Activity budgets for galagids are scarce, but the available data on long-term studies suggests that there is interspecific variation in activity. For example, small-eared greater galagos (*Otolemur garnettii*) spend the majority of their time traveling and Southern lesser galagos (*Galago moholi*) spend a large proportion of their time foraging (Nekaris and Bearder, 2011). The reasons for the variation are not known, but differences in diet and food distribution could be a factor. Around half of Southern lesser galagos' diet is comprised of tree gum, but half of small-eared greater galagos' food intake is fruit (Nekaris and Bearder, 2011), and longer periods of travel may be required to locate available fruit compared to tree gum. There are likely other factors contributing to variation in activity, such as habitat preferences and predation pressure.

Identifying the social system of nocturnal primates is challenging, but galagids are thought to have multi-female/single-male and promiscuous social systems (Poindexter and Nekaris, 2020). Galagids are often referred to as 'solitary foragers' (Bearder, 1987, in Müller et al., 1999), but maintain social networks through infrequent social interactions, and vocal and olfactory communication

(Clark, 1985). However, recent studies have challenged the view that they spend their active hours alone; for many species, 'social' time (the proportion of active time individuals were in close proximity to others) comprises a significant proportion of their time budgets (Nekaris and Bearder 2011). Southern lesser galagos often interact with others during the night and have been observed grooming and playing with each other in small groups for over an hour at a time (Bearder et al., 2002). Svensson and Bearder (2013) observed Northern lesser galagos in groups in the majority (60%) of encounters and one female large-eared greater galago (*Otolemur crassicaudatus*) was with conspecifics for half of their observed time (Harcourt, 1980, in Nash and Harcourt, 1986).

Galagids communicate using vocalisations and olfactory signals. Vocalisations serve as an important communicative function for nocturnal animals (Nekaris and Bearder, 2011) and their wide repertoires are used to portray a variety of messages. Detailed spectrographic descriptions are available for many species (e.g. small-eared greater galago: Becker et al., 2003) and are a valuable tool for aiding species identification (Zimmerman et al., 1988; Anderson et al., 2000). Olfaction is important in galagid communication (Nash and Chilton, 1986; Becker et al., 1999; Bearder and Doyle, 1974; Clark, 1982a, 1982b), conveying an array of messages to conspecifics across space and time. For example, when presented with a mirror image, male small-eared greater galagos foot scent mark using urine more than females, and the behaviour is believed to serve a social function as a male display behaviour (Becker et al., 1999). Androgens such as testosterone influence chest-rubbing behaviour of large-eared greater galagos, and individuals frequently ‘mark over’ areas previously used by conspecifics (Bullard, 1984). Although galagids collectively use visual, olfactory and auditory signals when introduced to an unknown object or individual, they are also able to recognise their conspecifics by visual stimuli alone (Becker et al., 1999). Visual stimuli can provoke ‘head-cocking’, the rotation of the head in response to a novel object or organism (Rogers et al., 1993) and there is interspecific variation in head-cocking, as the movement is more rapid and repetitive in Southern lesser galagos than in small-eared greater galagos (Cantalupo et al., 2002).

Social interactions have been recorded in many species (Nekaris and Bearder, 2011). Affiliative interactions include allogrooming, social play and olfactory investigation, often observed in captivity (Newell, 1971; Ehrlich, 1977; Roberts, 1971; Zimmerman, 1989), but also seen in wild populations (Bearder and Doyle, 1974; Clark, 1985; Svensson and Bearder, 2013). For example, Southern lesser galagos often interact with others during the night and have been observed grooming and playing with each other in small groups for over an hour at a time (Bearder et al., 2002). Agonistic behaviours (e.g. chasing, staring, tail-pulling, biting and pulling hair out) have been recorded in captivity (Bearder and Doyle, 1974; Ehrlich, 1977; Zimmerman, 1985; Zimmerman, 1989; Roberts, 1971) and in wild populations (Nash and Whitten, 1989; Bearder and Doyle, 1974). A study on both captive and wild populations of Southern lesser galagos found that overt fighting involving serious fights and loss of fur seen in the captive population did not seem to occur in the wild population; individuals descended to the ground and fled rather than fought (Bearder and Doyle, 1974). In the wild the ‘male call’ may alert other males of their presence and act as a spacing mechanism to avoid potential conflict (Bearder and Doyle, 1974).

Investigating social dominance can help to understand why social interactions are important to galagids. Dominance in captive Southern lesser galagos was determined by analysing dyadic interactions between conspecifics of different age and sex classes, and dominant individuals groomed, urine washed and fed more than subordinate individuals (Bearder and Doyle, 1974). Subordinate Southern lesser galagos use threatening signals and vocalisations to deter their opponent, while the dominant individual usually keeps silent and commences physical attacks (Bearder and Doyle, 1974). This information is difficult to obtain from wild populations, but could be possible where age and sex is known (e.g. if individuals can be been trapped and monitored). Without trapping the animals, detailed records of social interactions, information on group size, and investigations into the use and functions of vocal and olfactory communication, can help to understand the social complexity of galagids.

1.3 Ecology and distribution

Galagids occupy a wide variety of habitats throughout sub-Saharan Africa, including arid desert, woodland, tropical rainforest, savannah, riverine and montane forest (Nekaris and Bearder, 2011). Species are sympatric with each other in some areas, but can be ecologically separated in terms of diet and other resources (e.g. Zanzibar dwarf galagos and small-eared greater galagos in Kenya; Harcourt and Nash, 1986). Tanzania is home to the highest galagid species diversity, inhabited by 13 different species (Nekaris and Bearder, 2011).

Sleeping site ecology varies between species (Svensson et al., 2018). Generally, nests (Bearder et al., 2003), branches (Nash and Whitten, 1989; Butynski and de Jong, 2004; Svensson and Bearder, 2013) and tree cavities (Haddow and Ellice, 1964; Svensson and Bearder, 2013) are used as sleeping structures. Nests, used by species within the *Paragalago*, *Galagoides, Galago* and *Otolemur* genera, are usually open platform leaf constructions surrounded by thorny trees, providing crypsis and protection from predators (Bearder et al., 2003). Tree cavities are often used by *Galago* spp. and large-eared greater galagos, in addition to dense tangles of vegetation and branches/forks (Bearder et al., 2003).

Galagids are of great ecological importance. They are prey to many potential predators (Burnham et al., 2012) and are themselves predators of invertebrates (Estes, 2012; Bearder and Martin, 1980; Nash and Whitten, 1989), with some species (small-eared greater galagos and Southern lesser galagos) also predating on bird eggs and nestlings (Engelbrecht, 2016). Some species are known pollinators: Southern lesser galagos have been observed feeding on flower parts (Scheun et al., 2014) and *Galagoides* sp. nov. feed in banana trees, often leaving with pollen from the flowers sticking to their fur (Perkin et al., in Mittermeier et al., 2006). Although there is interspecific variation in galagid diet, all species feed on tree exudates (tree gum) from a variety of *Vachellia* and *Commiphora* spp. (Bearder and Martin, 1980; Nash and Whitten, 1989; Butynski and de Jong, 2004).

1.4 Predation

Predation is a significant selective force in primate evolution (Anderson, 1986). Compared to other primate groups, small, nocturnal and arboreal primates are particularly vulnerable to predation (Hart, 2007). Confirmed records of predation in nocturnal primates are extremely low, but a review found that non-felid carnivores were responsible for the majority of recorded predation events on nocturnal primates, with others by birds, snakes, felids and other primates (Burnham et al., 2012). In some areas throughout their range, galagids are taken by humans for bushmeat, traditional medicine and the pet trade (Svensson et al., 2021).

Few studies have investigated the ways in which nocturnal primates respond to potential predation when active at night, but the available research shows variation in antipredator responses. For example, gray mouse lemurs (*Microcebus murinus*) use 'freezing behaviour' in response to potential aerial predators, perhaps due to raptors relying heavily on visual cues to catch their prey (Rahlfs and Fichtel, 2010). In contrast, spectral tarsiers (*Tarsius spectrum*) show mobbing behaviour in response to threat from snakes (Gursky, 2005). This behaviour was more common in adults compared to subadults and juveniles, and was mostly initiated by adult males (Gursky, 2005). Southern lesser galagos use alarm calls when carnivores are nearby, sometimes as a communal mobbing response with others, until the predators move away (Bearder et al., 2002). The discovery of Southern lesser galago carcasses confirmed that predation by small carnivores occurs during the night (Bearder et al., 2002).

Nocturnal primates are particularly vulnerable during the day while asleep (Lima et al., 2005) and for many species predation avoidance is a prominent factor in their sleeping site selection (Svensson et al., 2018). An overview of the wide range of potential diurnal and crepuscular predators for each galagid species is in Svensson et al. (2018). There are records of two great ape species, bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*), predating on galagids during the day (Svensson et al., 2018). A population of Northern lesser galagos in South-eastern Senegal are particularly at risk from day time predation because they are systematically hunted by Western chimpanzees (*P. t. verus)* at their sleeping sites during the wet season (Pruetz and Bertolani, 2007; Pruetz et al., 2015). The way in which that population respond to this predation pressure is not currently understood.

1.5 Non-invasive genetic sampling

Non-invasive genetic sampling allows researchers to obtain samples from wild animals without making contact with them (Taberlet and Luikart, 1999; Taberlet et al., 1999), therefore minimising any possible disturbance to the animals involved. Non-invasive sampling is particularly useful for studying elusive or cryptic species (Waits and Paetkau, 2005; Smith and Wang, 2014) and has a wide range of applications, from detecting rare species to evaluating social structure (see Waits and Paetkau, 2005 for review). A recent review found that only 22% of wildlife genetic studies (but not including studies on primates) employed a non-invasive sampling method (Zemanova, 2019).

Non-invasive genetic sampling of free-ranging primates has become increasingly popular and been used to: investigate genetic diversity (Western chimpanzees: Morin et al., 2001; golden-crowned sifakas, *Propithecus tattersalli*: Quéméré et al., 2010; Assamese macaques, *Macaca assamensis*: Müller et al., 2014; Hainan gibbons, *Nomascus hainanus*: Bryant et al., 2016); understand zoonotic disease ecology (olive baboons, *Papio anubis*: Smiley Evans et al., 2015) and the potential transmission of human pathogens to other primates (great apes and lemurs: Schaumburg et al., 2013); estimate population size and monitor populations (Arandjelovic and Vigilant, 2018); and investigate reproductive and social dynamics (bonobos: Gerloff et al., 1999; Hanuman langurs, *Presbytis entellus*: Launhardt et al., 1998; savannah baboons, *Papio cynocephalus*: Smith et al., 2000; western lowland gorillas, *Gorilla gorilla gorilla*: Hagemann et al., 2018).
Primatologists often collect faecal samples non-invasively from wild primates (Assamese macaques: Müller et al., 2014; golden-crowned sifakas: Quéméré et al., 2010; western lowland gorillas: Hagemann et al., 2018; titi monkeys, *Callicebus brunneus*: Bunce et al., 2011; Hainan gibbons: Bryant et al., 2016; chimpanzees: Morin et al., 2001). If possible to find, shed hair can be collected non-invasively from wild primates as a source of DNA (chimpanzees: Morin et al., 2001). Researchers of black howler monkeys (*Alouatta pigra*) successfully obtained freshly-plucked

hairs using a novel method involving manufactured wooden darts (Améndola-Pimenta et al., 2009). Another useful source of DNA is buccal cells from saliva. Primatologists have retrieved primate saliva from vegetation partly consumed by bonobos (Ishizuka et al., 2019) and chimpanzees (Sugiyama et al., 1993). To obtain DNA non-invasively from habituated Tibetan macaques (*Macaca thibetana*), researchers created a device involving a PVC tube and baited cotton dental rope to obtain saliva (Simons et al., 2012). There are currently no published studies describing the use of non-invasive sampling to successfully obtain genetic samples from wild nocturnal primates. However, one study used swabs flavoured with diluted honey to measure salivary melatonin concentrations in captive nocturnal primates (aye ayes, *Daubentonia madagascariensis*: Fuller et al., 2016); a similar method may allow DNA extraction from wild nocturnal primates.

The available genetic studies on free-ranging nocturnal primates in mainland Africa and Asia used invasive methods such as live-trapping, mist-netting and capturing animals by hand to obtain samples. Researchers trapped Sulawesi tarsiers (*Tarsius* spp.) using mist-nets and captured them by hand to investigate the phylogeographic history of primates (Merker et al., 2009). On mainland Africa, live-trapping has been used to study galagid genetics, often using Chardonneret traps, which were first designed for catching galagids in Gabon (Charles-Dominique and Bearder, 1979). These traps were also used to catch Eastern dwarf galagos (Kenya coast galagos and Zanzibar dwarf galagos) to investigate species boundaries between them (Pozzi et al., 2019). Some studies give evidence of collecting samples by live-trapping African nocturnal primates, but the results of genetic analysis were not published (e.g. Pimley et al., 2005).

Using invasive methods to study nocturnal primates has proven successful, however it would be more ethical to obtain the samples non-invasively and avoid any potential negative effects on the animals. A novel approach is needed for obtaining non-invasive samples from nocturnal primates that is appropriate for their arboreal and elusive nature.

1.6 The Northern lesser galago

This thesis focuses on the most widely-distributed species of galagid (de Jong et al., 2019), the Northern lesser galago. The Northern lesser galago is a medium-sized galagid, with adults weighing just over 200 g on average in the wild (mean weight of males 225 g and 200 g for females: Butynski et al., 2013). Captive individuals are considerably greater in weight (mean weight of males 360 g and 266 g for females; Butynski et al., 2013).

The distribution of Northern lesser galagos stretches from Senegal and The Gambia in West Africa to Ethiopia, Kenya and Tanzania in East Africa (de Jong et al. 2019; see Figure 1.1). The four recognised subspecies are: *G. s. senegalensis*, *G. s. braccatus*, *G. s. dunni* and *G. s. sotikae* (see Figure 1.1 for geographic separation and Svensson et al. [2019] for phenotypic differences), but clear diagnosis of subspecies using genetics, vocalisations, behaviour and morphology is needed (Butynski et al., 2013).

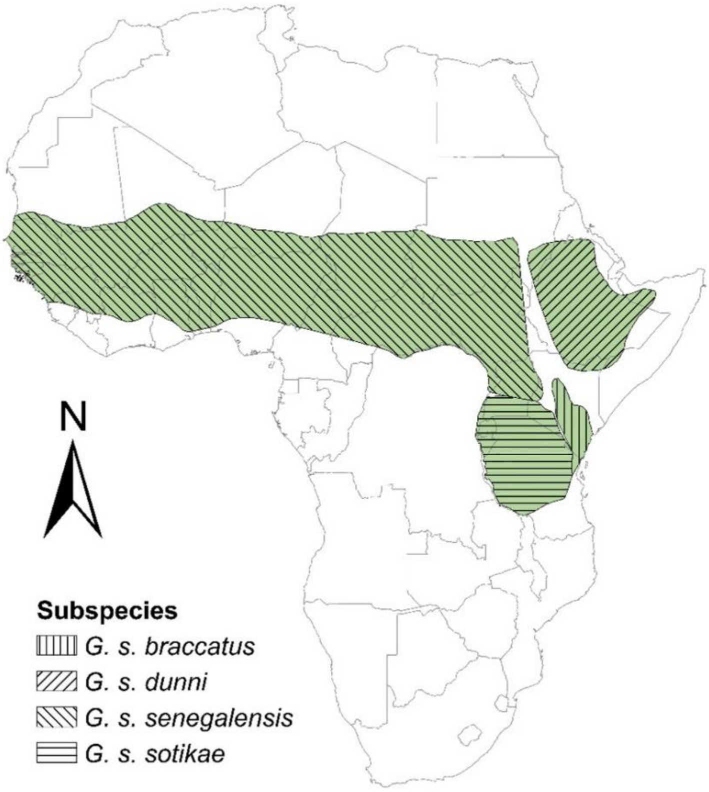


Figure 1.1 The geographical range of the Northern lesser galago according to data on the IUCN Red List (de Jong et al. 2019), shown in green. Proposed ranges for each subspecies are shown using different grid lines.

Data on wild populations is scarce and far less abundant than that on their closest relative, the Southern lesser galago, once thought to be a subspecies of the Northern lesser galago (‘*G. s. moholi*’). The Southern lesser galago is now recognised as a separate species, due to differences in reproductive parameters such as mean gestation length and age at puberty (Izard and Nash, 1988), morphology (Anderson, 2000; Anderson et al., 2000) and vocal repertoire (Zimmermann et al., 1988; Anderson et al., 2000). The taxonomy of lesser galagos is particularly problematic due to the misclassification of museum and captive samples (Pozzi et al., 2014; 2015) and further studies are needed to investigate their genetic variation. Research on the Southern lesser galago and studies of the Northern lesser galago in captivity (Izard and Nash, 1988; Butynski et al., 2013; Scheun et al., 2016; Schneiderová et al., 2016) form much of the assumed knowledge on the species because there have been few studies on *in situ* populations of Northern lesser galagos. The few studies carried out on wild populations are extremely valuable and summarised below.

Observations on wild Northern lesser galagos have provided insights into their habitat and feeding ecology. They occupy a range of habitats from savannah to riverine and dry bushland or woodland (Off et al., 2008; Butynski et al., 2013), but detailed information on their spatial distribution and contributing factors is unavailable. Throughout the day, Northern lesser galagos rest in varied sleeping structures such as tree branches/forks, leaf nests and tree cavities (Haddow and Ellice, 1964; Svensson and Bearder, 2013; Svensson et al., 2018), but have also been recorded sleeping in man-made nest boxes (Veiga et al., 2013) and unoccupied man-made bee hives (Butynski et al., 2013). Their omnivorous diet consists primarily of arthropods and tree exudates (Haddow and Ellice, 1964; Nash and Whitten, 1989) and foraging is carried out within trees or during short periods on the ground (Nash and Whitten, 1989).

Group size varies from 1–6 when sleeping and 1–3 when active (Haddow and Ellice, 1964; Off et al., 2008; Svensson and Bearder, 2013). In Kenya, Northern lesser galagos are mostly alone when active (Off et al., 2008) but in The Gambia they spend the majority of their active time in groups of two or more (Svensson and Bearder, 2013). They have an extensive vocal repertoire, but there is little variation in their commonly used ‘loud’ calls, or ‘honks’, across their geographic range

(Svensson et al., 2019). In The Gambia these calls were most likely used for reassembly at dawn, but also heard soon after leaving sleeping sites at dusk (Svensson and Bearder, 2013). In Senegal the same calls are uttered throughout the night, but are increased before and at dawn (Schneiderová et al., 2020). The function of Northern lesser galagos' loud call remains speculative (possible reasons include: territorial advertisement; group coordination; and reassembly at sleeping sites); further research on sleeping site distribution, sleeping groups and other social factors is needed to determine the purpose of the call (Schneiderová et al., 2020).

The locomotion of Northern lesser galagos is of great interest because they have a greater vertical jumping agility (2.2 metres per second) than any other animal (Haldane et al., 2016). The mechanics of their saltatory locomotion have been studied intensively in controlled environments in captivity (Hall-Crags, 1965; Ryan and Ketcham, 2002; Ryan and Van Rietbergen, 2005; Huq et al., 2018), but only briefly described from observations on wild populations when researchers attempted to catch free-ranging individuals in Uganda (Hall-Crags, 1965). The use and function of the different movements Northern lesser galagos use to travel through their habitat in the wild have not been described in detail. However, leaping may have evolved to enable swift evasion from predators, by allowing the animals to make sudden and unpredictable changes in direction when under threat (Crompton and Sellers, 2007).

The activity patterns of Northern lesser galagos have rarely been studied in the wild, but the activity of one wild female caught in an aktograph cage suggests that they may engage in biphasic activity, with a large peak of activity just after sunset and small peak before sunrise (Haddow and Ellice, 1964). Their home ranges were last studied over 30 years ago: researchers observed and followed individuals, marking trees every ten minutes and then returning to map the ranges the next day (estimated ranges were 0.01–0.02 km^2: Nash and Whitten, 1989). The available information on Northern lesser galago activity is both dated and limited. Detailed behavioural studies are needed to better understand the species and the ways in which they have adapted to survive.

There is a distinct lack of knowledge of this cryptic species and other closely-related nocturnal primates. 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.

1.7 Thesis aims

For this thesis I had the following aims:

1) Quantify the available literature on galagid behaviour and ecology and identify any taxonomic or geographic bias in the literature;

2) Investigate Northern lesser galago activity and social behaviour;

3) Determine the location of Northern lesser galago sleeping sites and factors contributing to sleeping site choice;

4) Assess the response of Northern lesser galagos to systematic predation from Western chimpanzees;

5) Develop a non-invasive sampling technique for obtaining amplifiable DNA from wild galagids.

1.8 Study sites

To collect data for this thesis I visited three study sites within the range of the Northern lesser galago. These were: 1) Kwakuchinja, Northern Tanzania; 2) Fongoli, South-eastern Senegal; and 3) Lolldaiga Hills Ranch, Central Kenya (see Figure 1.2).

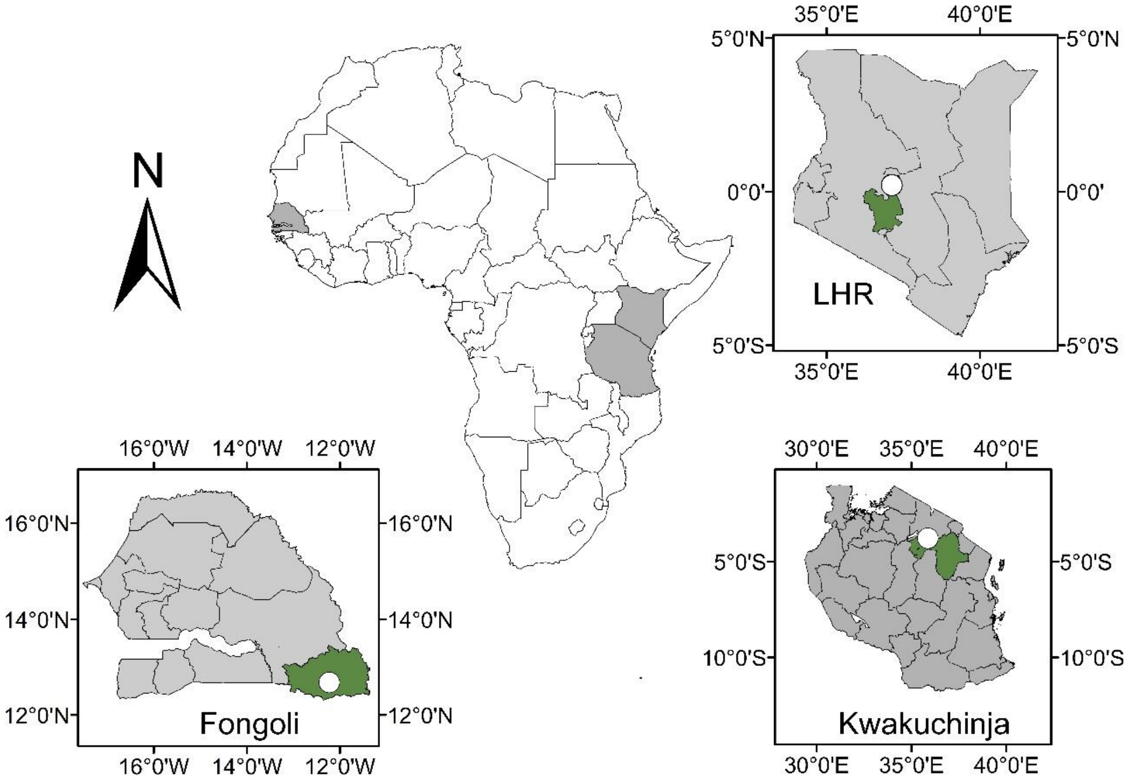


Figure 1.2 Study sites used to research populations of Northern lesser galagos in this thesis. The Kedougou region of Senegal, Central province of Kenya and Manyara region of Tanzania are shown in green. Locations of the study sites are indicated by white circles. Maps throughout this thesis were created using ArcGIS® software by Esri. 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 www.esri.com.

1.8.1 Kwakuchinja

In June–July 2016 and July 2017, I collected data in a 9.2 km^2 area within the Kwakuchinja wildlife corridor (‘Kwakuchinja’ hereafter), located in the Babati District of Northern Tanzania, between Lake Manyara and Tarangire National Parks (Figures 1.2 and 1.3). The Tarangire–Manyara ecosystem has a semiarid climate, with a mean annual rainfall of around 650 mm (Foley and Faust 2010; TCP 1997, given in Msoffe et al. 2007). The habitat in the study area is mainly woodland dominated by *Vachellia* and *Commiphora* species, with scattered Baobab (*Adansonia digitate*) and palm (*Hyphaene* and *Borassus* spp.) trees.

The site is home to two species of galagid, the small-eared greater galago and the focus of this study, the Northern lesser galago. The subspecies *G. s. sotikae* is present at Kwakuchinja. The corridor is frequently used by mammals such as Masai giraffes (*Giraffa tippelskirchi*); plains zebra (*Equus quagga*); and Grant's gazelles (*Nanger granti*; Kiffner et al., 2016). Some other mammals regularly seen at the site are: vervet monkeys (*Chlorocebus pygerythrus*); olive baboons; impala (*Aepyceros melampus*); warthogs (*Phacochoerus africanus*); Kirk's dikdik (*Madoqua kirkii*); spotted hyenas (*Crocuta crocuta*) and African savannah hares (*Lepus victoriae*). Birds of prey commonly seen at Kwakuchinja include Verreaux's eagle-owls (*Bubo lacteus*) and African goshawks (*Accipiter tachiro*). With the corridor being used by animals migrating between the two national parks, I also observed or found evidence of elephants (*Loxodonta africana*), lions (*Panthera leo*) and leopards (*Panthera pardus*) passing through the site. All research at Kwakuchinja was carried out on foot. Part of the study area is owned and protected by the College of African Wildlife Management, but the remainder of the Kwakuchinja wildlife corridor is unprotected and at risk from cattle grazing, tree felling for wood and charcoal production, and the creation of baskets from palm leaves. Roadkill affects medium-sized mammal populations at Kwakuchinja, particularly during the months of July to September, and species commonly affected are African savannah hares, impala and Kirk's dikdik (Njovu et al., 2019).

Figure 1.3 A giraffe in the Kwakuchinja wildlife corridor, Northern Tanzania.

1.8.2 Fongoli

In March–May 2018 I collected data at the Fongoli research site, situated outside of nationally protected park areas in the Kedougou region of South-eastern Senegal (Figures 1.2 and 1.4). The Fongoli study site encompasses the chimpanzee community's home range, an area covering more than 81.5 km^2, where topography ranges from 75–203 m in altitude, and the habitat is broadly composed of primarily woodland, plateau/open grassland, and bamboo woodland habitat types, with some agricultural fields and gallery forests (Pruetz, 2006; Lindshield et al., 2019). Annual rainfall is ~800 mm. The short wet season is from June to September, May and October are considered transitional months, and the long dry season is from November to April (Bogart and Pruetz, 2010; Pruetz and Herzog, 2017).

The Northern lesser galago is the only species of galagid present at Fongoli, and the subspecies there is *G. s. senegalensis*. Some other mammals regularly seen are: Western chimpanzees; green monkeys (*Chlorocebus sabaeus*); patas monkeys (*Erythrocebus patas*); Guinea baboons (*Papio papio*); hartebeest

(*Alcelaphus buselaphus*); common duiker (*Sylvicapra grimmia*); and warthogs. All research at Fongoli was carried out on foot or by motorbike and we made every effort to minimise our impact by using tracks when on the motorbike and the majority of the time when on foot. The wildlife at Fongoli is at risk from anthropogenic activities such as gold-mining, agriculture and man-made bushfires (Lindshield et al., 2019).

Figure 1.4 Chimpanzees at Fongoli, South-eastern Senegal.

1.8.3 Lolldaiga Hills Ranch

In July–August 2018, I collected data in Lolldaiga Hills Ranch, a livestock ranch and wildlife conservancy in Central Kenya (LHR; Figures 1.2 and 1.5). LHR is 200.1 km^2, ranges from 1737–2265 m in altitude and is broadly composed of woodland, bushland and other habitat types including forest and savannah. I 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 acacia (*Vachellia drepanolobium*), and some by other species such as fever trees (*V. xanthophloea*). Mean annual rainfall is between 750–1200 mm and temperatures average 16 °C in the coolest months and 26 °C in the warmest months (Butynski and de Jong, 2015, in Ngatia et al., 2019).

The Northern lesser galago is the only galagid species present at the site, and the subspecies there is *G. s. braccatus*. Some mammals regularly seen are: elephants; reticulated giraffes (*Giraffa reticulata*); vervet monkeys; olive baboons; plains zebra; Grevy's zebra (*Equus grevyi*); spotted hyenas; eland (*Taurotragus oryx*); oryx (*Oryx beisa*); and buffalos (*Syncerus caffer*). Birds of prey at Lolldaiga include secretary birds (*Sagittarius serpentarus*), steppe eagles (*Aquila nipalensis*) and Martial eagles (*Polemaetus bellicosus*). Due to safety risks from elephants and an abundance of other wildlife, all work at LHR was carried out by vehicle, or in very close proximity to the vehicle. We used tracks and roads the vast majority of the time to minimise our impact on the ranch, but on a few occasions drove across grassland to set camera traps, sound recorders, temperature recorders and string samples. Wildlife and livestock have shared pasture and water on LHR for over 80 years, and the total biomass density of livestock is far greater than that of wildlife (Mizutani et al., 2012). The impact of the presence of livestock on the wildlife is poorly understood.

Figure 1.5 A view of Lolldaiga Hills Ranch, Kenya.

1.9 Thesis overview

In Chapter 2, I systematically review all the literature on galagid behaviour and ecology from the last 50 years (January 1971 – December 2020) to identify and quantify taxonomic and geographic biases in the literature. The review acts as a guide to future researchers of galagids and encourages an equal sampling effort for a greater understanding of each species. **This chapter was published in PLoS ONE in December 2021 (Appendix 1A).**

In Chapter 3 I explore different elements of galagid sociality and assess differences in behavioural observations on free-ranging Northern lesser galagos at Kwakuchinja across three different stages of the night.

In Chapter 4 I investigate the sleeping site ecology of Northern lesser galagos at Kwakuchinja to test the impacts of thermoregulation and anti-predator behaviour on sleeping site ecology. **This chapter was published in the International Journal of Primatology in April 2019 (Appendix 1B).**

In Chapter 5 I explore the evidence for the influence of predation by Western chimpanzees at Fongoli on Northern lesser galago spatial distribution and sleeping site choice.

In Chapter 6 I describe the development of a non-invasive sampling technique for retrieving saliva samples from wild galagids. This involved hanging sterilised nylon strings in galagid sleeping trees, baiting them with sugary substances and monitoring their use using camera traps.

In Chapter 7 I discuss the significance of my findings and their contribution to the understanding of the Northern lesser galago and other nocturnal primates. I present several avenues for future research to further understand these cryptic animals.

1.10 Methods used and collaborators

I used a number of data collection and analysis methods throughout this thesis. I have summarised them in Table 1.1 below along with the contributions of local scientists, students and other helpers.

Collaboration with local scientists and students was invaluable in the success of my PhD. My collaborators at the College of African Wildlife Management (CAWM) have a strong bond with colleagues at my university, based on a memorandum of agreement and decades of collaborative research. CAWM own the Kwakuchinja site and recruited local guards to protect the area and assist the research, and local people to cook food so that our research was not disrupted. CAWM provided a local botanist to assist in vegetation sampling, without whose knowledge we would not have been able to complete our work. Senior researchers at CAWM provided ongoing support throughout the fieldwork and allowed me to recruit two research students from CAWM to assist in my non-invasive sampling project. This provided them with data collection skills for future careers in research and taught me about the views of young researchers on protecting their native wildlife.

At Fongoli, my collaborator Dr Jill Pruetz began the Fongoli Savannah Chimpanzee Project over 20 years ago and has made an exceptional contribution to the community and their involvement in chimpanzee and other wildlife conservation. The project is managed and run by local researchers, and the community have been educated on the importance of wildlife conservation. I was very lucky to have worked alongside the highly respected local researchers; my work was very much guided by their knowledge of the field sites and animals and plants within.

My collaborators at LHR recruited local rangers and researchers to assist in wildlife research and local people to cook for us. My collaborators at the National Museums of Kenya provided guidance throughout my time in Kenya and introduced me to their impressive taxidermy collection. Creating bonds with and listening to the views of local people in Kenya was a very valuable experience, given the colonial history in the country.

There is a long way to go to decolonize primatology. I am proud to have collaborated with local people at each field site and learnt their views on wildlife conservation and other issues. This was incredibly valuable for myself and my own research to grow, and hopefully for all parties involved at each field site. Importantly, the views of local people have been taken into account when proposing potential conservation strategies (section 7.3.2 of Chapter 7).

Table 1.1 Methods used throughout this thesis and collaborators.

Methods	Chapters contributed towards	Collaborators and their roles	Date
Data collection methods			
Systematic search of the literature	2	No collaborators.	May 2019 – January 2021
Behavioural observations including focal follows	3, 4 and 5	Kwakuchinja: My supervisor Caroline and the following students assisted in behavioural data collection: BSc students: Ryan Nolan; MSc students: Em Lane and Vicky Howard. Our rangers Augustino Mwageni, Nassoro Kapinga, and Michael Chaula ensured that we were safe during data collection. Professor Kidegesho, Dr Alex Kisingo and Dr Ladislaus Kahana from the College of African Wildlife Management provided logistical support.	June–July 2016 and July 2017
		Fongoli: Dondo Kante and Jacques Keita assisted in behavioural data collection. Dr Jill Pruetz provided financial and logistical support.	March–May 2018

Methods	Chapters contributed towards	Collaborators and their roles	Date
Vegetation surveys	4 and 5	Kwakuchinja: My colleague Dr Andy Wolfenden and the following students assisted in data collection: MSc students: John Jamieson, Em Lane and Vicky Howard; BSc students: Ryan Nolan, Sophie Halliwell, Jonny Holman, Maia Nicholson, Chloe Andrews, Aimee Waddicor, Chris Cockerill, Morwenna Moore, Vicky Howard, Sally Holdsworth, Rosa Aldridge, Harriet Bell. Our rangers Augustino Mwageni, Nassoro Kapinga, and Michael Chaula ensured that we were safe during data collection. Professor Kidegesho, Dr Alex Kisingo and Dr Ladislaus Kahana from the College of African Wildlife Management provided logistical support.	June–July 2016 and July 2017
		Fongoli: Dondo Kante and Jacques Keita assisted in vegetation data collection and were invaluable in plant identification.	March–May 2018
Line transect surveys	3 and 5	Fongoli: Dondo Kante and Jacques Keita assisted in line transect surveys and drove the motorbike whilst I collected data. Dr Jill Pruetz provided financial and logistical support.	March–May 2018
		LHR: My supervisor Caroline and MMU Research Assistants Simon Kenworthy and Amelia Ramage assisted in data collection during line transect surveys whilst I drove the car. Dr Tom Butynski and Dr Yvonne de Jong provided logistical support and advice. Our ranger Jackson ensured that we were safe during data collection. Dr Simon Musila at the National Museums of Kenya provided logistical support.	July–August 2018

Methods	Chapters contributed towards	Collaborators and their roles	Date
Non-invasive saliva sampling	6	Kwakuchinja: The following students assisted in data collection: BSc student Aimee Waddicor; College of African Wildlife management students: Happy Thadey and Gideon Titus. Our rangers Augustino Mwageni, Nassoro Kapinga, and Michael Chaula ensured that we were safe during data collection. Professor Kidegesho, Dr Alex Kisingo and Dr Ladislaus Kahana from the College of African Wildlife Management provided logistical support.	June–July 2016 and July 2017
		Fongoli and LHR: No collaborators for data collection. Dr Jill Pruetz provided financial and logistical support at Fongoli and Dr Tom Butynski and Dr Yvonne de Jong provided logistical support and advice at LHR. Our ranger Jackson ensured that I was safe during genetic sampling at LHR.	March–May 2018 (Fongoli) and July–August 2018 (LHR)
Analytical methods			
Hypothesis testing	3, 4, 5 and 6	My supervisors and my colleague Danny Norrey provided advice.	Throughout my PhD
Negative binomial regression	2	No collaborators.	January–March 2021

Methods	Chapters contributed towards	Collaborators and their roles	Date
Logistic regression	2	No collaborators.	January–March 2021
Text mining	2	My supervisor Caroline provided advice.	January–March 2021
Random forest classification analysis	4 and 5	My supervisor Martin and colleague Ed Harris provided advice on the analysis.	September–January 2016 and January 2020
Distance sampling	5	My supervisor Martin and colleague Christian Devenish provided advice on the analysis.	May 2019 – July 2019
Density surface modelling	5	My colleague Christian Devenish introduced me to the technique and assisted me with the analysis.	October 2019 – May 2020
DNA extraction and amplification	6	My colleague Tom Hughes shadowed me in the laboratory and my supervisor Brad provided advice.	November 2020 – February 2021

1.11 Ethics statement

The research in this thesis was approved by the Manchester Metropolitan University (MMU) Ethics Committee and the research complied with the International Primatological Society's Code of best practice for field primatology. In Tanzania I 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 I collected data 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. I adhered to the legal requirements of Tanzania, Senegal and Kenya at all times.

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Chapter 2. Taxonomic and geographic bias in 50 years of research on the behaviour and ecology of galagids

Abstract

Identifying knowledge gaps and taxonomic and geographic bias in the literature is invaluable for guiding research towards a more representative understanding of animal groups. Galagids are nocturnal African primates and, for many species, detailed information on their behaviour and ecology is unavailable. To identify gaps and bias in the literature, I reviewed published peer-reviewed research articles on galagid behaviour and ecology over a 50-year period from January 1971 to December 2020. Using the Web of Science and Google Scholar databases, I identified 758 articles, assessed 339 full texts for eligibility and included 211 in the review. Species of *Otolemur* have been extensively researched in comparison to other genera (78.2% of studies; *Euoticus*: 13.3% of studies; *Galago*: 66.4% of studies; *Galagoides*: 20.9% of studies; *Paragalago*: 22.3% of studies; *Sciurocheirus*: 15.2% of studies). The most common category of research was physiology (55.0% of studies), followed by behavioural ecology (47.4% of studies), and fewer studies were on genetics and taxonomy (16.1% of studies) and habitat and distribution (14.2% of studies). Text mining revealed that the word 'behaviour' was the most common word used in abstracts and keywords, and few words were related to ecology. Negative binomial regression revealed that mean body mass and geographic range size were significant positive predictors of the total number of scientific outputs on each species. Research on wild populations was carried out in only 24 (60%) of the 40 countries galagids are thought to inhabit. Studies were undertaken in locations with lower mean annual temperatures and higher human population densities over warmer and less populated areas. I encourage a more equal sampling effort both taxonomically and geographically that in particular addresses the paucity of research on smaller species and those with restricted ranges. Research on *in situ* populations, especially in warmer and remote areas, is urgently needed, particularly in West, Central and some Southern African countries.

Keywords**:** bushbaby, galago, strepsirrhine, systematic review, research effort.

2.1 Introduction

We are losing species worldwide at such an alarming rate that we may be in the midst of the sixth mass extinction (Ceballos et al., 2015). Species or populations lacking data on their behaviour and ecology are likely to be poorly understood and could be at greater risk of ‘silent’ extinction, where they may be overlooked by conservation management due to data deficiency and more likely to go extinct unnoticed (McKinney, 1999; Howard and Bickford, 2014). Despite this, research effort in animal behaviour and ecology is often dominated by a focus on certain taxonomic groups (Rosenthal et al., 2017) and geographical study areas or biomes (Reddy and Dávalos, 2003; Botts et al., 2011). Systematic reviews highlight the importance of evaluating the literature to quantify research outputs, reveal taxonomic or spatial biases, and identify areas in particular need of research (Clark and May, 2002; Reddy and Dávalos, 2003; Donaldson et al., 2016).

Reviews have revealed taxonomic bias (when organisms from a particular taxonomic group are researched disproportionately to others) in studies across a wide range of biological disciplines (Pawar, 2003; Fleming and Bateman, 2016) as well as a lack of species-specific data in subjects such as animal behaviour (Rosenthal et al., 2017) and conservation biology (Clark and May, 2002; Seddon et al., 2005; Lawler et al., 2006; Donaldson et al., 2016; Roberts et al., 2016; dos Santos et al., 2020). Within vertebrates, mammals and birds receive more research attention than any other group relative to their number of species (Bonnet et al., 2002; Bajomi et al., 2010). However, even within these well studied groups there can be imbalances, for example within European bird studies there is a strong focus on certain species (Murray et al., 2015), and the same has been found within studies on Australian terrestrial mammals (Fleming and Bateman, 2016) and Neotropical primates (Hawes et al., 2013).

Research effort into larger species is generally far greater than that into smaller species (e.g. felids: Brodie, 2009; Tensen, 2018; canids: Tensen, 2018; carnivores: Brooke et al., 2014; sharks: Ducatez, 2019; terrestrial mammals: dos Santos et al., 2020; Neotropical primates: Hawes et al., 2013; Australian birds: Yarwood et al., 2019), and for species with larger geographic ranges than those with smaller ranges (Neotropical primates: Hawes et al., 2013; carnivores: Brooke et al., 2014; Australian birds: Yarwood et al., 2019; sharks: Ducatez, 2019). Population size (Murray et al., 2015) and habitat type (Yarwood et al., 2019) were important factors explaining research effort in ornithological studies, and in felids and canids the likelihood of being a keystone species was strongly positively correlated with research effort (Tensen, 2018). A global analysis of non-marine mammals showed that introduced species had a greater number of outputs than native species (dos Santos et al., 2020), and in some taxa aesthetics can also play a role; one study found that 'ugly' native eutherian species were studied less than native monotremes and marsupial species (Fleming and Bateman, 2016).

In addition to taxonomic bias, geographic bias also pervades the literature in animal behaviour and ecology (Reddy and Dávalos, 2003; Botts et al., 2011; Kaschner et al., 2012; Archer et al., 2014; Roberts et al., 2016; Hugo and Altwegg, 2017) and conservation biology (Lawler et al., 2006; Fisher et al., 2011). Sampling effort in ecological research is often biased towards areas that are easily accessible to humans, such as near rivers (Reddy and Dávalos, 2003), cities, roads and other urban areas (Reddy and Dávalos, 2003; Botts et al., 2011; Hugo and Altwegg, 2017; Yarwood et al., 2019). For example, in Australia, records of koala presence closely mapped the road network (Margules and Austin, 1994). Furthermore, researchers of tropical coral reefs favoured sites in wealthy nations near top-ranking research institutions over those with greater species richness (Fisher et al., 2011). Conservation priority areas, national parks and other protected areas are also used as study sites more than other areas (Reddy and Dávalos, 2003; Botts et al., 2011; Hugo and Altwegg, 2017; Bezanson and McNamara, 2019). Alternatively, biologists may avoid using certain areas such as those affected by political instability and ongoing conflict (Parnell et al., 2003; Hopkins and Nunn, 2007).

The majority of primate populations are threatened with extinction (Estrada et al., 2017) and, like other animal groups, information on their behaviour and ecology is instrumental in the understanding of their conservation biology (Cowlishaw and Dunbar, 2000). Although better-studied than most other mammalian groups (Amori and Gippoliti, 2000), there are known biases in the research effort on primates. In recent years, primatologists showed a geographic bias for national parks and protected areas, using them as study sites in the vast majority of publications (73.3%; Bezanson and McNamara, 2019). Studies on parasites in wild primates are far more abundant on populations in East and South Africa than the rest of the world (Hopkins and Nunn, 2007). There is a taxonomic bias for specific groups, for example the great apes have been studied far more than other apes (Fan and Bartlett, 2017). A recent review found that between 2011 and 2015, the three non-human great ape genera (*Pan*, *Pongo* and *Gorilla*) were in the top ten most studied genera of primates (Bezanson and McNamara, 2019). *Pan* and *Macaca* species have been studied at a far higher rate than all other primate genera, and no nocturnal primates featured at all (Bezanson and McNamara, 2019). Furthermore, a review of Neotropical primate diet studies found very few on nocturnal primates (night monkeys, *Aotus* spp.: Hawes et al., 2013), and compared to diurnal primates, nocturnal species are underrepresented in scientific documentaries and films (Riley Koenig et al., 2019).

This review focuses on galagids, or ‘bushbabies’ (family: Galagidae); small, nocturnal, arboreal strepsirrhine primates distributed throughout sub-Saharan Africa. Due to their cryptic morphology and nocturnal lifestyles, nocturnal strepsirrhines were misclassified as just a few species for many years, but advances in their study revealed an incredibly diverse group of animals with varied social systems, locomotion and life histories (Nekaris and Bearder, 2011). Galagids are a useful model study group for understanding our earliest primate ancestors, which likely shared similar traits such as being small in size (Soligo and Martin, 2006) and nocturnal (Ross et al., 2007). Galagid behaviour and ecology varies greatly even within genera (Nash et al., 1989; Bearder et al., 2003; Svensson et al., 2018), and therefore extrapolating findings across even closely related species may be misleading and misinform conservation efforts.

My aim was to systematically review and quantify the available literature on galagid behaviour and ecology from the last 50 years to identify the level of disparity in research effort among galagid species and choice of study locations. Specifically, my objectives were to investigate taxonomic bias in the total number of scientific outputs per species, and geographic bias in the study of free-ranging populations, as well as identify the types of samples used (wild, captive, museum-type, bioinformatic, or unknown) and topics of behaviour and ecology most researched.

I expected species with a greater body mass and larger geographic range to have more publications than smaller, range-restricted species, as seen in Neotropical primate studies (Hawes et al., 2013), and expected areas with a greater human population density to be used as study sites more than less populated areas. I hypothesized that areas with lower mean annual temperatures would be preferred as study locations for logistical reasons such as increased accessibility and being less physiologically demanding for researchers. Similarly, I expected areas with lower mean annual rainfall to be popular as study sites, with the view that less dense vegetation from lower rainfall would allow greater visibility and accessibility.

2.2 Methods

2.2.1 *Data compilation*

I reviewed the available peer-reviewed research articles on the behaviour and ecology of galagids using a systematic approach. I largely adhered to the guidelines of Pullin and Stewart (2006), ensuring that data were searched for, selected, extracted and evaluated systematically to allow for replication. However, to avoid pseudoreplication and ensure that my methods are replicable, I only included published peer-reviewed research papers (Pawar, 2003; Lawler et al., 2006; Fisher et al., 2011; Donaldson et al., 2017; Rosenthal et al., 2017; Tensen, 2018; Yarwood et al., 2019) and excluded unpublished data (e.g. meeting abstracts, contacting experts in the field; Ziai et al., 2017). I completed the search in January 2021 on the Web of Science database, for publications from January 1971 to December 2020, using the following search terms: galag* AND: behav*; activity; social*; ecolog*; habitat; sleep*; feeding; distribution. The wildcard ‘galag*’ was also replaced by ‘bushbab*’ and ‘bush bab*’ for each of the 8 searches. Because galagids are African primates and the Web of Science does not support several African peer-reviewed scientific journals, I conducted a further search on the Google Scholar database using the ‘Advanced search’ tool, specifying that the word ‘African’ must be in the journal name. Google Scholar does not recognise wildcard searches (the use of asterisks to search for a word with the stated letters and any suffix) so I spelt all words out in full (all search terms are in Appendix 2A). I included articles published online or in print between, and including, 1st January 1971 and 31st December 2020.

2.2.2 *Data analysis*

I initially screened the literature and included any records that had any of the following target words in the title, abstract or keywords: ‘bush baby’; ‘bush babies’; ‘bushbaby’; ‘bushbabies’; ‘galagid’; ‘galagids’; ‘Galagidae’; ‘galago’; ‘galagos’; and the previously used family name ‘Galagonidae’, and ‘Galagonid’ and ‘Galagonids’ (Jenkins, 1987, in Grubb et al., 2003). I removed duplicate papers that appeared in more than one search.

I read all articles and only included those with primary data on galagids to avoid pseudoreplication. I excluded papers that contained data on galagids, but did not contribute towards the understanding of their behaviour and ecology, often where researchers used them as models for other areas of research (e.g. functional neuroscience or gene function). For studies containing data on several species, I only recorded the information related to galagids.

I recorded the following information from each paper: date of publication; species; sample type (captive, wild, museum-type, bioinformatic [from bioinformatics databases, such as GenBank from the National Centre for Biotechnology Information], or unknown); study location(s) with coordinates if available; the country of each authors’ affiliation(s) at the time of conducting the research; and categories of behaviour and ecology studied. Categories of behaviour and ecology were difficult to determine, as so many overlap (Estes, 2012), so I used four broad categories: behavioural ecology; habitat and distribution; physiology; and genetics and taxonomy. Some papers contributed to more than one area. For species that have had their taxonomy revised during the 50-year period, I used the location of the study site and geographic ranges to determine the current species name for studies on wild populations (e.g. between *G. senegalensis* and *G. moholi* [was *G. s. moholi*]). Study locations were those where researchers studied free-ranging galagids; I did not record the origin of museum specimens or captive samples. For studies on other sample types, it was not possible to distinguish changes in taxonomy. I classed any studies on ‘*O. montieri*’ as *O. crassicaudatus* (Masters and Bearder, 2019), and any on ‘*G. alleni*’ as *S. alleni* (Perkin et al., 2020a). I classed all eastern *Gd.* spp. under their new recognised genus *Paragalago* (Masters et al., 2017); this includes '*G. udzungwensis'* or '*Gd. udzungwensis*' now being classed as *P. zanzibaricus* (Perkin et al., 2020b) and *Gd. nyasae* as *P. granti* (de Jong et al., 2019a).

2.2.2.1 Taxonomic bias

I investigated body mass, as a proxy for body size (Brodie, 2009; Hawes et al., 2013; Brooke et al., 2014; Tensen, 2018; Ducatez, 2019; Yarwood et al., 2019; dos Santos et al., 2020), and geographic range size (Hawes et al., 2013; Brooke et al., 2014; Ducatez, 2019; Yarwood et al., 2019) as potential drivers of taxonomic bias. I used negative binomial regression models to model the log of the expected total number of research outputs per species as a function of covariates: body mass and geographic range size. I used negative binomial regression rather than poisson regression for count data due to over-dispersion (Zeileis et al., 2008). In addition to modelling the total number of research outputs per species, I used the same covariates to model the number of research outputs on wild populations only. I used separate models for total research and research only on wild populations instead of one model with random effects due to the small sample size ($N = 17$).

I used mean body mass data (g) from Butynski et al. (2013) as a covariate. Mean body mass data were for males and females combined, and I could not find any available body mass data for *G. gallarum*, *Gd. kumbirensis* or *S. makandensis;* these three species were not included in the models.

I downloaded data on geographic range size for each species from the IUCN Red List (downloaded on 17th August 2020 from https://www.iucnredlist.org) and combined any subspecies ranges into one for each species. I projected the ranges using the Africa Equal Area Conic projection to obtain one value for the area covered by each species in km^2.

There was no substantial collinearity between body mass and geographic range size ($r_s = 0.21$, $P = 0.417$). I included years since scientifically recognised as an offset in the models because *P. rondoensis* was formally described in 1996 (Honess 1996, in Butynski et al., 2013) and the other 16 species were known to science for the whole sampling period. I report the McFadden's pseudo R^2 for my best model and for each covariate: the coefficient; standard error; *z*-statistic; *P*-

value; 95% confidence intervals (95% CI); incident rate ratio; and 95% CI for the incident rate ratio.

2.2.2.2 Geographic bias

I created a map showing the number of studies published on galagid behaviour and ecology using wild samples from each country. I overlaid the locations of the populations studied and for papers where researchers used several study sites, I represented each study site separately on the map and in the models. If coordinates were not available in the paper, I entered the study site name into Google Earth (version 7.3.0.3830) and took the coordinates for the point chosen by the search (usually the mid-point) to include in the map. To investigate preference for study site locations I created an equal number of random points as there were study sites (N = 171) across the combined geographic range of all galagids and used logistic regression models with location (study site or random) as the dependent variable. I used data on local human population density as a measure of accessibility (Reddy and Dávalos, 2003; Botts et al., 2011; Hugo and Altwegg, 2017; Yarwood et al., 2019). I also investigated mean annual temperature, elevation and rainfall, as potential factors in choosing study locations. I projected all locations to the Africa Equal Area Conic projection, and created a 100 km buffer around the study sites and random locations to assess environmental variables in the areas surrounding study sites (Hawes et al., 2013).

I downloaded human population density (humans/km^2) raster data from near the mid-point of the survey period (2000) from the Socioeconomic Data and Applications Centre (SEDAC; https://sedac.ciesin.columbia.edu/gpw; 1 x 1 km resolution; on 9th September 2020). I also investigated mean annual temperature, elevation and rainfall, as potential factors in choosing study locations. I downloaded raster data for each covariate (mean annual temperature [°C]; annual precipitation [ml]; and digital elevation [m]) for the years 1970–2000 from WorldClim (https://www.worldclim.org; 1 x 1 km resolution; on 9th September 2020). I projected all rasters to the Africa Equal Area Conic projection and calculated the mean value for each of the buffers to use in analysis. Mean annual temperature and mean elevation were highly negatively correlated (R = -0.815) so I only used mean annual temperature in the analysis. I used logistic regression models with location (study site or random) as the dependent variable and mean annual temperature, mean precipitation and mean human population density as covariates. I chose the model with the lowest AIC score as the best model and report the performance statistics (McFadden's pseudo R^2 and associated *P*-value) for the model and for each covariate: the coefficient; standard error; 95% CI; *z*-statistic; *P*-value; odds ratio; and 95% CI for the odds ratio.

2.2.2.3 Topics of behaviour and ecology studied

I used broad categories of behaviour and ecology (behavioural ecology; habitat and distribution; physiology; and genetics and taxonomy) to provide a general overview of the types of studies, but also identified specific topics researched within those categories. To highlight the most common topics studied I conducted text mining using the package 'tm' in R (Fienerer, 2020) to extract the 30 most common words used in abstracts and keywords, including any abbreviations stated below abstracts. I converted all text to lower case and removed all variants of 'galagid', 'bushbaby', species and genera names, and any other words not related to behaviour or ecology. I removed all punctuation, white space and numbers. I stemmed words to avoid repetition (e.g. 'social' combines 'social', 'sociality' and 'socially') and for each of the 30 most used stemmed words I include the un-stemmed words in Appendix 2B. If any of the top 30 stemmed words used groupings that were not semantically similar, I separated them. This was the case for two stemmed words; I split 'activ' into 'active' (active / activities / activity / activity-dependent) and 'activate' (activate / activated / activating / activation / activations), and 'later' into 'later' (later) and 'lateral' (lateral / lateralis / lateralised / laterality / lateralization / lateralized). I carried out all statistical tests in R version 4.0.3 (R Development Core Team, 2021).

2.3 Results

2.3.1 *Article inclusion*

The 96 search terms generated 2398 items in total (758 without duplicates; see Appendix 2A for breakdown of results for each search term). I included 339 based on one or more of our target words being present in the title (*N* = 179), abstract (*N* = 293) or the authors' keywords (*N* = 107). Of the 339, I excluded 25 meeting abstracts, a further 8 because the full texts were not accessible, a further 58 articles for not including primary data on galagids and 37 more for having no contribution towards understanding the behaviour and ecology of galagids, leaving 211 for inclusion in the review (see Figure 2.1 for screening process, following Moher et al., 2009). There has been an increase in research into galagids from the late 1990s onwards (Figure 2.2) and the maximum number of studies published on galagid behaviour and ecology in any year (2016) was 13 (median = 4; IQR = 4.8).

2.3.2 *Author affiliations*

Of the 211 studies, 63 (29.9%) were carried out by at least one author affiliated with an organisation based in a galagid range country. Of these 63, 36 involved international collaboration between researchers from galagid range countries and non-range countries. At least one author from a USA-based affiliation contributed to 132 studies (62.6%), at least one South African affiliation was connected to authors of 42 studies (19.9%) and at least one UK affiliation featured in 32 studies (15.2%). At least one author from an institution based in Germany contributed to 20 studies (9.5%) and affiliations from all other countries were connected to fewer than 10 studies.

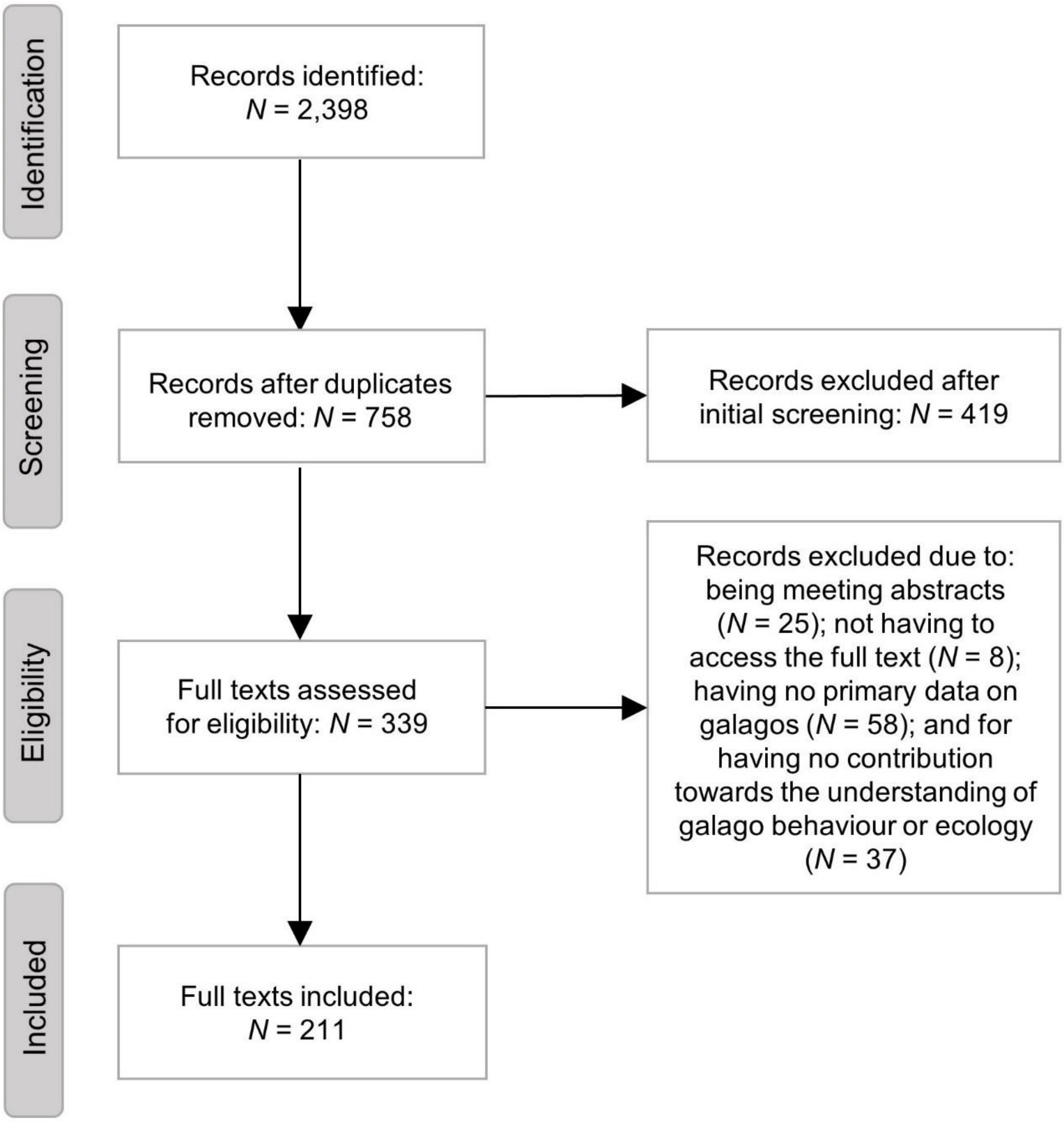

Figure 2.1 The screening process I used to review papers on galagid behaviour and ecology from January 1971 to December 2020.

2.3.3 *Sample type*

There were far more studies on captive galagids than any other sample type (47.4%; *N* = 100). Data on wild individuals were included in 30.8% of studies (*N* = 65), 23.7% (*N* = 50) included data from museum-type specimens and very few used bioinformatic data (1.9%; *N* = 4). For 1.4% of studies (*N* = 3) it was unclear which type of sample was used. The number of research outputs on wild populations increased at a faster rate in the last 5 years than the years before (see Table 2.1 and Figure 2.2).

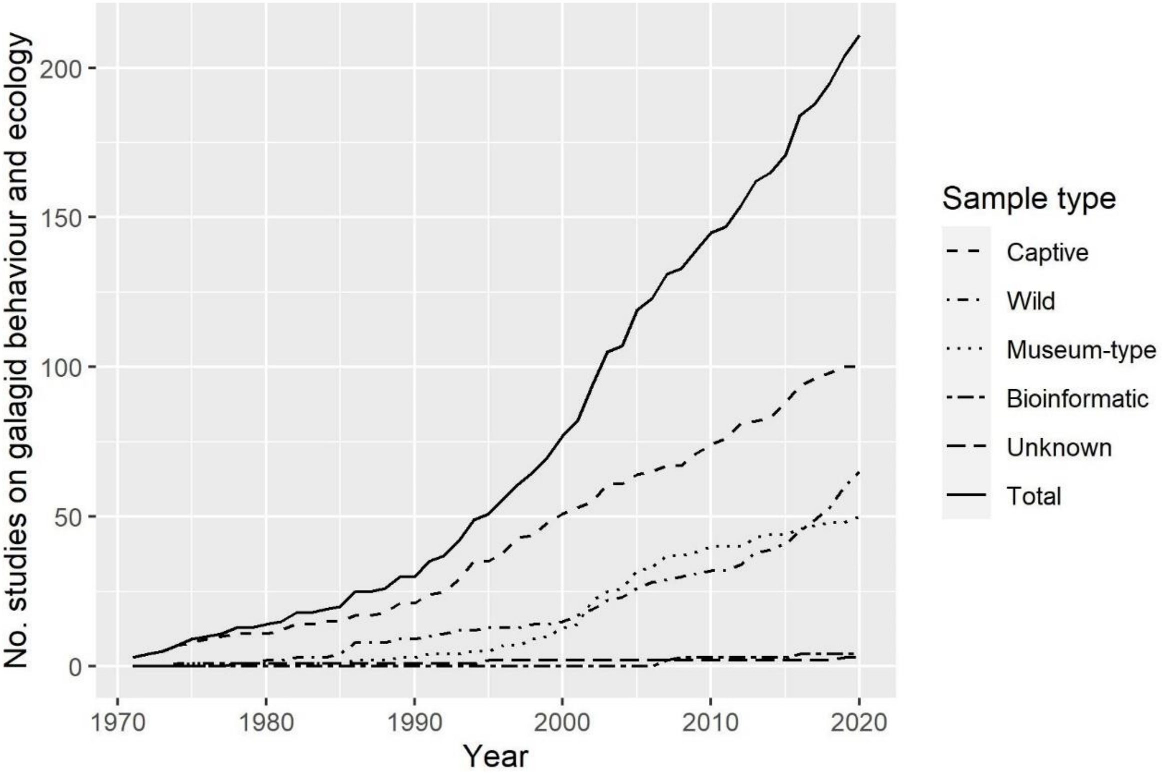

Figure 2.2 The number of research articles on galagid behaviour and ecology using captive, wild, museum-type, bioinformatic and unknown samples of galagids published between January 1971 and December 2020. The solid line denotes the cumulative number of studies.

2.3.4 *Taxonomic bias*

Species within the genus *Otolemur* featured in the majority of research outputs, and far more than other species (78.2%, *N* = 165; *Euoticus*: 13.3%, *N* = 28; *Galago*: 66.4%, *N* = 140; *Galagoides*: 20.9%, *N* = 44; *Paragalago*: 22.3%, *N* = 47; *Sciurocheirus*: 15.2%, *N* = 32; these values include outputs on unknown species within genera - see Table 2.1 for total outputs per individual species). Thirteen species featured in fewer than 20 publications and eight species were studied fewer than ten times. The number of studies on each genus using different sample types is in Figure 2.3. Three species of *Sciurocheirus* (*S. cameronensis*, *S. gabonensis* and *S. makandensis*) were vastly underrepresented, with *S. cameronensis* and *S.*

makandensis featuring in fewer articles than the recently described *Gd. kumbirensis* (described in 2017 by Svensson *et al*., 2017).

Table 2.1 The total number of research articles on galagid behaviour and ecology published between January 1971 and December 2020, the conservation status and reference to IUCN Red List web pages for each species. There is currently no IUCN Red List status for *Sciurocheirus cameronensis*.

Species	No. research outputs	IUCN status	Reference
Euoticus elegantulus	21	LC	(Oates and Butynski, 2019)
Euoticus pallidus	6	NT	(Cronin et al., 2020)
Galago gallarum	11	LC	(de Jong and Butynski, 2019)
Galago matschiei	11	LC	(Butynski and de Jong, 2019a)
Galago moholi	61	LC	(Bearder et al., 2019)
Galago senegalensis	55	LC	(de Jong et al., 2019b)
Galagoides demidovii	27	LC	(Svensson et al., 2019)
Galagoides kumbirensis	3	NT	(Svensson et al., 2020a)
Galagoides thomasi	12	LC	(Svensson and Bearder, 2019)
Otolemur garnettii	85	LC	(de Jong et al., 2019c)
Otolemur crassicaudatus	78	LC	(Masters and Bearder, 2019)
Paragalago cocos	5	LC	(Butynski and de Jong, 2019b)
Paragalago granti	10	LC	(de Jong et al., 2019a)
Paragalago orinus	7	VU	(Perkin, 2021)
Paragalago rondoensis	5	EN	(Perkin, 2020)
Paragalago zanzibaricus	19	NT	(Perkin et al., 2020b)
Sciurocheirus alleni	26	NT	(Perkin et al., 2020a)
Sciurocheirus cameronensis	1	NE	-
Sciurocheirus gabonensis	3	LC	(Oates, 2019)
Sciurocheirus makandensis	2	DD	(Svensson et al., 2020b)

IUCN Red List abbreviations used above: ‘LC’ = Least Concern, ‘NT’ = Near Threatened; ‘VU’ = Vulnerable; ‘EN’ = Endangered; ‘DD’ = Data Deficient; ‘NE’ = Not Evaluated.

The best negative binomial model to predict the total number of research outputs per species included both body mass (g) and geographic range size (1000 km^2) (AIC = 137.17; McFadden's pseudo R^2 = 0.880; see Table 2.2) rather than body mass only (AIC = 143.73) or geographic range size only (AIC = 162.50). Incident rate ratios revealed that, holding other variables in the model constant, for every one unit increase in body mass (1 g) the total research output is expected to increase by a factor of 1.002 (95% CI = 1.001–1.003). Holding other variables in the model constant, for every one unit increase in geographic range size (1000 km^2) the total research output is expected to increase by a factor of 1.0002 (95% CI = 1.0001–1.0004). Because of the high number of captive studies on *Otolemur* spp., I also ran the models with captive studies removed and both predictors were still significant in the best model (body mass: P = 0.027; geographic range size: P = 0.010). However, when only studies on wild populations were considered, neither body mass or geographic range size were significant predictors of the number of research outputs per species (see Table 2.2).

Table 2.2 Results from the negative binomial regression models used to investigate taxonomic bias in 50 years of research articles on galagid behaviour and ecology. For each covariate I report the coefficient, standard error (SE), 95% confidence intervals (95% CI), *z*-statistic and approximate *P*-value.

Dependent variable	Covariate	Coefficient	SE	95% CI	*z*	*P*-value
Total studies per species	Body mass[1]	0.002	6.04E-04	7.27E-04 – 0.003	3.137	0.002**
	Range size[2]	2.20E-04	6.97E-05	8.56E-05 – 3.70E-04	3.151	0.002**
Wild studies per species	Body mass[1]	5.84E-04	4.65E-04	-3.15E-04 – 0.002	1.256	0.209
	Range size[2]	9.60E-05	5.49E-05	-1.33E-05 – 2.09E-04	1.749	0.080

Data sources: 1. (Butynski et al., 2013); 2. www.iucnredlist.org

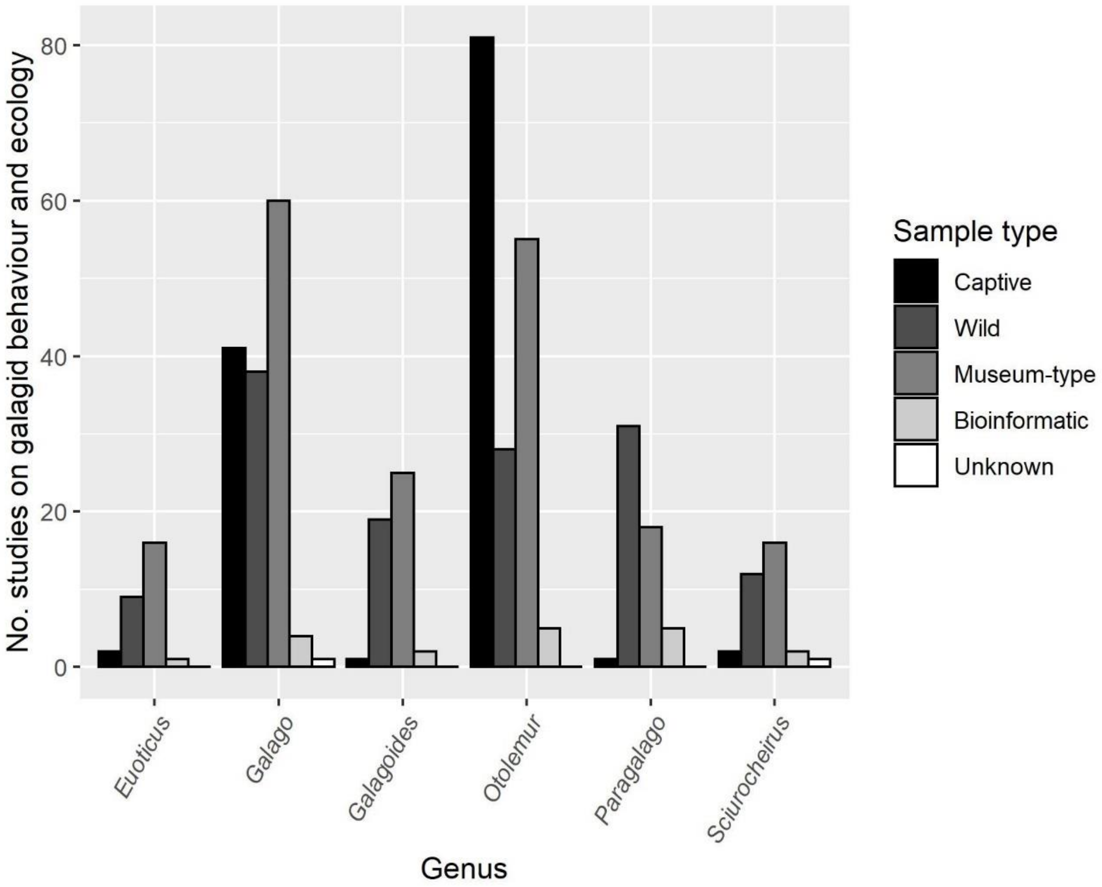

Figure 2.3 The number of research articles on captive, wild, museum-type, bioinformatic and unknown samples of each galagid genus published between January 1971 and December 2020.

2.3.5 *Geographic bias*

The included studies spanned 24 countries in Africa (60% of countries galagids are thought to inhabit). Twenty-four of the 65 studies on free-ranging populations included research on galagids resident to South Africa; 15 in Kenya; 12 in Tanzania; nine in Cameroon; six in Uganda and Malawi; four in Nigeria; three in Angola and Equatorial Guinea; two in Ethiopia, Gabon, The Gambia, Zambia and Zimbabwe; and one in each of: Botswana, Cote d'Ivoire, the Democratic Republic of Congo, Eswatini, Ghana, Mozambique, Namibia, Rwanda, Senegal and Togo (see Figure 2.4 for the number of studies per country and the distribution of all study sites). No studies on wild galagids were conducted in 16 countries they are thought to inhabit according to IUCN geographic range data. These countries are: Benin;

Burkina Faso; Burundi; Central African Republic; Chad; Congo; Eritrea; Guinea; Guinea-Bissau; Liberia; Mali; Niger; Sierra Leone; Somalia; South Sudan; Sudan. The distribution of study sites for each species are in Figure 2.5.

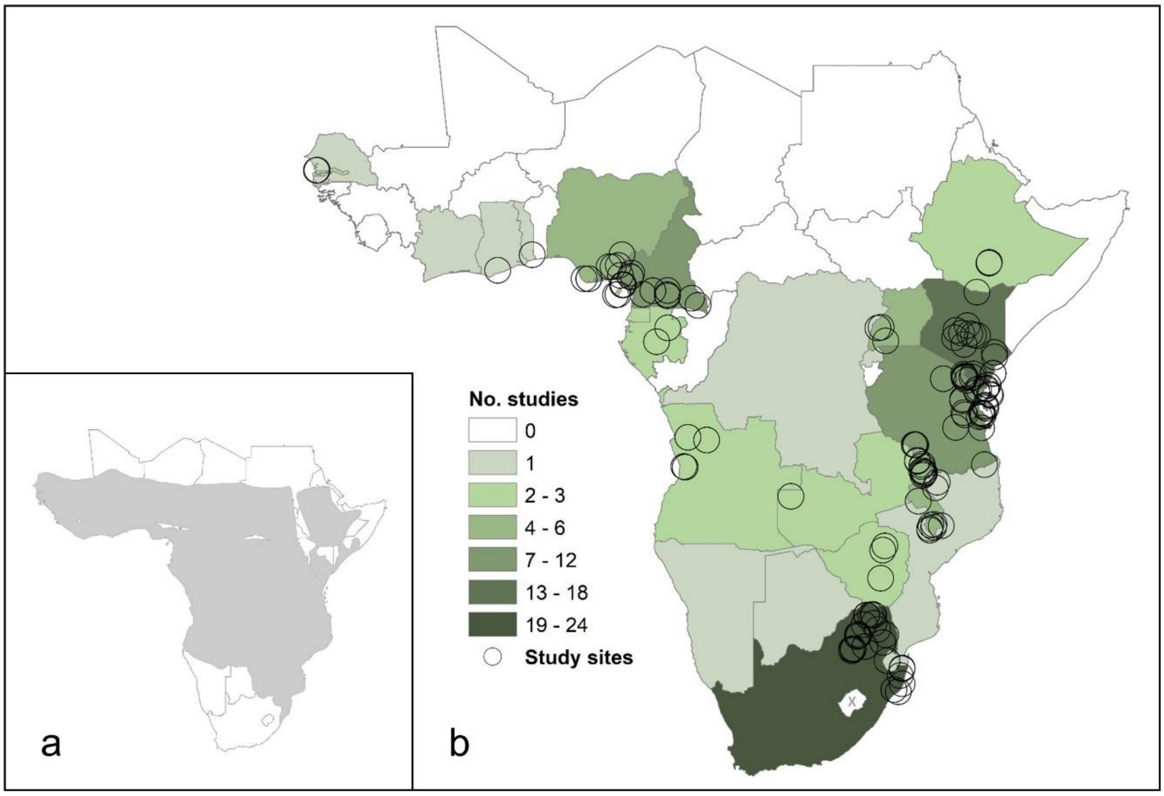

Figure 2.4 a) The combined geographic range of all galagids according to IUCN data; b) The number of research articles on galagid behaviour and ecology using wild samples from each country published between January 1971 and December 2020. White countries are those inhabited by at least one species of galagid according to IUCN geographic range data, but where no studies have yet been conducted. Lesotho is landlocked and therefore seen in the map above, marked with a grey cross because no free-ranging galagids are confirmed to be there based on IUCN data. South Sudan is also landlocked but the presence of one species, *Gd. thomasi*, is uncertain there (Svensson and Bearder, 2019) so I include it as a country galagids are thought to inhabit. The black circles mark the locations of study sites used to research galagids; for some studies there were several sites.

The best logistic regression model to predict study locations included mean annual temperature and mean human population density as covariates (AIC = 426.50; McFadden’s pseudo $R^2 = 0.113$; $P < 0.001$; see Appendix 2C for comparison of model performance). Mean human population density (humans/km^2; coefficient = 0.007; SE = 0.002; 95% CI = 0.004–0.011; $z = 4.010$, $P < 0.001$) and mean annual temperature (°*C*; coefficient = -0.233; SE = 0.044; 95% CI = -0.322 – -0.148; $z = -5.262$; $P < 0.001$) were significant predictors of galagid study locations compared to random locations. The odds ratio for mean annual temperature suggests that, holding other variables at a fixed value, for a one unit increase in temperature (1 °*C*) the odds of that location being chosen as a study site decreases by 20.8% (odds ratio = 0.792; 95% CI = 0.724–0.862). The odds ratio for mean human population density suggests that, holding other variables at a fixed value, for a one unit increase in human population density (humans/km^2) the odds of that location being chosen as a study site increases by 0.7% (odds ratio = 1.007; 95% CI = 1.004–1.011).

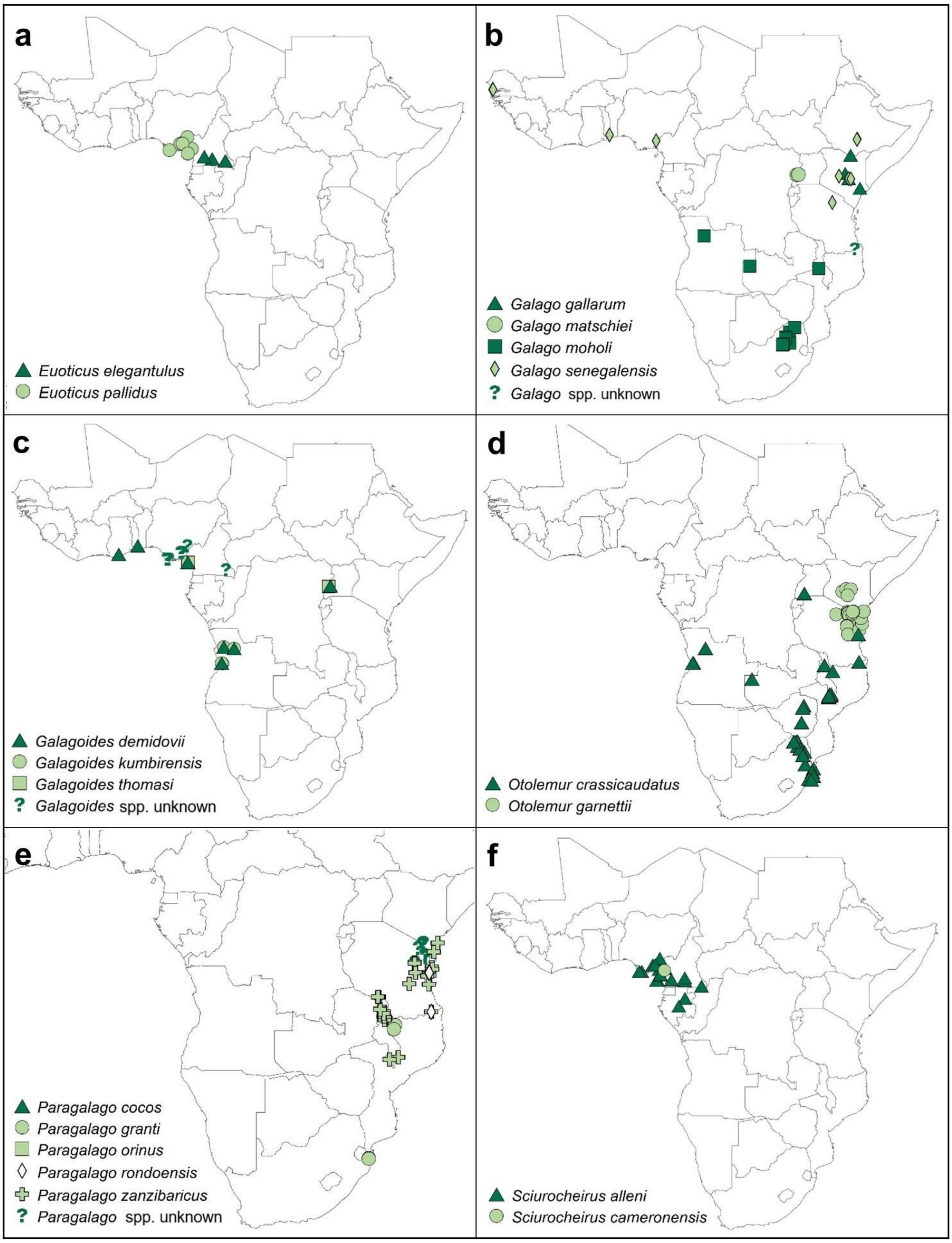

Figure 2.5 The location of study sites for each galagid species in research articles published between January 1971 and December 2020. I split any study sites for unknown dwarf galagid species into '*Galagoides* spp. unknown' or '*Paragalago* spp. unknown' based on the location and IUCN geographic range data.

2.3.6 *Topics of behaviour and ecology*

Of the 211 publications, I classified 116 studies as contributing to the knowledge of galagid physiology (55.0%), 100 to behavioural ecology (47.4%), 34 to genetics and taxonomy (16.1%) and 30 to habitat and distribution (14.2%; see Figure 2.6).

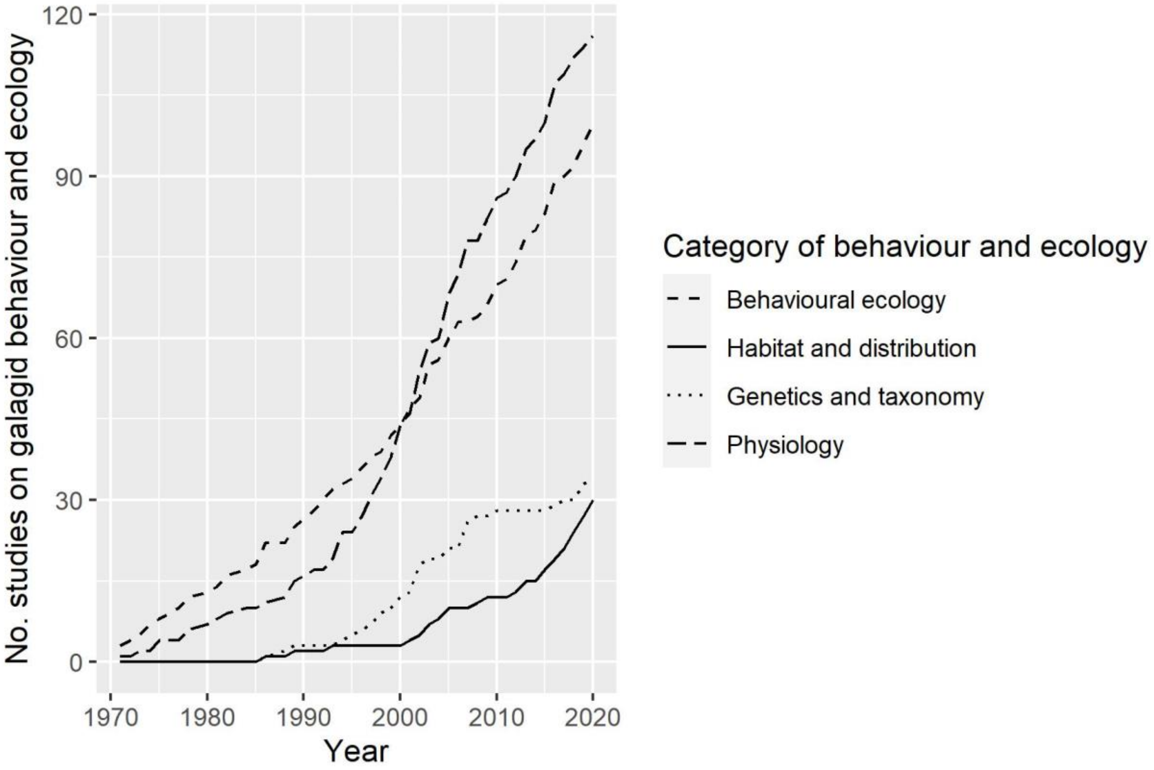

Figure 2.6 The number of research articles on each category of galagid behaviour and ecology published between January 1971 and December 2020.

Text mining revealed that the most common word used by researchers studying galagid behaviour and ecology was ‘behaviour’ (see Figure 2.7). Many words can refer to general areas of behaviour (e.g. ‘behaviour’, ‘activ*’, ‘social’), with some more focused on particular topics such as locomotion (e.g. ‘movement’, ‘muscle’, ‘force’). Galagid appearance and physiology were commonly referred to (e.g. ‘morpholog’, ‘bodi’, ‘function’) with brain research being a popular topic of study (e.g. ‘cortex’, ‘region’, ‘lateral’).

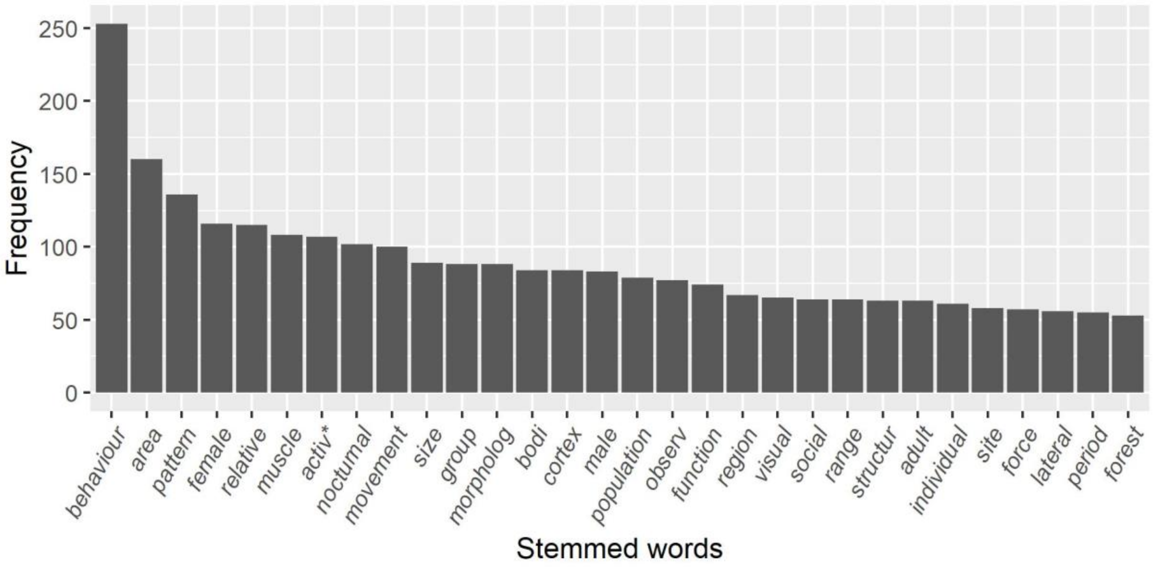

Figure 2.7 The 30 most used (stemmed) words in abstracts and keywords of research articles on galagid behaviour and ecology from January 1971 to December 2020. I excluded words not related to behaviour and ecology.

**'activ' refers to the following words: 'active', 'activities', 'activity', 'activity-dependent'; not: 'activate', 'activated', 'activating', 'activation', or 'activations'.*

2.4 Discussion

In 50 years of research, 211 articles contributed to the understanding of galagid behaviour and ecology. The total research effort on galagids was not equally distributed among the species, and was generally higher for those with a greater body mass and larger geographic range; we know far less about smaller and range-restricted galagids. However, neither variable was a significant predictor when only the number of wild studies for each species were considered. Studies on wild galagids were more abundant in areas with a greater human population density and lower temperatures, suggesting that the behaviour and ecology of galagids in rural areas and those with higher temperatures may be poorly understood. Captive galagids were researched far more than wild populations or museum-type specimens, therefore many of the findings on galagids may not apply to wild populations.

2.4.1 *Taxonomic bias*

Consistent with the literature on other animal groups (Bonnet et al., 2002; Bajomi et al., 2010; Trimble and Van Aarde, 2010; Hawes et al., 2013; Murray et al., 2015; Fleming and Bateman, 2016), I found a taxonomic bias in the literature on galagid behaviour and ecology. The total research effort was generally greater for species with a larger body mass (Brodie, 2009; Hawes et al., 2013; Brooke et al., 2014; Tensen, 2018; Ducatez, 2019; Yarwood et al., 2019; dos Santos et al., 2020) and larger geographic range (Hawes et al., 2013; Brooke et al., 2014; Yarwood et al., 2019). Species of *Otolemur* were studied far more than any other species, with a large number of studies on captive populations of *Otolemur*; but both body mass and geographic range size were still significant predictors of research output when captive studies were removed. However, neither predictors were significant when only studies on wild populations were considered. There are a number of possible explanations for this. I have not accounted for the number of each species that exist in captive facilities or museums, which could have influenced the results. If species with larger body masses are more abundant in captivity and museums, it may be because they have been spotted with greater ease in the wild, and consequently captured more for zoos and museums. *Otolemur garnettii* are known for their loud vocalisations (Bettridge et al., 2019), making them more conspicuous than other species, which could have resulted in the abundance of *Otolemur* in captivity. Larger species such as *O. garnettii* may be easier to keep in captivity owing to their varied diet (Nekaris and Bearder, 2011) whereas specialists such as *E. elegantulus* (Nekaris and Bearder, 2011), which rely more on tree gum, may be more difficult to provide for in captivity. A further possible explanation is that larger species are intrinsically more popular and charismatic to researchers. Larger bodied animals are favoured by visitors to zoos over smaller animals (Ward et al., 1998; Moss and Esson, 2010), so it is possible that they were preferred model species by researchers, or that this knowledge encouraged captive facilities and museums to keep larger species that were therefore available for research.

For many animal species, geographic distribution and abundance are positively associated (Gaston, 1996; Blackburn et al., 1997), so species with larger geographic ranges may be more likely to be encountered. Our results suggest that species with larger geographic ranges have not necessarily had more studies on wild populations, but their larger spatial distributions have likely allowed a greater presence in captive facilities and museums than those with smaller ranges. It is important to note that the sample size (N = 17 species) was fairly small and a larger sample size, if available, would have increased the power of the models.

Understanding the behaviour and ecology of a species is essential for effective conservation management (Sutherland, 1998) and the conservation implications that arise from taxonomic bias should not be ignored. Of the six species classified as NT, VU, and EN, four (*P. rondoensis*, *P. orinus, Gd. kumbirensis and E. pallidus)* featured in fewer than 10 articles. Owing to their extinction risks, research on these species should be prioritised for their conservation. *Sciurocheirus cameronensis* has not been assessed by the IUCN Red List and must be done so in the near future. Many species of galagid are currently classed as Least Concern, even when very few studies have been conducted on those species (Table 2.1). This is concerning because species may not receive the conservation attention they need if categorised as Least Concern unnecessarily; Data Deficient may be more suitable for many species of galagid. Knowing so little about some galagid species has potentially devastating consequences for their conservation; understudied species may be at greater risk of extinction than those well studied, and could be more susceptible to 'silent' extinction (McKinney, 1999; Howard and Bickford, 2014).

2.4.2 *Geographic bias*

Geographic bias is present in the literature on galagid behaviour and ecology, as seen in other animal groups (Reddy and Dávalos, 2003; Botts et al., 2011; Kaschner et al., 2012; Archer et al., 2014; Roberts et al., 2016; Hugo and Altwegg, 2017; Bezanson and McNamara, 2019). In 50 years of research, just under half of the countries galagids are thought to inhabit were not represented. The most common country visited to research them was South Africa, followed by Kenya, Tanzania and Cameroon. West Africa, Central Africa and some areas of Southern Africa (Namibia, Botswana and Mozambique), are in urgent need of research on galagids for us to understand the requirements of populations and obtain sufficient knowledge to conserve them.

Studies on wild galagids were generally carried out in areas with a greater human population density, suggesting that accessibility is an important factor in choosing a study site, likely due to the abundance of roads, cities and other urban areas (Reddy and Dávalos, 2003; Botts et al., 2011; Hawes et al., 2013; Hugo and Altwegg, 2017; Yarwood et al., 2019). Some of the countries with few or no published studies may be considered as difficult to travel to for foreign researchers or unsafe due to ongoing conflict (Kieh and Mukenge, 2002; Aghedo and Osumah, 2015). In Angola for example, research on galagids has only been possible in recent years following the end of the war (Bersacola et al., 2015). Similarly, conducting research, particularly during the night, may be more difficult in countries home to potentially dangerous animals. It is also possible that researchers avoided areas for political reasons (Parnell et al., 2003; Hopkins and Nunn, 2007). It is likely that other factors such as gross domestic product (GDP) affect research output. GDP was positively associated with the number of papers a country produced on seabird distribution data (Mott and Clarke, 2018) and citation rates of conservation research are higher in countries of greater wealth (Meijaard et al., 2015).

Study site locations were in areas with cooler mean annual temperatures than random locations across the combined geographic range of all galagids. The combined range crosses the equator and stretches up to the southern end of the Sahara desert, supporting some of the highest temperatures in the world. This could explain why researchers of galagids preferred cooler sites that may not have posed as much physiological stress on the body as those in extremely hot areas. It would be beneficial to confirm that galagids are present in the warmer and more remote areas of their proposed ranges, and to investigate the coping strategies they adopt to survive under warmer conditions.

Collaboration with local researchers could help expand research to the less-studied areas and species (Reboredo Segovia et al., 2020). Less than one third (29.9%) of the studies on galagid behaviour and ecology were carried out by at least one author with an affiliation in a galagid range country. Just over half of those studies involved collaboration between researchers living in galagid range countries and those living in other parts of the world. Collaboration with local researchers can increase knowledge transfer and help to implement conservation policies (Stocks et al., 2016). By using the countries where the institutions are based in this review, I did not account for the possibility that researchers from galagid range countries may be affiliated with organisations in non-range countries.

For a better understanding of galagid behaviour and ecology, we must ensure that the study locations are representative of their whole geographic range, where feasible and safe to do so. Geographic sampling bias could skew the biological knowledge necessary for conservation management (Botts et al., 2011; Archer et al., 2014) and sampling previously unrepresented populations may lead to new discoveries about the behaviour of a species (Reddy and Dávalos, 2003). I hope that my results, particularly the distribution of study locations in Figures 2.4 and 2.5, can guide future research towards less-visited study areas if a target species is in mind.

2.4.3 *Sample type*

Although the greater galagos *O. crassicaudatus* and *O. garnettii* featured in the largest number of studies, most of those studies focused on captive or museum-type samples rather than wild populations. I found a similar pattern with all other genera except for *Paragalago*, in which the majority of the studies were on wild populations. With primate populations threatened with extinction on a global scale (Estrada et al., 2017) it is imperative that further research into the behaviour and ecology of *in situ* populations is carried out and that populations are monitored over the long term. I anticipate that advances in genetics and technology will lead to an increase in bioinformatic studies. Currently, due to the many taxonomic revisions within the galagids, the number of studies on each species may not be entirely accurate, particularly for those using captive or museum-type samples.

2.4.4 *Categories and topics of behaviour and ecology studied*

Physiology was the most common category of behaviour and ecology studied, followed by behavioural ecology. Galagid locomotion is of great interest (Off and Gebo, 2005; Ryan and Ketcham, 2005; Wright-fitzgerald et al., 2010), particularly the saltatory locomotion of the leapers (Aerts, 1998; Connour et al., 2000; Ryan and Ketcham, 2005; Huq et al., 2015, 2018; Haldane et al., 2016), which may have increased the number of studies on their physiology substantially. Correspondingly, three of the most common words used by researchers in abstracts and keywords were ‘movement’, ‘muscle’ and ‘force’, highlighting the abundance of studies on galagid locomotion.

‘Behaviour’ was the most commonly used stemmed word and researchers used ‘activ’ and ‘social’ more than most other words. Galagids are often described as ‘solitary foragers’ (Bearder, 1987, in Müller et al., 1999), but decades of research has highlighted elements of their social behaviour (Newell, 1971; Bearder and Doyle, 1974; Ehrlich, 1977; Clark, 1982a, 1982b, 1985; Harcourt and Nash, 1986; Nash and Harcourt, 1986; Bearder, 1999; Nekaris and Bearder, 2011; Svensson and Bearder, 2013), and the prominent use of the word ‘social’ is in accordance with this.

From the articles reviewed here, research on galagid habitat and distribution, and genetics and taxonomy, is much less frequent. Fewer studies contributed to the habitat and distribution category than any other category. Moreover, ‘ecology’, or a stemmed version of the word, was not one of the 30 most used words in abstracts and keywords. However, there has been a steady increase in studies on habitat and distribution in the last 20 years, following a similar pattern to the increase in the number of studies on wild populations, and some of the most commonly used words may indicate the study of wild populations (e.g. ‘population’, ‘range’, ‘area’, ‘region’). It is no surprise that taxonomic revisions within the Galagidae family have occurred in recent years and that further revisions are expected (Nash et al., 1989; Grubb et al., 2003; Masters et al., 2017; Svensson et al., 2017) when so few studies have investigated their genetics and taxonomy. It is possible that my choice of search terms influenced the number of papers on genetics and taxonomy. I did not include the words ‘genetics’, ‘taxonomy’ and ‘physiology’ as search terms because these were not the focus of my review, but this is unlikely to have biased the results because ‘physiology’ was still the most common category of behaviour and ecology studied.

A possible limitation with this review is that it does not include books and book chapters, without which we would know far less about this diverse group of animals. These types of sources often include overviews, summaries, and collated knowledge from researchers on the taxonomy, physiology, behaviour and conservation of each species (Alterman et al., 1995; Nekaris and Bearder, 2011; Butynski et al., 2013; Masters et al., 2013; Nekaris, 2013). Others investigated the behaviour and ecology of particular species of galagid in greater depth. For example, Charles-Dominique (1977) described the ecology and behaviour of galagids (*E. elegantulus*, *S. alleni* and *Gd. demidovii*) in Gabon in detail, including how these species live sympatrically along with two other nocturnal primates (pottos: *Perodicticus potto*; and Calabar angwantibos: *Arctocebus calabarensis*) by occupying separate ecological niches within the forest. The influence of predators on foraging in *G. moholi* is compared to that of the grey slender loris (*Loris lydekkerianus*) in Bearder et al. (2002).

There may also be some studies I did not find due to my chosen search criteria. Some may not be published due to issues such as small sample size, non-significant results, or other methodological handicaps (Pawar, 2003), but could have contributed to our knowledge on galagids. Due to known taxonomic bias within the Primate family (Bezanson and McNamara, 2019) it is possible that there is a publication bias, with studies on certain groups favoured over galagids. Galagid research may also be reported in the grey literature, on websites, in languages other than English and in technical reports. However, I did not find any evidence of technical reports or studies in non-English languages during my literature search. For future research, it would be interesting to investigate whether the books and any other sources on galagid behaviour and ecology support or contradict the findings in this review.

2.4.5 *Conclusion*

Taxonomic and geographic bias in research effort skews our knowledge of animal behaviour and ecology, presenting challenges for conservation. In the case of the galagids, research is urgently needed on the smaller and range-restricted species. Further research on galagid behaviour and ecology is needed across most of sub-Saharan Africa, and urgently in West, Central and some Southern African countries. Logistical and financial constraints can understandably compromise the questions researchers are able to answer and the animals they can study to answer those questions. Unfortunately, as a result, our understanding of animal behaviour and ecology is skewed and limited, but there is potential for a wealth of new discoveries. Researchers may inevitably continue to show bias for particular species or study sites, but I hope that my review can act as a guide to direct future research on galagids and alleviate some of the biases found here.

2.5 References

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Chapter 3. Sociality and diel temporal variation in the activity of Northern lesser galagos

Abstract

The ancestral primate was most likely small and nocturnal; studying the behaviour of nocturnal primates is therefore fundamental to understanding the evolutionary origins of primate behaviour and ecology. Galagids, like most nocturnal primates, are generally thought to be solitary foragers. However, there is increasing evidence to suggest that they live in social networks, connected through different modes of communication and group-sleeping. I investigated group size, communication and social interactions in free ranging Northern lesser galagos, and present the first activity budget and assessment of temporal variation in their behaviour. I collected continuous behavioural data using focal follows at three different stages of the night from the population at Kwakuchinja. I also collected group size data from Northern lesser galagos at Fongoli and LHR. I 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. I analysed 140 focal follows (31.4 hours 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 most prevalent in the evening. Group size at Kwakuchinja was significantly larger than at Fongoli or LHR. Galagos were in groups of 2 or more in the majority of encounters at Kwakuchinja (55.4%; *N* = 76) rather than alone, but spent most of their night time activity alone at Fongoli (79.4%; *N* = 185) and LHR (79.8%; *N* = 142). Only a small proportion of their time involved observable social behaviours, and both affiliative and agonistic social interactions were recorded. My preliminary investigation into the social structure of Northern lesser galagos suggests that they connect through infrequent social interactions and communicate using vocalisations and olfactory signals, whilst avoiding some of the potential costs associated with group-living.

Keywords: *behavioural ecology, bushbaby, consolation behaviour, Galagidae, strepsirrhine*

3.1 Introduction

Primates exhibit a range of social systems and structures with considerable inter- and intra-specific variation. 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 social living is a response to increased predation risk during the day (Van Schaik, 1983). Diurnal primate species predominantly live in groups, but social complexity is not limited to these gregarious species (Clark, 1985; Poindexter and Nekaris, 2020). 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). Quantifying group size may be the easiest way to measure animal sociality (Reiczigel et al., 2008), but observations of social behaviour, interactions and sleeping associations enhance our understanding of social relationships within a species (Kutsukake, 2009; Clark, 1985; Poindexter and Nekaris, 2020).

Studying nocturnal primate behaviour can contribute to the understanding of our earliest primate ancestors, which were also likely small (Soligo and Martin, 2006) and nocturnal (Ross et al., 2007). However, very few studies have been published on the behaviour and ecology of galagids (Nekaris and Bearder, 2011; Chapter 2), and activity budgets are scarcely reported in the literature (Nekaris and Bearder, 2011). Researching nocturnal primate sociality is particularly problematic because behaviours are difficult to perceive in low light levels and many interactions occur via auditory or olfactory signals, which can be challenging to measure (Sterling et al., 2000). Furthermore, nocturnal primates do not use facial expressions to convey information to the same degree as some of their diurnal counterparts (Newell, 1971; Burrows et al., 2016).

When nocturnal research is so challenging, and sociality is often measured by recording group sizes, it is not surprising that many researchers do not consider galagids to be highly social compared to other primate groups (e.g. Shultz et al., 2011). However, many species have been observed sleeping with others during the day, with groupings of up to 9 individuals recorded in Eastern dwarf galagos and 10 individuals in Demidoff’s dwarf galagos (see Svensson et al., 2013 for a review). Researchers have also observed grouping when galagids are active, with some individuals spending a large proportion of their time with others. For example, Northern lesser galagos in The Gambia were in groups of at least two in 60% of encounters (Svensson and Bearder, 2013), and one female large-eared greater galago (*Otolemur crassicaudatus*) spent approximately 50% of observed time with others (Harcourt, 1980, in Nash and Harcourt, 1986). Rather than solitary animals, some researchers prefer the term ‘solitary foragers’ (Bearder, 1987, in Müller et al., 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 (Chapter 2), 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 and Doyle, 1974; Nekaris and 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 mobbing potential predators (Zimmermann, 1985, 1989; Nash and Harcourt, 1986; Bearder, 1999; Bearder et al., 2003; Becker et al., 2003a; Becker et al., 2003b; Nekaris and Bearder, 2011; Bettridge et al., 2019). Like many nocturnal strepsirrhines (Drea et al., 2019), galagids have a moist rhinarium and olfactory communication is very important for marking territories and assessing the sex and age of conspecifics (Newell, 1971; Bearder and Doyle, 1974; Charles-Dominique, 1977; Katsir and Crewe, 1980; Clark, 1982a; Clark, 1982b).

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

Affiliative social behaviours are far more common and long lasting than agonistic behaviours in free-ranging large-eared greater galagos (Clark, 1985), but agonistic social behaviours have been recorded in many species, primarily from those kept in captivity. In captive large-eared greater galagos these range from ‘low intensity’ behaviours such as chasing and tail-pulling to ‘high intensity’ attacks involving vigorous fights and pulling hair out (Newell, 1971; Ehrlich, 1977). Similar high intensity attacks were observed in Southern lesser galagos in the laboratory, but agonistic interactions were far less common in the wild and did not appear to be as severe (Bearder and Doyle, 1974).

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 and Bearder, 2013). My primary aim was to investigate sociality in Northern lesser galagos by using group size as a quantitative measure of sociality (Reiczigel et al., 2008), and to record observations of vocal and olfactory communication and social interactions. There is very little basic information on the behaviour and ecology of Northern lesser galagos. My second aim was therefore to provide an activity budget and assess temporal variation in activity.

3.2 Methods

3.2.1 Study sites

The first part of the study took place over eight weeks from July to August 2016 and three weeks in July 2017 at Kwakuchinja (section 1.8.1 of Chapter 1). I also obtained group size data from Fongoli (section 1.8.2 of Chapter 1) between March and May 2018 and LHR (section 1.8.3 of Chapter 1) in June and July 2018.

3.2.2 Data collection

3.2.2.1 Group size

At Kwakuchinja I collected group size data when carrying out focal follows, which are detailed in section 3.2.2.2 below. I collected group size data during line transect surveys on foot and by motorbike at Fongoli, and by car in LHR (see section 5.2.2.1

of Chapter 5 for detailed description). I considered individuals within 20 metres of each other to be in the same group.

3.2.2.2 Focal follows

At Kwakuchinja I conducted focal follows, assisted by at least one other researcher. We located Northern lesser galagos using torches fitted with red filters (Finley, 1959) and collected behavioural data using continuous sampling of focal individuals (Altmann, 1974) at three different stages of the night. In the 'morning' (pre-dawn: 05:30–07:00 h) we located galagos and aimed to stay with them until they returned to their nest sites. Each 'evening' (from dusk: 18:30–20:00 h) we revisited one known nest site to observe the waking behaviour of focal individuals and then followed for as long as possible, and later in the night ('night' hereafter; 20:30–22:30 h) we located and observed galagos across the study site. We visited different areas across the study site each night to ensure an even sampling effort. Focal follows began when we first spotted a Northern lesser galago and were able to observe their behaviour. We recorded behaviours continuously, noting the distance to any other individuals within 20 metres of the focal individual ad hoc. Due to the visual restrictions of night work, all behavioural data were recorded 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 minutes, 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). I was not able to collect such detailed behavioural data at Fongoli and LHR due to time constraints and safety restrictions.

We used the following behavioural categories to record state behaviours, which we mostly pre-determined using a short pilot study: 'crawl'; 'sleep'; 'still'; 'scratch'; 'stretch'; 'scan environment'; 'watch observer'; 'forage' (including feeding; arthropods or tree plant exudates); 'self-groom'; 'allogroom' (directed or received); 'scent mark'; 'urine wash'; 'play'; 'chase'; 'stare'; 'freeze'. I categorised all behaviours into the following: 'antipredator'; 'foraging'; 'inactive'; 'locomotion';

‘olfaction’; ‘self-maintenance’; ‘social: affiliative’; ‘social: agonistic’; ‘vigilance’. A full ethogram of the behaviours is shown in Table 3.1.

I 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 tree); ‘trunk-leaps’ (from the trunk of one tree to another tree); and ‘ground-leaps’ (across the ground or to a tree from the ground). We recorded the number of each 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.

3.2.2.3 Vocalisations

I quantified vocalisations using counts of behavioural events: ‘honks’ (Svensson et al., 2019); or ‘other vocalisations’ for any Northern lesser galago vocalisation other than a honk. If galagos vocalised again within 5 seconds of the last call I counted that as one ‘bout’. I analysed vocalisations separately to the activity budgets and recorded all vocalisations heard during focal follows, not just those of the focal individual, as it was difficult to determine which galago was vocalising.

3.2.3 Data analysis

3.2.3.1 Group size

I used Kruskal-Wallis tests to assess 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 (morning/evening/night) at Kwakuchinja).

3.2.3.2 Activity budget

I included all focal follows in the overall activity budget for the morning, evening, night, and total. For additional analysis, I only included focal follows with a duration of ≥30 seconds. For each focal follow I 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 duration. Although not a natural behaviour, I 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. I tested all variables for normality using the Shapiro-Wilk test and no variables were normally distributed (*P* <0.001). Consequently, I used Kruskal-Wallis tests to assess significant differences in the ranks of activity across the three periods of the night. For any significant results I used Dunn's tests for multiple comparisons to compare the ranks between groups, which retains the rank sums from the Kruskal-Wallis test (Dunn, 1964).

3.2.3.3 Locomotion

To investigate the types of movements used at different stages of the night, I totalled the number of times each individual leapt, crawled, canopy-leapt, ground-leapt and trunk-leapt. Because of the different lengths of the focal follows, I calculated the proportion of recorded movements for each individual followed for ≥30 seconds. The Shapiro-Wilk test revealed that none of the variables were normally distributed (*P* <0.001) so I used Kruskal-Wallis tests to assess significant differences in the ranks of the types of locomotion across the three periods of the night and used the Dunn's test for multiple comparisons where necessary.

3.2.3.4 Vocalisations

I 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 I also calculated the calling rate for each time period. To do this I 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. I did not exclude the time the focal galago spent sleeping or out of sight here because we recorded all Northern lesser galago vocalisations heard during focal follows.

3.3 Results

3.3.1 Group size

Active Northern lesser galagos were found in groups of 1–5 individuals at Kwakuchinja (mean ± SD = 1.79 ± 0.87 individuals) and Fongoli (mean ± SD = 1.28 ± 0.63 individuals), and in groups of 1–3 individuals at LHR (mean ± SD = 1.24 ±

0.50 individuals). There was a significant difference in the ranks of group size between the three populations (Kruskal-Wallis test: $H = 63.749$, $df = 2$, $P < 0.001$; see Figure 3.1). Dunn's post hoc tests revealed that group size was significantly greater at Kwakuchinja compared to LHR ($z = 7.04$, $P < 0.001$) 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 at Kwakuchinja (Kruskal-Wallis test: $H = 3.506$, $df = 2$, $P = 0.173$; morning: mean ± SD = 2.02 ± 1.01 individuals; evening: mean ± SD = 1.74 ± 0.82 individuals; night: mean ± SD = 1.66 ± 0.76 individuals).

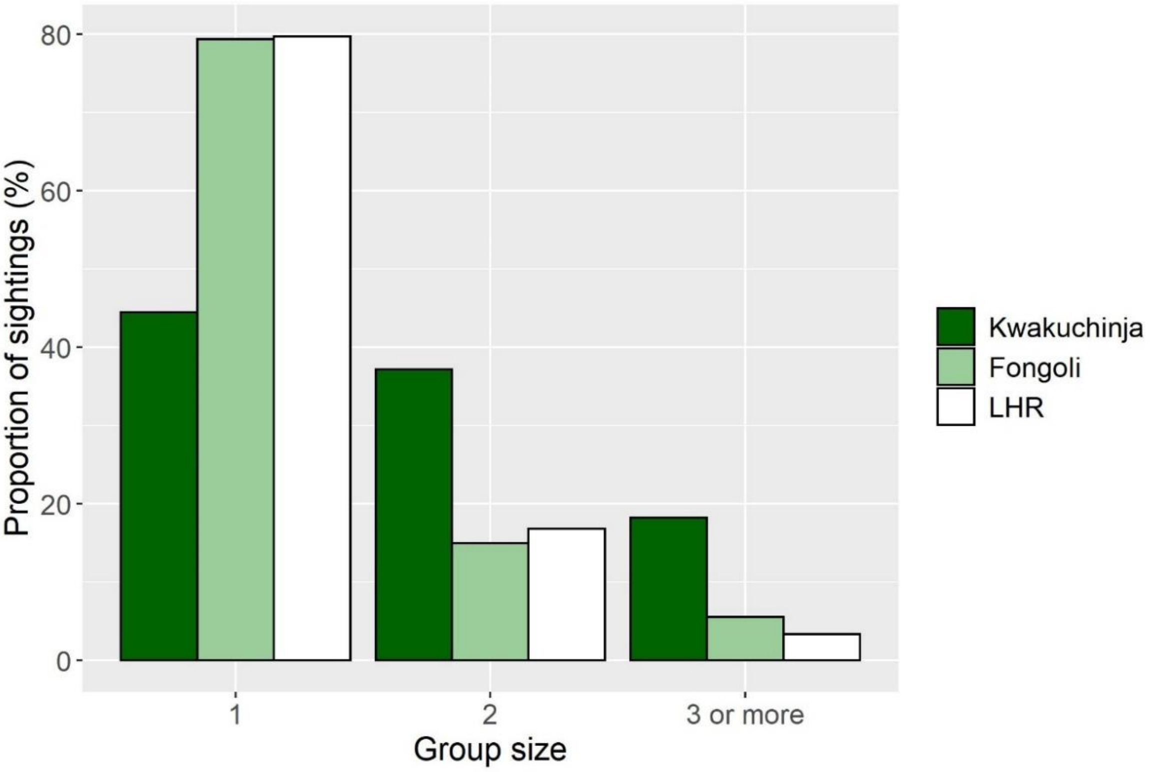

Figure 3.1 Group size of active Northern lesser galagos at Kwakuchinja in Tanzania, Fongoli in Senegal and Lolldaiga Hills Ranch (LHR) in Kenya.

3.3.2 Activity budget

In total, I carried out 180 focal follows. Of these, 140 had a duration ≥30 seconds (median duration = 6.4 minutes; IQR = 16.9 minutes; 31.4 hours of continuous behavioural observations in total) and were therefore included in the analysis. An ethogram for all observed behaviours is in Table 3.1.

Table 3.1 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 long duration (>10 seconds) when in the presence of a nearby potential predator (e.g. an African civet; *Civettictis civetta*).
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 also classed as foraging arthropods.
	Tree exudates (gum)	Licking and eating gum that exudes from tree bark using tooth comb on lower jaw (Bearder and Martin, 1980; Burrows and 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 in some area of the body, 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, prior to a chase.
Social: affiliative	Allogroom	Reciprocal licking exchanging salivary secretions. May be directed or received.
	Play	Tumbling over others, grabbing others, pulling and pushing others.
Vigilance	Scan environment	Moving head around to check different directions, sometimes assisted by head-cocking (rotating of head in response to novel object; Rogers et al., 1993).
	Watch observer	Looking towards ≥1 observer for more than two seconds, often assisted by head-cocking.
Vocalisation	Honk	Creating an advertising call consisting of a single, low pitched note uttered persistently at a regular tempo (Svensson et al., 2019).
	Unknown call	Creating a call that varies from that of a honk.

Northern lesser galagos spent the majority of their time exhibiting the following behaviours: vigilance (median 38.4%; IQR: 49.2%); inactive (median: 19.5%; IQR: 32.2%); locomotion (median: 15.8%; IQR: 26.4%); self-maintenance (median: 0.0%; IQR: 2.2%); and foraging (median: 0.0%; IQR: 0.0%; see Figure 3.2, Figure 3.3 and Table 3.2). Results from Kruskal-Wallis tests for these five behaviours are in Table 3.2 with the median, inter-quartile ranges and ranges. Of the vigilance behaviours, the majority were ‘scan environment’ (median: 25.8% IQR: 44.3%) rather than ‘watch observer’ (median: 0.0% IQR: 6.0%).

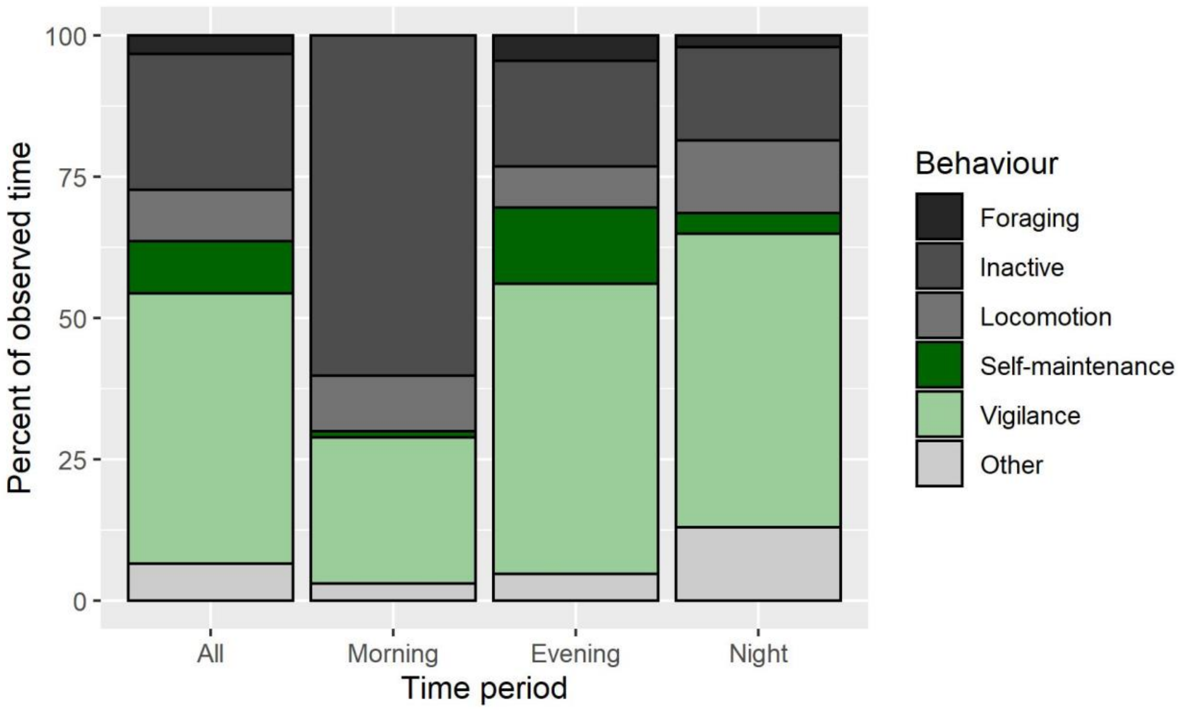

Figure 3.2 The percent of observed time Northern lesser galagos at Kwakuchinja were observed in each behaviour category. The category 'other' contains all other behaviours (antipredator; social: affiliative; social: agonistic; territorial; and unknown). Time spent sleeping or out of sight was not included.

Dunn's post hoc tests revealed that galagos were significantly more inactive in the morning than the evening (z = -4.09, P <0.001) or the night (z = 4.60, P <0.001). They foraged significantly more in the evening compared to 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 = -3.76, P <0.001). Galagos spent a significantly longer proportion of their time showing self-maintenance behaviours in the evening than the morning (z = 4.71, P <0.001) or 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 to the evening (z = 3.54, P <0.001) and night (z = -2.82, P = 0.002).

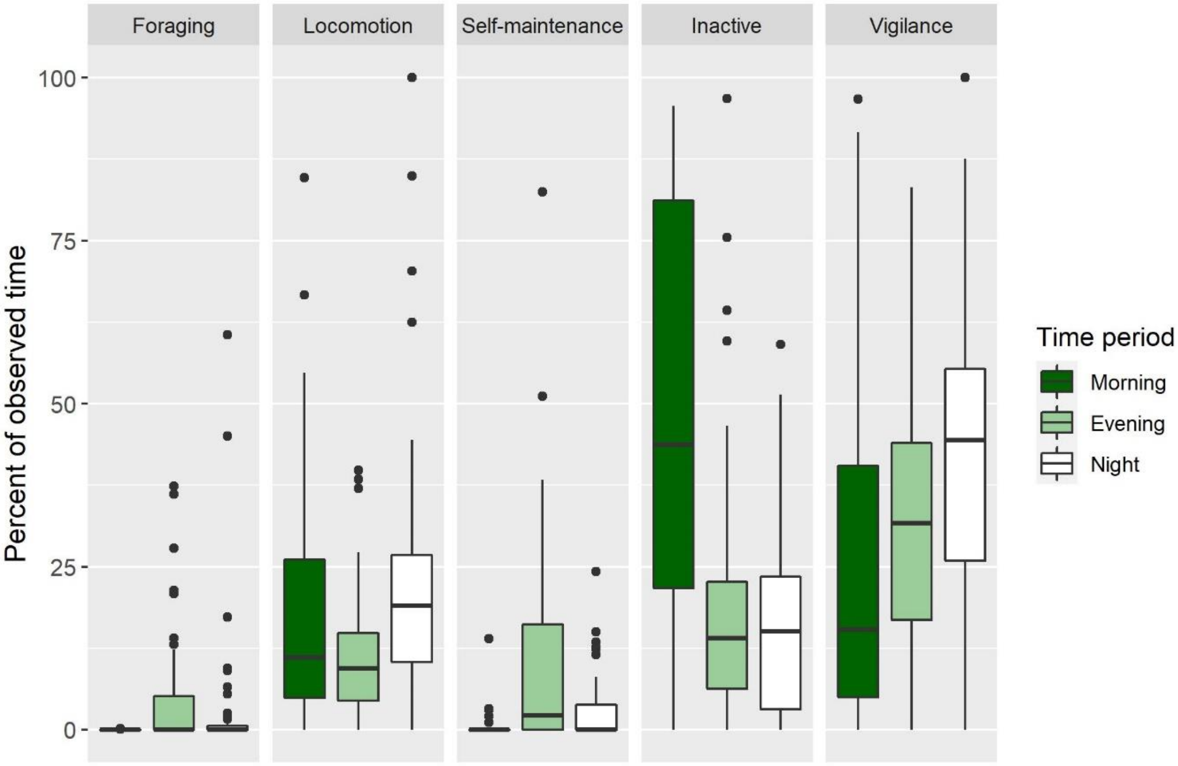

Figure 3.2 The differences in median and IQR of percent of observed time Northern lesser galagos spent showing each of the above behaviours in the morning, evening and night in June–July of 2016 and 2017 in Kwakuchinja, Northern Tanzania. The black dots represent outliers and the whiskers represent 1.5 × IQR.

3.3.3 Locomotion

Northern lesser galagos leapt (within one tree) and crawled more than any other type of locomotion (see Table 3.2). The use of some types of locomotion in the night varied from that used during the morning and evening. Galagos 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 leapt significantly more in the night than the morning (z = -2.46, P = 0.007) and evening (z = -2.34, P = 0.010).

Table 3.2 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 in June–July of 2016 and 2017. For each behaviour type I report the median (med), inter-quartile range (IQR) and range for the three periods of the night. I report the test statistic (*H*, 2 degrees of freedom) and *P*-value for Kruskal-Wallis tests between the ranks of behaviour for each time period.

	Morning			Evening			Night				
Behaviour	**med**	**IQR**	**range**	**med**	**IQR**	**range**	**Med**	**IQR**	**range**	***H***	***P***
Activity											
Antipredator	0.0	0.0	0.0–0.0	0.0	0.0	0.0–0.0	0.0	0.0	0.0–21.1	NA	NA
Foraging	0.0	0.0	0.0–0.2	0.0	5.1	0.0–37.4	0.0	0.6	0.0–60.6	19.67	<0.001***
Inactive	43.7	59.5	0.0–95.7	14.0	16.4	0.0–96.8	15.1	20.3	0.0–59.1	23.94	<0.001***
Locomotion	11.1	21.2	0.0–84.6	9.4	10.4	0.0–39.8	19.0	16.3	0.0–100.0	14.6	<0.001***
Olfaction	0.0	0.0	0.0–6.7	0.0	0.0	0.0–3.8	0.0	0.0	0.0–12.9	NA	NA
Self-maintenance	0.0	0.0	0.0–14.0	2.2	16.1	0.0–82.4	0.0	3.8	0.0–24.2	22.55	<0.001***
Social: agonistic	0.0	0.0	0.0–0.0	0.0	0.0	0.0–0.0	0.0	0.0	0.0–12.3	NA	NA
Social: affiliative	0.0	0.0	0.0–27.4	0.0	0.0	0.0–24.4	0.0	0.0	0.0–17.7	NA	NA
Vigilance	16.4	41.9	0.0–100.0	50.9	27.6	2.1–86.1	47.3	22.5	0.0–100.0	13.32	0.001**
Unknown	0.0	0.0	0.0–16.4	0.0	0.8	0.0–26.6	0.0	6.0	0.0–90.0	NA	NA
Locomotion type											
Canopy-leap	5.2	10.8	0.0–38.1	5.0	8.0	0.0–30.4	0.0	3.0	0.0–21.2	15.08	<0.001***
Crawl	25.0	25.7	0.0–100.0	24.6	14.9	8.3–100.0	27.0	16.0	0.0–80.0	0.01	0.993
Ground-leap	0.0	0.0	0.0–83.3	0.0	2.0	0.0–36.0	0.0	0.0	0.0–18.8	5.93	0.052
Leap	61.9	32.7	0.0–100.0	63.5	17.1	0.0–91.7	70.0	16.3	20.0–100.0	8.01	0.018*
Trunk-leap	0.0	0.0	0.0–2.6	0.0	1.0	0.0–17.2	0.0	0.0	0.0–11.8	4.23	0.121

3.3.4 Vocalisations

The total frequencies of bouts of honks and other calls heard every half hour are shown in Figure 3.4. The calling rate (combined bouts of honks and other) was 4.2 calls per hour in the morning, 0.9 per hour in the evening and 2.0 per hour at night.

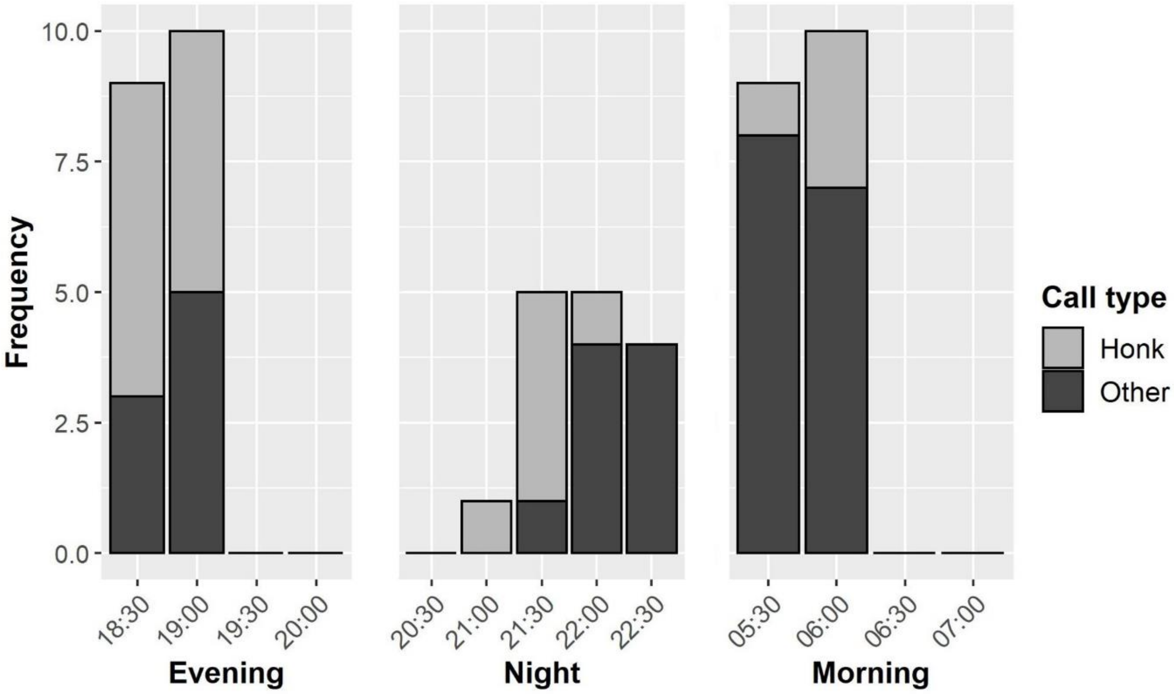

Figure 3.3 The total frequency of bouts of honks and bouts of other calls made by Northern lesser galagos each half-hour (e.g. '18:30' = 18:30–18:59) at Kwakuchinja in June–July of 2016 and 2017. I did not collect any data between the hours of 20:00–20:30 and 22:30–05:30, or during the day (07:00–18:30). The three time periods were not sampled equally.

3.3.5 Qualitative observations

I 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 (Preston and de Waal, 2002; de Waal and van Roosmalen, 1979). The observation happened on the 12th July 2017 during a waxing crescent moon and usual temperature of around 18 °C for the time of the night. I was with one other observer and one guard at the time. 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. A civet appeared approximately 4 metres away and stopped. It sat upright and looked in the direction of the galago. The galago crawled for 20 sec and then froze still with one arm close to the body and the other stretched out on the branch for 2 min 34 sec. The civet then moved off and out of sight, and the galago then leapt in the other direction, back to near the where the other two individuals were seen. After 1 min and 44 sec the galago began producing frequent ‘attention/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 a minute later a third individual was spotted within a few metres of the other two and three 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 sec. It was not possible to determine the focal individual after that but two galagos moved off together around 1 min later.

3.4 Discussion

3.4.1 Galagid sociality

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

There are likely several different factors affecting group size (Clutton-Brock and Harvey, 1977). One possibility is that resources (e.g. tree gum) could be limited at Kwakuchinja, which might encourage grouping. Small-eared greater galagos

(*Otolemur garnettii*), whose diet contains a greater arthropod component than large-eared greater galagos, are less often observed in groups, possibly due to insect foraging being more of a solitary activity (Nash and Harcourt, 1986). Alternatively, food resources could be more plentiful at Kwakuchinja; the group size of some primate species is constrained by resource availability (Chapman, 1990). The differences in habitat between the sites could have been a factor in group size, which again could have impacted resource distribution. The effect of ecological variables such as food distribution on group size has been studied intensively in (mostly diurnal) primates (Terborgh and Janson, 1986; Clutton-Brock and Janson, 2012) and other mammals (e.g. ungulates: Bowyer et al., 2020), and would be a very interesting area of further study on galagids.

The methods used to collect group size data could also have influenced the results. At Fongoli and LHR we relied on transects to collect group size data and therefore were not in as close proximity to galagos as we were in Kwakuchinja, which could have affected our ability to detect other galagos within 20 m of the one spotted. Alternatively, the difference could be due to differences between subspecies, with *G*. *s*. *sotikae* being naturally more social than *G*. *s*. *braccatus* and *G*. *s*. *senegalensis;* however, this is unlikely as *G. s. senegalensis* in The Gambia were predominantly observed in groups (Svensson and Bearder, 2013).

Observable social groupings are one indicator of animal sociality. Although some populations of Northern lesser galagos do not spend their time in close proximity to others, they should not be categorised as solitary animals; many other factors should be taken into account to understand their sociality. Vocalisations are important indicators of social behaviour in galagids, with many using calls to keep or regain contact with others (Zimmermann, 1985; Bearder et al., 2003; Becker et al., 2003a; Becker et al., 2003b). I found that Northern lesser galagos called at a higher rate in the morning than any other time, which was likely important for social cohesion when traveling back to sleeping sites (Bettridge et al., 2019). The night time 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 were often already with others and usually moved off in the same direction, and may not have needed to call to keep contact during that time.

In addition to vocalisations, olfactory communication is common in nocturnal strepsirrhines and allows communication without being in close proximity (Nekaris and Bearder, 2011; Drea et al., 2019). I observed scent marking and urine washing at each stage of the night, consistent with the behaviour of Allen's galagos (*Sciurocheirus alleni*) in Gabon (Charles-Dominique, 1977), but not as frequent. 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. This may be extremely important in Northern lesser galago sociality.

Although agonistic encounters are fairly common in studies on captive galagids (e.g. large-eared 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 and Doyle, 1974). The majority of social interactions recorded were affiliative, and although they only comprised a small proportion of the total time budgets, I observed play and allogrooming on many occasions involving both adults and infants, mostly when at sleeping sites (see also Nekaris and Bearder, 2011). To the best of my knowledge, these behaviours have not been recorded in wild Northern lesser galagos before but have been seen in captive populations during early development (Zimmermann, 1989; Nash, 2003). Play and allogrooming have also been observed in free-ranging populations of Southern lesser galagos (Bearder and Doyle, 1974) and large-eared greater galagos (Clark, 1985), but were not specifically recorded at sleeping sites.

In addition to the above social behaviours, I recorded one observation that resembled consolation behaviour. The behaviour observed was in response to an encounter with a potential predator (an African civet), not aggression from a conspecific, but the individual seemed extremely distressed, producing frequent 'attention/alarm' calls ("tjong": Zimmermann, 1989; Anderson et al., 2000; Schneiderová et al., 2016), and two uninvolved galagos appeared and engaged in allogrooming with the victim until the vocalisations stopped. Consolation is a very complex behaviour once thought to be unique to apes (Preston and 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 and

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 is evidence for galagids potentially interacting socially in a highly developed way.

Group-living should not define the social complexity of galagids (Clark, 1985; Poindexter and Nekaris, 2020). My study supports the possibility that they 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). It is important to note that there may have been observer effects on the galagos' perceived sociality. For example, the galagos researched in this study were not habituated and the presence of researchers may have reduced their social time.

3.4.2 Activity

I presented the first activity budget for free-ranging Northern lesser galagos and found that their behaviour varied between different stages of the night. 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 leapt 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 location.

Northern lesser galagos, along with some other galagid species, are known for their characteristic saltatory (leaping) locomotion (Napier and Walker, 1967; Crompton et al., 1993; Sellers, 1996; Aerts, 1998; Crompton and Sellers, 2007; Shapiro, 2007; Nekaris and Bearder, 2011; Huq et al., 2015, 2018). By categorising their leaping locomotion into leaps (within one tree), ground-leaps (across the ground or to a tree from the ground), trunk-leaps (from the trunk of one tree to another tree) and canopy leaps (from the canopy of one tree to another tree) I was 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. I observed individuals canopy-leaping between trees more than 6 metres apart on several occasions, making them very difficult to follow and supporting the idea that leaping evolved for predator avoidance (Crompton and Sellers, 2007).

Foraging behaviour has been a focus of a number of studies on galagids (Bearder and Martin, 1980; Clark, 1985; Harcourt, 1986; Nash and Whitten, 1989; Butynski and de Jong, 2004; Scheun et al., 2014). Unfortunately, I did not collect enough data to study the diet of Northern lesser galagos in detail, but we observed them eating tree exudates, or ‘gum’ (Bearder and Martin, 1980; Clark, 1985; Nash and Whitten, 1989; Butynski and de Jong, 2004; Nekaris and Bearder, 2011; Svensson and Bearder, 2013; Scheun et al., 2014; Génin et al., 2016), and arthropods (Clark, 1985; Nash and Whitten, 1989; Butynski and de Jong, 2004; Nekaris and Bearder, 2011; Svensson and Bearder, 2013; Scheun et al., 2014; Génin et al., 2016). On some occasions individuals used our torchlight to their advantage and caught flying arthropods attracted to the beam of the light. Unlike some other species (Nekaris and Bearder, 2011; Scheun et al., 2014) and a population of Northern lesser galagos in The Gambia (Svensson and Bearder, 2013), I did not observe galagos eating fruit (Nash and Whitten, 1989). However, our study was limited to the dry season (June to July), and their diet may change throughout the year (Harcourt, 1986) perhaps with the addition of available fruit. The most important time for Northern lesser galagos to forage is the evening, soon after leaving sleeping sites, but foraging was also prevalent later in the night. We observed very little foraging in the morning, when individuals seemed to be either fixated on moving swiftly to their sleeping sites or settling in to them.

Vigilance behaviours are obviously of great importance to Northern lesser galagos as they comprise a large proportion of the activity budgets in my study. They were less vigilant during the morning observations compared to 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 galagos feel secure when settled in to their sleeping sites in the morning but remain alert for a short while before sleep. We know very little about galagid predation but potential predators are aerial (e.g. birds of prey), terrestrial (e.g. small carnivores such as African civets; *Civettictis civetta*), and scansorial animals (e.g. snakes and genets; Burnham et al., 2012). Because predators approach from above, below and within trees, it is understandable why Northern lesser galagos spend so long being vigilant, and in particular, scanning the environment. We note that although we kept in ‘watch observer’ as a vigilance behaviour, the majority of vigilance behaviours were ‘scan environment’.

Self-maintenance behaviours increase the well-being of the individual and keep the body in a good condition (Bolhuis and Giraldeau, 2005), and in our study these included self-grooming, stretching and scratching. I 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 aforementioned 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.

3.4.3 Future research

This study is limited in that I was not able to follow galagos for a longer period of time or compare between the different seasons (Diete et al., 2017). I also did not observe galagos later at night or in the early hours of the morning (22:30–05:30 h) so I have no data on their behaviour at that time. It is vital that future research on galagid activity takes all hours of darkness into account if possible so that valuable observation data on activity and social behaviour is not missed.

The influence of the level of moonlight on Northern lesser galago behaviour would be another important future avenue of study, as moonlight was positively associated with foraging activity in Mysore slender lorises (*Loris lydekkerianus lydekkerianus*), and increased the travel speed but decreased the night range length of male Southern lesser galagos (Bearder and Nekaris, 2002). Foraging behaviour and predator avoidance were also influenced by moon phase in spectral tarsiers (*Tarsius spectrum*: Gursky 2003).

Understanding the ranging behaviour of Northern lesser galagos is important for their conservation and would provide further insights into their sociality; observations on ranging behaviour have contributed to understanding the social organization of free-ranging Zanzibar galagos (*Paragalago zanzibaricus*) and small-eared greater galagos (Harcourt and Nash, 1986; Nash and Harcourt, 1986). Studying range overlap in Northern lesser galagos and other galagids would allow a much clearer understanding of their sociality.

These results are only preliminary, and my ethogram is likely to be limited, but they provide a basic understanding of Northern lesser galago activity and form a basis for comparative studies. Olfactory behaviour and vocalisations should be researched rigorously in future research on free-ranging galagids to determine their function and importance in sociality, which should not be underestimated. The social interactions and different types of communication noted here are crucial for understanding Northern lesser galago sociality and with more data could reveal the extent to which they are connected by networks.

3.4.4 Conclusion

Nocturnal primates are a socially diverse group of animals with interspecific variation in behaviour and ecology. I 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. Future research on Northern lesser galago social interactions, ranging behaviour, and olfactory and vocal communication is vital to greater understand their sociality.

3.5 References

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Chapter 4. Sleeping site selection in the nocturnal Northern lesser galago supports antipredator and thermoregulatory hypotheses

Abstract

Sleep is an important and time-consuming activity, during which animals may be particularly vulnerable. Selecting a suitable sleeping site is therefore essential for an individual’s fitness. Here I test the importance of antipredator and thermoregulatory hypotheses for the sleeping site preference of Northern lesser galagos at Kwakuchinja. During June to August of 2015 and 2016 I conducted daily surveys of sleeping sites to record the number of galagos and their location within the sleeping tree, and used focal follows to record when galagos reached and left sleeping sites. I collected vegetation data for sleeping sites (*N* = 47) and matched controls, and placed data loggers in sleeping (*N* = 14) and control locations to compare temperature and humidity. Sleeping group sizes were similar to that of Northern lesser galagos in The Gambia, and the mean proportion of visits in which galagos were present at each site was 27 ± SD 25%. Galagos slept on branches (*N* = 29), nests (*N* = 6), palm leaves (*N* = 6) and in tree cavities (*N* = 1). Palm leaves have not been previously recorded as regular sleeping sites for galagos and were overrepresented relative to their occurrence in the habitat. Random forest classification analysis revealed that galagos sleep in areas with greater canopy cover and connectivity, greater mid-level vegetation cover, higher tree density and a greater number of acacia (*Vachellia* spp.) trees. Sleeping locations had significantly lower mean temperatures but greater mean humidity than control locations. My findings support predator avoidance and thermoregulation as drivers of nesting behaviour. In particular, the characteristics of galago sleeping sites correspond well to those expected for protection from aerial predators, while those related to protection from terrestrial predators seem to play a minor role.

Key words: ecology, galago, microclimate, predation, primate behaviour, sleep.

4.1 Introduction

Sleep is a widespread behaviour, argued to provide essential restorative effects (Siegel, 2005) and memory consolidation (Diekelmann and Born, 2010). Many animals spend a large proportion of their time asleep, and can be especially vulnerable to predation and other environmental risks during this time (Lima et al., 2005). Selecting a suitable sleeping site is therefore crucial for fitness, as it provides shelter and safety, and can facilitate social contact (Di Bitetti et al., 2000; Hamilton, 1982; Takahashi, 1997). Studies of sleeping behaviour in mammals generally find that either predation avoidance (e.g. degus, *Octodon degus*: Lagos et al., 1995); thermoregulation (e.g. koalas, *Phascolarctos cinereus*: Briscoe et al., 2014) or both (e.g. pine martens, *Martes martes*: Birks et al., 2005; Eastern spotted skunks, *Spilogale putorius*: Lesmeister et al., 2008; North American porcupines, *Erethizon dorsatum*: Mabille and Berteaux, 2014; and roe deer, *Capreolus capreolus*: Van Moorter et al., 2009) are prominent factors affecting sleeping behaviour, including site selection.

Predation risk appears to be the main factor driving sleeping site selection in primates. Olive baboons (*Papio anubis*) prefer to sleep in higher areas that are less accessible to leopards (*Panthera pardus*: Hamilton, 1982); black-tufted marmosets (*Callithrix penicillata*) in urban areas choose tall trees to avoid predation from cats (Duarte and Young, 2011); pileated gibbons (*Hylobates pileatus*) seek tall trees with few lower branches to avoid terrestrial predators (Phoonjampa et al., 2010); and chimpanzees (*Pan troglodytes ellioti*) choose to build terrestrial nests only in areas where they are not under threat from humans (Last and Muh, 2013). However, it is unlikely that predation risk exclusively influences where primates sleep, and some species such as pigtailed macaques (*Macaca leonine*) combine predation avoidance with other environmental factors (e.g. distance to food resources) when selecting sleeping sites (Albert et al., 2011).

Microhabitat features known to influence primate sleeping site selection may offer antipredator benefits, e.g.: tree height (Albert et al., 2011; Di Bitetti et al., 2000; Rode et al., 2013) offers a vantage point from which to spot terrestrial predators, and inaccessibility to predators; greater tree diameter at breast height (DBH; Cheyne et al., 2013; Di Bitetti et al., 2000; Hankerson et al., 2007; Rode et al., 2013) indicates structural stability in case of need for evasive or defensive action; greater tree connectivity (Kenyon et al., 2014) and density of undergrowth (Dagosto et al., 2001) offer escape routes; and canopy cover (Hankerson et al., 2007; Rode et al., 2013) may offer concealment, especially from aerial predators. By sleeping in dense foliage, animals such as Northern giant mouse lemurs (*Mirza zaza*: Rode et al., 2013) and green monkeys (*Cercopithecus sabaeus*: Harrison, 1985) remain cryptic yet able to sense vibrations from approaching scansorial and aerial predators. Dense vegetation is also favoured by Neotropical primates for parasite avoidance (Nunn and Heymann, 2005). Alternatively, dense ground vegetation may provide cover for terrestrial predators, thus increasing predation risk (Bettridge and Dunbar, 2012; Cowlishaw, 1997a; 1997b). The relative importance of each of the above factors is subject to the ecological pressures on the population, and to gain further insight into the sleeping site ecology of primates, repeated use of sites should be monitored (Anderson, 1984). Individuals may trade-off conflicting pressures meaning that in order to reduce detection by predators, even the most desirable sleeping sites may not be used consistently (Day and Elwood, 1999).

Thermoregulatory hypotheses, where animals adapt their sleeping site behaviour for thermoregulatory advantages, also explain elements of primate sleeping site selection (Anderson, 1984; Stewart et al., 2018). Western chimpanzees (*Pan troglodytes verus*) use a humidity-avoidance strategy when building arboreal nests (Koops et al., 2012). Thermoregulation is likely to be a greater consideration for smaller primate species; golden-brown mouse lemurs (*Microcebus ravelobensis*) use leaf nests more frequently in low temperatures (Thorén et al., 2010) and Japanese macaques (*Macaca fuscata*) sleep on lower ground to facilitate larger groupings for huddling in cold winters (Takahashi, 1997). Thermoregulatory pressures may also vary seasonally, or throughout an animal’s life. For example, the importance of thermoregulation in female grey mouse lemurs (*Microcebus murinus*) sleeping site choice changes with seasonality and increases when they have offspring (Lutermann et al., 2010). Some nocturnal primates may select particular microclimates to sleep in to reduce overheating from the sun. For example, mouse lemurs (*Microcebus* spp.) favour insulated sleeping sites with less extreme fluctuations in temperature when ambient daytime temperatures are high (Karanewsky and Wright, 2015; Schmid, 1998), and less insulated sites during periods of heavy rainfall (Lutermann et al., 2010). Dense canopy cover can be an important factor in providing protection from the ambient temperature by shading animals from the sun (Duncan and Pillay, 2013).

Much of the previous research into primate sleeping behaviour has focused on diurnal primates. The earliest primates were thought to be small (Soligo and Martin, 2006) and nocturnal (Ross et al., 2007), similar to the nocturnal strepsirrhines of today (Crook and Gartlan, 1966). Therefore, knowledge on the behaviour and ecology of extant nocturnal primates aids our understanding of the selection pressures that acted upon some of the earliest primate species before the appearance of diurnality. Some nocturnal primates (owl monkeys, *Aotus* spp.; and mouse lemurs, *Microcebus* spp.) are ‘marathon sleepers’, spending a much greater time asleep than diurnal primates (Nunn et al., 2010). The importance of a safe sleeping site is therefore paramount in nocturnal primates, but detailed information on the sleeping behaviour of many species in Asia and mainland Africa is unavailable (Bearder et al., 2003; Svensson et al., 2018).

Nocturnal primates are likely to be vulnerable to a different predator guild to their diurnal counterparts due to high levels of inactivity during daytime hours. Small, arboreal, nocturnal primates are estimated to be predated on at a greater rate than other primate groups (Hart, 2007) but reports of predation on nocturnal primates are scarce (Burnham et al., 2012; Hart, 2007). Known predators of nocturnal primates include snakes, felids, non-felid carnivores, raptors, and other primates including humans (Burnham et al., 2012; Svensson et al., 2018). Nocturnal primates may be especially vulnerable to predation during the daytime (Butynski, 1982; Pruetz and Bertolani, 2007), therefore a level of crypsis is required when sleeping (Bearder et al., 2002; Burnham et al., 2012; Nekaris and Bearder, 2011; Svensson et al., 2018).

Galagid species vary in sleeping behaviour and ecology (Svensson et al., 2018), but generally, galagids sleep in groups with variable membership during the day and forage alone at night (Bearder, 1999; Bearder et al., 2003; Bearder and Doyle, 1974; Charles-Dominique, 1977; Harcourt and Nash, 1986), with particular sleeping sites used repeatedly by different individuals (Bearder et al., 2003). Galagid nests, built by a number of species within the *Galagoides, Galago* and *Otolemur* genera, are usually leaf and twig, open platform constructions within thorny trees, presumably to provide protection from predators (Bearder et al., 2003). In addition, *Galago* spp. and thick-tailed galagos (*Otolemur crassicaudatus*) use tree cavities, dense tangles of vegetation and branches as sleeping sites (Bearder et al., 2003; Svensson et al., 2018). Some species sleep in areas of dense forest canopy and understory cover (e.g. Allen's squirrel galago, *Sciurocheirus alleni*; and elegant needle-clawed galago, *Euoticus elegantulus*: Laurance et al., 2008). Brief periods of torpor have been recorded in Southern lesser galagos (*Galago moholi)* but they largely favour behavioural and ecological adaptations, such as increased huddling behaviour and choosing insulated sleeping sites (enclosed cavities and nests rather than open branches), over torpor use for survival in cold, dry winters (Nowack et al., 2013).

Reptiles such as snakes (Svensson et al., 2018), and raptors such as Verreaux’s eagle (*Aquila verreauxii*: Baker, 2013, given in Svensson et al., 2018) and hawks (Ambrose and Butynski, given in Svensson et al., 2018), are either observed or suspected predators of galago species. Genets (*Genetta* spp.) are also predators of galagos (Burnham et al., 2012; Mzilikazi et al., 2006), but are more likely to hunt galagos at night or at dusk when they are active, rather than when they are sleeping (Bearder et al., 2002). Western chimpanzees (Pruetz and Bertolani, 2007) hunt Northern lesser galagos from tree cavities but are not present at Kwakuchinja, and researchers have observed vervet monkeys (*Chlorocebus pygerythrus*) eating (though not catching) a Northern lesser galago (Phyllis Lee, pers. comm. to CB).

Details of Northern lesser galago sleeping site ecology and sociality featured in a review of galagids (Bearder et al., 2003) and two short-term studies focused on the habitat ecology of populations in Kenya (Off et al., 2008) and The Gambia (Svensson and Bearder, 2013). However, no studies have addressed the sleeping site ecology of this species in great detail. In East Africa, populations of Northern lesser galagos are associated with *Vachellia* spp. (Nash and Whitten, 1989; Off et al., 2008), which provide both sleeping sites (Haddow and Ellice, 1964; Nash and Whitten, 1989) and food sources (*Vachellia* gum: Nash and Whitten, 1989; Off et al., 2008). Non-*Vachellia* trees also provide suitable sleeping sites for the Kenyan sub-species *G. s. braccatus* (Nash and Whitten, 1989). Known structure types to support sleep in Northern lesser galagos are: nests (Bearder et al., 2003); in tree cavities (Haddow and Ellice, 1964; Svensson and Bearder, 2013); on tree branches; or in dense tangles of vegetation (Nash and Whitten, 1989; Svensson and Bearder, 2013).

Here I describe the nesting behaviour and sleeping site preferences of Northern lesser galagos at Kwakuchinja, investigating the ecological importance of environmental variables on their sleeping site choice. If predation risk is a strong selective pressure influencing sleeping behaviour galagos will sleep in trees with greater connectivity and canopy cover, and in areas with greater tree and mid-level vegetation density, but lower levels of ground cover. If thermoregulation is important to Northern lesser galagos I predict that cooler, more sheltered sites will be preferred. I aim to identify the levels of tree density, canopy cover and vegetation cover that are preferred for sleeping sites with a view to establishing the habitat requirements for this and similar species.

4.2 Methods

4.2.1 Study site

The study took place at Kwakuchinja (section 1.8.1 of Chapter 1) prior to starting my PhD in June–July 2015 and during my PhD in June–July 2016. A pilot study was conducted by CB in 2014.

4.2.2 Location of galagos and sleeping trees

I collected data as part of a small team. In 2015, we generated six 1 km^2 blocks using QuantumGIS software (QGIS Development Team, 2017). For the first 4 weeks, we surveyed a block each morning before sunrise (04:30–07:00 h) for galagos and followed them back to their sleeping sites. Sleeping sites are the places where individuals sleep, and I define them in this study as the area around and including the sleeping tree within a 10 m radius. I define the sleeping tree as the tree that galagos sleep in. In the evening (19:00–23:00 h) we searched for galagos on foot to determine the best areas for locating sleeping sites in the morning. For the final two weeks, we concentrated our survey effort on one of the blocks, as we observed very few galagos in the other areas. In 2016 we increased the total survey area to 9.2 km^2, including the previous area. We used a similar sampling strategy:

we divided the area into five larger blocks (mean area 1.8 ± SD 0.4 km^2, range = 1.2–2.3 km^2), and randomised the order in which we sampled them. As in the previous year we initially sampled all blocks equally (this time for three weeks) to determine galago distribution, and then concentrated on the most heavily used areas (two blocks or 3.83 km^2 in total in 2016) for the final three weeks.

We used torches fitted with red filters (LED Lenser, Clulite and Maglite 3-Cell D LED flashlight) to minimise disturbance to the animals (Bearder and Doyle, 1974; Finley, 1959; Svensson and Bearder, 2013). We relied on visual detections from galagos' eye shine reflecting in the torch light, and also used their vocalisations as an aid to locate them. We recorded the time each galago settled into their sleeping location, stopped moving and, if in view, closed their eyes. It is clear from the behaviour of the galago when they are settling to sleep: their movements become very deliberate, slow and they assume a recognisable position, often curling their tail over their head or around their body. We waited a minimum of 10 minutes or until light levels increased, to make sure that the individual had settled. We recorded the location of sleeping trees with a handheld Garmin 62 GPS, and marked sleeping trees with biodegradable coloured tape to assist in identification on return. We revisited occupied galago sleeping sites in the evening (17:30–19:30 h) to record time of awakening; the time the first galago left their sleeping location in the tree; and the time of departure from the sleeping tree.

4.2.3 Sleeping site surveys

We surveyed all previously recorded sleeping trees each day to monitor their use and record group size of galagos. We recorded height of the sleeping location, number of individuals and structure type. I use the term 'structure type' to refer to the kind of structure used to support the animal when sleeping, and 'sleeping location' to refer to the location of the individual in the tree. To calculate the height of sleeping locations, one researcher used a TruPulse range finder while another stood directly beneath the sleeping galago(s). The range finder required three points to calculate height: the horizontal distance to the researcher stood beneath the animal(s); the angle up towards the animal(s); and the base angle, towards the feet of the researcher stood beneath the galago(s). I defined four categories of structure types: (i) branch: no visible leaf structure; (ii) nest: platform or cup constructed of plant material; (iii) palm leaf: individuals sleeping in the folded sections of a palm tree; and (iv) tree cavity: within a tree trunk or branch. In some sleeping trees (*N* = 5) galagos were seen in both nests and on branches, in such cases I report the most commonly used structure type for each sleeping tree. When we observed different numbers of galagos using a particular sleeping location on different days I report the first recorded group size for each tree instead of all observations in the results. For the same purpose, I report mean height of sleeping location and mean distance of sleeping location from the top of the tree canopy for each sleeping site. I calculated the mean occupancy of all sleeping sites, where occupancy for each sleeping site was the proportion of visits in which at least one sleeping galago was using the site.

4.2.4 Vegetation data

We used sleeping trees as the centres of vegetation plots 10 metres in radius. We marked them using 2 x 20 metre bisecting measuring tape transects, each pointing in the direction of the four cardinal points. We selected control plots by using the minute hand on an analogue watch and travelling 100 metres in this direction from the sleeping tree; the closest tree to this point acted as the centre of control plots. To assess the habitat, we recorded 9 variables from all plots: (1) the number; (2) species; (3) height and; (4) diameter at breast height (DBH) of all trees in the plot; (5) the number of trees with any part of their canopy touching any part of the sleeping or control tree; (6) canopy cover; (7) the number of shrubs and (8) the number of shrub species within the plot. Lastly, where applicable, (9) we estimated the diameter of the sleeping branch where the galago(s) slept (0–5 cm, 5–10 cm, >10 cm). We defined trees as having a DBH ≥7.5 cm (Benavides et al., 2016; Motta et al., 2006); and shrubs as woody plants with a DBH of <7.5 cm. We measured DBH at 1.3 m from the ground using a diameter measuring tape; for multi-stemmed trees we calculated the mean for all stems ≥7.5 cm. We used either a clinometer or a TruPulse range finder to measure tree height and then calculated the mean height and DBH of all trees in the plot for use in analyses. We recorded unidentified tree or shrub species and included them in total number of trees or shrubs in the plot but not in any other analysis. I categorized non-sleeping tree species into ‘*Vachellia*’ or ‘non-*Vachellia*’ to reduce the number of levels in the tree species variable. I chose these categories because the *Vachellia* species share broadly similar structural features such as thorns, and seasonally shed their leaves in the dry season; they also comprised a large proportion of the habitat. I grouped together non-*Vachellia* trees, as each individual species were represented in relatively low numbers. Similarly, I categorized distance to nearest yellow fever tree (*V. xanthophloea*), a known food source for Northern lesser galagos (Nash and Whitten, 1989; Off et al., 2008), into two levels (<30 m, ≥30 m), based on our usual range of sight.

We measured canopy cover every 5 m along the plot transects and at the centre point, recording 9 points for each plot. One observer looked through the reverse end of binoculars perpendicular to the ground and estimated the proportion of canopy cover as: 0%; 1-20%; 21–40%; 41–60%; 61–80%; 81–100%. To measure mid-level vegetation density one researcher held a pole with 1 cm red bands positioned every 10 cm along its length horizontally at approximately 1 m above the ground at each of the four cardinal points; another researcher stood at the centre of the plot and counted the number of red bands they could see using binoculars (8 x 42 or 10 x 42). We subtracted the total number of red bands in view from the total number of bands on the pole; a lower value represents lower mid-level density. There was a small variation in the number of red bands used in the different years (10 in 2015 and 15 in 2016) so I calculated proportions before any analyses. To record ground cover; in 2015, we used four quadrats of 1 m^2, each 5 m from the central tree along the plot transects; in 2016 we used a circle with a 10 cm diameter every 1 m along the measuring tape (41 points in total). We then recorded the percentage of bare ground, and the height of vegetation in each quadrat or circle. The second method is more thorough, so I tested whether this difference in method affected the results using 'year' as a factor in the model with two levels: the 2015 and 2016 field seasons. To measure human disturbance, we counted the number of cut tree and shrub stems in the vegetation plot and in 2016 also recorded counts of dung in the vegetation plot, categorized into 'domestic herbivore', 'wild herbivore' and 'wild carnivore'.

4.2.5 Abiotic measures

I compared abiotic measures between sleeping and control trees. Portable Reed ST-171 data loggers recorded temperature and humidity of the microhabitat around galago sleeping locations every 30 minutes. I used a 4 m long wooden stick to place data loggers as close as possible to the galago sleeping locations, and at the same height in control trees (defined as the closest tree of the same species and of similar height to the sleeping tree). In total I placed twenty-eight data loggers (fourteen in sleeping trees and fourteen in controls) for seven days each in 2016 (ten in week four, ten in week five and eight in week six). I was unable to reach palm trees to place any data loggers, and I only analysed data from currently unoccupied sleeping locations to ensure that body heat from the animals did not bias the results.

4.2.6 Statistical analysis

4.2.6.1 Comparison between sleeping trees and the general population of trees

I compared data on height and DBH of sleeping trees to the general population of trees (the other trees in sleeping site plots and all trees in control plots from 2016). Data on both height and DBH violated assumptions of normality (Shapiro-Wilks test) in at least one of the levels (sleeping trees/general population of trees); all variables P <0.05. Therefore, I used Wilcoxon matched-pairs signed-rank tests to compare the ranks of data on height and DBH between sleeping and control trees from the general population. I also compared tree species of sleeping trees with the composition of the wider habitat. I created four categories of tree species, the first two being the most used tree species, *Vachellia tortilis* and *V. kirkii,* and all others were categorised into ‘palm’ (*Hyphaene* and *Borassus* spp.) or ‘other’. I used a chi-squared test of goodness-of-fit to test whether the number of sleeping tree species were significantly different to the expected proportion of the general population of trees.

4.2.6.2 Predictors of galago sleeping sites

I used random forest classification analysis (Breiman, 1996; 2001) to determine the best predictors of galago sleeping sites when compared to control sites. Random forests are built as a combination of generated classifier trees, which ‘vote’ for the best predicted class and ultimately provide a measure of variable importance. The approach uses bootstrapping to create new samples, with replacement, from the known observations. For each of the bootstrap samples, the mean classification error is calculated using only the predictions from the trees not containing the training data in their bootstrap sample. This is called the ‘out of bag’ error, generalised across the number of trees constructed, and a lower value indicates greater strength and lower correlation between classifiers. I included the following variables in the analysis: height of sleeping/control tree; DBH of sleeping/control tree; number of trees in the plot (including the sleeping/control tree);

number of acacia (*Vachellia* spp.) trees in the plot (including the sleeping/control tree); number of shrubs in the plot; mean height of surrounding trees in the plot; mean DBH of surrounding trees in the plot; species of sleeping/control tree (*Vachellia*/non-*Vachellia*); number of connected trees; distance to nearest yellow fever tree (<30 / ≥30 m); number of *V*. *tortilis* trees in the plot; percentage of canopy cover; percentage of mid-level vegetation density; number of trees and shrubs cut down; proportion of bare ground in ground cover; mean height of ground cover; number of domestic herbivore dung; number of wild herbivore dung; and year (field season). I excluded all other variables due to insufficient data.

I used the ‘cforest’ function in the ‘party’ package (Hothorn et al. 2015) in R version 3.3.1 (R Development Core Team, 2016). Cforest takes into account potential collinearity between predictor variables and is argued to provide unbiased variable selection (Strobl et al., 2007). The cforest function allows both continuous and categorical variables to be used in the analysis, with continuous variables varying in range (Strobl et al., 2007). Variable importance is measured by mean decrease in classification accuracy, where greater values indicate that they are more important to the classification.

4.2.6.3 Abiotic measures

I obtained the mean temperature and humidity from each full day (06:00–18:00 h) of data collection for each data logger and with these values calculated the mean of all full days for each data logger ($N = 13$). I calculated the standard deviation of the mean temperature (Tsd) and humidity (Hsd) for each day to measure fluctuation of the two variables (Bettridge et al., 2010; Korstjens et al., 2010). I did not use data from one data logger and its control in the analysis, as there was always a galago present at the sleeping location.

I tested all variables for normality using the Shapiro-Wilk test. Mean humidity and Hsd were normally distributed (mean humidity: sleeping: $W = 0.91$, $P = 0.16$, control: $W = 0.92$, $P = 0.24$; Hsd: sleeping: $W = 0.89$, $P = 0.10$, control: $W = 0.92$, $P = 0.24$), but mean temperature and Tsd did not have a normal distribution in at least one of the levels (mean temperature: sleeping: $W = 0.85$, $P = 0.03$, control: $W = 0.95$, $P = 0.52$; Tsd: sleeping: $W = 0.95$, $P = 0.56$, control: $W = 0.85$, $P = 0.03$). I used paired T-tests (for mean humidity and Hsd) and Wilcoxon matched-pairs signed-rank tests (for mean temperature and Tsd) for comparisons between sleeping and control locations.

4.2.6.4 Human disturbance

I used Fisher’s Exact tests to compare the counts of cut stems and domestic herbivore dung in sleeping and control sites. I also compared the number of wild herbivore dung, and data were insufficient for testing between wild carnivore dung, between sleeping sites and controls.

4.3 Results

4.3.1 Sleeping sites

In 2015 we recorded 26 sleeping sites, including 3 that were located during a pilot study by CB in 2014. In 2016 we located 31 sleeping sites, 8 of which were reused from previous years; giving a total of 49 independent sleeping sites (Figure 3.2) located over 60 survey nights. Some sleeping trees from 2015 had been damaged in 2016; a small palm tree (*Hyphaene petersiana*) had mostly broken leaves and a large *V*. *polycantha* had fallen. We revisited sleeping sites 2–48 times, depending on when we first located them. Mean occupancy of all sleeping sites was 27 ± SD 25%.

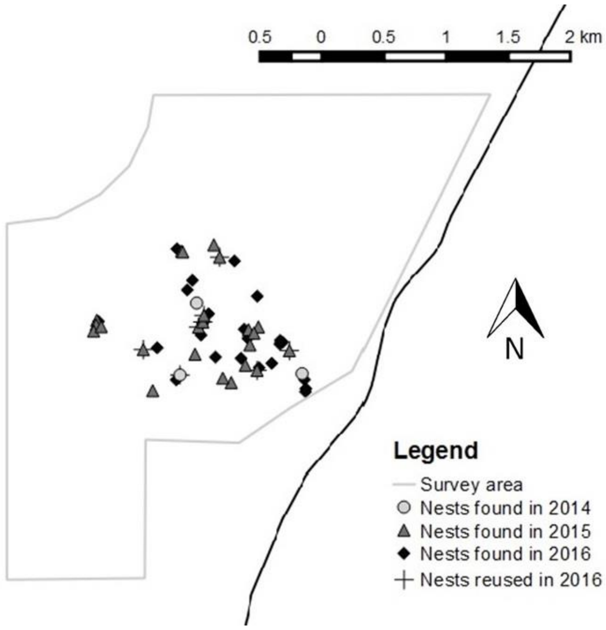

Figure 4.1 Distribution of sleeping sites of Northern lesser galagos found in July 2014, and from June to August of 2015 and 2016, at Kwakuchinja.

4.3.2 Sleeping tree characteristics

We collected vegetation data for 47 of the 49 sleeping sites and 47 random controls. Mean height of sleeping trees was 9.78 ± SD 3.42 m and mean DBH was 18.95 ± SD 10.81 cm. Mean number of connected trees to the sleeping tree was 2.57 ± SD 1.96 and mean percentage of canopy cover at sleeping sites was 48 ± SD 21%.

The most commonly used tree species was *Vachellia tortilis* (*N* = 21) followed by: *V*. *kirkii* (*N* = 7); *Hyphaene petersiana* (*N* = 6); *V*. *polycantha* (*N* = 3); *Borassus aethiopum* (*N* = 2); *Balanites glabra* (*N* = 2); *V*. *mellifera* (*N* = 2); *Lannea* spp. (*N* = 1); *Balanites aegyptiaca* (*N* = 1); *Albizia* spp. (*N* = 1); and *V*. *xanthophloea* (*N* = 1). The species of sleeping trees differed from the composition of the wider habitat (χ^2_3 = 8.68, *P* = 0.03). Galagos slept in palm trees more than expected (Expected: 3; Observed: 8), in *V. tortilis* and *V. kirkii* as expected (*V. tortilis*: Expected: 22; Observed: 21; *V. kirkii*: Expected: 6; Observed: 7), and in ‘other species’ less than expected (Expected: 16; Observed: 11).

4.3.3 Structure type and sleeping location

The majority of the structure types used to support sleep were branches (65%; *N* = 32). Galagos used nests in 14% of sleeping trees (*N* = 7) and palm leaves in 18% (*N* = 9). We observed galagos using a tree cavity for the first time in 2016 (*N* = 1; Fig. 3); this was the only tree cavity recorded during the study. Of the 32 branches used to sleep on, the majority had a diameter of <5 cm (*N* = 24), four were 5–10 cm in diameter and only one branch was >10 cm; we did not collect data for the remaining three branches due to poor visibility. Nests were usually crude leaf constructions and we did not observe galagos building the nests. When using palm leaves, galagos slept towards the central spine of the leaf, usually covered by other towering palm leaves. The tree cavity was situated in the fork of a *V. polycantha*, at a height of approximately 9 m, with a closed canopy above (Fig. 3).

Mean height of sleeping locations was 5.95 ± SD 2.38 m (range 2.50–12.00 m; *N* = 39) and mean distance of sleeping locations from the top of the tree was 4.30 ± SD 2.92 m (range 0.41–10.83 m; *N* = 38). We could not collect data from some trees with poor visibility.

Figure 4.2 Examples of the four different structure types used by Northern lesser galagos in the Kwakuchinja wildlife corridor, Northern Tanzania from June to August of 2015 and 2016: a) galago sleeping on a branch; b) galagos sleeping on a leaf nest; c) galago awake from sleeping in a palm leaf; d) a tree cavity used by galagos.

4.3.4 Group size

Of the first recorded group size for each sleeping site, 51% were solitary individuals (*N* = 22), 30% were a pair (*N* = 13), 14% were a group of three (*N* = 6) and 5% were a group of 4 (*N* = 2). We could not reliably determine group size for the remaining four trees.

4.3.5 Sleep patterns

Galagos reached their sleeping trees at a mean of 29 ± SD 14 min before sunrise (*N* = 10, range = 12–53 min) and settled in to their sleeping location, with no further movement, at a mean of 17 ± SD 17 min before sunrise (*N* = 7, range = -5–41 min). In the evening, galagos first showed signs of awakening (eyes open or first movement) at a mean of 11 ± SD 10 min before sunset (N = 11, range = -1–34 min). They left their sleeping location at a mean of 8 ± SD 8 min after sunset (N = 15, range = -5–23 min) and moved on from the sleeping tree at a mean of 15 ± SD 7 min after sunset (N = 16, range = -1–26 min). These sample sizes are variable because quite often the animals were not visible enough for us to detect small movements or whether their eyes were open or not.

4.3.6 Habitat predictors of galago sleeping sites

Sleeping trees did not differ significantly from the general population of trees in height (Wilcoxon signed-rank test: Z = 2969, P = 0.72) or DBH (Wilcoxon signed-rank test: Z = 2999, P = 0.79). Random forest classification analysis (Table 4.1 and Figure 4.1), showed that galagos select sleeping trees with greater connectivity than control trees. They also sleep in areas with greater mid-level vegetation and tree density; higher percentage of canopy cover; and more acacia (*Vachellia* spp.) trees than control plots. Measures of ground cover (% bare ground and vegetation height) were not important predictors of sleeping sites (Appendix 4) and ‘year’ was one of the least important predictors of all the variables I tested. The mean out of sample prediction error rate (‘out of bag’ error rate) for 500 repetitions was 9% (5% for sleeping trees and 12% for control trees; see the confusion matrix in Table 4.2). My model correctly predicted forty-two sleeping sites as sleeping sites and thirty-five controls sites as control sites.

Table 4.1 The five best predictors of sleeping sites of Northern lesser galagos within the Kwakuchinja wildlife corridor, Northern Tanzania from June to August of 2015 and 2016, identified by random forest classification analysis.

	Sleeping trees		**Control trees**	
Habitat predictor	Mean ± SE	Range	Mean ± SE	Range
Connected trees	2.57 ± 0.29	0–9	1.02 ± 0.23	0–7
Number of trees	4.98 ± 0.42	1–15	2.89 ± 0.36	1–14
Mid-level density (% covered)	22.68 ± 3.81	0–100	7.94 ± 3.02	0–100
Canopy cover (% covered)	48.90 ± 3.12	12–95	32.54 ± 4.18	0–96
Number of *Vachellia* trees	3.19 ± 0.33	0–10	1.80 ± 0.23	0–7

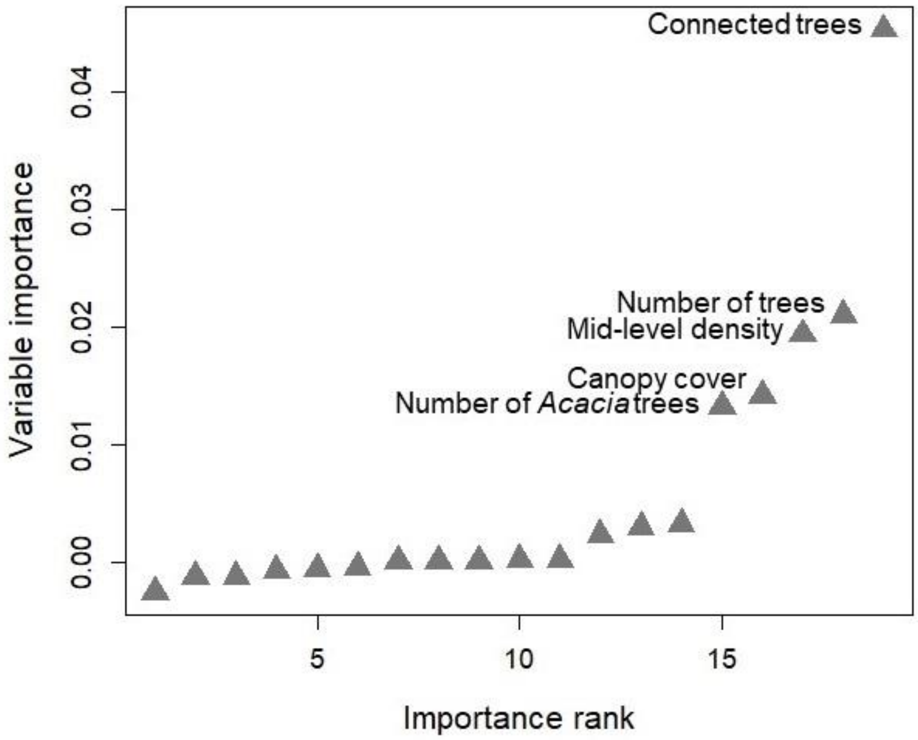

Figure 4.3 The five best predictors of sleeping sites of Northern lesser galagos within the Kwakuchinja wildlife corridor, Northern Tanzania from June to August of 2015 and 2016. They are ranked 19 to 15 with 19 being the best classifier. The importance rank of all other variables can be found in Appendix 4.

Table 4.2 Confusion matrix showing the performance of my random forest model in determining sleeping site predictors of Northern lesser galagos in the Kwakuchinja wildlife corridor, Northern Tanzania from June to August of 2015 and 2016.

	Predicted presence		
Observed presence	Control	Sleeping	Out of bag error
Control	36	11	0.117
Sleeping	5	42	0.053

4.3.7 Abiotic measures

Mean humidity was significantly higher, and mean temperature and Tsd were significantly lower in sleeping locations than in control locations. There was no significant difference in Hsd between sleeping and control locations (Table 4.3).

Table 4.3 Summary of abiotic measures (mean ± SD) of 13 sleeping locations used by Northern lesser galagos and control locations, in Kwakuchinja, Northern Tanzania from June to August of 2015 and 2016. Results of paired *t*-tests (*t*, *df* = 12) and Wilcoxon matched-pairs signed-rank tests (*T*). Tsd: standard deviation of daily temperature; Hsd: standard deviation of daily humidity. Significant results in bold.

Habitat predictor	**Sleeping trees**	**Control trees**	**Statistic**	***P*-value**
Mean temperature (°C)	24.42 ± 1.79	25.27 ± 1.81	*T* = 10	**0.01**
Tsd	0.71 ± 0.30	0.85 ± 0.45	*T* = 15	**0.03**
Mean humidity (%)	52.56 ± 6.13	49.77 ± 5.60	*t* = 2.34	**0.04**
Hsd	3.37 ± 1.16	3.60 ± 1.51	*t* = -0.83	0.42

4.3.8 Human disturbance

There was no significant difference in the number of cut stems (Fisher's exact test: *P* = 0.42; *N* = 47; mean: sleeping: 5.64 ± SD 6.20 control: 5.72 ± SD 7.14), domestic herbivore dung (Fisher's exact test: *P* = 0.89; *N* = 21, mean: sleeping: 29.27 ± SD 18.58 control: 50.24 ± SD 36.96) or wild herbivore dung (Fisher's exact test: *P* = 0.55; *N* = 21, mean: sleeping: 17.73 ± SD 11.29 control: 42.14 ± SD 33.03) between sleeping and control sites.

4.4 Discussion

I have shown that sleeping site selection by Northern lesser galagos at Kwakuchinja supports both anti-predator and thermoregulatory hypotheses. The most important predictor of galago sleeping sites was connectivity between the sleeping tree and neighbouring trees; a means of escape or safe departure from the sleeping tree. Greater mid-level vegetation and number of trees are also predictors of sleeping sites and provide escape routes from the sleeping tree. Dense canopy cover was also an important predictor, and can provide both antipredator benefits in concealment from aerial predators and thermoregulatory benefits in protection from direct sunlight.

4.4.1 Evidence for antipredator hypotheses

The most important predictors of sleeping sites in this study can all be attributed to the importance of predator avoidance by aiding cover and concealment (Anderson, 2000; Albert et al., 2011; Birks et al., 2005; Duarte and Young, 2011; Hamilton, 1982; Last and Muh, 2013; Phoonjampa et al., 2010; Svensson et al., 2018). Connectivity, and tree and mid-level density, relate to the galagos' ability to easily move throughout their habitat and evade predators without the need for terrestrial locomotion. Mid-level vegetation density may be of particular importance for predator avoidance because galagos are light enough to move swiftly through shrubs, where their larger-bodied predators may not be. In this study galagos prioritised their defence from aerial predators over the threat from potential terrestrial predators. Dense canopy cover could increase crypsis from aerial predators and may provide more escape routes from other predators (Fan and Jiang, 2008; Xiang et al., 2010). In contrast to diurnal primates who are argued to counter predation risk through increased gregariousness (Cheney and Wrangham, 1987; Shultz et al., 2004; Shultz et al., 2011; van Schaik, 1983), nocturnal primates probably counter predation risk through crypsis (Bearder et al., 2002; Nekaris and Bearder, 2011).

Reports of predation on nocturnal primates are far fewer than those related to their diurnal counterparts (Burnham et al., 2012; Hart, 2007), most likely due to the comparatively smaller number of studies addressing this. The main predators of galagos are thought to be genets and other viverrids, raptors, jackals (*Canis mesomelas*) and snakes (Bearder et al., 2002; Burnham et al., 2012; Svennson et al., 2018) and in some populations, chimpanzees (Pruetz and Bertolani, 2007). There are also reports of blue monkeys (*Cercopithecus mitis*: Butynski, 1982) and vervet monkeys (Phyllis Lee, pers. comm. to CB) predating lesser galagos. Aside from reports of genets (Simon Bearder, pers. obs., Burnham et al., 2012) all other reports of galago predation occurred during the day, when galagos are asleep and at their most vulnerable (Lima et al., 2005), reflecting the importance of predator avoidance in selecting a sleeping site. Galagos do not have the means for active defence against predators so avoidance through crypsis or escape are their only options for reducing predation risk.

Whilst the influence of predation risk is considered a major evolutionary pressure on sociality in diurnal primates (Hill and Lee, 1998; van Schaik, 1983), its effect on the behavioural ecology of nocturnal primates is less understood. The tendency for animals in this study to sleep in groups is similar to that observed in Northern lesser galagos in The Gambia (Svensson and Bearder, 2013), where animals slept alone only 30% of the time, and the closely related Southern lesser galagos (Bearder and Doyle, 1974), which slept alone around 40% of the time. We mostly found sleeping sites in small clusters within 150 metres of each other. It is possible that the sharing of sleeping sites and/or being in close vicinity to other sites provides safety from potential predators through the use of alarm calls and the mobbing response of other galagos (Bearder et al., 2002). The clustering of sleeping sites may also be due to the limited suitable habitat available, as most of the areas in the control plots exhibited lower connectivity and vegetation density than the sleeping sites.

The low mean occupancy rate of sleeping sites in this study could suggest that galagos experience a trade-off between choosing favourable sites and avoiding detection from predators, and move to reduce their detectability (Day and Elwood, 1999). The fact that galagos move between sleeping trees suggests that the population density is low enough to allow this; if the habitat were saturated, or sleeping trees were a limited resource, we might expect to see more and larger groups at sleeping sites and more consistent use of each site. My model incorrectly predicted a small number (11 of 49) of the control sites as sleeping sites, again suggesting that the population does not saturate its habitat, although with a longer study we may well have observed these control trees being used as sleeping sites. Alternatively, there may be factors unaccounted for in the model, such as presence of sympatric galago species; one tree used by Northern lesser galagos in 2015 instead housed small-eared greater galagos in 2016.

4.4.2 Evidence for thermoregulatory hypotheses

Although the most important variables in determining sleeping sites in this study can relate to predator avoidance, one of the best predictors (canopy cover) can also offer thermoregulatory benefits. Data from data loggers also showed that galagos sleep in cooler, more humid locations, with less temperature variation than control sites. Thermoregulatory hypotheses are well-supported by data from diurnal primate nesting behaviour (Fruth and Hohmann, 1996), and are thought to be of greater importance than predator avoidance for chimpanzees (Koops et al., 2012). Much of the existing literature focuses on the need for diurnal primates to insulate themselves against low ambient temperatures overnight (McGrew, 2004; Takahashi, 1997) or humidity avoidance (Koops et al., 2012). In this study, the thermoregulatory pressure likely comes from reducing overheating in the high daytime temperatures.

Tree holes provide good insulation properties and so may be preferred sleeping locations for small primates, especially those that undergo torpor in order to save energy, such as the *Microcebus* spp. (Schmid, 1998). Previous studies on the closely related Southern lesser galagos, which are subject to lower temperatures than the study population, show that although they are capable of torpor, they only rarely employ this tactic and instead rely on behavioural adjustments to thermoregulation (Nowack et al., 2013). The most commonly used structure type in this study were open branches, where galagos hugged the branch with their four limbs (Fig. 3). Whilst this posture may allow the cool microenvironment of the branches to prevent the animals from overheating (Briscoe et al., 2014), clinging to thinner lateral branches is likely to have been more important for avoiding a fall. We only recorded one tree cavity in this study, contrasting with other populations of Northern lesser galagos (Svensson and Bearder, 2013) and closely related species (e.g. Southern lesser galagos; and Spectacled lesser galagos, *Galago matschiei*: Bearder et al., 2003). It is unclear from this study why galagos did not use more tree cavities. It could be that the temperature conditions are not extreme enough for cavities to be important; female grey mouse lemurs show a seasonal shift from tree holes, which provide superior thermoregulatory advantages, to nests during the wet season (Lutermann et al., 2010). Alternatively, due to the level of human activity in the area, it is possible that there are not many trees large or old enough to house suitable cavities.

Human activity is prevalent in the area and I observed tree cutting almost daily. Deforestation of other tree species may be one reason that this study is the first to record the use of palm trees as sleeping sites for any galago species (Svensson et al., 2018). Galagos used palms more than would be expected based on their representation in the habitat, which may be due to a lack of tree cavities (Haddow and Ellice, 1964; Svensson and Bearder, 2013) or other suitable resources. Palm leaves may provide shelter from direct sunlight, but based on personal observations they may not offer good protection from predators – on several occasions we saw vervet monkeys, baboons and raptors in the palm trees, and the raptors appeared to be actively searching amongst the leaves.

4.4.3 Habitat requirements of Northern lesser galagos

My study reveals that, unsurprisingly for an arboreal primate, galagos need areas with high tree connectivity and high tree and mid-level vegetation density. However, the height and DBH of trees (indicators of age, and structural stability) seem less important, and there was no difference in these variables between sleeping sites and control areas. Galagos preferred a higher density of acacia (*Vachellia* spp.) trees in their sleeping sites. It is likely that galagos favour the protection from predators offered by the trees' spines and thorns over their use as food resources, as we did not observe any animals feeding at sleeping sites. De Jong and Butynski (2004) made a similar argument for the use of *Vachellia* trees by the closely related Somali lesser galago (*Galago gallarum*). The prevalence of cut stems and domestic herbivore dung across both sleeping and control sites suggests that Northern lesser galagos are able to persist in areas with high human activity. Just how much they are affected by anthropogenic activity cannot be determined from this study as I do not have any comparison areas where humans are not having an impact. Now that I have provided a greater understanding of galago sleeping site ecology the effect of anthropogenic pressure should be a focus of future research.

4.4.4 Conclusion

This study reveals the nesting behaviour of a poorly understood nocturnal primate and highlights the importance of anti-predation and thermoregulation on sleeping site choice; it is possible that both influence sleeping site selection in other small nocturnal mammals. Future research should focus on the effects of human impact on galagos, aided by the knowledge of the sleeping site ecology provided here. Nocturnal primates are underrepresented in the scientific literature and further research into their behavioural ecology, including the effect of anthropogenic threats, is paramount for understanding the selective pressures on their evolutionary past and aiding their conservation.

4.5 References

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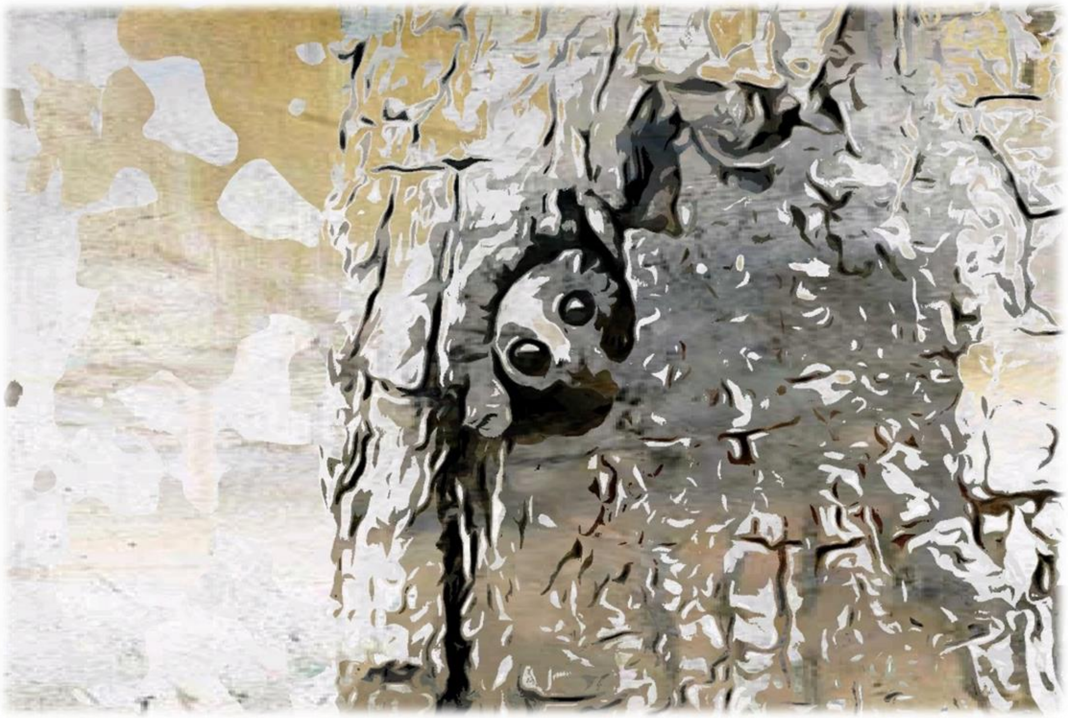
Chapter 5. The spatial abundance and sleeping site ecology of Northern lesser galagos in a landscape of fear



Abstract

Spatial variation in predation risk can influence the way prey animals use their environment, creating a ‘landscape of fear’. For many animals, predation avoidance is a prominent factor when choosing an adequate place to sleep. Predation is particularly costly to primates, owing to their long life spans and slow life histories. Western chimpanzees (*Pan troglodytes verus*) hunt Northern lesser galagos in the area the chimpanzee community use as their home range at the Fongoli study site (81.5 km^2) in South-eastern Senegal. The chimpanzees use self-constructed stick tools to target galagos in their sleeping sites and until now we knew very little about the way galagos respond to this risk. I investigated the spatial abundance of galagos at Fongoli and Lolldaiga Hills Ranch (LHR; 200.1 km^2), where galagos are not subject to predation from chimpanzees. I collected locational data using line transects and used density surface modelling to estimate the spatial distribution and abundance of galago populations at Fongoli and LHR. I used the normalized difference vegetation index (NDVI), as a correlate of vegetation productivity, and elevation as predictors for both sites. At Fongoli I used the additional predictors: distance to human settlements; distance to mining operations; and density of chimpanzee sleeping locations. I also investigated aspects of the sleeping site ecology of galagos at Fongoli that could increase predator avoidance by collecting vegetation data from sleeping sites and control sites, and used random forest classification analysis to determine the best predictors of sleeping sites compared to controls. The estimated abundance of galagos at Fongoli was 2404 (95% CI: 1728–3346; estimated overall density: 29.5 individuals/km^2) and estimated abundance was higher in areas with a lower density of chimpanzee sleeping locations and lower overall vegetation density (with lower NDVI scores: 0.22–0.43). At LHR I estimate that there were 3169 individuals (95% CI: 1721–5834; estimated overall density: 15.8 individuals/km^2) and that galagos were predominantly found in areas of lower elevation (<1950 m). Galagos at Fongoli maximised concealment at sleeping sites by always sleeping in tree cavities and preferred large sleeping trees that supported several cavities for predator evasion. I found evidence for predation risk being a driver of both spatial distribution and sleeping site selection of galagos at Fongoli.

Keywords: bushbaby; distance sampling; nocturnal primate; primate-primate predation; strepsirrhine.

5.1 Introduction

Spatial variation in predation risk can affect how animals use the landscape they inhabit, generating a 'landscape of fear' (Laundre et al., 2010). Investigating the influence of predation on prey species reveals the tactics the latter may use in response to the perceived risk of predation. An important technique some prey animals adopt to survive in response to a landscape of fear is to populate areas with lower predator abundance. For example, on a large spatial scale, fish species in the Northwest Atlantic shifted their distribution to safer areas in response to increased predation risk by grey seals (*Halichoerus grypus*: Swain et al., 2015). On a smaller scale, at Karongwe Game Reserve in South Africa, small African ungulates such as warthogs (*Phacochoerus africanus*) and impala (*Aepyceros melampus*) avoid the space used by known predators, and warthogs showed stronger avoidance for predators of greater threat to them (Thaker et al., 2011).

Due to their relatively slow life histories, predation is extremely costly for primate populations. Predation risk is known to impact primate group size and activity patterns (Terborgh and Janson, 1986; Isbell, 1994; Hill and Lee, 1998; Colquhoun, 2006; Karpanty, 2006; Kamilar and Beaudrot, 2018), and some primates respond to a landscape of fear, adjusting their spatial distribution to avoid areas with greater risk of predation. For example, there is strong evidence for samango monkeys (*Cercopithecus mitis erythrarchus*) in South Africa avoiding areas considered high risk of predation from eagles (African crowned eagle, *Stephanoaetus coronatus*; and African black eagle, *Aquila verreauxii*: Coleman and Hill, 2014). Secondly, in contiguous forests in North-east Madagascar, mouse lemurs (*Microcebus rufus*) show evidence of avoidance from all predator species, while White-fronted brown lemurs (*Eulemur albifrons*) show avoidance from fossas (*Cryptoprocta ferox*) in particular (Farris et al., 2014).

Primates spend a large proportion of their time asleep and are especially vulnerable to predation whilst sleeping (Lima et al., 2005; Nunn et al., 2010); this is particularly the case for nocturnal primates, which sleep for longer durations than diurnal species (Nunn et al. 2010). Selection of an adequate sleeping site is therefore essential for fitness, and predator avoidance is a prominent factor in primate sleeping site selection (Hamilton, 1982; Anderson, 2000; Schreier and

Swedell, 2008; Matsuda et al., 2008; Xiang et al., 2010; Phoonjampa et al., 2010; Bernard et al., 2011; Teichroeb et al., 2012; Rode et al., 2013; Last and Muh, 2013; Thiry et al., 2016; Markham et al., 2016; Caselli et al., 2017; Svensson et al., 2018; Chu et al., 2018; Chapter 4).

Connectivity of vegetation to the sleeping tree or within the sleeping site is important to many primate species, as high connectivity can provide more escape routes from predators (Albert et al., 2011; Bernard et al., 2011; Thiry et al., 2016; Chapter 4). To maximise escape routes and enhance concealment, many primates favour dense vegetation around their sleeping site; this could be provided by canopy cover (Hamilton, 1982; Xiang et al., 2010; Seiler et al., 2013), surrounding trees (Markham et al., 2016; Chapter 4), lianas (Rode et al., 2013; Caselli et al., 2017), or mid-level vegetation (Chapter 4). However, there seems to be a trade-off between remaining hidden and reducing accessibility to predators, with some species choosing sleeping sites with less surrounding vegetation (e.g., fewer lianas: Phoonjampa et al., 2010; Cheyne et al., 2013). Sleeping tree height is an important factor in sleeping site choice of many primates, with tall trees likely reducing accessibility to predators (Day and Elwood, 1999; Xiang et al., 2010; Albert et al., 2011; Bernard et al., 2011; Teichroeb et al., 2012; Rode et al., 2013; Thiry et al., 2016; Caselli et al., 2017) and increasing the chances of detecting them (Feilen and Marshall, 2014). Many species also choose sleeping trees with a large diameter at breast height (Hankerson et al., 2007; Teichroeb et al., 2012; Cheyne et al., 2013; Seiler et al., 2013; Caselli et al., 2017). Tree cavities are particularly important for small primates, whether sleeping throughout the night (e.g., golden lion tamarins: Hankerson et al., 2007) or the day (gray mouse lemurs, *Microcebus murinus*: Schmid, 1998; Lutermann et al., 2010; galagos: Bearder et al., 2003; Svensson et al., 2018).

Galagos are small, arboreal, nocturnal primates, and species with these characteristics generally have higher predation rates than other primates (Hart, 2007). Like other nocturnal primates (Karpanty, 2006), galagos employ cryptic antipredator tactics when active and use concealed sleeping sites to avoid predation. Many predators of galagos are thought to be opportunistic hunters, including birds of prey (e.g., spotted eagle owls, *Bubo africanus*: Burnham et al., 2012), snakes (Burnham et al., 2012; Svensson et al., 2018) and small mammals such as genets (*Gennetta* spp.: Burnham et al., 2012), jackals (*Canis mesomelas*: Burnham et al., 2012) and caracals (*Caracal caracal*: Cuozzo et al., 2021). One study recorded a three-legged domestic dog carrying a small-eared greater galago carcass in its mouth, and partly consuming it (Pihlström et al., 2021). Some primates such as blue monkeys (*Cercopithecus mitis stuhlmanni*: Butynski, 1982) and vervet monkeys (*Chlorocebus pygerythrus*: Phyllis Lee, pers. comm. to CB) are known to predate lesser galagos.

Whilst the above animals pose a threat to lesser galagos across much of their range, at Fongoli in South-eastern Senegal, Western chimpanzees (*Pan troglodytes verus*) living in a savannah landscape systematically hunt Northern lesser galagos by constructing spear-like tools and targeting sleeping individuals (Pruetz and Bertolani, 2007; Pruetz et al., 2015). Researchers have recorded over 500 of these hunting events at Fongoli (Fongoli Savanna Chimpanzee Project [FSCP], unpublished data), yet we know very little about the impact on galago behaviour and ecology. Owing to such a predation pressure on sleeping galagos, effective sleeping site choice and spatial distribution may be crucial for their survival. I have access to longitudinal data on chimpanzee locations at Fongoli, which enabled me to quantify the spatial distribution of predation risk. This study therefore presents a unique opportunity to examine the influence of predation on distribution and sleeping site preferences of galagos, using another site with very different predation pressures as a comparison.

My first objective was to provide abundance estimates for galagos and identify significant predictors of their spatial abundance for two populations: 1) Fongoli, Senegal, where chimpanzees actively hunt galagos at their sleeping sites; and 2) Lolldaiga Hills Ranch (LHR), Kenya, where only opportunistic predators such as snakes and birds of prey are a threat to galagos. I expected galagos to avoid areas with a high density of chimpanzees at Fongoli. My second objective was to investigate the importance of predation avoidance from chimpanzees in the sleeping site choice of galagos at Fongoli. I expected galagos to prefer sleeping sites with a high number of tree cavities for evasion from chimpanzees and therefore sleeping trees would be greater in height and DBH than controls to support more cavities. For concealment and more escape routes from predators, I predicted that sleeping sites would have higher levels of canopy cover, mid-level vegetation density and more connected trees to the sleeping tree than in control sites (Chapter 4).

5.2 Methods

5.2.1 Study sites

I studied Northern lesser galagos at Fongoli from March to May 2018 (section 1.8.2 of Chapter 1), and at LHR from July to August 2018 (section 1.8.3 of Chapter 1).

5.2.2 Data collection

5.2.2.1 Line transect surveys

At Fongoli I divided the area into five roughly even sized areas of approximately 17.0 km^2 each (mean = 17.1 ± SD 0.3 km^2, range = 16.7–17.5 km^2) using ArcGIS version 10.8. One observer and I visited one area per night to ensure we were not only surveying areas close to camp. We surveyed one transect within the chosen area between 19:00 and 23:00 h to collect detection data for distance sampling of galagos. I chose the longest transects available that would allow the most coverage within the grid, and visited each area four times on foot and three times by motorbike; the order visited was different every week but was not random due to logistical reasons (e.g., accessibility – some areas were easier to access than others). When on foot, one observer and I walked at a pace of approximately 2–5 km/h and searched for galagos using hand-held torches (always LEDLenser p7.2), scanning all strata from the ground to the top of the tree. When surveying by motorbike, we travelled at approximately 5–10 km/h with myself searching from the passenger seat using a torch. At LHR I predetermined 16 transects using known tracks and randomly chose one to survey each night. We surveyed using a car, driving slowly (5–10 km/h) along each transect between the same hours as in Senegal (19:00 and 23:00 h) with one observer searching with a torch from each side of the vehicle. At Fongoli some transects on foot overlapped with those by motorbike but at LHR they were all independent of each other. At both sites we used existing paths or roads as transects to minimise disturbance and meet logistical and safety considerations.

When we spotted a galago I recorded: 1) the estimated perpendicular distance between the location of the observer and the first location of a detected galago or centre of the group of galagos (m); 2) group size; 3) broad habitat type (as defined above); and 4) the estimated height of the vegetation stratum each galago was using at first sight (ground [0 m]; >0–<4 m; ≥4–<8 m; ≥8–<12 m; ≥12 m). We estimated distance because we could not reliably use range finders due to the lack of light, which meant we were not able to ascertain which object the laser was reflecting from. I always took the mean of at least two observers' estimates. I considered galagos within 20 m of each other to be in a group.

5.2.2.2 Sleeping site and vegetation surveys (Fongoli only)

We visited a different area each morning, again to ensure we were not only surveying areas close to camp, but did not use specific transects. One observer and I searched for galagos on foot using torchlight and auditory cues between 05:30–07:00 h, and followed individuals to their sleeping sites where possible. When we were within 20 m of galagos we used red filters on our torches to minimise disturbance to the animals (Finley, 1959). I recorded the time that galagos reached their sleeping trees and returned in the evening (18:30–20:00 h) to confirm the use of a tree as a galago sleeping tree and to record group size. I also recorded the height and estimated diameter of the cavity used as an entrance or exit hole (<5 cm; ≥5–<10 cm; ≥10–<15 cm; ≥15 cm).

As in Chapter 4, we created vegetation plots with a 10 m radius around sleeping trees ('sleeping sites' hereafter) and selected control sites by standing at the centre of the sleeping site facing north and walking for 100 m in a random direction; we chose the nearest tree as the control tree and centre of the control site. From each sleeping and control site I collected the following data: 1) species of the sleeping or control tree; 2) the height (m) and 3) diameter at breast height (DBH; cm) of all trees in the plot; 4) the number of trees touching any part of the sleeping or control tree [the 'number of connected trees' hereafter]; 5) the number of shrubs and 6) lianas; 7) the number of tree cavities on the sleeping or control tree and 8) within the plot; 9) the percentage of canopy cover and 10) mid-level vegetation density in the plot; 11) height of ground cover (cm); 12) and any evidence of burning (Y/N). We defined trees as plants with a DBH ≥7.5 cm (Motta et al., 2006; Benavides et al., 2016; Chapter 4); other woody plants were classified as shrubs or lianas.

Detailed data collection methods for percentage of canopy cover, mid-level vegetation density, and height of ground cover, are in section 4.2.4 of Chapter 4.

5.2.3 Data analysis

5.2.3.1 Detection

I recorded group size for active galagos (both populations) and galagos at sleeping sites (Fongoli only). To assess differences in the ranks of detection distance for each group size with sufficient data, I used a Wilcoxon rank sum test (for the Fongoli population; group sizes 1 and 2) and a Kruskal-Wallis test (for the LHR population; group sizes 1, 2 and 3). I used Wilcoxon rank sum tests to assess differences in the ranks of: a) detection distance; and b) galago encounters per km by researchers on foot or on motorbike at Fongoli.

To investigate the different levels of vegetation used by galagos at each site I used a Chi-square test for homogeneity. I used the vegetation level from the first galago detected from each group.

5.2.3.2 Abundance and spatial distribution

Distance sampling

Distance sampling uses observation data from point or line transects to fit a ‘detection function’, accounting for uncertain detection by estimating the proportion of data missed by the observers (Buckland et al., 2015). I used the ‘Distance’ package in R (Miller, 2020) to calculate the detection function. For the LHR data I included broad habitat type as a covariate, categorised into three broad categories: woodland; bushland; and mixed other. At Fongoli, the vast majority of detections were in woodland habitat so I had insufficient variation in data to include habitat as a covariate in the Fongoli analysis.

Following best practice guidelines (Miller, 2020), I first truncated the data by plotting histograms using different truncation points and varied number of binned distances, or ‘bins’. I chose the maximum distance of 80 m as a truncation point for Fongoli (N = 143 detections) and 100 m for LHR (N = 178 detections) due to the histograms presenting the best fit for the detection functions (see Appendix 5A). Using the Distance package I built models using the half normal and hazard rate (this distribution is more flexible; Buckland et al., 2015, section 5.2.1) key functions

(Buckland et al., 2015, section 5.2.1; Miller, 2020). I determined the best model by choosing the model with the lowest Akaike information criterion (AIC; Akaike, 1974) score and visually assessing the histograms. All models chosen passed the goodness of fit test.

Density surface modelling

Density surface modeling (DSM) is used to visualise the spatial abundance of a population and identify environmental variables that may influence the distribution of that population (Miller et al., 2013). A spatial modeling approach does not require the line transects to be randomly placed within the study area (Hedley et al., 2004) and can improve accuracy of abundance estimates from distance sampling by accounting for spatial variability in the model (Hedley et al., 2004; Miller et al., 2013). Density surface modeling relies on line transects being continuously segmented, and count data are then summarised for each segment (Miller et al., 2013). These counts are used as the response variable in generalized additive models (GAMs), modeled as a sum of smooth functions (used in GAMs to capture the relationship of the data without fitting the noise) of covariates along with the detection function from distance sampling to account for detectability (Miller et al., 2013). To prepare the data for DSM I split each transect into segments (~160 m in length for Fongoli and ~200 m in length for LHR). I chose these values because they are double the truncation distance used to create the detection function (80 m for Fongoli and 100 m for LHR; Hedley et al., 2004; Miller et al., 2013). This resulted in 512 segments in total for the Fongoli data and 506 for LHR. I joined the detection data to the corresponding segments from which we detected them.

Using Landsat 8 data I created rasters for median and SD annual NDVI between July 2017 and June 2018 for Fongoli and September 2017 to August 2018 for LHR (downloaded from https://earthengine.google.com on 1st July 2020; 30 m resolution) as a correlate of vegetation productivity useful in predicting animal abundance (Pettorelli et al., 2005, 2011). I used digital elevation raster data (Elevation Derivatives for National Applications [EDNA]; downloaded from https://earthexplorer.usgs.gov on 9th July 2020; 30 m resolution). To calculate the density of chimpanzee sleeping locations I used data collected by the FSCP, as part of a longitudinal study on chimpanzee behaviour and ecology. Researchers documented the locations at which chimpanzees built their nests in the evening ('chimpanzee sleeping locations' hereafter), where they were likely to remain for the night. Data were predominantly from the months of January to June in the years 2016, 2017 and 2018 ($N = 155$). I created a kernel density raster in ArcGIS version 10.8 with the data using a search radius of 1000 m to identify hotspots of chimpanzee sleeping locations. Because chimpanzees hunt galagos during the day, I used the same method to extract data for two estimates including diurnal locations: 1) all of the known locations of chimpanzees from the three years (day and night in 2016–2018); and 2) all of the known locations from the year of study only (day and night in January–June 2018). The values per segment for chimpanzee sleeping locations were highly correlated with those for both 1) all of the known chimpanzee sleeping locations from the three years ($r_s = 0.95$, $P < 0.001$) and 2) chimpanzee sleeping locations from January–June 2018 only ($r_s = 0.71$, $P < 0.001$). I chose to use chimpanzee sleeping locations (nocturnal) rather than both diurnal and nocturnal locations because it is likely that chimpanzees remained in those locations for a long period of the night while galagos were active.

Using location data on human settlements and mining operations at Fongoli, collected as part of JP's longitudinal study, I used the 'Euclidean Distance' tool in ArcGIS to create two rasters with the following values per 30 x 30 m cell: distance to human settlements (m); and distance to mining operations (m). Using the same method I created a raster containing values for distance to water (m) for LHR, but not Fongoli because there were no observed natural water sources during the study period. All rasters used in the DSMs are in Appendix 5B.

I created a buffer the size of the truncation distance (80 m for Fongoli and 100 m for LHR) around each segment and calculated the mean value of each covariate within each segment buffer to use in the analysis. Using these values I evaluated the collinearity between the covariates for each population, and for LHR elevation and median NDVI were highly correlated ($r_s = 0.74$, $P < 0.001$) so I only used elevation in the models. There was no substantial collinearity between any other covariates ($r_s < 0.70$). I therefore used the following covariates: Fongoli: median NDVI; SD NDVI; elevation [m]; density of chimpanzee sleeping locations; distance to human settlements [m]; distance to mining operations [m]; LHR: SD NDVI;

elevation [m]; distance to water [m]). I used these data in addition to the x and y coordinates as covariates in DSMs using the ‘dsm’ package in R (Miller et al., 2020).

I created DSMs with all the covariates using the quasi-Poisson (can be used if the counts are overdispersed or underdispersed; Buckland et al., 2015, section 7.2.2), negative binomial (useful for overdispersed counts; Buckland et al., 2015, section 7.2.2) and Tweedie (a more flexible distribution than the others, and particularly useful when there are a large proportion of zeroes in the data; Miller et al., 2013) distributions (Miller et al., 2013). I determined the best model distribution based on the lowest restricted maximum likelihood (REML) score. I used the REML score instead of the generalized cross-validation (GVC) score because REML is more likely to give stable, reliable results (Marra and Wood, 2011; Wood, 2011; Miller et al., 2013). I then selected covariates by removing any that were non-significant (approximate *P*-values ≥0.05). It was important to balance the smooth terms in the model; the smooth terms should be close to the data (avoiding under-fitting) without fitting the noise (avoiding over-fitting). I set the maximum basis dimension size to 20 for univariate smooth terms and 30 for bivariate smooth terms, which reduced the complexity of the smooth terms to an appropriate level whilst allowing enough flexibility (Wood, 2006, 4.1.7). For my chosen models I checked for correlation between segment residuals using the function ‘dsm.cor’ in the dsm package (Miller et al., 2020).

I created a prediction grid with square grid cells of 900 m^2 in size for each study site and used the ‘predict’ function in the dsm package (Miller et al., 2020) to estimate the abundance of galagos in each cell. I report the estimated abundance, the total coefficient of variation (CV;%) and the 95% confidence intervals (95% CI) for each DSM. Prior to the analysis I converted all spatial locations from longitude and latitude into UTM format (WGS 84 / UTM 28N for Fongoli and WGS 84 / UTM 37N for LHR).

5.2.3.3 Sleeping site ecology

Sleeping tree characteristics

I used Wilcoxon rank sum tests to compare the height and DBH of sleeping trees compared to all other trees measured (all other trees in sleeping and control sites).

Predictors of sleeping sites

I ran a random forest classification analysis to reveal the best predictors of sleeping sites compared to controls. Because sleeping trees were far greater in height and DBH than all other trees measured, I did not include them in this analysis. In addition, the total number of tree cavities in the plot (very highly correlated with the number of cavities on the sleeping or control tree: $r_s = 0.97$, P <0.001) was highly correlated with DBH ($r_s = 0.72$, $P < 0.001$) and height ($r_s = 0.70$, $P < 0.001$) of the sleeping or control tree, so I also excluded that variable. No other variables were highly correlated ($r_s < 0.7$).

I therefore included the following variables: the total number of trees in the site (including the sleeping or control tree); the number of shrubs in the site; the number of lianas in the site; the number of connected trees to the sleeping or control tree; mean height of the surrounding trees in the site (m); mean DBH of the surrounding trees in the site (cm); number of *Pterocarpus erinaceus* trees, the most common nesting tree species; percentage of canopy cover; percentage of mid-level vegetation density; mean height of ground cover (cm); and density of chimpanzee sleeping locations. I used the party package (Hothorn et al., 2017) in R to determine variable importance, measured by mean decrease in classification accuracy.

As a measure of chimpanzee density while galagos were sleeping, I used the day time locations of chimpanzees to identify hotpots of chimpanzee day locations by creating a kernel density raster in ArcGIS version 10.8 using a search radius of 1000 m. I used a Wilcoxon rank sum test to investigate significant differences in the ranks of density of chimpanzee sleeping locations for galago sleeping sites and 25 randomly generated control locations within Fongoli (these were different to the control sites used as a comparison for sleeping site measures). I used a Pearson's correlation test to test for a significant correlation between the minutes that galagos left their sleeping sites after waking in the evening and the density of chimpanzee sleeping locations at the sleeping sites.

Unless stated otherwise, I carried out all statistical tests in R version 4.0.3 (R Development Core Team, 2021) or ArcGIS version 10.8 (ESRI, 2021).

5.3 Results

5.3.1 Detection

At Fongoli we surveyed 81.7 km of transects (*N* = 37; mean length = 2.2 ± SD 1.1 km; range = 0.5–4.4 km) and encountered 143 groups of active galagos (*N* = 165 individuals). At LHR we surveyed 101.1 km of transects (*N* = 17; mean length = 5.9 ± SD 2.8 km; range = 2.9–11.8 km) and encountered 178 groups of active galagos (*N* = 220 individuals). Median estimated detection distance was 20 m (IQR = 35.5 m) at Fongoli; and 40 m (IQR = 40.0 m) at LHR.

We detected galagos in larger groups when sleeping than when active (see Figure 5.1). Mean group size when active was 1.2 ± 0.4 (range = 1–3) at Fongoli and 1.2 ± SD 0.5 (range = 1–3) at LHR. Mean group size of sleeping galagos at Fongoli was 1.9 ± SD 1.0 (range = 1–5 and 1–6 including infants; see Figure 5.1). Group size did not affect detectability of active galagos at either study site. There was no significant difference in the ranks of estimated detection distance between all group sizes of active galagos with sufficient data at Fongoli (group sizes 1 and 2; Wilcoxon rank sum test: *W* = 1151.5, *P* = 0.065; see Appendix 5C) or LHR (group sizes 1, 2 and 3; Kruskal-Wallis rank sum test: *H* = 0.954, *df* = 2, *P* = 0.621).

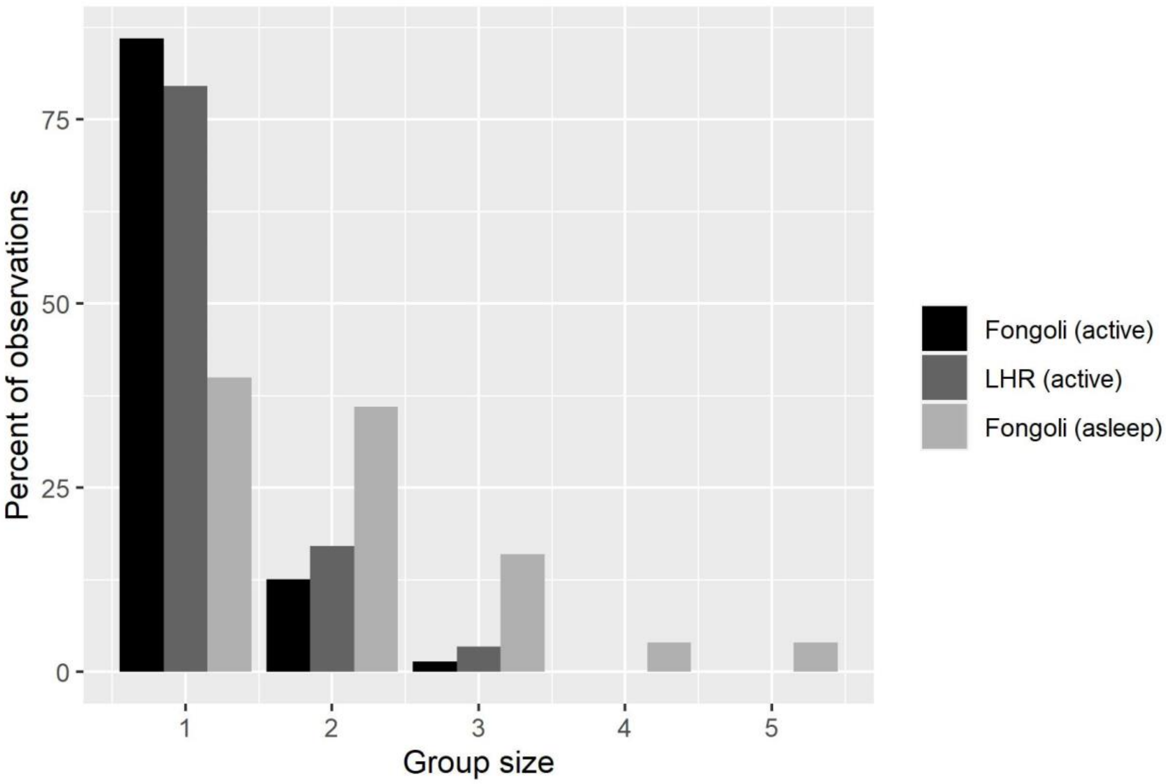


Figure 5.1 Group size of Northern lesser galagos at Fongoli, Senegal and Lolldaiga Hills Ranch, Kenya.

The observer method did not affect detectability of active galagos at Fongoli. I found no significant difference in the number of encounters per km between two researchers searching on foot (median = 2.05; inter-quartile range = 1.81) or one researcher searching from a motorbike (median = 1.13; inter-quartile range = 1.68; Wilcoxon rank sum test: W = 164.5, P = 0.641; see Appendix 5D) at Fongoli. I also found no significant difference in the ranks of distance between those detected on foot or by motorbike (Wilcoxon rank sum test: W = 1886.5, P = 0.308).

Galagos in both populations used all levels of vegetation strata from the ground to heights ≥12 m and generally used higher strata at Fongoli. I found a significant difference in the number of times we spotted individuals at different heights at Fongoli and LHR (Chi-squared test for homogeneity: X^2 = 45.78, df = 4, P <0.001). At heights of ≥12 m we detected more galagos at Fongoli than expected, but fewer at LHR than expected (see Table 5.1). At heights of <0–<4 m we saw an opposite pattern again, with fewer galagos detected at Fongoli than expected, but more galagos at LHR than expected (see Table 5.1).

Table 5.1 Observed (O) and expected (E) values from the chi-squared test for homogeneity between the vegetation levels used by Northern lesser galagos (the first spotted individual detected per group) at Fongoli, Senegal and Lolldaiga Hills Ranch, Kenya. Significant differences (*P*<0.05) in the vegetation levels used between populations are underlined.

	Ground (0 m)		**>0–<4 m**		**≥4–<8 m**		**≥8–<12 m**		**≥12 m**	
Study site	O	E	O	E	O	E	O	E	O	E
Fongoli	8	5.5	29	41.9	34	41.1	23	24.1	36	17.4
LHR	5	7.5	70	57.1	63	55.9	34	32.9	5	23.7

5.3.2 Abundance and spatial distribution

5.3.2.1 Distance sampling

The best detection function model for Fongoli used the hazard-rate key function with no adjustments (AIC = 405.9); and the best for LHR used the half-normal key function with broad habitat type as an additional covariate (AIC = 750.4; see Appendix 5E). My data did not differ significantly from the curve for either model (Fongoli: Chi-squared goodness-of-fit test: P = 0.284, df = 4; LHR: Chi-squared goodness-of-fit test: P = 0.780, df = 5).

5.3.2.2 Density surface modelling

The best DSM for Fongoli used a Tweedie distribution and included median NDVI and density of chimpanzee sleeping locations, but not x and y coordinates of detection locations, as covariates. The model estimates that there were 2404 galagos at the 81.5 km^2 Fongoli field site (95% CI: 1728–3346; CV = 16.99%) with an estimated overall density (no. individuals / area) of 29.5 individuals/km^2. Both covariates were significant (median NDVI: $P = 0.022$; density of chimpanzee sleeping locations: $P = 0.004$; see Table 5.2 and Figure 2). The x and y coordinates, SD NDVI, distance to mining and distance to human settlements did not improve the performance of DSMs for the Fongoli data (see Table 5.2).

The best DSM for LHR used a quasi-Poisson distribution and included elevation in addition to x and y coordinates as covariates, and estimates that there were 3169 galagos at the 200.1 km^2 LHR field site (95% CI: 1721–5834; CV = 31.92%) with an estimated overall density of 15.8 individuals/km^2. Median or SD NDVI did not improve the performance of DSMs for LHR (see Table 5.2). I removed distance to water from all models for creating extremely wide confidence intervals and very high total coefficient of variation, and for not being a significant predictor of galago abundance. Significant smooth terms for LHR were spatial location ($P < 0.001$) and elevation ($P = 0.011$; see Figure 5.2). Estimated spatial abundance of galagos and CV for each site are in Figure 5.3. The correlograms indicated no problems, showing only a very small amount of residual correlation between segments (see Appendix 5F).

Table 5.2 Comparison between percent deviance explained (DE; %), restricted maximum likelihood (REML) score and the total coefficient of variation (CV; %) for each DSM. I include the estimated *P*-value and effective degrees of freedom (edf) for each smooth term. The best DSMs for Northern lesser galagos at Fongoli, Senegal and Lolldaiga Hills Ranch (LHR), Kenya are in bold. Chimpanzee density = density of chimpanzee sleeping locations.

Study site	Model	Response distribution	Covariates	*P*–value	edf	DE (%)	REML score	CV (%)
Fongoli	mod.s.1	Quasi–poisson	x, y	0.361	2.00	12.7	406.7	20.67
			chimpanzee density	0.003**	1.59			
			median NDVI	0.018*	3.26			
			SD NDVI	0.525	1.56			
			elevation	0.649	1.00			
			distance to humans	0.260	2.46			
			distance to mining	0.440	1.00			
Fongoli	mod.s.2	Tweedie	x, y	0.305	2.00	12.2	280.5	18.99
			chimpanzee density	<0.001***	1.02			
			median NDVI	0.003**	3.05			

Study site	Model	Response distribution	Covariates	*P*–value	edf	DE (%)	REML score	CV (%)
			SD NDVI	0.326	1.14			
			elevation	0.601	1.00			
			distance to humans	0.145	2.32			
			distance to mining	0.339	1.00			
Fongoli	mod.s.3	Negative binomial	x, y	0.692	2.00	13.3	446.4	25.49
			chimpanzee density	0.004**	1.88			
			median NDVI	0.017*	2.92			
			SD NDVI	0.439	1.00			
			elevation	0.617	1.00			
			distance to humans	0.279	2.01			
			distance to mining	0.617	1.00			
Fongoli	**mod.s.4**	Tweedie	chimpanzee density	0.004**	1.48	6.3	286.0	16.99
			median NDVI	0.022*	3.08			
LHR	mod.k.1	Quasi–poisson	x, y	<0.001***	17.65	61.1	271.3	38.26

Study site	**Model**	**Response distribution**	**Covariates**	***P*–value**	**edf**	**DE (%)**	**REML score**	**CV (%)**
			elevation	<0.001***	13.38			
			SD NDVI	0.083	4.91			
LHR	mod.k.2	Tweedie	x, y	<0.001***	15.68	55.9	367.9	15.70
			elevation	0.029*	6.57			
			SD NDVI	0.113	2.86			
LHR	mod.k.3	Negative binomial	x, y	<0.001***	16.11	64.2	387.6	20.97
			elevation	0.001**	9.65			
			SD NDVI	0.058	3.19			
LHR	**mod.k.4**	Quasi–poisson	x, y	<0.001***	17.54	57.9	280.0	31.92
			elevation	0.011*	12.54			

The best DSM for Fongoli estimates that the highest densities of galagos occurred in areas with a median annual NDVI score between 0.22 and 0.43 (Figure 5.2) and the estimated abundance of galagos decreases with increasing density of chimpanzee sleeping locations (Figure 5.2). For LHR the best DSM estimates that galago abundance is higher in areas with an elevation less than 1950 m, and abundance decreases with increasing elevation (Figure 5.2).

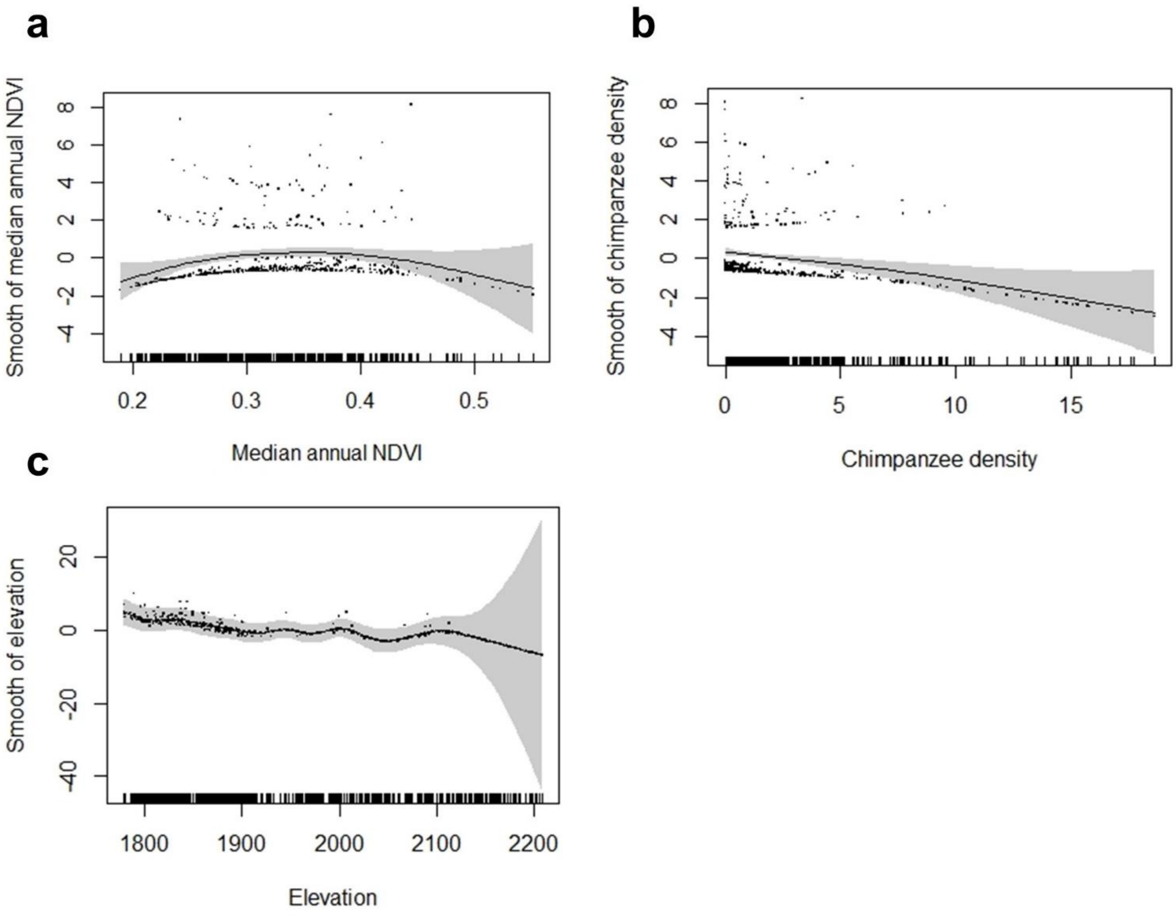
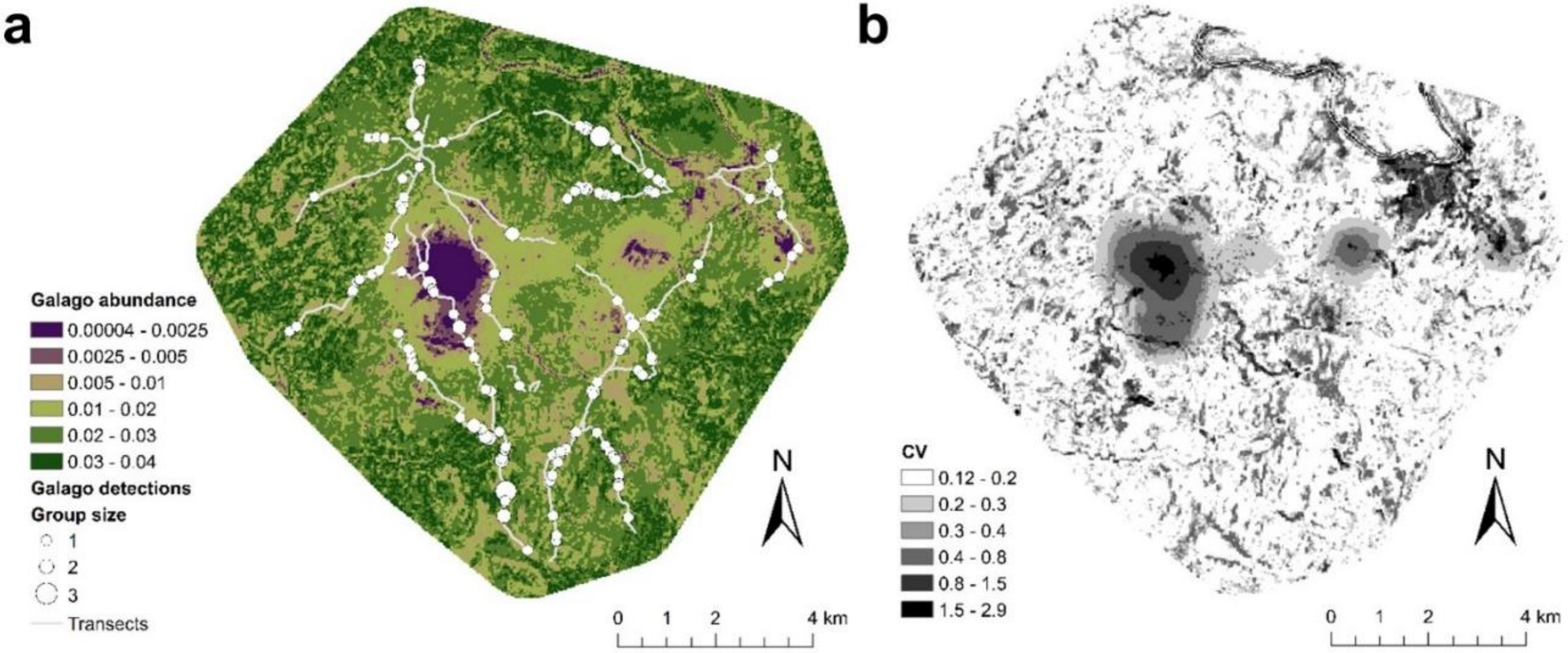


Figure 5.2 The effect on the response of smooths from the best DSMs: a) median NDVI at Fongoli; b) density of chimpanzee sleeping locations at Fongoli; c) elevation at LHR. Approximate 95% confidence intervals are shown in grey and the black dots represent the residuals. The rug ticks along the x-axes indicate the coverage of the range of values for each covariate.


a
Galago abundance
0.00004 - 0.0025
0.0025 - 0.005
0.005 - 0.01
0.01 - 0.02
0.02 - 0.03
0.03 - 0.04
Galago detections
Group size
1
2
3
Transects
N
0 1 2 4 km
b
CV
0.12 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.8
0.8 - 1.5
1.5 - 2.9
N
0 1 2 4 km

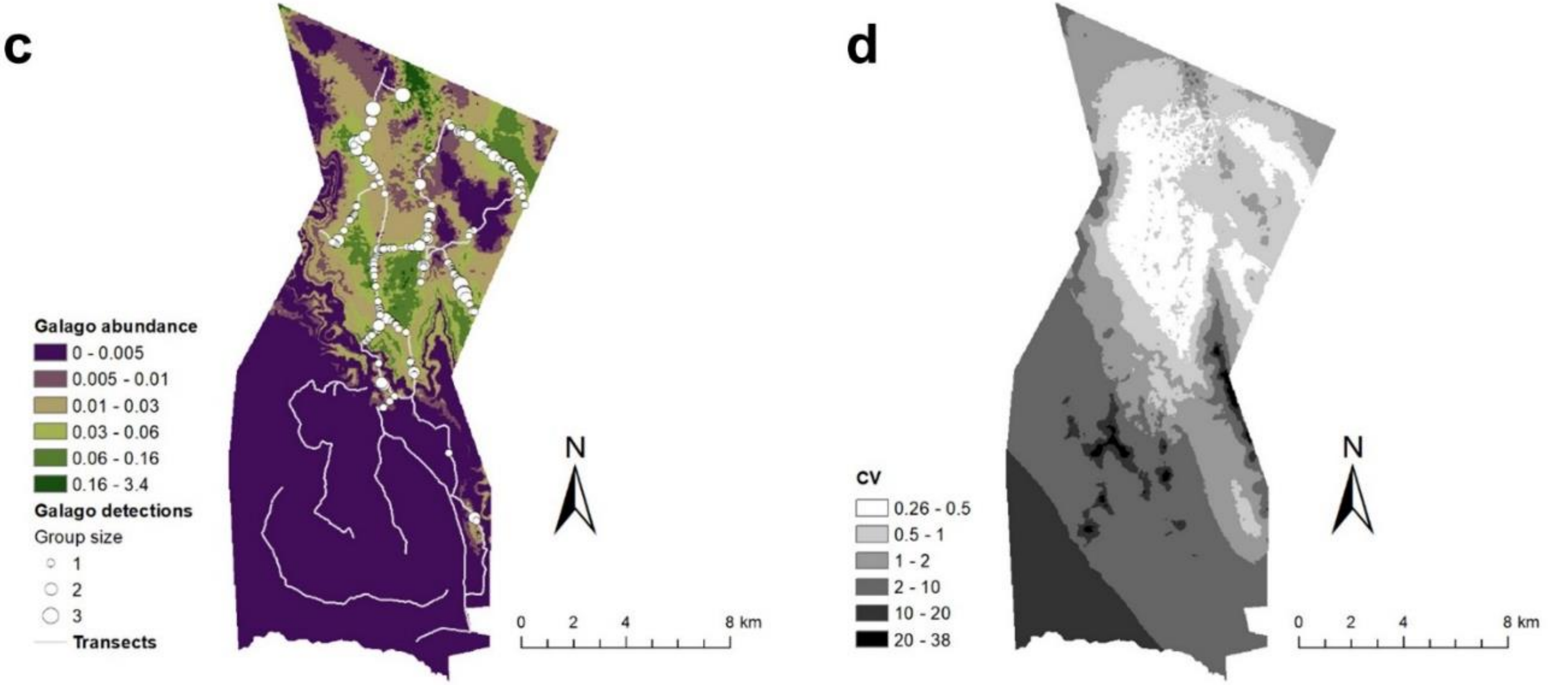


Figure 5.3 Density surface models showing the a) estimated abundance and b) coefficient of variation (CV) of Northern lesser galagos at Fongoli, Senegal, and the c) estimated abundance and d) CV of Northern lesser galagos at Lolldaiga Hills Ranch, Kenya. Abundance and CV estimates are per 900 m^2 grid cell. Greener areas represent higher abundance (a and c) and darker areas represent higher CV (b and d).

5.3.3 Sleeping site ecology

5.3.3.1 Sleeping tree characteristics at Fongoli

We located 25 sleeping trees at Fongoli. The most commonly used sleeping tree species was *Pterocarpus erinaceus* (*N* = 15) followed by: *Vitellaria paradoxa* (*N* = 2); *Terminalia macropterous* (*N* = 2); *Bombax costatum* (*N* = 1); *Anogeissus leiocarpus* (*N* = 1); *Hannoa undulata* (*N* = 1); *Spondias monbin* (*N* = 1); *Parkia biglobosia* (*N* = 1); and *Daniella oliveri* (*N* = 1).

Mean height of sleeping trees was 14.06 ± SD 3.88 m (range = 5.42–20.49 m; *N* = 25) and mean DBH was 49.56 ± SD 9.65 cm (range = 26.5–71.4 cm; *N* = 25). Sleeping trees were significantly greater in height (Wilcoxon rank sum test: *W* = 654.5, *P* <0.001) and DBH (Wilcoxon rank sum test: *W* = 302.0, *P* <0.001) than all other measured trees (surrounding trees in sleeping sites and all trees in control sites; *N* = 419). Sleeping tree cavities ranged from small round sleeping holes <5 cm in diameter to large open branches or holes ≥15 cm in diameter and long fissures (see Figure 5.4 for some examples). Mean height of tree cavities used by galagos was 5.91 ± SD 1.82 m (range = 3.57–9.60 m; *N* = 24). Mean distance between tree cavities and the top of the tree was 8.50 ± SD 3.63 m (range = 2.23–15.08 m; *N* = 24). We could not reliably determine the height of the tree cavity used in one sleeping tree. I recorded evidence of burning in almost all of the sleeping and control sites for which I have data (94.9%; *N* = 39).

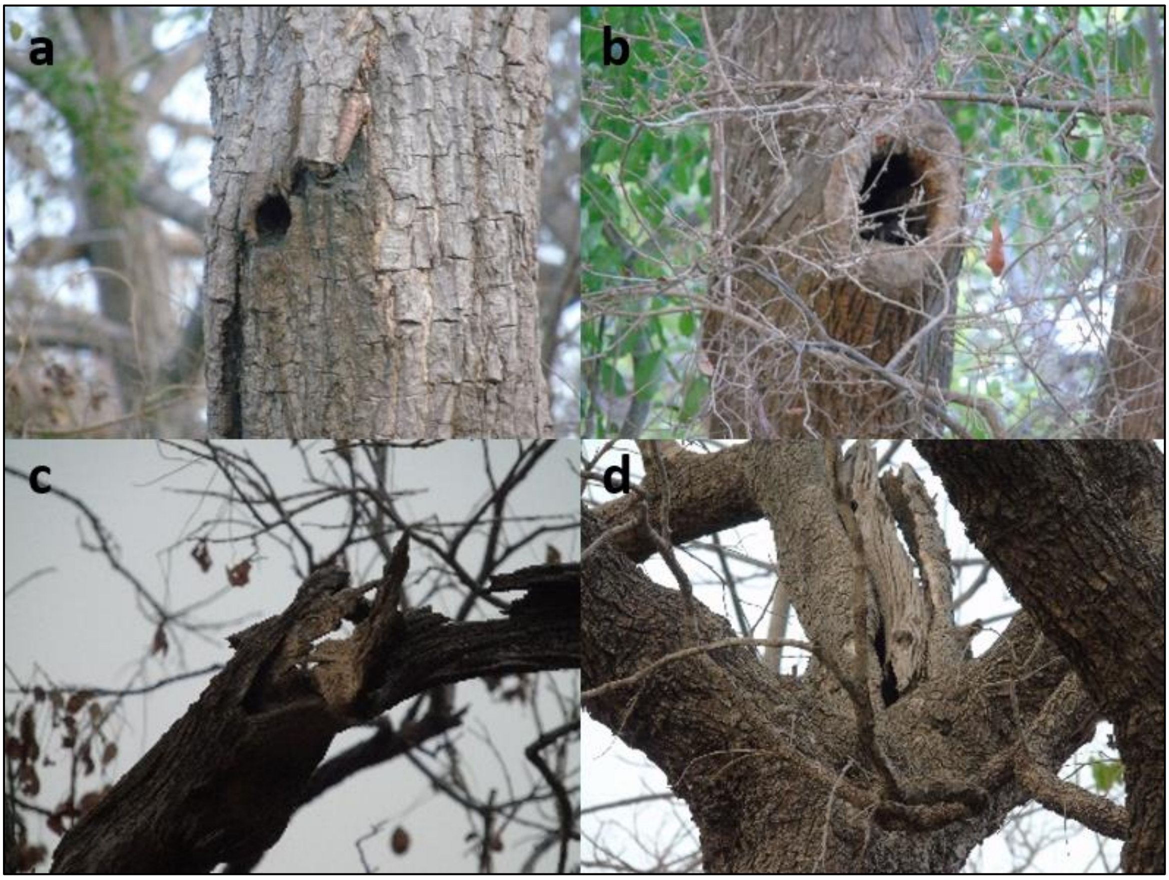


Figure 5.4 Tree cavities used by galagos: a) small hole with a diameter <5 cm; b) large hole with diameter ≥15 cm; c) broken branch; d) long fissure in branch.

5.3.3.2 Predictors of sleeping sites

I collected data from 25 sleeping sites and 25 control sites at Fongoli. Random forest classification analysis revealed that the number of connected trees to the sleeping or control tree and percentage of canopy cover were the most important predictors of sleeping sites compared to control sites (see Table 5.3). The mean out of sample prediction rate for 500 repetitions was 6% (8% for sleeping sites and 4% for control sites; see the confusion matrix in Table 5.4). The model correctly predicted 21 sleeping sites as sleeping sites and 23 control sites as control sites.

Table 5.3 The two best predictors of sleeping sites of Northern lesser galagos at Fongoli, Senegal from March to May of 2018, identified by random forest classification analysis. The variable importance scores for all other variables are in Appendix 5G.

	Sleeping sites		**Control sites**		**Variable importance score**
Habitat predictor	**Mean ± SE**	**Range**	**Mean ± SE**	**Range**	
Number of connected trees	3.54 ± 0.46	0–8	0.68 ± 0.21	0–4	0.148
Canopy cover (%)	34.09 ± 2.86	8.89–66.67	16.89 ± 2.68	2.11–55.56	0.074

Table 5.4 Confusion matrix showing the performance of the random forest model in determining sleeping site predictors of Northern lesser galagos at Fongoli, Senegal from March to May of 2018.

	Predicted presence		
Observed presence	Control	Sleeping	Out of bag error
Control	23	2	0.04
Sleeping	4	21	0.08

I found no significant difference in the density of chimpanzee sleeping locations at galago sleeping site locations (*N* = 25) compared to random control locations (*W* = 409, *P* = 0.061). There was no significant correlation between the minutes after sunset that galagos left their sleeping sites (*N* = 20) and the density of chimpanzee sleeping locations at those sites (r_s = -0.15, *P* = 0.534). For five sleeping sites we could not reliably determine the time galagos left due to poor visibility.

5.4 Discussion

Western chimpanzees living in a savannah landscape systematically hunt Northern lesser galagos at Fongoli, Senegal, and until now, we had very limited knowledge on how this influences the galagos' behaviour and ecology. I found that the spatial distribution of active galagos at Fongoli, and their sleeping site ecology, suggest predation avoidance from chimpanzees. The density of chimpanzee sleeping locations was the strongest predictor of galago abundance at Fongoli; estimated abundance was higher in areas with a lower density of chimpanzee sleeping locations. Estimated galago abundance at Fongoli was also greater in areas with lower vegetation productivity (median NDVI scores between 0.22 and 0.43). There was no significant difference in density of chimpanzee day locations between galago sleeping sites and random locations, which suggests that galagos do not avoid chimpanzees spatially when sleeping during the day as they do when active at night. Instead, they choose well-concealed sleeping sites that allow for crypsis and swift evasion from chimpanzees. At LHR, where there are no chimpanzees, the model predicted that galagos were more abundant in areas of lower elevation (<1950 m).

5.4.1 Spatial distribution and predator avoidance

Researchers at Fongoli have recorded Western chimpanzees systematically hunting galagos since 2005 with >500 cases documented via the FSCP (FSCP, unpublished data). The DSM for Fongoli revealed that estimated galago abundance (when active) was lower in areas where the density of chimpanzee sleeping locations was higher, suggesting that galagos avoided the sleeping locations of their predators, the chimpanzees, when active. The vast majority (95%) of reported predation events on galagos occurred during the wet season (June–September) or transitional months (May and October; Pruetz et al., 2015); my study was carried out in the dry season (March to May) before the start of the rains, which suggests that galagos are fearful of their predators even during the dry season when they are less likely to be hunted. However, researchers at Fongoli have observed chimpanzees active at night, mostly for feeding, socialising or soaking in water, particularly in the dry season (Pruetz, 2018). This could explain their avoidance of chimpanzees during the dry season, even though chimpanzees have only been recorded eating vegetation, not hunting, during the night (Pruetz, 2018).

The percent deviance explained, one of the indicators of model performance, for DSMs at Fongoli were all much lower than DSMs for LHR, suggesting that there are other factors influencing the distribution of galagos at Fongoli. Chimpanzee community size at Fongoli fluctuates but consists of around 32 individuals on average (community size varied between 28 and 36 individuals between 2005 and 2006; Pruetz, 2018), and chimpanzees at Fongoli spend their time in larger parties than other populations (Pruetz and Bertolani, 2009). I do not have the sleeping location for every individual each night, usually just the largest group of individuals, and mean nesting party size of chimpanzees at Fongoli is 20.8 ($N = 39$; Pruetz, 2018). If I knew the location of every chimpanzee every night, the performance of the model in terms of deviance explained could have improved. Other factors such as food availability may be important in galago spatial abundance; in order to investigate this in future research, knowledge of the production and availability of the animals' food in the ecosystem is needed (Hanya and Chapman, 2013).

Galago detections at Fongoli were fairly evenly distributed across the transects. In contrast, at LHR the detections were predominantly in the north of the study site with very few in the southeast and none in the southwest. This was reflected in my DSMs, where a large proportion of the distribution at LHR can be explained by geographic location alone, but the best DSM for Fongoli did not include spatial location as a covariate. At LHR, the north is generally lower in elevation than the south, with less green vegetation (see Appendix 5B, which corresponds with elevation - highly positively correlated with median NDVI) being a significant predictor of galago distribution. At Fongoli, median NDVI scores were more homogenous across the study site, which could explain why galagos were distributed more evenly. Another explanation could be that galagos avoided occupying a more confined area to reduce the chance of being located easily by chimpanzees. At LHR, they are only prey to opportunistic predators and it may have been less risky to inhabit areas confined to the North and Eastern parts of the study site.

Fongoli has a lower mammal species richness than the nearby protected Assirik area within the Parc National du Niokolo-Koba (Lindshield et al., 2019). Researchers hypothesised that this is due to the higher degree of human activity at Fongoli (Lindshield et al., 2019), but here I found that the distribution of galagos is not influenced by human settlements or mining operations. Galagos may be more easily adapted to anthropogenic disturbance than other mammals, owing to their nocturnal lifestyle.

5.4.2 Sleeping site selection and predator avoidance

At Fongoli, galagos preferred sleeping sites that enhanced concealment and allowed several means of escape from predators. Galago sleeping trees were significantly greater in DBH than all other measured trees (Hankerson et al., 2007; Teichroeb et al., 2012; Cheyne et al., 2013; Seiler et al., 2013; Caselli et al., 2017). Trees housing sleeping primates inside cavities often have a large DBH (Hankerson et al., 2007; Seiler et al., 2013) and I found that DBH was highly correlated with the total number of tree cavities in the site. Mean tool length used by chimpanzees is 63 cm (range = 40–120 cm; Pruetz and Bertolani, 2007) so trees with a large DBH and a greater number of tree holes can likely facilitate more internal movement when being targeted by a tool-bearing chimpanzee, and may provide more escape routes through the sleeping tree and to surrounding trees with cavities. However there may also be a thermoregulatory benefit to galagos using tree cavities in extremely hot weather, particularly in large trees, as they are likely to provide fewer fluctuations in temperature (Schmid, 1998).

Galagos chose sleeping trees that were significantly taller than all other measured trees, which are likely advantageous for detecting approaching predators and reducing accessibility for them (see also: Day and Elwood, 1999; Xiang et al., 2010; Bernard et al., 2011; Teichroeb et al., 2012; Rode et al., 2013; Feilen and Marshall, 2014; Thiry et al., 2016; Caselli et al., 2017). Mean height of tree cavities galagos used (5.91 m) was very similar to the mean height of sleeping locations of Northern lesser galagos at Kwakuchinja (5.95 m; Chapter 4). However, mean distance between tree cavities used as entrances/exits and the top of the tree was much greater at Fongoli than between sleeping locations and the top of trees for the population at Kwakuchinja (8.50 m and 4.30 m respectively; Chapter 4). The significantly taller sleeping trees and considerable distance between the sleeping location and the top of the tree could allow for larger hollow spaces within the tree or more escape routes from hunting chimpanzees. The use of lower entrance holes is consistent with the idea that lower holes may lead to deeper usable cavities than those higher up the trunk (Hankerson et al., 2007).

Both connectivity (Albert et al., 2011; Bernard et al., 2011; Thiry et al., 2016; Chapter 4) and canopy cover (Hamilton, 1982; Xiang et al., 2010) provide more avenues for escape from predators. They are the most important factors in the sleeping site selection of galagos at Fongoli, and two of the most important for galagos at Kwakuchinja (Chapter 4), increasing their chances of staying hidden from predators and maximising the likelihood of escape. One clear difference between the two populations is that the galagos at Fongoli use only tree cavities, choosing larger trees with holes, whereas galagos in Kwakuchinja mostly slept out on branches, in leaf nests, or in palm leaves (Chapter 4). It is likely that the risk of sleeping on the external parts of a tree are too high for galagos at Fongoli when hunted by chimpanzees, but dense canopy and connectivity to the sleeping tree allows them to escape through the canopy using thinner branches that may not support chimpanzees. Dense canopy cover could also allow galagos to remain hidden from aerial predators (Seiler et al., 2013; Chapter 4) and provide some relief from extremely hot temperatures when sleeping during the day (Chapter 4).

Contrary to my predictions, and the sleeping ecology of galagos at Kwakuchinja (Chapter 4), mid-level vegetation density was not a significant predictor of sleeping sites at Fongoli. At Fongoli, galagos sleep in extremely large trees with many tree cavities to escape through, therefore mid-level vegetation density may be unnecessary for escape routes when so low down the tree. A greater density of trees or lianas were also not important factors of galago sleeping sites. Mid-level vegetation, lianas and surrounding trees may provide ways of chimpanzees and other scansorial predators such as snakes to approach tree cavities quicker than they could from the ground (Phoonjampa et al., 2010). The time for galagos to detect chimpanzees and escape from them would therefore be greater, especially when sleeping in such tall trees, which could explain why vegetation surrounding the sleeping tree (except the canopy above) was not a predictor at Fongoli. With no preference for vegetation surrounding the trunk of the sleeping tree, and their swift locomotive abilities, maximising opportunities to escape seems to be more important to galagos than staying hidden.

The way primates respond to predation risk is a growing and very important area of research (Terborgh and Janson, 1986; Isbell, 1994; Hill and Lee, 1998; Colquhoun, 2006; Karpanty, 2006; Coleman and Hill, 2014; Farris et al., 2014;

Kamilar and Beaudrot, 2018). However, primate on primate predation is a fairly understudied field. The unique interaction between Western chimpanzees and Northern lesser galagos was first documented in 2007 (Pruetz and Bertolani, 2007), but until now we knew very little about the potential effects of the hunting behaviour on galago behaviour and ecology. My study found evidence for galagos living in a landscape of fear, with predation avoidance from chimpanzees being a driver of spatial abundance and sleeping site choice at Fongoli.

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Chapter 6. Successful non-invasive sampling method for the retrieval of DNA from a nocturnal primate

Abstract

Genetics has revolutionised the study and conservation of natural populations by revealing novel information such as population structure and genetic diversity, and identifying cryptic species and inbred populations for genetic rescue. However, obtaining samples for genetic analysis is often challenging. Non-invasive methods are increasingly used in wildlife research and advantageous to both researchers (e.g. no specialised training needed) and the animals involved (e.g. reduced stress). Particularly challenging to sample are nocturnal primates, which are generally small, arboreal and elusive. As a result, taxonomic uncertainties have not been resolved and there is a paucity of literature on nocturnal primate mating systems. Researchers have obtained genetic samples from nocturnal primates using live-trapping, mist-netting and catching them by hand. For some of the larger diurnal primates, it is possible to collect faeces and urine non-invasively to retrieve DNA, but for nocturnal primates such samples are difficult to obtain. I adapted a technique originally developed for disease surveillance in olive baboons (*Papio anubis*) and rhesus macaques (*Macaca mulatta*), to collect saliva non-invasively, from free-ranging Northern lesser galagos (*Galago senegalensis*) at Kwakuchinja to yield amplifiable DNA template. I hung sterile nylon strings in occupied sleeping trees, baited them with different sugary solutions and monitored them using camera traps to confirm that the strings had been chewed by galagos. I returned before dawn to collect any strings that were chewed during the night. I also trialled the same methods at Fongoli and LHR. In total, I collected 25 samples at Kwakuchinja and the overall success rate was 0.27 samples collected per trap night (25 samples collected from 92 strings). Northern lesser galagos showed no preference for the different bait types but some retrieved higher quantities of DNA than others. I extracted DNA from each of the samples and amplified the cytochrome b region of the mitochondrial genome (217 bp). I did not obtain any samples from Fongoli or LHR; it is not clear why that is, but possible reasons include resource availability and differences in sleeping ecology. For further verification, quantitative PCR (qPCR) and sequencing are needed, but this study shows that it is possible to obtain genetic material non-invasively from free-ranging galagids using baited strings, reducing the requirement to trap them. This method may be applicable to, or could be adapted for, other nocturnal, arboreal, or cryptic species.

Keywords: buccal cells; bushbaby; noninvasive; strepsirrhine.

6.1 Introduction

The application of genetic methods is integral to the study of natural populations and has positively influenced the conservation of wildlife (Allendorf, 2017). Genetics is particularly useful for revealing information on elusive species that are difficult to study in the wild, for example: the genetic diversity of the nocturnal Annamite striped rabbit (*Nesolagus timminsi*: Nguyen et al. 2021); kinship and dispersal of the elusive Cabrera vole (*Microtus cabrerae;* Ferreira et al., 2018); and population genetics of the rarely-observed noisy scrub-bird (*Atrichornis clamosus*, once thought to be extinct: Cowen et al., 2021). Invasive genetic sampling of wild animals (making contact with them to take the sample) has utility but can be time and money consuming, risks negatively impacting the behaviour (potentially causing stress and mortality) of the individuals involved (Taberlet and Luikart, 1999), and often requires specialist equipment or training to handle the animals (Smith and Wang, 2014).

Nocturnal primates are small, arboreal and notoriously cryptic, and invasive genetic sampling methods have proven valuable in learning more about these animals. Studies on Madagascan nocturnal primates used live-trapping to reveal valuable information on their behaviour and ecology using genetics (Fredsted et al., 2005; Schliehe-Diecks et al., 2012; Eberle and Kappeler, 2004; Kessler et al., 2014; Radespiel et al., 2001, 2009; 2019). However, published studies on the genetics of free-ranging nocturnal primates outside of Madagascar are far less abundant and genetics studies on galagids are lacking (Chapter 2). This is likely due to the difficulty of obtaining genetic samples from nocturnal primates; therefore a robust non-invasive technique is needed.

Non-invasive sampling involves the collection of DNA from animals without making contact with them (Taberlet et al., 1999). This type of sampling is increasingly used and advantageous for having little effect on the behaviour of the animals, often requiring lower field work costs, enabling the sampling of cryptic species (Taberlet et al., 1999; Ferreira et al., 2018), and can identify a higher number of individuals than live-trapping (Ferreira et al., 2018). The relatively poor quality and quantity of template DNA recovered from non-invasive sampling can be prone to genotyping errors (e.g. allelic dropout) and issues from contamination or PCR inhibitors (Taberlet and Luikhart, 1999). In potentially degraded non-invasive samples the amplification success of mitochondrial DNA (mtDNA) should be greater than for single copy loci, because eukaryotic cells have multiple copies of mtDNA (Foran, 2006). Sufficient information for conservation genetics studies can be obtained from samples collected non-invasively even with small (e.g. $N \geq 10$: Smith and Wang, 2014) sample sizes (Smith and Wang, 2014; Shultz et al., 2022). Nocturnal primate researchers have used mtDNA in phylogenetic studies to reveal new species (mouse lemurs, *Microcebus* spp.: Yoder et al., 2000; Pastorini et al., 2001) and to study population structure (gray mouse lemurs, *Microcebus murinus*: Fredsted et al., 2005; tarsiers, *Tarsius* spp.: Merker et al., 2009).

Non-invasive samples are usually sourced from faeces, hairs or feathers (Goossens and Bruford, 2009). Faecal-based genetic sampling has been used for genotyping (Müller et al., 2014; Davis et al., 2013) and investigating genetic diversity (Taberlet et al., 1997; Quéméré et al., 2010), population size and marking behaviour (Lampa et al., 2015), and social dynamics such as group stability (Hagemann et al., 2018). Although scat may be easily obtained for terrestrial and non-elusive species, non-invasive sampling for other sources of DNA often involves creative methods. Hair samples have been retrieved using hair snares, often involving Velcro® and sharp tools such as nails or barbed wire, from species that are elusive and occur in low densities (e.g. grizzly bears, *Ursus arctos*: Phoebus et al., 2020; felids and other mammals: Garcia-Alaniz et al., 2010). Researchers adapt the hair snare approach for their chosen species; for example hair samples were collected from Eurasian otters using an innovative hair trap involving Velcro® within a tunnel (Anderson et al., 2006). However, such methods have a limited application to small, arboreal and nocturnal mammals like galagids when they move swiftly through different heights of trees.

Buccal cells from saliva can be a valuable source of DNA and can be collected invasively from animals using sterile swabs (wolves, *Canis lupus*: Sastre et al., 2009; other canids: Sundqvist et al., 2008), FTA® Classic Cards (titi monkeys: Bunce et al., 2011) and absorbent sponges (domestic canids: Yokoyama et al., 2010). Although buccal cells from saliva are a potentially useful source of DNA, relatively few studies have attempted to retrieve saliva samples non-invasively in natural populations. Researchers have successfully obtained saliva non-invasively from the wounds of animals preyed upon by coyotes (*Canis latrans*: Williams et al.,

2003) and other canids (Sundqvist et al., 2008). A recent innovative study used saliva from bite marks in artificial prey (clay models) to amplify and sequence the mitochondrial cytochrome c oxidase subunit I (COI) gene to aid in the identification of predators of European fire salamanders (*Salamandra salamandra*: Rößler et al., 2020). DNA has also been collected by swabbing the area of fruit showing saliva after being eaten and discarded by scarlet macaws (*Ara macao*: Monge et al., 2020). A similar method was used for bonobos (*Pan paniscus*), where cotton swabs were used to retrieve saliva from partly consumed vegetation (Ishizuka et al., 2019), and researchers of wild chimpanzees collected remains of fruit, or 'wadges', for saliva recovery (Sugiyama et al., 1993). Researchers of free-ranging but habituated Tibetan macaques (*Macaca thibetana*) created a device using a PVC tube containing absorbent cotton dental rope baited with fruit juice to obtain saliva (Simons et al., 2012); after the monkey chewed for several seconds the rope was pulled into the sterile collection cartridge to obtain the sample.

Collecting samples non-invasively from nocturnal primates is particularly challenging because their faecal and urine deposits, often collected from free-ranging diurnal primates (Launhardt et al., 1998; Gerloff et al., 1999; Smith et al., 2000; Quéméré et al., 2010; Müller et al., 2014; Bryant et al., 2016; Hagemann et al., 2018), are extremely small and difficult to find and retrieve in the field at night. It is possible to obtain saliva from captive aye ayes using swabs baited with diluted honey to measure salivary melatonin concentrations (Fuller et al., 2016); a similar technique could be used to obtain genetic samples from wild nocturnal primates. No published studies have yet used non-invasive sampling to research the genetics of free-ranging nocturnal primates. An ideal method is one that does not directly harm or cause distress to the study animal, but yields sufficient DNA for downstream analysis and is cheap and reproducible at scale.

I adapted an oral sampling method that involved baited sterile swabs or strings to retrieve saliva samples from primates chewing on the baited object (Smiley Evans et al., 2015). Although previously used for disease surveillance, I adapted the method to retrieve DNA non-invasively from wild Northern lesser galagos to confirm the species using the mtDNA obtained.

6.2 Materials and methods

6.2.1 String preparation

I cut 4 mm braided nylon string into pieces 16.5 cm in length (Smiley Evans et al., 2015). To sterilise and remove any contaminating DNA I autoclaved them for 20 minutes at 121 °C. I then placed each string into an individual transparent zip-lock bag and exposed each one to a 15-Watt, 365 nm UV bench lamp light for 30 min on the front side of the bag and 30 min on the back to degrade any remaining DNA.

6.2.2 Data collection

6.2.2.1 Kwakuchinja

I located sleeping sites of Northern lesser galagos by following them back to their sleeping sites in the morning (05:30–07:00 h) as part of a separate project on their sleeping site ecology (see section 4.2.2 of Chapter 4). In the evening (17:00–18:30 h) I tied two or four sterile nylon strings to each sleeping tree (or nearby tree if it was inaccessible) using twine. I looked for places on the tree where I could hang the strings and galagos would easily be able to reach them; there was usually a branch beneath the strings. I soaked the lower 3–4 cm of the strings in one of four sugary bait types (honey / strawberry jam / white sugar syrup / Tang: https://www.mondelezinternational.com/Our-Brands/Tang; I changed the types of bait each time), based on the knowledge that other species of galagid (Nekaris and Bearder, 2011; Scheun et al., 2014) and Northern lesser galagos in The Gambia (Svensson and Bearder, 2013) eat fruit. I monitored the baited strings using a camera trap at each site (camera traps were set to record 20 s videos with a 1 s interval; see Figure 6.1).

Figure 6.1 Camera trap and baited strings (left: jam; right: honey) set before sunset in a tree occupied by sleeping Northern lesser galagos at Kwakuchinja in July 2017.

Before sunrise the next day, I inspected the strings and checked the camera trap videos to see whether galagos had chewed on the strings or not. If there was evidence that they had been chewed, I cut 2–3 cm off the base of the strings, placed each one into an individual sterilised universal or bijou container, preserved them in 1–2 ml RNA*later*® buffer and stored them in a dark room. Samples remained at room temperature for 1–2 years before being exported to the UK and were frozen at -20 °C when they arrived at Manchester Metropolitan University.

6.2.2.2 Fongoli and LHR

I trialled the same methods as above at Fongoli in March–May 2018 and LHR in July 2018. At Fongoli, I located sleeping sites (as described in section 5.2.2.2 of Chapter 5) and hung baited strings in the sleeping tree and nearby trees. At LHR, where I had not located any sleeping sites, I hung strings in whistling-thorn acacia

(*Vachellia drepanolobium*) trees within woodland, where I had spotted galagids during line transects (section 5.2.2.1 of Chapter 5).

6.2.2.3 Captive populations

I also obtained samples collected by keepers from captive Northern lesser galagos at Prague Zoological Garden (10 buccal swabs collected as part of routine care), which I used to optimise the polymerase chain reaction (PCR).

6.2.3 DNA extraction and amplification

I used a petri dish and sterile scalpel to cut each string sample in half in order to not overload the spin columns. I extracted DNA from the samples using the ISOLATE II Genomic DNA Kit (https://www.bioline.com/isolate-ii-genomic-dna-kit.html), following the standard protocol provided by the manufacturer with an addition step during preparation: I added 500ul of Phosphate buffer saline (PBS) to each sample and then vortexed and centrifuged each sample two times (2 x: 1 min vortex and 5 min centrifuge). After the extractions were complete, I measured the quantity and purity (measured by 260/280 ratio) of each extracted sample using a NanoDrop spectrophotometer.

I used primers 14850F and 15068R from Pozzi et al. (2019; see Appendix 6A), which were used to amplify the mtDNA cytochrome b region in Kenya coast galagos, *Paragalago cocos*, and Zanzibar galagos, *P. zanzibaricus*. I performed PCR using the MyTaq Red Mix kit from Bioline (www.bioline.com) with a reaction volume of 10 μL containing 5 μL Taq mastermix (containing MgCl2 at a concentration of 3 mM, dNTPs and polymerase), 4 μL primer mix at a concentration of 2mM, and DNA at a set volume of 1 μL (0.1–25.1 ng/μL). I used the same PCR parameters as in Pozzi et al. (2019) but with slightly lower annealing temperatures. These were: 95 °C for 10 min; followed by a first round of 25 cycles denaturing at 95 °C for 15 s, primer annealing starting at 58 °C (and gradually decreasing to 48 °C across 25 cycles; by -0.4 per cycle) for 30 s and extension at 72 °C for 1 min; then a subsequent round of 25 cycles of 95 °C for 15 s, 48 °C for 30 s and 72 °C for 1 min; and a final extension at 72 °C for 7 min.

Positive PCR products were visualised on a 1% agarose gel stained with Midori green next to a 1 kb ladder. I then cleaned the samples using ExoSAP-IT^{TM}

(following the protocol provided by the manufacturer) and used a Qubit Fluorometer to quantify the DNA in each sample.

6.2.3.3 Precautions taken

To reduce the chances of contamination in the laboratory, I used separate rooms for pre and post PCR experiments. I used previously amplified samples from the captive galagos as positive controls and a negative control (containing molecular grade water in place of sample) in each experiment to monitor potential exogenous contamination in the reagents.

6.3 Results

6.3.1 Success of sample collection

From Northern lesser galagos at Kwakuchinja I retrieved 25 string samples in total (16 from 2016 and 9 from 2017; see Figure 6.2). I hung strings at 13 different sites at Kwakuchinja and the 25 samples came from 4 of the 13 sites. The mean latency from setting and baiting the strings to them being chewed was 8.5 ± SD 7.6 days (range 1–18 days) and the overall success rate (number of samples obtained / number of trap nights) was 0.27 samples per trap night (25 samples obtained / 92 baited string samples; 0.26 samples per trap night in 2016 and 0.29 samples per trap night in 2017). I retrieved 9 samples baited with jam, 7 with honey, 6 with Tang and 3 with sugar syrup. Of the 25 samples, 15 yielded amplifiable DNA (see Appendix 6B). Of the 15 that showed bands, 4 were originally baited with jam, 6 with honey, 3 with Tang and 2 with sugar syrup (see Table 6.1).

No chewed string samples were retrieved from Fongoli or LHR.

Figure 6.2 A Northern lesser galago chewing on a string baited with honey at Kwakuchinja in July 2017.

6.3.2 Extractions

The median quantity of DNA reported by the NanoDrop spectrophotometer was 3.2 ng/µl (IQR = 2.6; range = 0.1–25.1 ng/µl, *N* = 25; see Table 6.1 for the breakdown by each bait type). The median purity reported by the NanoDrop spectrophotometer, measured by 260/280 ratio, was 1.37 (IQR: 0.33; range = 1.12–15.00, *N* = 25; see Table 6.1).

6.3.3 Amplicons

The median quantity of DNA reported by the Qubit Fluorometer was 26.4 ng/µl (IQR = 19.3 ng/µl; range = 16.6–43.4 ng/µl, *N* = 15; see Table 6.1).

Table 6.1 The extract quantity and purity, amplicon quantity, and percent of positive PCR samples for each of the four bait types

	Extract quantity (ng/µl)			**Extract purity (260:280)**			**Amplicon quantity (ng/µl)**			**Positive PCR (%)**
Bait type	mean ± SD	range	*N*	mean ± SD	range	*N*	mean ± SD	range	*N*	
Honey	3.3 ± SD 3.2	0.1–9.5	7	1.57 ± SD 0.54	1.16–2.73	7	32.1 ± SD 10.7	21.2–43.4	6	85.7
Jam	3.6 ± SD 1.3	1.8–6.3	9	1.42 ± SD 0.23	1.12–1.82	9	25.6 ± SD 9.4	16.6–38.4	4	44.4
Sugar	1.7 ± SD 1.0	0.6–2.4	3	6.0 ± SD 7.8	1.38–15.00	3	41.2 ± SD 0.0	41.2–41.2	2	66.7
Tang	10.2 ± SD 9.3	2.0–25.1	6	1.39 ± SD 0.16	1.21–1.64	6	23.6 ± SD 6.7	16.9–30.2	3	0.5

6.4 Discussion

This study demonstrates that it is possible to collect saliva samples non-invasively from wild nocturnal primates and successfully extract and amplify DNA from them; even for samples that have been preserved for over 4 years. This method does not require any specialised training to collect the samples, is low in cost, and, unlike other ways of collecting saliva non-invasively from wild primates (e.g. Simons et al., 2012; Ishizuka et al., 2019), does not require habituating primates, being in close proximity to them or being present while the samples are deposited. When live-trapping galagids, traps must be checked regularly (4–5 times a night: Pozzi et al., 2014, 2019; every hour: Scheun et al., 2015, 2016), but with this approach the strings are left at dusk and collected just before dawn, allowing researchers time to engage in other aspects of nocturnal research within that period. It is important that this method is further verified using qPCR and sequencing.

The trap rate of 0.27 samples per trap night at Kwakuchinja is lower than the success rate of hair traps on felids (0.36 samples per trap night outside the protected area and 0.48 samples per trap night within it: Garcia-Alaniz et al., 2010) and Eurasian otters (0.71 samples per trap night: Anderson et al., 2006). I could not find any comparison trap rates for small mammals but the trap rate demonstrates the potential for this method to obtain a large number of samples for genetic studies.

Given the suboptimal storage conditions (long-term storage at room temperature), I retrieved higher quantities of DNA than expected. The latency between collecting samples and extracting DNA can negatively affect the stability of the DNA and in this study it was 3–4 years before I made extractions from the samples due to logistical constraints. Fortunately, there should have been very little degradation from UV light because I collected the strings before sunrise and stored the collected strings in the dark. Saliva maintains high quality DNA over different storage conditions and times (Sun and Reichenberger, 2014) and in this study RNA*later*® preserved the samples well at room temperature before they reached the UK. For future studies, I recommend minimising freeze-thawing and conducting the PCRs as soon as possible after extraction.

The sample size is small but allows a preliminary comparison of the effectiveness of the four bait types for retrieving amplifiable DNA. For future studies

I recommend researchers to use honey as bait because it reported the highest purity and the highest percentage of positive PCR results (85.7%). Although extracts of samples baited with Tang retrieved the highest DNA quantities, the variance was far greater than for honey. I was not able to determine any preference for bait type using the camera trap videos. The quantity and purity values obtained from the extracts are not as high as those from the amplicons due to both DNA and sugar absorbing light at a wave length of ~260 nm (Kaijanen et al., 2015); both the DNA and any leftover sugar may have contributed to the values from the extracts. Since the average purity value was less than 1.8 (pure DNA; Desjardins and Conklin, 2010), I recommend a further clean-up step of the DNA extracts prior to PCR to increase success. The addition of PCR adjuvants such as Bovine Serum Albumin (BSA) at a concentration of 0.1–1.2 µg/µL may also positively increase amplification success, since it is routinely used with difficult templates (e.g. those from non-invasive samples; Beja-Pereira et al., 2009). It is important that quantitative PCR (qPCR) and Sanger sequencing are used to verify the results.

I also trialled the data collection methods at Fongoli and LHR, but did not retrieve any samples. There are a number of possible explanations as to why that might be. There were remarkable differences in the sleeping site ecology of Northern lesser galagos at Kwakuchinja and Fongoli (e.g. galagos at Fongoli slept inside tree cavities of large trees and those in Kwakuchinja slept out on branches of smaller trees: see Chapters 4 and 5), which could have affected their ability to detect the baited strings. At Fongoli, galagos are subjected to systematic hunting by Western chimpanzees (Pruetz and Bertolani, 2007; Pruetz et al., 2015) and may be more fearful of approaching novel objects or want to move swiftly to avoid detection near sleeping sites. Furthermore, I witnessed significant tree felling in areas of Kwakuchinja and it is possible that the galagids' habitat and potential food sources (e.g. tree gum: Nash and Whitten, 1989; Svensson and Bearder, 2013) are diminishing (Chapter 7) but food sources may be more abundant at Fongoli or LHR. However, I have no evidence that this is the case.

This method is not only limited to Northern lesser galagos. When staying at a hotel 13 km northeast of Kwakuchinja, on the border of Tarangire National Park, I heard small-eared greater galagos (*Otolemur garnettii*) calling and left four baited strings in the trees on the hotel site. I retrieved four samples from small-eared greater galagos and successfully amplified DNA from them, which demonstrates that this method could be effective for many other species.

Logistical issues could affect the way researchers are able to use this method. If researchers do not have access to camera traps, they can visibly assess the strings, but the footage is useful for determining that only the target species have chewed the strings. The absence of rainfall was undoubtedly a contributing factor in the success of this experiment at Kwakuchinja. In the wet season or other areas with greater rainfall, researchers may need to use further adaptations to the technique to protect the collection area from the rain (e.g. use tarpaulin as a shelter). If feasible to do so, I recommend extracting DNA and conducting analysis in a laboratory in the country of study instead of exporting the samples, to reduce time and costs.

Using invasive or non-invasive samples presents a trade-off between high quality DNA and ethical, safety and logistic considerations. Although the method needs to be verified using qPCR and sequencing, it has the potential to obtain a large number of samples over a short period of time and, most importantly, minimises any possible stress to the animals. The quantities of mtDNA retrieved in this study allow for a wide variety of applications and, for studies where these are sufficient, non-invasive sampling is encouraged.

6.5 References

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Chapter 7. General conclusions and future research

7.1 Introduction

Nocturnal primates are a diverse group of animals with significant variation in their behaviour and ecology. Before beginning my PhD, there were very few studies on wild populations of Northern lesser galagos, with secondary references to their behaviour stemming from studies on Southern lesser galagos. As a result, the knowledge on Northern lesser galagos, particularly wild populations, was limited. In this thesis I endeavoured to learn as much as possible about the most widely-distributed, yet poorly-understood, species of galagid and inform their conservation.

I first aimed to quantify the available literature on the behaviour and ecology of all species of galagid to identify any taxonomic or geographic bias in the literature. I then aimed to investigate Northern lesser galago activity and social behaviour; determine the location of Northern lesser galago sleeping sites and factors contributing to sleeping site choice; and assess the response of Northern lesser galagos to systematic predation from Western chimpanzees. Finally, I aimed to develop a non-invasive sampling technique for obtaining amplifiable DNA from wild galagids.

In this final chapter, I summarise the main findings from Chapters 2–6; discuss the implications of my findings on galagid conservation, and the contributions of this thesis to understanding Northern lesser galago behaviour and ecology; consider the limitations of the thesis; suggest recommendations for future research; and provide overall conclusions.

7.2 Summary of key chapter findings

7.2.1 Chapter 2: Taxonomic and geographic bias in 50 years of literature on galagid behaviour and ecology

Research on the greater galagos (*Otolemur* spp.) was far more abundant than that of any other genera, followed by: the lesser galagos, *Galago* spp.; the Eastern dwarf galagos, *Paragalago* spp.; the Western dwarf galagos, *Galagoides* spp.; the squirrel galagos, *Sciurocheirus* spp.; and the needle-clawed galagos (*Euoticus* spp.) were the least studied. The total research output was generally higher for larger species and those with greater geographic ranges. These results were consistent when captive studies were removed from the models, but neither covariates were significant predictors of research outputs on wild studies only.

Galagids were most studied in South Africa, Tanzania, Kenya and Cameroon. Study locations were generally lower in temperature and in areas with a higher human population density. Galagid physiology and behavioural ecology were the most common categories of research, followed by 'habitat and distribution' and 'genetics and taxonomy'. The most commonly used (stemmed) word was 'behaviour', and 'social' was often referred to, with few words related to ecology.

The findings of this chapter allow researchers to address the gaps in the literature, by expanding the distribution of study sites to other areas within the geographic range of galagids and researching the lesser-studied species.

7.2.2 Chapter 3: Sociality and diel temporal variation in the activity of Northern lesser galagos

At Kwakuchinja, Northern lesser galagos were in groups when active in the majority of the observations, but at Fongoli and LHR I detected them alone in most observations.

Behavioural observations at Kwakuchinja revealed that Northern lesser galagos engage in infrequent social (mostly affiliative, but sometimes agonistic) interactions. I observed Northern lesser galagos leaving olfactory signals through urine washing and scent marking, and I recorded vocalisations at different stages of the night, with a higher rate of vocalising in the morning (pre-dawn). I recorded evidence of consolation behaviour, a highly developed social act, in Northern lesser galagos following an encounter between an individual and potential predator.

There was temporal variation in the behaviour of Northern lesser galagos across three stages of the night (morning: pre-dawn; evening: from dusk; night: later in the night). In the morning they spent a large proportion of their time inactive and foraging was most prevalent in the evening.

The findings of this chapter suggest that group size of Northern lesser galagos varies between populations, and at Kwakuchinja they are connected by vocalisations and olfactory communication, as well as infrequent social interactions.

7.2.3 Chapter 4: Sleeping site selection in the nocturnal Northern lesser galago supports antipredator and thermoregulatory hypotheses

Northern lesser galagos at Kwakuchinja slept mostly on the exterior of trees (e.g. on branches or in leaf nests). They frequently slept in palm leaves, which has not been recorded in any species of galagid before. Northern lesser galagos slept at sites with a higher proportion of canopy cover and mid-level vegetation, more surrounding trees and acacia (*Vachellia* spp.) trees, and better connectivity to the sleeping or control tree than that of the control sites (control sites were 100 m away in a random direction). Sleeping locations were lower in temperature but higher in humidity than control locations (control locations were at the same height in the nearest tree of the same species and height).

The findings of this chapter reveal that the sleeping site ecology of Northern lesser galagos at Kwakuchinja has been influenced by pressures from predation and increasing temperatures.

7.3.4 Chapter 5: The spatial abundance and sleeping site ecology of Northern lesser galagos in a landscape of fear

The strongest predictor of Northern lesser galago spatial abundance was the density of chimpanzee sleeping locations. Estimated abundance was also greater in areas with lower NDVI scores. The locations of chimpanzees during the day did not influence where galagos chose to sleep. Instead, they maximised concealment by sleeping inside cavities of large trees surrounded by vegetation, with many potential escape routes from chimpanzees. At LHR, where Northern lesser galagos are not subject to predation from chimpanzees, their estimated abundance was greater in areas of lower elevation.

The findings of this chapter suggest that the galagos at Fongoli have adapted their sleeping behaviour and spatial distribution when active in response to predation from chimpanzees.

7.2.5 Chapter 6: Successful non-invasive sampling method for the retrieval of DNA from a nocturnal primate

I successfully obtained 25 samples in Tanzania with an overall success rate of 0.27 samples obtained per trap night. Samples had greater quantities of DNA than expected based on their suboptimal storage conditions and of the four bait types, honey retrieved the highest quantities of DNA. I also retrieved samples from small-eared greater galagos at another site. Verification of the method using both qPCR and sequencing is needed.

This method opens a window of opportunities for galagid genetics and could be used or adapted to obtain DNA from other nocturnal, arboreal or elusive species.

7.3 Conservation implications

Although the study species, like many of the galagids, is currently classified as Least Concern (LC) on the IUCN Red List (de Jong et al. 2019), it is important to have extensive behavioural and ecological data on this species before it becomes threatened to help prevent irreversible, detrimental population changes. It is likely that with more data, Northern lesser galagos may not be considered as LC. For example, the ecotone habitats in which they survive are likely under increasing pressure from human activities and climate change (Rehm et al., 2015). A global assessment of the percent of species threatened with extinction within each primate family revealed Galagidae to have the lowest proportion of threatened species (Estrada et al., 2017). However, the authors suggested that the galagids are likely to follow a similar pattern to the Malagasy lemurs, with species being more threatened than currently recognised, and new range-restricted species (e.g. the Angolan dwarf galago, *Galagoides kumbirensis*: Svensson et al., 2017) are being discovered (Estrada et al., 2017).

Since the predictions for Galagidae by Estrada et al. (2017), the following changes to the IUCN Red List have occurred: *E. pallidus* was then LC but is now Near Threatened (NT) due to losing ~20% of its habitat in 15 years (Cronin et al., 2020); *Paragalago orinus* is now VU (Vulnerable), not NT, due to habitat degradation and loss (Perkin, 2021); *P. zanzibaricus* moved from LC to NT to reflect their severely fragmented population (Perkin et al. 2020a); and *Sciurocheirus alleni* is now NT, not LC, because of a rising human population and associated habitat loss (Perkin et al., 2020b). One positive category move occurred: *P*. *rondoensis* recently moved from Critically Endangered (CR) to Endangered (EN: Perkin, 2020). Today, most species of galagid are classified as LC on the IUCN Red List database, with the following exceptions: *Euoticus pallidus* (NT: Cronin et al., 2020); *Galagoides kumbirensis* (NT: Svensson et al., 2020a); *P*. *orinus* (VU: Perkin, 2021); *P*. *rondoensis* (EN: Perkin, 2020); *P*. *zanzibaricus* (NT: Perkin et al., 2020a); *S*. *alleni* (NT: Perkin et al., 2020b); and *S*. *makandensis* (Data Deficient; DD: Svensson et al., 2020b). *Sciurocheirus cameronensis* has not yet been evaluated and should be in the near future.

It must be noted that many species of galagid currently classed as LC have not been studied in great detail (Table 2.1) and therefore may not warrant that classification. For some species, a classification of DD may be more appropriate. For others, based on known and increasing anthropogenic threats, and the negative category moves aforementioned, classifications of NT or VU may be more suitable to protect those species.

7.3.1 Anthropogenic threats to galagids

Known anthropogenic threats to galagids are habitat reduction and fragmentation; this is mainly for logging (Dinesen et al., 2001; Laurance et al., 2008; Bersacola et al., 2015; Forbanka, 2018), agriculture (Svensson and Bearder, 2013; Bersacola et al., 2015), and charcoal production (Bersacola et al., 2015). Galagids were recently revealed to be under threat from the illegal wildlife trade (Svensson et al., 2021). They are sold or consumed as bushmeat (most common in Central and West Africa), sold or used for traditional medicine (mostly recorded in West Africa) and sold as pets (most prevalent in East Africa; Svensson et al., 2021). Images and videos of pet galagids on social media are likely driving an increase in the illegal pet trade of galagids (Svensson et al., 2022). They are sought after in Japan and Southeast Asia in particular, and many are kept in negative conditions where their welfare is greatly compromised (e.g. dressed up in clothes and in daylight or other unnatural environments). These findings are extremely concerning and action needs to be taken to prevent further exploitation of galagids for the pet trade.

During my time in the field and traveling through galagid-range countries I did not find any evidence of galagids being exploited for the illegal wildlife trade. However, the findings from my thesis show that, like other populations of galagids, Northern lesser galagos at both Kwakuchinja and Fongoli are threatened by habitat degradation and likely habitat fragmentation and loss.

Wood is a valuable resource to local communities near the Kwakuchinja study site and I frequently observed tree-felling; the prevalence of cut stems recorded in Chapter 4 is evidence of this. Only one tree cavity was used as a sleeping site at Kwakuchinja (Chapter 4), which is unusual compared to other populations of Northern lesser galagos (e.g. in The Gambia: Svensson and Bearder, 2013; at Fongoli: Chapter 5). This could be because there are few trees big enough to support tree cavities at Kwakuchinja. Similarly, the use of palm leaves as sleeping sites (Chapter 4), not recorded in any other galagids, could be a result of a lack of other available trees. Local people use palm leaves for weaving baskets, which could affect the remaining useable palm sleeping sites. I surveyed the areas surrounding the study site at Kwakuchinja by driving at night and searching for eye-shine using torches, but did not find any galagids. It may be that the population at Kwakuchinja are range-restricted and isolated due to habitat loss and degradation.

Burning is prevalent at Fongoli, affecting 75% of the Western chimpanzees' habitat during the dry season (Pruetz and Herzog, 2017). Burning at Fongoli is often started by wildfires but humans also intentionally initiate illegal fires to clear space for cultivation, hunting and easier navigation around the area (Pruetz and Herzog, 2017). It is very likely that the fires at Fongoli negatively impact the habitat and resources available to Northern lesser galagos, and may cause habitat degradation. I visited a previously-located sleeping tree at Fongoli but the tree had been destroyed from burning and was still emitting smoke. The results of Chapter 5 revealed that the location of human settlements and mining operations did not significantly predict the estimated spatial distribution of Northern lesser galagos at Fongoli. This may imply that the galagos at Fongoli are extremely resilient to human activities (e.g. due to their nocturnal lifestyle), or it could be that the threat of predation from chimpanzees is far greater and so avoiding chimpanzees is most important for their survival. To test how effective the galagos' avoidance strategies are at Fongoli, future research should use the same methods as in Chapter 5 to monitor their estimated abundance and determine whether the population is in decline or not.

In the face of the aforementioned threats, if we understand the requirements of galagids we will have more chance of implementing effective conservation strategies where needed. The results of Chapters 4 and 5, on sleeping site ecology and spatial distribution, are useful in determining which vegetation and areas are most important to protect to conserve the Northern lesser galagos.

7.3.2 Proposed conservation action / management strategies

7.3.2.1 Kwakuchinja

Wildlife corridors connect protected areas and serve many vital functions in conservation, with some examples being: ensuring animal populations can reach suitable habitat and resources; increasing genetic flow and reducing inbreeding; and minimising the risk of local extinction (Caro et al., 2009). The Kwakuchinja wildlife corridor connects Tarangire and Lake Manyara National Parks and is approximately 407 km^2 in size (Martin et al., 2019).

In 2009, the Kwakuchinja wildlife corridor was categorised as a ‘land connection with movements’ wildlife corridor and labelled ‘critical’, meaning it was likely to have less than 5 years left before disappearing, due to the rate of land use change (Caro et al., 2009). A recent study on land change in the Kwakuchinja wildlife corridor found that woodland areas declined by 67.4% between 2002 and 2017, and agriculture increased by 35.6% (Martin et al., 2019). The increase of farming activities around the A104 since it was improved and paved in 2005 is particularly concerning (Martin et al., 2019). The Kwakuchinja study site is an area of approximately 9.2 km^2 within the Kwakuchinja wildlife corridor, bordered by the A104 on the east side. When I visited Kwakuchinja in 2017, the change to the habitat over one year was clearly visible; the Northern lesser galagos are undoubtedly under pressure from habitat degradation at Kwakuchinja.

It is clear that action needs to be taken to protect the corridor and the biodiversity that depends on it. The Northern lesser galagos at Kwakuchinja are facing habitat degradation and loss of habitat and other resources, and may be vulnerable to local extinction. Fortunately, the College of African Wildlife

Management own some of land at Kwakuchinja to protect the remaining wildlife and reduce further habitat degradation and loss. The expansion of protected areas may be vital for the health of the corridor and the wildlife that uses it, but may not be possible in some areas. There is a paucity of research on galagid taxonomy and in the future ‘new’ species of galagid may be recognised as a result of widespread species’ ranges being divided up into much smaller, fragmented populations.

In order for Northern lesser galagos at the Kwakuchinja study site to live sympatrically with an increasing human population, the results on microhabitat preference from Chapter 4 suggest that:

- *Vachellia* trees (*V. tortilis*, *V. kirkii* and *V. polycantha*) and palm trees (*Hyphaene petersiana* and *Borassus aethiopum*) and their surrounding trees (within 10 m) are important for Northern lesser galago sleeping sites at Kwakuchinja and should not be cut down;
- Mid-level and any other connected vegetation (within 10 m) should also not be removed;
- Any trees large enough to house galagos in tree cavities at Kwakuchinja should be conserved.

7.3.2.2 Fongoli

Fongoli is situated outside of nationally protected park areas in the Kedougou region of South-eastern Senegal. In recent decades the area has been under increasing pressure from artisanal small-scale gold mining and an associated increase in human population density, mercury pollution, risk of disease transmission from humans, and poaching for bushmeat and the illegal pet trade (Boyer-Ontl, 2017). This has impacted the home range of Western chimpanzees at Fongoli, increasing their use of poor-quality habitat and limiting their access to food sources (Boyer-Ontl, 2017).

Ironically, the Western chimpanzees, although predators of the Northern lesser galagos at Fongoli, may be their best hope of being conserved. They are CR on the IUCN Red List (Humle et al., 2016) and therefore far more likely to receive conservation attention. Researchers, non-government organizations and governing bodies have joined forces to try to conserve the remaining chimpanzee populations in Senegal (Boyer-Ontl, 2017). If the Western chimpanzees and their habitat are protected, they could act as an umbrella species for the wider ecosystem at Fongoli and indirectly save the galagids from habitat degradation.

The findings on the microhabitat requirements of Northern lesser galagos at Fongoli in Chapter 5 suggest that:

- Trees greater in both height and DBH than the general population of trees should not be burnt or cut down, particularly large *Pterocarpus erinaceus* (the majority of sleeping trees were this species);
- Trees connected to large potential sleeping trees and vegetation contributing to the canopy (particularly within 10 m) should not be burnt or cut down;
- Trees large enough to support multiple cavities should be conserved.

7.3.2.3 Lolldaiga Hills Ranch (LHR)

Unlike Kwakuchinja and Fongoli, Lolldaiga Hills Ranch (LHR) is privately owned and functions as both a livestock ranch and wildlife conservancy. Wildlife can move freely from LHR to surrounding areas using gaps in the electric fences to the west and north-east, but there are stable populations of wildlife at the ranch, which also take advantage of the water sources provided for livestock (Mizutani et al., 2012). It is unlikely that the presence of humans and livestock affect the behaviour of Northern lesser galagos at LHR because the livestock are kept in bomas (fenced enclosures) during the night (from 18:00 h to between 08:00 and 09:00 h: Mizutani et al., 2012). This is believed to be one of the reasons for the successful cohabitation and resource-sharing of livestock and wildlife at LHR (Mizutani et al., 2012).

In Chapter 5 I revealed the estimated abundance of Northern lesser galagos at LHR; the same methods should be used in the future to monitor the stability of the population. The habitat requirements, including sleeping site preference, should be investigated in the future to ensure that the needs of the galagos at LHR are met.

7.4 Limitations, lessons learnt and recommendations for future research

7.4.1 Logistical constraints

Three proposed field seasons (and opportunities to collect data) were compromised due to reasons out of my control. This was unfortunately due to: 1) safety risks from lions (*Panthera leo*) at the Kwakuchinja study site in 2017, which meant I had to leave the area and terminate data collection prematurely; 2) medical reasons preventing me from travelling to Fongoli for fieldwork in 2019; and 3) cancelling my final field season to Kwakuchinja in 2020 because of the COVID-19 pandemic. As a result, Chapters 3 and 6 are not as data-rich as I had initially intended them to be. Due to COVID-19 lockdowns and reduced availability in the lab, I was unable to complete the verification of the non-invasive technique (using qPCR and sequencing) in Chapter 6.

7.4.2 The available literature on galagid behaviour and ecology

Chapter 2 acts as a guide for future research on galagid behaviour and ecology. Prior to this study, it was likely that galagid researchers were aware of the disparity in research effort amongst the species and study areas, but the systematic quantitative literature review identified clear gaps to inform where the biases lie. I only included peer-reviewed scientific research articles in the review and it would be interesting to investigate whether other sources (e.g. books, book chapters and grey literature) support or contradict the findings in the review.

Future research should monitor the published output on each species and the areas visited (e.g. every 10 years). The main findings from the review (taxonomic and geographic bias in the literature, and contributing factors) support the results on similar studies of other taxa, from carnivores (Brooke et al., 2014) to tropical coral reefs (Fisher et al., 2011). The methods are therefore easily applicable to other nocturnal primates and many other taxonomic groups.

7.4.3 The study of nocturnal primate activity and social behaviour

The continuous behavioural data collected at Kwakuchinja for Chapter 3 revealed valuable insights into the activity and social behaviour of Northern lesser galagos. Studying nocturnal primate behaviour is challenging due to the low light levels and arboreal nature of the animals, and continuously observing their behaviour is particularly difficult. Behavioural studies on *in situ* populations of nocturnal primates often use instantaneous sampling (Pullen et al., 2000; Nekaris, 2001, 2003; Bearder et al., 2006; Starr et al., 2012). Continuous observations of nocturnal primates may be more feasible in captivity (e.g. Fuller et al., 2016) but previous studies have successfully carried out focal follows on nocturnal primates in the wild (sportive lemurs, *Lepilemur* spp.: Rasoloharijaona et al., 2006). Although focal follows demanded a high level of concentration, calculating the duration of behaviours was necessary to learn as much as possible about Northern lesser galagos in a short space of time.

The time available to collect data for this study was limited, and for future research, with more data, it would be interesting to see whether or not there are differences in the types of behaviour that I only obtained some data for here (e.g. social interactions - both affiliative and agonistic; and olfactory communication). Comparisons with behavioural observations from other populations is necessary to learn more about how galagos have adapted to their different habitats. During my field season at Fongoli, I noticed that the Northern lesser galagos did not tolerate my presence and moved off very quickly after detecting us. This may have been because the high frequency of predation incidents by chimpanzees (Pruetz et al., 2015) has contributed to galagids being more fearful of humans (perhaps even associating humans with chimpanzees due to the fact that researchers are often following them), or that they are simply not familiar with humans showing them interest. Collecting continuous behavioural data from Fongoli would have been more difficult than at Kwakuchinja, and likely have required a habituation period, but this is possible with further research. At LHR I had to stay in close proximity to the vehicle for safety from the abundance of elephants and buffalo, so behavioural observations were not feasible.

Chapter 3 presents the first ethogram specific to free-ranging Northern lesser galagos and describes behaviours not seen in wild populations before. For future research, it would be interesting to learn more about the function and use of play and allogrooming in Northern lesser galagos, and the extent to which they are connected through complex behavioural interactions. The recording of consolation behaviour, a highly developed social act, challenges previous assumptions regarding the sociality of Northern lesser galagos (e.g. Shultz et al., 2011), and more continuous behavioural observations (ideally with video recordings) should be carried out in the future. Another fascinating area of future study would be to learn how frequently and under what circumstances Northern lesser galagos at Fongoli have twins, and compare the alloparental care between Fongoli and other populations.

Camera traps were incredibly useful for monitoring galagids chewing strings. Galagids are small so the camera traps did not move when they jumped on them if secured tightly to the tree. Camera traps could be used in future research to monitor the presence, distribution and possibly activity of galagids. Other forms of technology could advance the knowledge on nocturnal primate behaviour. Attaching accelerometers is effective for continuous locomotor monitoring (e.g. tarsiers: Costantini et al., 2017) and radio trackers are valuable for continuous location monitoring (e.g. tarsiers: Neri-Arboleda et al., 2002; Southern lesser galagos: Bearder et al., 2002), but both require trapping the animals in order to attach the device. Acoustic monitors have proven useful in studying the behavioural context of galagid vocalisations (Schneiderová et al., 2020; Bettridge et al., 2019) and would be a very useful tool for future research on Northern lesser galago sociality.

7.4.4 Northern lesser galago sleeping site ecology

In Chapters 4 and 5 I investigated the sleeping site ecology of Northern lesser galagos at Kwakuchinja and Fongoli, respectively. Random forest classification models enabled me to identify, out of a large number of environmental variables, the best predictors of sleeping sites compared to control sites. There are likely other factors influencing sleeping site preference that I did not test for in Chapters 4 and 5, such as water level (Matsuda et al., 2010) and distance to food resources (Day and Elwood, 1999).

I obtained some data at Kwakuchinja that I could not collect at Fongoli using the same methods. For example, at Kwakuchinja I conducted daily surveys to monitor the use of known sleeping sites (with the one tree cavity sleeping site being an exception). By doing this I was able to determine that the Northern lesser galago population have not saturated the habitat and frequently reuse sleeping sites, although there is a likely trade-off between using optimal sites frequently and reducing the use of those sites to avoid detection by predators. I could not obtain this data from the sleeping sites at Fongoli because the sleeping locations were inside the tree and out of sight. Secondly, the sleeping behaviour of Northern lesser galagos at Kwakuchinja was easily observable using binoculars from a nearby area. All of the located sleeping sites at Fongoli were within the cavities of trees and it was difficult to observe their sleep chronology and behaviours, and interactions within the sleeping sites. Thirdly, I could not test for differences in temperature and humidity at Fongoli because the tree cavities were in very large (and inaccessible) trees.

For future research it would be interesting to observe the re-use of sleeping sites and sleeping behaviour of Northern lesser galagos at Fongoli and other populations using remote cameras inside the cavities (Zárybnická et al., 2016). This could reveal the actions taken when under attack from chimpanzees. Measuring the temperature and humidity of sleeping locations at Fongoli, as we did at Kwakuchinja, could reveal whether or not there is a thermoregulatory benefit to sleeping inside the trees during the hot days (as with the population at Kwakuchinja; Chapter 4); perhaps they provide fewer fluctuations in temperature (Schmid, 1998). At both Kwakuchinja and Fongoli, it would be interesting to see how sleeping site use changes during the mating season and at other times of the year; western woolly lemurs (*Avahi occidentalis*) changed their sleeping location and site use between the dry and wet seasons (Ramanankirahina et al., 2012).

7.4.5 Predation avoidance from Western chimpanzees at Fongoli

Northern lesser galagos at Fongoli chose sleeping sites in very large trees that were concealed and had several escape routes from chimpanzees. The spatial distribution of the population at Fongoli also supports avoidance from chimpanzees. I carried out my research at Fongoli towards the end of the dry season, but the majority of recorded hunting occurrences happen during the wet season (Pruetz et al., 2015). It would therefore be interesting to see whether galagos employ additional avoidance tactics during the wet season. For example, I found no relationship between sleeping site selection of galagos and the location of the chimpanzees during the day. Future research should investigate whether this changes during the wet season, such that the daytime locations of chimpanzees during the wet season influence where galagos at Fongoli choose to sleep.

Other factors may influence Northern lesser galago spatial distribution and sleeping ecology at Fongoli. If the local human population and presence of mining operations increase, they may become contributing factors in the future and this should be monitored.

To study the spatial abundance of Northern lesser galagos at Fongoli and LHR I used density surface modelling (DSM); a valuable tool for conservation that uses detection data and environmental variables to estimate the abundance and spatial distribution of a population (Miller et al., 2013). Although the technique is fairly new it has identified areas for conservation action, for example, by revealing the influence of human presence on animal abundance (Antún et al., 2018; Nuttall, 2017) and assessing habitat requirements prior to or following planned developments (Buckland et al., 2012). Few primate studies have yet used DSM, but one used the technique to show that the predicted abundance of chimpanzees is high at a location where there are plans to build a bauxite mine in Guinea-Bissau (Dias et al., 2019). Another identified differences in the spatial abundance of several primate species in Cambodia (Nuttall et al., 2021). Density surface modelling has been used to study marine (Herr et al., 2009; Williamson et al., 2016), avian (Buckland et al., 2012; Antún et al., 2018; Kubečka et al., 2019), and terrestrial (Schroeder et al., 2014; Valente et al., 2016; Boulanger et al., 2018; Dias et al., 2019) populations of animals. Chapter 5 and Nuttall et al. (2021) show that DSM also has utility in studying the spatial abundance of arboreal animals, and could be used in future studies to investigate factors influencing the spatial distribution of other primate populations.

7.4.6 Using non-invasive methods to study nocturnal primate genetics

In Chapter 6 I showed that it is possible to obtain genetic material from Northern lesser galagos non-invasively and extract and amplify DNA from them for genetic analysis. The method was, however, not successful at Fongoli or LHR, but with a longer sampling period I may have retrieved some samples.

There are two important limitations to this study. Firstly, due to factors associated with the COVID-19 pandemic (e.g. lab lockdowns), I could not provide further verification that the samples had originated from Northern lesser galagos; verification using both sequencing and qPCR is needed and will be a focus of future research. Secondly, the sample size for this chapter was limited and with more time in the field I could have retrieved enough samples for genetic analysis.

Obtaining samples from other populations would allow the investigation of phylogenetic differences between those and the population at Kwakuchinja and clarify the taxonomy of Northern lesser galagos. This is unclear from previous phylogenetic reconstructions of the group; most likely because morphologically similar samples in museum collections and captivity were misclassified (Pozzi et al., 2014; 2015). Since studying Northern lesser galagos at two different ends of their geographic range (Fongoli and Kwakuchinja), I noticed some significant differences such as differences in pelage (Figure 7.1).

Figure 7.1 *Galago senegalensis sotikae* at Kwakuchinja; Right: *G. s. senegalensis* at Fongoli. The dark rings around the eyes of Northern lesser galagos at Kwakuchinja were not as prominent on those at Fongoli and the shape of their faces at Fongoli were slightly different.

The most striking difference noted was that during the breeding season at Fongoli, many females had more than one dependent young with them. Northern lesser galagos most often give birth to one young, with twinning being uncommon (see Butynski et al., 2013 for overview of Northern lesser galago reproduction). For future research, genetic samples from the population at Fongoli should be collected to determine whether they are indeed the same species as at Kwakuchinja, or if there is significant genetic variation to warrant separation into different species.

Ecological differences such as variation in predation pressure between populations could also explain the many observations of twinning at Fongoli (in response to the high predation pressure from chimpanzees).

The non-invasive method could allow the study of genetic elements of sociality. For example, information on the mating system of Northern lesser galagos is lacking and should be investigated in the future. I often observed an adult (presumably the mother) and infant being joined by at least one other adult (perhaps a related female or the father of the young) at their sleeping site. ‘Grandmothering’ occurs in captive Northern lesser galagos (Kessler et al., 2010) so in some of my observations it was likely a close kin joining the mother and infant at their sleeping site; this could be determined through genetics.

7.5 General conclusions

Northern lesser galagos exhibit variation in behaviour and ecology between subspecies (e.g. in their sleeping ecology and spatial distribution). They show clear temporal patterns of activity and are connected through infrequent social interactions and different modes of communication. There is evidence for predation avoidance from Western chimpanzees and their response to different anthropogenic pressures should be monitored in the future. It is possible to obtain genetic samples from galagids non-invasively and this method could allow future genetics studies to reveal a wealth of new discoveries about cryptic species.

7.6 References

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Appendices

Appendix 1A

Ellison, G., Jones, M., Cain, B. and Bettridge, C. M. (2021) Taxonomic and geographic bias in 50 years of research on the behaviour and ecology of galagids. *PLoS ONE*, 16(12), p. e0261379.

https://doi.org/10.1371/journal.pone.0261379

PLOS ONE

RESEARCH ARTICLE

Taxonomic and geographic bias in 50 years of research on the behaviour and ecology of galagids

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Abstract

Identifying knowledge gaps and taxonomic and geographic bias in the literature is invaluable for guiding research towards a more representative understanding of animal groups. Galagids are nocturnal African primates and, for many species, detailed information on their behaviour and ecology is unavailable. To identify gaps and bias in the literature we reviewed published peer-reviewed research articles on galagid behaviour and ecology over a 50-year period from January 1971 to December 2020. Using the Web of Science and Google Scholar databases, we identified 758 articles, assessed 339 full texts for eligibility and included 211 in the review. Species of *Otolemur* have been extensively researched in comparison to other genera (78.2% of studies; *Euoticus*: 13.3% of studies; *Galago*: 66.4% of studies; *Galagoides*: 20.9% of studies; *Paragalago*: 22.3% of studies; *Sciurocheirus*: 15.2% of studies). The most common category of research was physiology (55.0% of studies), followed by behavioural ecology (47.4% of studies), and fewer studies were on genetics and taxonomy (16.1% of studies) and habitat and distribution (14.2% of studies). Text mining revealed that the word 'behaviour' was the most common word used in abstracts and keywords, and few words were related to ecology. Negative binomial regression revealed that mean body mass and geographic range size were significant positive predictors of the total number of scientific outputs on each species. Research on wild populations was carried out in only 24 (60%) of the 40 countries galagids are thought to inhabit. Studies were undertaken in locations with lower mean annual temperatures and higher human population densities over warmer and less populated areas. We encourage a more equal sampling effort both taxonomically and geographically that in particular addresses the paucity of research on smaller species and those with restricted ranges. Research on *in situ* populations, especially in warmer and remote areas, is urgently needed, particularly in West, Central and some Southern African countries.

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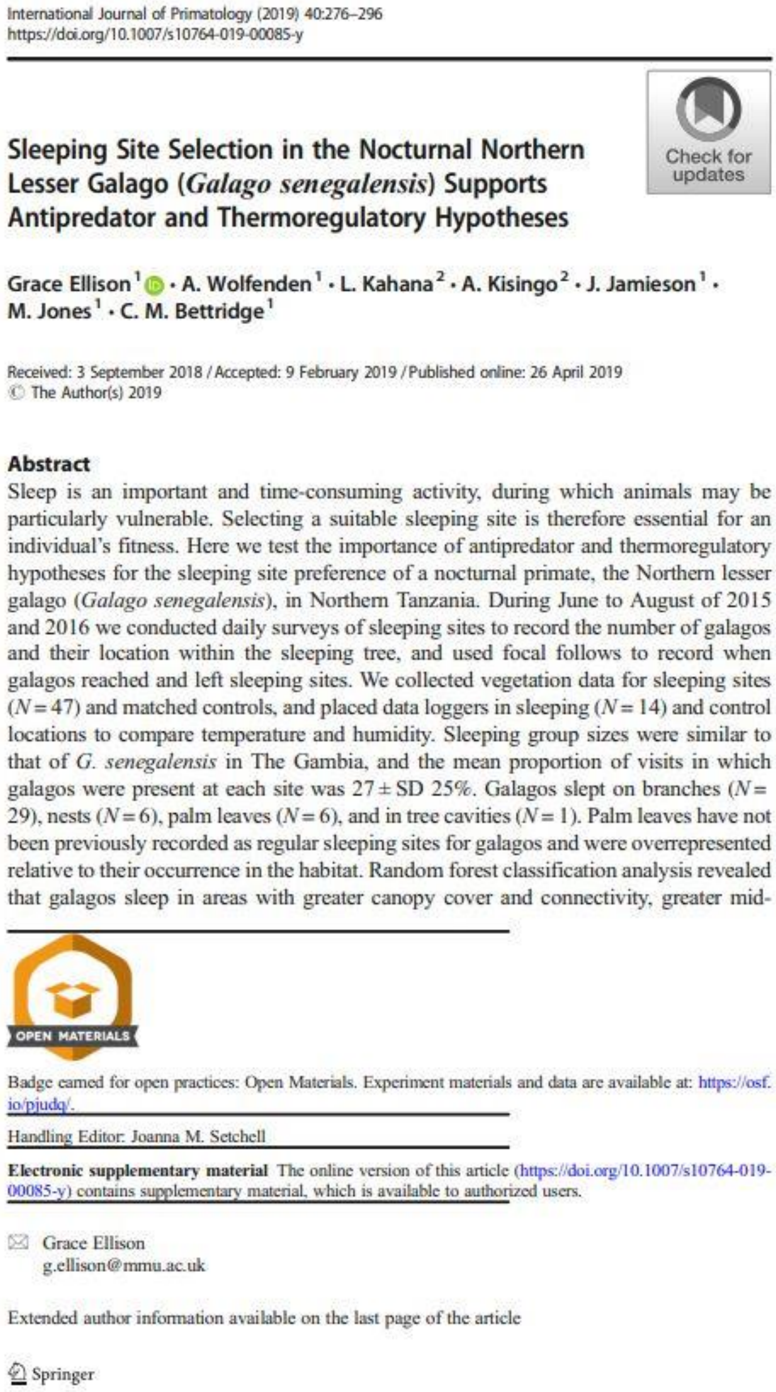
Introduction

We are losing species worldwide at such an alarming rate that we may be in the midst of the sixth mass extinction [1]. Species or populations lacking data on their behaviour and ecology

Appendix 1B

Ellison, G., Wolfenden, A., Kahana, L., Kisingo, A., Jamieson, J., Jones, M. and Bettridge, C. M. (2019) Sleeping site selection in the nocturnal northern lesser galago (*Galago senegalensis*) supports antipredator and thermoregulatory hypotheses. *International Journal of Primatology*, 40(2) pp. 276–296.

https://doi.org/10.1007/s10764-019-00085-y



International Journal of Primatology (2019) 40:276–296
https://doi.org/10.1007/s10764-019-00085-y

Sleeping Site Selection in the Nocturnal Northern Lesser Galago (*Galago senegalensis*) Supports Antipredator and Thermoregulatory Hypotheses

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Abstract

Sleep is an important and time-consuming activity, during which animals may be particularly vulnerable. Selecting a suitable sleeping site is therefore essential for an individual's fitness. Here we test the importance of antipredator and thermoregulatory hypotheses for the sleeping site preference of a nocturnal primate, the Northern lesser galago (*Galago senegalensis*), in Northern Tanzania. During June to August of 2015 and 2016 we conducted daily surveys of sleeping sites to record the number of galagos and their location within the sleeping tree, and used focal follows to record when galagos reached and left sleeping sites. We collected vegetation data for sleeping sites ($N = 47$) and matched controls, and placed data loggers in sleeping ($N = 14$) and control locations to compare temperature and humidity. Sleeping group sizes were similar to that of *G. senegalensis* in The Gambia, and the mean proportion of visits in which galagos were present at each site was 27 ± SD 25%. Galagos slept on branches ($N = 29$), nests ($N = 6$), palm leaves ($N = 6$), and in tree cavities ($N = 1$). Palm leaves have not been previously recorded as regular sleeping sites for galagos and were overrepresented relative to their occurrence in the habitat. Random forest classification analysis revealed that galagos sleep in areas with greater canopy cover and connectivity, greater mid-

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Badge earned for open practices: Open Materials. Experiment materials and data are available at: https://osf.io/pjudq/.

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Springer

Appendix 2A

Search terms used in Web of Science and Google Scholar to find articles on galagid behaviour and ecology published between January 1971 and December 2020. For the Google Scholar search, I specified to search only journals with the word 'African' in the journal name.

Search engine	**Search term**	**No. results**
Web of Science	galag* AND behav*	182
Web of Science	bushbab* AND behav*	54
Web of Science	bush bab* AND behav*	38
Web of Science	galag* AND activity	104
Web of Science	bushbab* AND activity	24
Web of Science	bush bab* AND activity	10
Web of Science	galag* and social*	59
Web of Science	bushbab* and social*	16
Web of Science	bush bab* and social*	15
Web of Science	galag* AND ecolog*	48
Web of Science	bushbab* AND ecolog*	10
Web of Science	bush bab* AND ecolog*	11
Web of Science	galag* AND habitat	46
Web of Science	bushbab* AND habitat	15
Web of Science	bush bab* AND habitat	9
Web of Science	galag* AND sleep*	13
Web of Science	bushbab* AND sleep*	3
Web of Science	bush bab* AND sleep*	1
Web of Science	galag* AND feeding	37
Web of Science	bushbab* AND feeding	11
Web of Science	bush bab* AND feeding	7
Web of Science	galag* AND distribution	101
Web of Science	bushbab* AND distribution	14
Web of Science	bush bab* AND distribution	12
Google Scholar	galago and behaviour	98

Google Scholar	galago AND behavior	50
Google Scholar	galagos AND behaviour	20
Google Scholar	galagos AND behavior	18
Google Scholar	bushbaby AND behaviour	21
Google Scholar	bushbaby AND behavior	12
Google Scholar	bushbabies AND behaviour	21
Google Scholar	bushbabies AND behavior	14
Google Scholar	bush baby AND behaviour	11
Google Scholar	bush baby AND behavior	7
Google Scholar	bush babies AND behaviour	13
Google Scholar	bush babies AND behavior	5
Google Scholar	galago AND activity	121
Google Scholar	galagos AND activity	18
Google Scholar	bushbaby AND activity	15
Google Scholar	bushbabies AND activity	16
Google Scholar	bush baby AND activity	10
Google Scholar	bush babies AND activity	11
Google Scholar	galago AND social behaviour	11
Google Scholar	galago AND social behavior	4
Google Scholar	galagos AND social behaviour	1
Google Scholar	galagos AND social behavior	3
Google Scholar	bushbaby AND social behaviour	3
Google Scholar	bushbaby AND social behavior	1
Google Scholar	bushbabies AND social behaviour	3
Google Scholar	bushbabies AND social behavior	1
Google Scholar	bush baby AND social behaviour	1
Google Scholar	bush baby AND social behavior	1
Google Scholar	bush babies AND social behaviour	1
Google Scholar	bush babies AND social behavior	0
Google Scholar	galago AND sociality	4
Google Scholar	galagos AND sociality	4
Google Scholar	bushbaby AND sociality	2
Google Scholar	bushbabies AND sociality	2

Google Scholar	bush baby AND sociality	1
Google Scholar	bush babies AND sociality	1
Google Scholar	galago AND ecology	121
Google Scholar	galagos AND ecology	37
Google Scholar	bushbaby AND ecology	29
Google Scholar	bushbabies AND ecology	29
Google Scholar	bush baby AND ecology	10
Google Scholar	bush babies AND ecology	11
Google Scholar	galago AND ecological	93
Google Scholar	galagos AND ecological	32
Google Scholar	bushbaby AND ecological	20
Google Scholar	bushbabies AND ecological	22
Google Scholar	bush baby AND ecological	11
Google Scholar	bush babies AND ecological	10
Google Scholar	galago AND habitat	101
Google Scholar	galagos AND habitat	35
Google Scholar	bushbaby AND habitat	27
Google Scholar	bushbabies AND habitat	24
Google Scholar	bush baby AND habitat	13
Google Scholar	bush babies AND habitat	10
Google Scholar	galago AND sleeping site	9
Google Scholar	galagos AND sleeping site	7
Google Scholar	bushbaby AND sleeping site	3
Google Scholar	bushbabies AND sleeping site	6
Google Scholar	bush baby AND sleeping site	1
Google Scholar	bush babies AND sleeping site	4
Google Scholar	galago AND feeding	59
Google Scholar	galagos AND feeding	18
Google Scholar	bushbaby AND feeding	11
Google Scholar	bushbabies AND feeding	15
Google Scholar	bush baby AND feeding	4
Google Scholar	bush babies AND feeding	7
Google Scholar	galago AND distribution	138

Google Scholar	galagos AND distribution	36
Google Scholar	bushbaby AND distribution	33
Google Scholar	bushbabies AND distribution	27
Google Scholar	bush baby AND distribution	11
Google Scholar	bush babies AND distribution	11
Total		2398 (758 without duplicates)

Appendix 2B

The 30 most common stemmed words and corresponding un-stemmed words relating to galagid behaviour and ecology, used in scientific papers from January 1971 and December 2020.

Stemmed word	Combination of words included
behaviour	behave / behaved/ behavior / behavioral / behaviorally / behaviors / behavior-specific / behaviour / behavioural / behaviours
area	area / areas
pattern	pattern / patterns
female	female / females
relative	relative / relatives
muscle	muscle / muscles / muscle-force / muscle-induced
activ*	active / activity / activities / activity / activity-dependent
nocturnal	nocturnal / nocturnal-diurnal / nocturnality
movement	movement / movements
size	size / sizes / sized / size-matched
group	group / groups / grouped / grouping / groupings
morpholog	morpohlogic / morphological / morphologically / morphology / morphologies
bodi	body / bodies
cortex	cortex
male	male / males / male-female
population	population / populations
observ	observation / observational / observations / observe / observed / observer / observing
function	function / functional / functionally / function-altering / functions
region	region / regional / regions
visual	visual / visually
social	social / sociality / socially
range	range / ranged / ranges
structur	structural / structure / structures
adult	adult / adulthood / adult-like / adults

individual	individual / individualized / individually / individuals
site	site / sites
force	force / forceful / force-production / forces
lateral	lateral / lateralis / lateralised / laterality / lateralization / lateralized / laterally
period	period / periodically / periods
forest	forest / forest-agricultural / forests

Appendix 2C

Comparison of model performance (AIC) of logistic regression models used to investigate geographic bias in the locations of study sites used to research galagids between January 1971 and December 2020. Covariates are: mean annual temperature (‘temperature’; °C); mean human population density from the year 2000 (‘human population density’; humans/km^2); and mean annual precipitation (‘precipitation’; ml). My best model is in bold.

Covariates	**AIC**
temperature	445.98
human population density	455.98
precipitation	477.48
temperature + human population density	**426.50**
temperature + precipitation	445.00
human population density + precipitation	457.86
temperature + human population density + precipitation	428.26

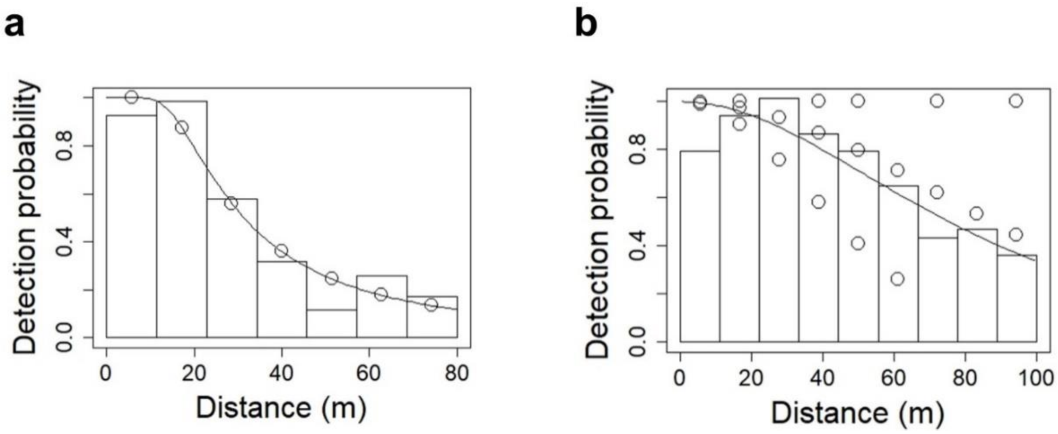
Appendix 4

Variable importance scores for each of the measures compared between sleeping and control sites of Northern lesser galagos at Kwakuchinja, from June to August of 2015 and 2016, as determined by random forest classification analysis.

Rank	**Variable**	**Variable importance score**
19	Number of connected trees	4.53E-02
18	Number of trees	2.10E-02
17	Mid-level vegetation density	1.94E-02
16	Canopy cover	1.42E-02
15	Number of acacia (*Vachellia* spp.) trees	1.32E-02
14	Number of shrubs	3.24E-03
13	Mean height of ground cover	2.94E-03
12	Number of wild herbivore dung	2.35E-03
11	Number of domestic herbivore dung	2.35E-04
10	Number of trees and shrubs cut down	1.76E-04
9	Proportion of bare ground in ground cover	1.18E-04
8	Species of sleeping/control tree	5.88E-05
7	Number of *Vachellia tortilis* trees	5.88E-05
6	Mean height of surrounding trees	-4.12E-04
5	Distance to nearest yellow fever tree	-5.88E-04
4	DBH of sleeping/control tree	-7.65E-04
3	Year	-1.29E-03
2	Height of sleeping/control tree	-1.29E-03
1	Mean DBH of surrounding trees	-2.53E-03

Appendix 5A

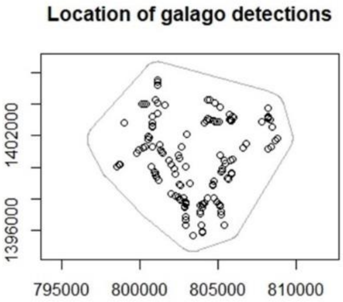
The fit of each distance sampling model to the distribution of the detection data for Northern lesser galagos: a) at Fongoli, Senegal; and b) at Lolldaiga Hills Ranch, Kenya. The blocks represent binned distances, or 'bins', and the line represents the fit of the model to the data. The points indicate the detection probability for individual detections at the recorded perpendicular distance and, for b), the covariate values for each level.

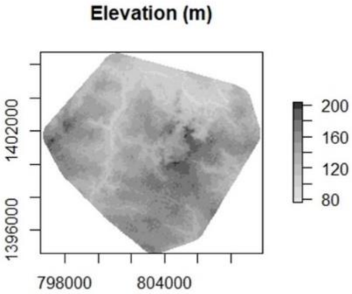


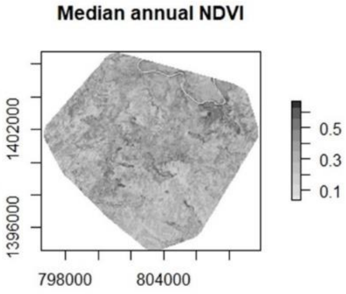
Appendix 5B

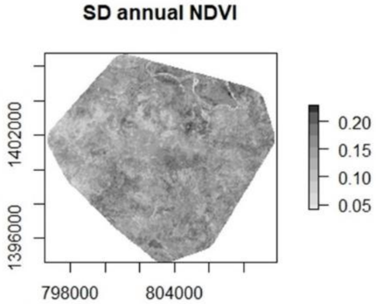
All rasters used in density surface models for Northern lesser galago populations at a) Fongoli, Senegal and b) Lolldaiga Hills Ranch, Kenya.

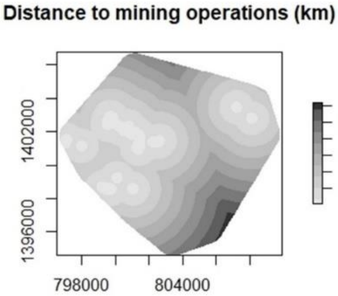
5B.1 Fongoli, Senegal

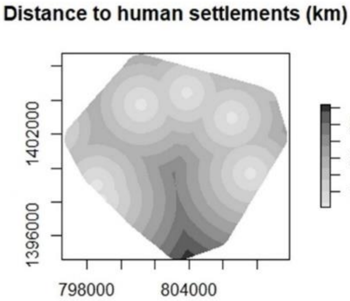

Location of galago detections

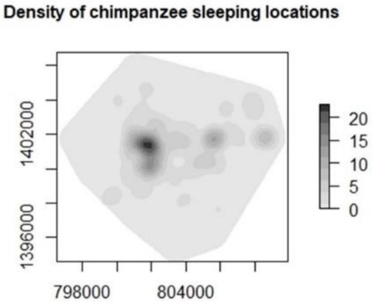

Elevation (m)


Median annual NDVI

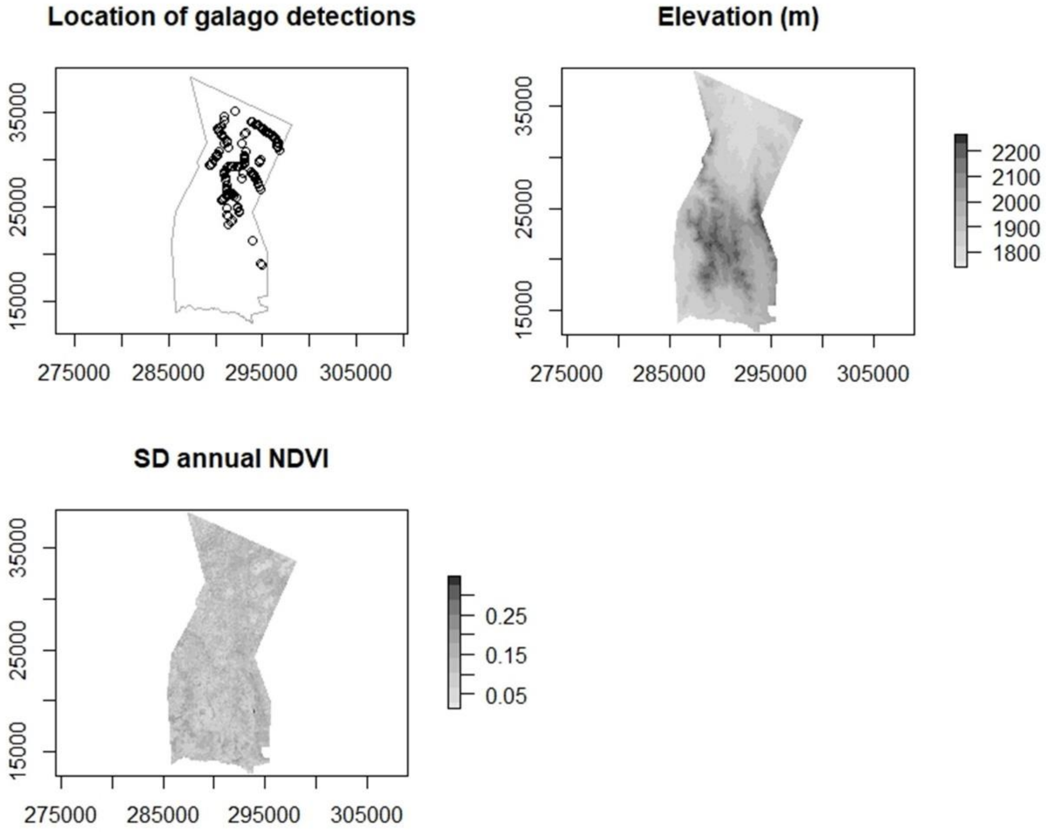

SD annual NDVI


Distance to mining operations (km)


Distance to human settlements (km)


Density of chimpanzee sleeping locations

5B.2 Lolldaiga Hills Ranch, Kenya



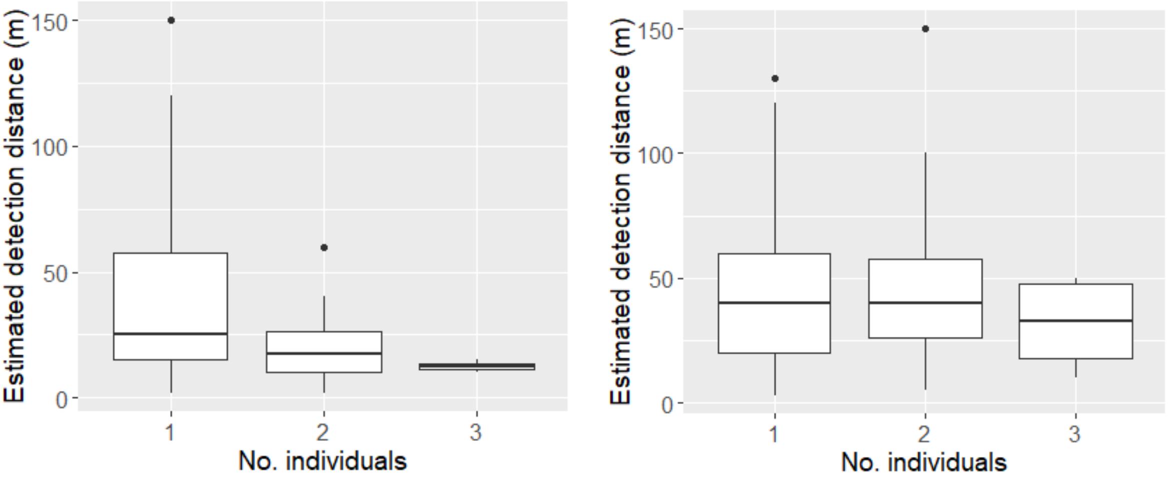
Location of galago detections

Elevation (m)

SD annual NDVI

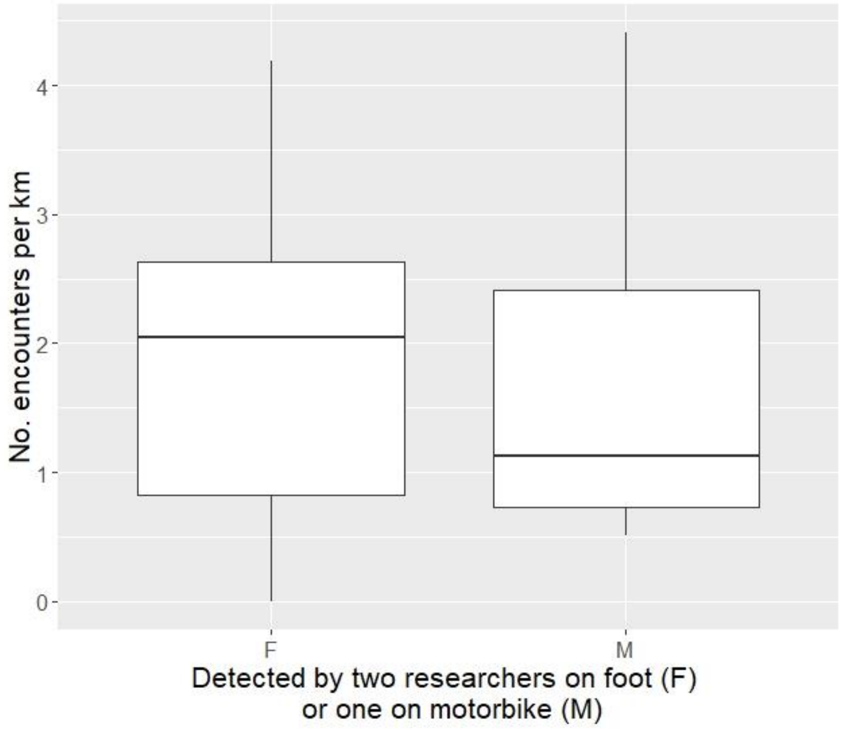
Appendix 5C

Boxplot to show the distribution of estimated detection distances (m) of Northern lesser galagos depending on whether the group size was 1, 2 or 3 in: left: Fongoli, Senegal; right: Lolldaiga Hills Ranch, Kenya.



Appendix 5D

The number of groups of Northern lesser galagos encountered per km by two researchers on foot (F) or one on a motorbike (M) at Fongoli, Senegal.



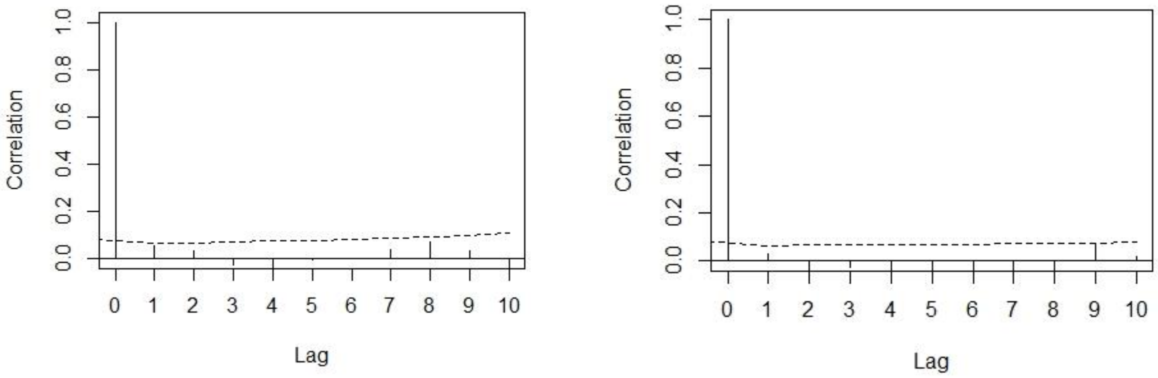
Appendix 5E

Model selection table for modeling the detection functions for Fongoli and LHR. I selected Fongoli_2 and LHR_3 (in bold) as the best models for each population and used these in the further modeling process.

Model name	Study site	Key function	Covariates	AIC
Fongoli_1	Fongoli	Half-normal	-	410.3
Fongoli_2	**Fongoli**	**Hazard-rate**	**-**	**405.9**
LHR_1	LHR	Half-normal	-	754.9
LHR_2	LHR	Hazard-rate	-	756.0
LHR_3	**LHR**	**Half-normal**	**broad habitat type**	**750.4**
LHR_4	LHR	Hazard-rate	broad habitat type	751.1

Appendix 5F

Spatial autocorrelation for the best DSMs for Fongoli (left) and LHR (right). Lag 0 is the correlation between a segment and itself, lag 1 is the correlation between a segment and its neighbouring segments, lag 2 is the correlation between a segment and those one segment away, etc. (Winiarski et al., 2013). The dotted lines represent 95% confidence intervals.



Appendix 5G

Variable importance scored for each of the measures compared between sleeping and control sites of Northern lesser galagos at Fongoli, Senegal, from March to May of 2018, as determined by random forest classification analysis.

Rank	Variable	Variable importance score
11	Number of connected trees	0.148
10	Canopy cover (%)	0.074
9	Total number of trees	0.010
8	Mean height of surrounding trees (m)	1.89E-03
7	Number of shrubs	2.22E-04
6	Number of *Pterocarpus erinaceus* trees	2.22E-04
5	Density of chimpanzee sleeping locations	2.22E-04
4	Mid-level vegetation density (%)	2.78E-19
3	Number of lianas	-3.33E-04
2	Mean DBH of surrounding trees (cm)	-4.44E-04
1	Mean height of ground cover (cm)	-8.89E-04

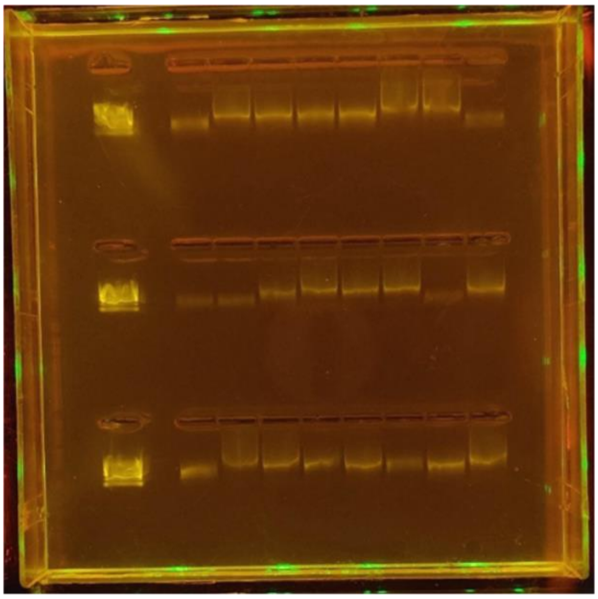
Appendix 6A

Primers used for DNA amplification.

Primer name	Sequence	Location	Reference
14850F	GACAAAATCCCCTTCCACCC	cyt b	Pozzi et al. (2019)
15068R	AGTTTGTTGGGAATGGATCG	cyt b	Pozzi et al. (2019)

Appendix 6B

Results of electrophoresis showing bands of successful samples. Ladder length is 1 kb and sequence length is 217 base pairs.



Appendix 7

Curriculum vitae.

GRACE ELLISON

Stafford, UK

27.09.1990

grace.ellison@hotmail.co.uk

@gracellison

Summary

I am an experienced research scientist and recently completed my PhD. During my part-time PhD, I worked as a postgraduate teaching assistant for Manchester Metropolitan University, teaching biology students from foundation to Masters level. My background is in social research and wildlife biology, and I am currently a Research Integrity Specialist for a scientific publisher looking for a new, challenging role.

Professional skills

- Scientific writing and editing
- Project management
- Supervising and mentoring
- Communicating to both public and scientific audiences
- Creating novel research methods
- Research integrity and ethics
- Critical thinking and decision making
- Time management

Technical skills

- R for data handling and statistics
- GIS (using ArcGIS and qGIS)
- Social network analysis
- Statistical modelling
- Systematic reviewing
- Laboratory skills (e.g. PCR)
- Use of CRMs (e.g. Salesforce)

Achievements

Charles A. Lockwood prize and medal
Best student talk at a Primate Society of Great Britain conference in 2017

3rd Prize for a poster presentation
MMU SciEng Symposium in both 2016 and 2017

Employment history

Research Integrity Specialist
Frontiers Media SA, UK
February 2021 to present

- Ensure manuscripts uphold the highest level of integrity
- Lead of the Bioethics working group to improve workflow
- Initiator and organiser of a monthly research seminar

Postgraduate Teaching Assistant
Manchester Metropolitan University, UK
January 2016 to January 2021 (5-year fixed-term contract)

- Delivered lectures, tutorials and seminars
- Marked written work and oral presentations
- Supervised large groups of students in the field
- Provided pastoral care to students

Clinical Support Worker
John Munroe Hospital, Staffordshire, UK
March 2014 to July 2015

- Managed challenging behaviour of patients
- Made life-saving decisions in critical situations

Education

PhD: 'Behaviour and ecology of the Northern lesser galago (*Galago senegalensis*)'
Manchester Metropolitan University
2016–2022

MSc Animal Behaviour: Distinction
Manchester Metropolitan University
2014–2015

BSc Psychology: 2:1
The University of Manchester
2010–2013

Publications

Ellison, G., Jones, M., Cain, B. and Bettridge, C. M. (2021) Taxonomic and geographic bias in 50 years of research on the behaviour and ecology of galagids. *PloS one, 16*(12), p.e0261379. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0261379

Ellison, G., Wolfenden, A., Kahana, L., Kisingo, A., Jamieson, J., Jones, M. and Bettridge, C. M. (2019) Sleeping site selection in the nocturnal Northern lesser galago (*Galago senegalensis*) supports antipredator and thermoregulatory hypotheses. *International Journal of Primatology, 40*(2), pp. 276-296. https://doi.org/10.1007/s10764-019-00085-y

Ellison, G., Devenish, C., Jones, M., Cain, B. and Bettridge, C. M. (in prep.) Galagos live in a landscape of fear.

Ellison, G., Hughes, T., Cain, B., Jones, M. and Bettridge, C. M. (in prep.) Successful non-invasive sampling method for the retrieval of DNA from a nocturnal primate

Invited talks / lectures

The University of Salford
January 2020
Primate Behaviour and Conservation (2nd year BSc; 2 hours) "Behaviour and ecology of *Galago senegalensis*"

Oxford Brookes University
March 2019
Primate Conservation Seminar (MSc; 1 hour) "Behaviour and ecology of *Galago senegalensis*"

The University of Salford
November 2018
Primate Behaviour and Conservation (2nd year BSc; 2 hours) "Nocturnal primate behaviour"

Volunteer work

Wildlife Researcher
Sri Lanka Wildlife Conservation Society, Sri Lanka; September 2013

Wildlife Researcher
African Impact, South Africa; July 2012 to August 2012

Wildlife Researcher
GVI, South Africa; June 2011 to July 2011

Conference talks

European Primate Federation/Primate Society of Great Britain joint meeting in Oxford, UK (September 2019; 15 minutes)
"The use of distance sampling and density surface modelling to estimate the population density of the nocturnal primate *Galago senegalensis*"

International Primatological Society 27th Congress in Nairobi, Kenya (August 2018; 15 minutes)
"New insights into the social behaviour of the Northern lesser galago (*Galago senegalensis*) in Kwakuchinja, Northern Tanzania"

International Primatological Society 27th Congress in Nairobi, Kenya (August 2018; 15 minutes)
"Predation risk and microclimate influence sleeping site selection in the Northern lesser galago (*Galago senegalensis*) in Kwakuchinja, Northern Tanzania"

Manchester Metropolitan University SciEng Symposium in Manchester, UK (September 2017; 3 minutes)
"New insights into the social behaviour of an African nocturnal primate"

Primate Society of Great Britain in Manchester, UK (April 2017; 15 minutes)
"The behaviour and ecology of a nocturnal primate, *Galago senegalensis*, in Northern Tanzania"

Association for the Study of Animal Behaviour in Liverpool, UK (April 2017; 10 minutes)
"More social than we think? New insights into the behaviour and ecology of the Northern lesser galago in Northern Tanzania"

Primate Society of Great Britain in Durham, UK (January 2017; Lightning talk – 2 minutes)
"Effective methods for the study of a nocturnal African primate"