



Looking Ahead: Predicting the Possible Ecological and Physiological Response of *Galago Moholi* to Environmental Change

Juan Scheun¹ · Julia Nowack²

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Abstract

Large scale changes to the natural environment, due to both climate change and direct human activities (e.g., urbanization), pose a great risk to biodiversity. As this realization has set in, the number of studies modelling and monitoring the effect of environmental change on species response and survival has increased significantly; however, these studies focus on flagship species, often neglecting the lesser-known, cryptic species, which include the nocturnal primates. This is especially true for the 20 species of galago who, despite their large distribution throughout Africa, have had little to no research conducted on the effect of environmental change on population fitness and long-term survival. With urbanization set to increase throughout their distribution range, along with an increase in climate change parameters (e.g., increased temperature and a decrease in annual rainfall), the most studied species of the family, namely the African lesser bushbaby *Galago moholi*, provides an ideal model to assess the impact of future environmental change on galago species. In this review, we discuss the possible impact of environmental change on *G. moholi* and specifically focus on the effect of environmental change on feeding ecology, genetics, thermal biology, and reproduction, all of which contribute to the fitness and survival of the species. We also highlight the need for specific, long-term research to be conducted on the effect of environmental change on the survival likelihood of *G. moholi* and other galago species.

Keywords Climate change · Urbanisation · Physiology · Ecology · Genetics · *Galago moholi*

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✉ Juan Scheun
Scheunj@tut.ac.za

¹ Department Nature Conservation, Tshwane University of Technology, Pretoria Campus, Pretoria, South Africa

² School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK

Introduction

Climate change and habitat destruction pose some of the greatest, long-term risks to species conservation (Thuiller, 2007). An increase in average global temperature will push many species beyond their thermal limits (Somero, 2010; Sunday et al., 2012), and the effects are amplified by other human-induced environmental changes, such as progressing habitat fragmentation and urbanisation. Furthermore, a change in seasonal rainfall and temperature patterns will significantly influence on the timing of reproduction, reproductive output, and sociality (Campos et al., 2017; Mazaris et al., 2008; Visser et al., 2004). Although the effect of climate change on species survivability depends on the distribution, physiology, and adaptability of a species, it is thought that one out of six species will be threatened with extinction due to elevated temperatures and associated environmental changes (Urban, 2015).

Non-human primates are often considered protected from the effects of climate change thanks to specific biological attributes such as behavioural, physiological, and dietary plasticity (Bernard & Marshall, 2020; Korstjens & Hillyer, 2016). Unfortunately, this is erroneous, as recent studies have shown that primates, among all endotherms, are disproportionately at risk to climate change (Pacifici et al., 2017). According to the International Union for the Conservation of Nature (IUCN, 15 February 2023), 62.6% of primates of threatened globally; on the African continent, 52.3% of mainland African species are threatened, with 42% in decline (Estrada et al., 2017). Several reasons are responsible for this: Firstly, most primates inhabit tropical habitats, which are known to have mild, seasonal fluctuations. As a result of this, a slight increase in environmental temperature will reach and exceed the thermal tolerance of these populations (Tewksbury et al., 2008). Next, as primates have evolved to survive in specific, stable habitats, most of these species are incapable of long-distance migration because of biological or anthropogenic factors, which would assist in mitigating any negative change in their present environment (Gnanadesikan et al., 2017; Zhao et al., 2019). Finally, because of the long generation times inherent in primates, the likelihood of accumulating beneficial adaptations fast enough to mitigate the harmful effects of climate change will be limited (Meyer & Pie, 2022).

Found in the strepsirrhine suborder is the family galagidae, which consists of 20 species spread across Africa, making it one of the most widespread primate families (Bearder, 1999; Bearder et al., 1995; Nekaris & Bearder, 2007). Despite their widespread distribution, to date, little to no research has been conducted to determine the effect of climate change and habitat alteration on any African galago species. There is a large size variation between species of the family, ranging from 60 g in the Rondo dwarf galago (*Galagoides rondoensis*; Honess et al., 2008) to 1500 g in the largest species, the thick-tailed bushbaby (*Otolemur crassicaudatus*; Nekaris & Bearder, 2007). Despite this difference in size, all species in the family display nocturnal activity patterns (Ellison et al., 2021; Svensson, 2017) and a diet which is generally thought to be specialised, ranging from insectivores, and gummivores to

frugivores (Forbanka, 2018; Nekaris & Bearder, 2007). The African lesser bushbaby, *G. moholi* (Fig. 1), is the most well-known species of galagos (Table 1) with an estimated lifespan of 3–5 years in the wild (Dausmann et al., 2012) and a wide distribution range over Southern Africa. Despite the use of the species as bushmeat, traditional medicine or in the pet trade, these activities are not thought to lead to widespread population decreases (Masters et al., 2016). Rather, it is the effects of factors such as climate change and urbanisation which are likely to be the biggest threat to the species. We aim to review the current information available for *G. moholi* and make predictions on how the species might adapt to environmental and climatic changes in its natural distribution. In this review, we discuss the possible ecological and physiological response of *G. moholi* to climate change and urbanisation. Specifically, we discuss the effect of habitat quality and fragmented habitats on population density, genetic diversity and population fitness. As habitat alteration will likely lead to a change in resource availability, we discuss the possible change in *G. moholi* feeding ecology in order for the species to survive. This is followed by a review of the thermoregulatory response of the species to extreme weather events, before discussing the likely change in reproductive activity which could occur when habitat quality and resource availability change considerably.



Fig. 1 The African lesser bushbaby, *Galago moholi* (Photo credit: Polley, 2019).

Table 1 Summary of life- and natural-history parameters for *Galago moholi*

Parameter	Details	Reference
Population trend (IUCN)	Least Concern	Bearder <i>et al.</i> (2021)
Body mass	About 160–210 g (Males are heavier than females)	Masters <i>et al.</i> (2016) Scheun <i>et al.</i> (2015)
Diet	Depending on habitat: mainly gum and small arthropods; fruit	Harcourt and Bearder (1989) Scheun <i>et al.</i> (2014) Nowack <i>et al.</i> (2013b)
Social system	Solitary foraging, but sharing of nesting sites	Ray <i>et al.</i> (2016) Nowack <i>et al.</i> (2013b) Bearder (2008)
Activity pattern	Nocturnal	Bearder and Martin (1980) Nekaris and Bearder (2007)
Torpor use	Irregular use of daily torpor during winter	Scheun <i>et al.</i> (2019) Nowack <i>et al.</i> (2010)
Home range size	1.8–5.2 ha 4.4–22.9 ha	Nowack <i>et al.</i> (2013a) Nowack <i>et al.</i> (2013b)
Gestation length	120–141 days	Nekaris and Bearder (2007) Scheun <i>et al.</i> (2016)
Birth period	January/February and September/November	Izard and Simons (1987) Doyle <i>et al.</i> , 1967
Litter size	Mostly twins	Scheun <i>et al.</i> (2016) Scheun <i>et al.</i> (2017)
Predators	Mongoose, genets, owls, eagles, snakes, domestic cats	Izard and Nash (1988) Scheun <i>et al.</i> (2016) Mzilikazi <i>et al.</i> (2006)
Estimated average lifespan in the wild	3–5 years	pers observation J.N Dausmann <i>et al.</i> (2012)

Climate Change and Habitat Alteration Will Affect the Natural Habitat of *Galago Moholi*

To determine the correct conservation measures required to ensure species survival, it is crucial to assess species vulnerability in terms of sensitivity, resilience, and potential for adaptation (Huey et al., 2012). While current estimates show an average global temperature increase of 1.09 °C since the start of the twentieth century, the Intergovernmental Panel on Climate Change (2021) suggests this will reach 1.5 °C by 2030. An increase in global temperature along with a predicted decrease in rainfall will have a significant effect on habitat quality and carrying capacity globally (Meadows & Hoffman, 2003; Parnell & Walawege, 2011). Climate change is a significant concern in southern Africa, where the annual, terrestrial temperature increase is 1.1–1.5 times the observed global average of 0.65 °C, (Davis-Reddy & Vincent, 2017; Ziervogel et al., 2014). Unfortunately, it is difficult to monitor and link rainfall patterns to climate change due to its high spatial and year-to-year variability (Engelbrecht et al. 2013). However, there is a clear increase in the number of extreme climate events, for both temperature and rainfall, which includes frequent dry spells and daily rainfall intensity (Davis-Reddy & Vincent, 2017). A permanent increase in annual temperature and extreme weather events, along with the two-fold increase in carbon dioxide concentration, will likely result in the change of terrestrial ecosystems throughout southern Africa, including several vegetation biome shifts (Higgins & Scheiter, 2012). The change in habitat parameters and quality will have several important impacts on wildlife species, including altered distribution limits, population fitness, growth, and survival (Davis-Reddy & Vincent, 2017). Due to the large-scale threat climate change poses in southern Africa, conservation strategies focusing on habitat protection or increasing connectivity between protected land patches seem to be inadequate to assist in species conservation practices (Gillson et al., 2013). Thus, to enhance any conservation event, an adaptive response method is required, which can only be implemented if sufficient species-specific data are available (Prober et al., 2019).

In addition to climate change, countries in southern Africa are experiencing rapid urbanisation, in many cases above the global average (Gambe et al., 2023); however, despite the growth in infrastructure, urban human population growth rates in South Africa are steadily declining and could perhaps indicate a decline in urbanisation rates in the future (Turok & Borel-Saladin, 2014). Population growth in South Africa correlates with infrastructure development and thus urban growth (Marais & Cloete, 2016). Thus, in the period 2001–2011, nearly 60% of the observed population increase in South Africa occurred in metropolitan sections of the country, which led to further urban development (Turok & Borel-Saladin, 2014). One of the hallmarks of urbanisation is the complete transformation, in the form of progressive replacement or fragmentation, of the natural habitat (Antrop, 2004; Güneralp et al., 2017). Such considerable change in the natural habitat will result in several outcomes for wildlife species. Many wildlife populations will be unable to adapt to novel environments and resources, becoming locally extinct

(DeVictor et al. 2007; de Andrade et al., 2019; Fenoglio et al., 2021). In contrast to this, several species seem to be able to adapt and survive in the urban landscape (Castillo-Contreras et al., 2021; Tait et al., 2014). These species must contend with several novel stressors and environmental conditions, including linear infrastructure, fragmented habitat, electrocution, and direct human-wildlife interactions, such as vehicle collisions (Cunneyworth & Duke, 2020; Cunneyworth & Slade, 2021; Linden et al., 2022a, b; Tigas et al., 2002).

As species unable to adapt to rapidly altered environments will go locally extinct, both climate change and urbanisation poses some of the greatest risk to the survival of wildlife species (Acevedo-Whitehouse & Duffus, 2009; Soulsbury & White, 2015; Taylor-Brown et al., 2019). With a distribution ranging throughout southern Africa, including South Africa, Namibia, Botswana, Angola, and the Democratic Republic of the Congo (Fig. 2; Bearder et al., 2021; Masters et al., 2016), *G. moholi* is sure to experience the effects of climate change and urbanisation quite drastically. Long-term data from the Lajuma Research Station (23°02'18.0"S 29°26'34.1"E), in Limpopo, South Africa, an area inhabited by *G. moholi*, already show an upward trend in average annual temperature and a decrease in rainfall between 2012 to 2018 (Fig. 3). Moreover, South Africa experienced a flash drought during the 2015–2016 period (Xuan et al., 2018). Such extreme weather events are known to occur more frequently due to climate change and will likely be an important driver of *G. moholi* population stability. In addition to this, the change in land use from rural, rural environments to an urban landscape will result in further ecological- and fitness-related changes in the species.

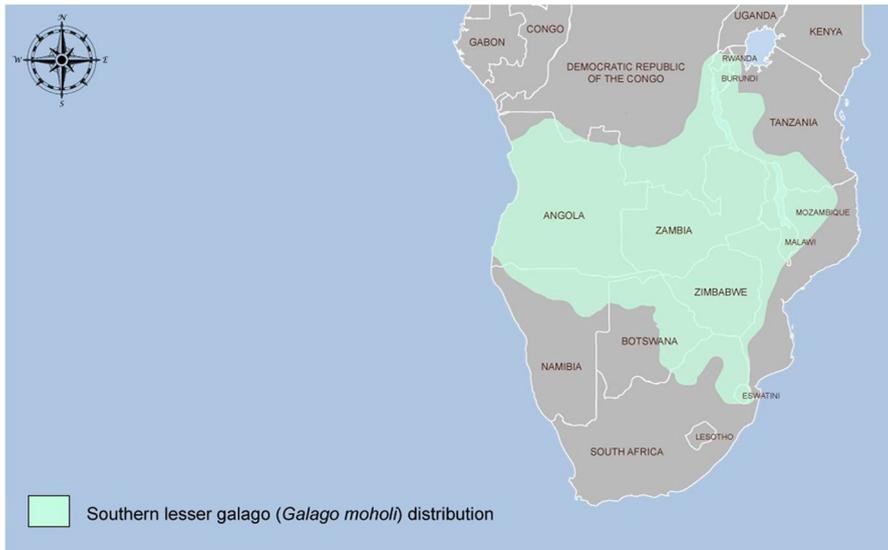


Fig. 2 The distribution range of the African lesser bushbaby, *Galago moholi* (Picture credit: African Geographic)

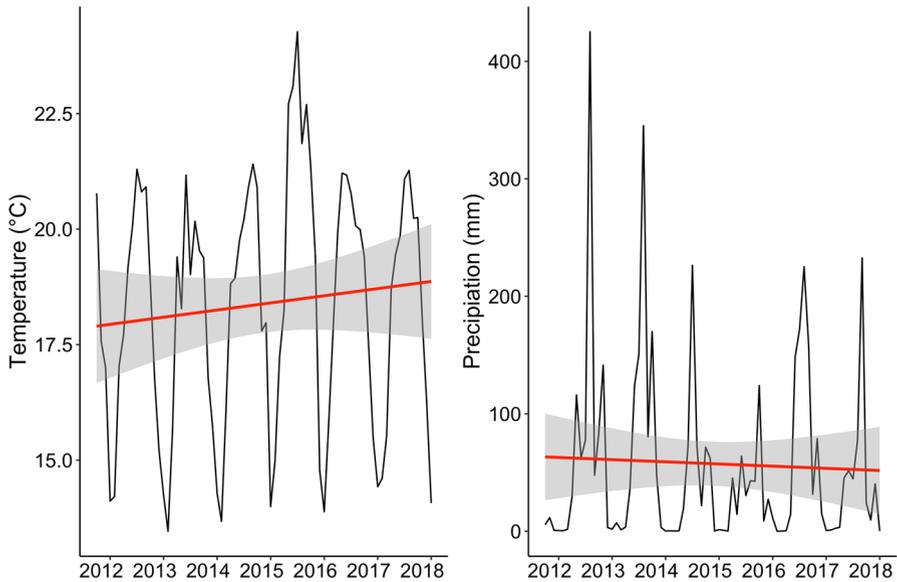


Fig. 3 The annual temperature and rainfall patterns (2012–2018) at the Lajuma Research Centre, Limpopo, South Africa. Temperature and rainfall data were collected by weather stations at the Lajuma Research centre and made available by the South African Environmental Observation Network (SAEON) and Lajuma Research centre

Habitat Quality is Shaping Population Density

The ecology of *G. moholi* is relatively well studied, with the first documented systematic field study in 1966 (Bearder, 1987; Nekaris & Bearder, 2007). However, despite the species' wide distribution range (Bearder et al., 2021), most studies have been conducted in north-eastern South Africa, specifically in the Gauteng and Limpopo provinces. As such, population-specific information on behaviour, physiology, and ecology, especially across different environments/climatic conditions, are absent for the species and we will focus our review on South African populations.

Both climate change and anthropogenic activities (deforestation, urbanisation, agriculture) are known to cause large-scale habitat fragmentation, leading to a reduction in habitat area, quality and carrying capacity, while limiting the dispersal ability of primates (see Arroyo-Rodríguez & Mandujano, 2006, 2009; Happold, 1995; Scanes, 2018). *Galago moholi* is generally found in semi-arid bushveld woodland, where individuals spend most of their time in trees, though foraging at ground-level is frequently observed (see Bearder et al., 2006; Nekaris & Bearder, 2007). Although galagos can survive in less preferred, natural habitats, most species show a clear preference for areas with dense trees due to their arboreal nature (Nekaris & Bearder, 2007). Initial density estimates of *G. moholi* in the natural environment was determined to be 0.87 animals/ha (Naboomspruit, Gauteng province; Bearder & Doyle, 1974), though later studies at the same study site found the density to be much lower at 0.31 animals/ha (Naboomspruit, Gauteng province; Bearder, 1987; Bearder & Martin, 1980) and 0.01

animals/ha (Loskop Dam Nature Reserve, Mpumalanga province; Ray et al., 2017). The difference observed between study populations could relate to several environmental factors, including the habitat size (dispersal ability), as well as resource availability. High dependence on environmental factors is also suggested by seasonally varying home range sizes of *G. moholi*. Home range estimates show male territories can range from 5–22 ha, while females maintain a smaller home range of 2–11 ha, but almost double their home range in the winter months when resource availability is drastically reduced (Nekaris & Bearder, 2007; Nowack et al., 2013b). In contrast to this, males seem to maintain a relatively constant home range, which overlaps with that of surrounding females (Nekaris & Bearder, 2007; Nowack et al., 2013a, b).

Due to their arboreal nature and dependence on forest connectivity, *G. moholi* may be at considerable risk to land transformation, habitat fragmentation and population seclusion (Masters et al., 2016). Furthermore, initial observations of the effect of climate change in the Limpopo province of South Africa, where *G. moholi* is abundant, shows that there will be a shift in vegetation type, from grasslands to tree-dominated landscapes (Scheiter et al., 2018); this might well be an advantage for galago species should it occur in most grasslands of southern Africa. Habitat fragmentation/alteration is known to cause a decrease in galago population densities, as shown for the dusky galago (*G. matschiei*; Weisenseel et al., 1993), Demidoff's galago (*G. demidovii*; Omifolaji et al., 2020), as well as several other nocturnal primate species (Pimley, 2009). This effect is not as simple, and the impact of habitat alteration on galago population dynamics may be driven by a complex relationship between habitat quality and the ability to disperse into and from neighbouring populations (Campos et al., 2012). This should be taken into consideration when predicting the possible effect of habitat alteration on galago densities.

Although no information regarding the effect of habitat fragmentation or alteration on *G. moholi* densities exists, the differences in range size and population density between different studies and habitats may indicate the importance of habitat quality (e.g., resource availability, climate etc.) and mating partner availability in driving population ecology and fitness. The removal of endemic tree species during urbanisation or tree-harvesting events, such as the gum-producing *Vachellia karroo* (formerly *Acacia karroo*), will remove important nesting and food sources, limiting the number of *G. moholi* which can survive in the environment (Masters et al., 2016). Studies on urban *G. moholi* populations indicate that the carrying capacity in urban environments are higher than observed in the rural environment (Scheun et al., 2015) in. Groups of up to ten *G. moholi* were observed in small fragmented suburban gardens (<1 ha) with anthropogenic feeding sources but limited to no connectivity to adjacent green spaces. It is largely thanks to the constant availability of exotic and anthropogenic food sources that *G. moholi* can maintain such high population densities in the urban environment.

Fragmented Habitats Can Alter Genetic Diversity and Population Fitness

As high levels of genetic diversity in a population are beneficial in terms of adaptation to environmental change, managers and conservationists often use genetic diversity as a marker of population health and fitness (Frankham, 2005; Grogan

et al., 2017; Markert et al., 2010; Toro & Caballero, 2005). High genetic diversity is often highlighted as an important parameter to consider when developing climate change species loss projections. Populations with high genetic diversity generally display higher behavioural and genetic adaptability to climate change and habitat alteration thanks to their genetic make-up (Pauls et al., 2013; Razgour et al., 2019; Willi & Hoffmann, 2009). However, several studies have shown that large-scale fragmentation, a shift in distribution range and habitat conservatism can all lead to the erosion of genetic variability and increased genetic divergence through reduced gene flow and increased genetic drift, especially in smaller wildlife populations (Marsh, 2003; Mhemmed et al., 2008; Razgour et al., 2013; Sousa et al., 2008).

While the ability of an individual to disperse into neighbouring populations can counteract the effect of genetic drift and inbreeding depression, the removal of natural habitat and migration corridors will limit such movement in many arboreal primate species (Ćosić et al., 2013; Jones, 2005). This pattern of genetic diversity loss due to the inability of individuals to disperse is often observed in small, captive primate populations (Charpentier et al., 2008; Neveu et al., 1998; Schulze et al., 1998). In wild, free-ranging primate populations a decrease in genetic diversity, because of habitat fragmentation/alteration, has been found in several primate species, including the samango monkey (*Cercopithecus albogularis*; Linden et al., 2022a, b), white-headed langur (*Trachypithecus leucocephalus*; Wang et al., 2017), pied tamarin (*Saguinus bicolor*; Farias et al., 2015), golden lion tamarin (*Leontopithecus rosalia*; Dietz et al., 2000) and silvery marmoset (*Mico argentatus*; Gonçalves et al., 2003). Unfortunately, specific information on the effect of habitat fragmentation on galago genetic diversity is not available. Many species in the family Galagidae are known to be philopatric, with females remaining in or around the home range of their mother; males, however, disperse to distant habitats (Nekaris & Bearder, 2007). As such, it is the males who are essentially responsible for the exchange of genetic material between populations.

In the thick-tailed bushbaby (*Otolemur crassicaudatus*), genetic diversity was low at various fragmented sites (fixation of mitochondrial haplotypes) likely due to limited migratory patterns observed in females (Phukuntsi et al., 2020); any native genetic material observed in the population was likely due to the movement of males between populations. While genetic diversity was found between several *G. moholi* populations, differentiation levels among populations were low, likely due to historic migration of males or translocation of individuals by the pet trade industry (Phukuntsi et al., 2021). It is clear from the highlighted studies that movement corridors must remain intact to maintain high levels of genetic variability, and thus population health and fitness. Like most primate species, *G. moholi* populations trapped in fragmented habitats are at risk of the erosion of genetic variability, and a reduction in the ability to react/adapt to climate change and further habitat alteration. While many other galago species have been observed living in fragmented habitats (Haji & Bakuza, 2022; Hanson et al., 2007; Zungu et al., 2018), no information exists on the effect thereof on the genetic fitness of any of these populations.

Climate Change and Urbanisation Can Lead to a Change in Food Resource Use

Urbanisation and climate change will not only affect habitat connectivity but alter food availability in once natural and now urbanised environments. *Galago moholi* has historically been described as a food specialist, exclusively feeding on insects, as well as gum from *Vachellia karroo* trees (Bearder, 1987; Nekaris & Bearder, 2007). Insects are known to be a nutrient dense food resource, consisting of protein, vitamins, mineral and fibre (Belluco et al., 2013; Rothman et al., 2014), making them an ideal food source to meet the high metabolic rates characteristic for small mammals (Clarke et al., 2010). Gum on the other hand seems to be mostly used as a secondary food source. It contains β -linked complex polysaccharides, which are resistant to digestive enzymes as part of the digestive process, and require long gut passage times, fermentation and specific gut microbes (Power, 2010; Caton et al., 2000). Consequently, it has considerably less nutritional value than protein-rich insects, but may provide an important source of calcium and minerals for the species (Bearder & Martin, 1980; Cabana et al., 2018; Jayne, 2020). Furthermore, the nutrient content of gum increases when insect biomass decreases during the cold, dry winter periods (Nowack et al., 2013b; Williams et al., 2015), which may explain why *G. moholi* shifts its dietary strategy from insects to *Vachellia* gum during the winter (Bearder & Martin, 1980; Harcourt, 1986; Nash, 1986; Nowack et al., 2013b).

Climate change and habitat modification have led to a permanent, global decrease in insect biomass over the past 25 years (Cardoso et al., 2020; Sánchez-Bayo & Wyckhuys, 2019). The reduction in preferred food sources, as well as the alteration and fragmentation of the natural environment, through both climate change and urbanisation, will pose a considerable threat to *G. moholi*. In support of this theory, Haji and Bakuza (2023) recently noted that a possible decrease in insect density in the similarly insect-specialised Rondo galago (*G. rondoensis*) will be one of the greatest threats to the survival of the species throughout its natural distribution. In response to food shortages, primates will need to adapt their movement and foraging behaviours to lower resource availability. One option to adapt to lower food availability could be an increased dependence on secondary foods such as gum to meet metabolic demands as already observed in winter (Nowack et al., 2013b). However, the extended use of gum throughout the year as a primary food source, alongside a decrease in insect consumption, may well lead to developmental constraints, changes in social ecology, elevated physiological stress and a decrease in general health and fitness. This has been noted for other primates using secondary food sources over prolonged periods (Cabana et al., 2018; Chapman et al., 2015; Koenig et al., 1997; Lea et al., 2015).

In addition to the increased use of gum, *G. moholi* would likely also need to extend the time spent foraging to meet metabolic requirements. For example, Bearder and Martin (1980) found that in periods of extreme food shortages, *G. moholi* foraged for additional food sources during the day. This shift in foraging behaviour and movement patterns, to meet metabolic requirements, has also been observed in several other primate species including the colobus monkeys

(*Colobus guereza*; Harris et al., 2010), chimpanzees (*Pan troglodytes schweinfurthii*; Giuliano, 2021), lowland woolly monkeys (*Lagothrix lagotricha poeppigii*; Fiore & Rodman, 2001) and Yunnan snub-nosed monkeys (*Rhinopithecus bieti*; Grueter et al., 2013). Additional foraging activity will not only limit time spent on reproductive, social, and resting activities but increase the number of possible predator–prey encounters. In fact, the nocturnal, solitary foraging and limited social interaction seen in *G. moholi* are thought to be important antipredator mechanisms (Burnham et al., 2013). In support of the predator avoidance theory, *G. senegalensis*, of which *G. moholi* was a subspecies until recently (i.e., *G. senegalensis moholi*), is considered more gregarious in regions where predators are largely absent (Svensson, 2017). Thus, an increase in nocturnal and diurnal foraging behaviours will likely increase the risk of predator encounters and mortality in *G. moholi*.

Several studies have shown that feeding specialists, who depend on specific resources and are unable to use additional food sources, are most at risk of extinction should these primary sources be unavailable (Foden et al., 2013; Garnett et al., 2013; Sánchez-Bayo & Wyckhuys, 2021). In contrast, feeding generalists or species able to adapt to rapidly changing environments tend to survive where specialists go locally extinct (Colles et al., 2009; Isabirye-Basuta & Lwanga, 2008). Despite the historic classification of *G. moholi* as a specialised feeder, several studies have recently shown that the species can act as a generalist feeder under various environmental conditions, highlighting the dietary flexibility of the species. Anecdotal observations during our fieldwork in the urban and natural environment found that galagos can opportunistically supplement their diet with fruits from the jacket plum tree (*Pappea capensis*) or nectar from the bird of paradise flower (*Strelitzia nicolai*) (Scheun et al., 2014, 2019). Similarly, wild *G. moholi* were observed consuming fruit from the sickle bush tree, *Dichrostachys cinerea* (Ray et al., 2016), as well as feeding on several bird species and their eggs during a drought (Engelbrecht, 2016). As noted by the authors, in the absence of insects, birds and their eggs offer *G. moholi* a nutrient-rich resource which is easily accessible. Although such a permanent shift in dietary preference will allow the species to survive in altered habitats, it will likely lead to a considerable loss in avian populations that experience elevated nest predation (Kubelka et al., 2022).

Galago moholi populations found in urban, fragmented habitats have been shown to integrate anthropogenic food sources into their diet, which include breadcrumbs and yoghurt (Scheun et al., 2015, 2019). Despite the advantage such dietary plasticity holds for species inhabiting altered habitats, long-term consumption of anthropogenic food sources may have deleterious effects on populations. Several studies have shown that supplementary feeding can have a range of negative effects on wildlife species, including an increase in disease, stress, injury, and malnutrition (Kirby et al., 2019; Murray et al., 2016; Strandin et al., 2018; Wimberger et al., 2017). Furthermore, urban *G. moholi* populations feeding on anthropogenic food sources also had (1) significantly higher body mass index levels, (2) higher levels of intergroup aggression, (3) as well as a change in group/social dynamics compared to rural populations using natural sources (Scheun et al., 2015). Thus, although food provisioning can assist in short term survival of populations in altered

environments, the negative effects of long-term consumption on the general health and reproductive success may well have several deleterious effects on population stability and survivability.

Torpor Use May Facilitate Survival During Drought Conditions

Galagos in South Africa inhabit a highly seasonal habitat with a cold and dry winter and wet and hot summer period where the daily variation can be substantial. Absolute temperatures up to 40°C during daytime have been observed and the daily difference between night and daytime temperature can be up to 35°C (recorded in October 2009 in a study in north-east South Africa; Nowack *et al.*, 2013b). Due to the high seasonality in their habitat, the low food availability during the colder season, and the high energy demands of mammals this size, the use of energy saving torpor (i.e., a controlled reduction in body temperature and energy expenditure) had long been suggested based on anecdotal evidence (Skinner & Smithers, 1990), but was only confirmed in 2010 (Nowack *et al.*, 2010). Earlier studies on the thermoregulation of *G. moholi* did not find any incidence of torpor use (Dobler, 1976; Knox & Wright, 1989; Mzilikazi *et al.*, 2006), which is likely due to the use of mostly shallow and hard to detect bouts of torpor (body temperature > 30 °C) that are restricted to the rest phase (Nowack *et al.*, 2023). Deeper bouts of torpor (body temperature < 30 °C) are only occasionally used (Nowack *et al.*, 2010, 2013a). Instead, *G. moholi* does seem to mainly rely on behavioural means, such as changes in nesting sites, increased huddling, and a change in activity pattern to survive the cold and resource-low winter period (Nowack *et al.*, 2013b).

While we have a good idea of how *G. moholi* cope with cold conditions there are virtually no data on how the species may respond to an increase in heat waves, droughts, or climate change related natural disasters. Exposure to heat is more dangerous than cold-exposure for endothermic mammals and birds and we are already seeing an increase in heat-associated mortality (McKechnie & Wolf, 2019). The upper limit of the thermal neutral zone of *G. moholi*, i.e., the temperature threshold above which animals must start using evaporative cooling to maintain a stable body temperature, has been determined as 35 °C (Dobler, 1978), but *G. moholi* are regularly exposed to daily maximum temperatures above this temperature in summer (Nowack *et al.*, 2013b). Nocturnal activity, i.e., inactivity during the hottest time of the day and selection of well-buffered resting sites – if available – likely limits exposure to extreme temperature conditions. Laboratory studies on grey mouse lemurs (*Microcebus murinus*) suggest that the closely related lemurs cope well with chronic heat exposure up to 34 °C in the laboratory, although aged animals showed greater difficulties coping with heat exposure (Terrien *et al.*, 2011). However, in the wild, heat waves often co-occur with droughts and reduced water availability, which can affect how well animals are able to cope with heat. At ambient temperatures above body temperature, evaporative water loss is the only option for an animal to cool down and limited water availability will thus have a large impact. There are two general physiological adaptations of animals to reduce evaporative water loss when water is scarce: (1) reducing metabolic rate through

the use of torpor and thereby reducing water loss through feces, urine as well as respiratory water loss from breathing or (2) thermoconforming behaviour (*adaptive or regulated heterothermy*), i.e., a voluntary increase in body temperature to reduce the need of evaporative cooling (Nowack *et al.*, 2017). Adaptive heterothermy is well known from many species coping with high ambient temperatures, such as Malagasy bats (Reher & Dausmann, 2021), Australian ring-tailed possums (Turner, 2020) as well as diurnal primates, i.e., baboons (*Papio hamadryas*; Mitchell *et al.*, 2009). However, so far, an adaptive increase in body temperature to deal with high daytime ambient temperatures has not been observed in any galago species. *G. moholi* are, however, able to improve their water balance using torpor (Nowack *et al.*, 2010). In addition to water loss through the skin, water is lost through the production of urine and faeces as well as during respiration, all of which are reduced to lower levels during torpor (Cooper *et al.*, 2005). Furthermore, lower levels of metabolisms also lower the need for evaporative cooling as a mechanism of heat dissipation, allowing animals to conserve water for the times when evaporative cooling is crucial (Bondarenco *et al.*, 2013).

While torpor use is mainly considered to be an adaptation to low food availability, a negative water balance can also be a strong trigger for torpor use in species in arid habitats (Cooper *et al.*, 2005) and water availability is also suggested as a main trigger of torpor use in grey-mouse lemurs inhabiting Madagascar's dry forest (Schmid & Speakman, 2009). Although torpor use in *G. moholi* has so far only been recorded in the winter period, galagos are able to undergo opportunistic torpor as a last resort strategy and it is thus likely that opportunistic torpor use can also aid survival under extreme temperatures and drought conditions or even climate-change related natural disasters, such as storms and fires, as reported for other species (reviewed in Nowack *et al.*, 2017).

Long-Term Reproductive Change in *G. moholi* in Response to Climate Change and Urbanisation

Although several species exist that breed throughout the year (non-seasonal breeders), most mammal species outside of the tropical regions tend to breed during specific periods annually (seasonal breeders) (Guh *et al.*, 2019). Seasonal breeding is an adaptive trait and allows an individual to avoid reproductive activity during inappropriate times of the year, while ensuring the survival of offspring who are born during periods of resource abundance and a mild climate (Bronson & Heideman, 1994; Guh *et al.*, 2019; Nakane & Yoshimura, 2014).

Like most galagids, *G. moholi* is a seasonal, polygynous breeder (Bearder, 1987); in this regard, mating activity is restricted to two periods annually (Scheun *et al.*, 2016). Several behavioural and physiological studies found that these mating periods occur during May/early June and late September/early October, when resources are abundant and temperatures favourable (Bearder & Martin, 1979; Doyle *et al.*, 1971; Pullen *et al.* 2000; Scheun *et al.*, 2016). However, the latter mating period is thought to be used as a 'back-up' mating period by females who did not become pregnant during the May period (Pullen

et al. 2000). Scheun *et al.* (2017) also found that testosterone levels, testis volume and mating behaviour did not differ between mating seasons; thus, while the September mating period might act as a ‘back-up’ mating period for females, males may attempt to maximise their reproductive output over both mating periods. According to observational data, as determined from intromission to birth, the gestation length in *G. moholi* ranges from 120–141 days (Doyle *et al.*, 1967; Izard & Nash, 1988; Nekaris & Bearder, 2007). Behavioural and endocrine monitoring in a captive population showed a gestational length of 128 days (Scheun *et al.*, 2016). Taking into consideration the 4-month pregnancy period, most births occur around September and January (Scheun *et al.*, 2016), where the nutritional needs of a lactating female can be met, while ensuring new-borns are not exposed to the extreme colds experienced in winter. In fact, it has been hypothesised that a trade-off with reproduction is one of the major factors explaining why *G. moholi* does not use torpor on a regular basis during winter (Nowack *et al.*, 2010). Lower body temperatures associated with torpor use would delay parturition and thus shift the second mating period, making it unlikely for juveniles born before winter to reach a sufficient body mass to survive the resource poor period.

Climate change and habitat alteration are set to drastically change both abiotic and biotic parameters in the environment (Boutin & Lane, 2014; Skogen *et al.*, 2018). While an increase in extreme weather events may reduce the mating season length, and lead to lower reproductive success (McNutt *et al.*, 2019; Moss *et al.*, 2001), an increase in favourable conditions (milder winters, early onset of spring, increased resource abundance) would lead to an increase in mating season length and reproductive success (Isaac, 2009; Moyes *et al.*, 2011; Wegge & Rolstad, 2017). For example, late-born pied flycatchers (*Ficedula hypoleuca*) had an increased rate of survival, albeit at the cost of a reduced fattening phase prior to migration (Tomotani *et al.*, 2016, 2018). Similar patterns will likely be observed in *G. moholi* in both natural and considerably altered environments, with prolonged or early onset mating and birthing periods occurring. Interestingly, a < 1 month old juvenile has been seen carried around and parked by the mother in July 2022, i.e., about 2 months prior to the normal birthing period, in an urban environment in South Africa (personal observation, JS).

Urban environments may well provide *G. moholi* populations with not only a mild climate throughout the year, but an abundance of resources which could remove the need for seasonal breeding. Similarly, an increase in insect availability due to warmer temperatures may also assist females who became pregnant in May and carrying the young across winter and into spring. Several studies have shown an increase in insect biomass when environmental temperature increase, providing an important food source for many insectivore species (Cornelissen, 2010; de Sassi & Tylianakis, 2012; Wolf *et al.*, 2008). However, the opposite may be the case during the summer pregnancy period, where an increase in temperature throughout the savannah-like highveld distribution of *G. moholi* may result in temperatures exceeding the physiological limits of both insect and plant species (Cornelissen, 2010; de Sassi & Tylianakis, 2012). This will drastically decrease the resources available to meet metabolic demands linked to reproduction in the

species. Furthermore, extreme fluctuations in environmental temperature may lead to suboptimal development and even genetic deficiency of the embryo (Nord & Giroud, 2020). Thus, although elevated temperature may have little to no direct effect on *G. moholi* reproduction, aspects such as resource decline and habitat isolation may influence population stability.

Finally, environmental stressors may influence the general and reproductive ecology of a species. The presence of an environmental stressor, be it injury, predator presence, aggressive interactions or low resource availability, will lead to the activation of the physiological stress response (Kersey & Dehnhard, 2014). One component thereof is the hyper-activation of the hypothalamic–pituitary–adrenal axis and an increase in secreted glucocorticoids (GCs; Beehner & Bergman, 2017). While an acute increase in GC concentrations can be adaptive in nature (Crespi *et al.*, 2013), chronic elevated GC levels can have a host of deleterious effects on an organism, including immune and reproductive suppression (Charmandari *et al.*, 2005; Hing *et al.*, 2016). As such, monitoring GCs, or the excreted metabolites thereof in faeces, provides an ideal method for monitoring the perceived physiological stress experienced by an organism within its environment (Kersey & Dehnhard, 2014). Urban *G. moholi* populations displayed significantly elevated faecal glucocorticoid metabolites (fGCM) concentrations compared to conspecifics inhabiting rural environments (Scheun *et al.*, 2015). The elevated fGCM levels observed in urban *G. moholi* may likely be because of insufficient resource availability, the use of anthropogenic food sources, altered group dynamics and aggression, as well as interactions with novel stressors. While the activation of the physiological stress response, and an acute increase in glucocorticoid levels, are adaptive in nature and can assist in the survival of an organism (Breuner & Hahn, 2003; Sapolsky *et al.*, 2000; Wingfield *et al.*, 1997), GC increase over extended periods may have several deleterious effects. Aside from the suppression of the immune response, and thus an increase in disease, ‘stressed’ individuals may also experience a suppression of reproductive function (Whirlledge & Cidlowski, 2017). While several studies have noted the ability of certain wildlife species to exploit the urban environment (Lyons *et al.*, 2017; Maibeche *et al.*, 2015; Teixeira *et al.*, 2015) and even enhance reproductive success as a result (Kettel *et al.*, 2018; Narango *et al.*, 2018), little to no information exists on the effect of long-term GC elevation on reproduction success in any urban species. Furthermore, as maternal GC levels may alter offspring temperament, fitness, and adult longevity (Hinde *et al.*, 2014; Monaghan & Haussmann, 2015; Petelle *et al.*, 2017; Todd, 2020), elevated GC levels throughout pregnancy may have a significant impact on long-term population growth and fitness.

Conclusion

Primates are currently threatened and nearing extinction due to anthropogenic activities, including factors such as habitat modification (e.g., climate change logging/urbanisation/mining/agriculture), overuse (e.g., bushmeat/traditional medicine), novel predators (e.g., domesticated pets) and disease (Estrada *et al.*, 2017). Because of the

number of threats facing primates, they are at risk of local or global extinction due to environmental change (Pacifci *et al.*, 2017). Climate change and human induced environmental change will undoubtedly have drastic effects on *G. moholi* and other galago species and may affect reproductive timing and success as well as limit gene flow. However, each species of galagos has evolved unique ecological and physiological adaptations to survive in their specific habitat, making general predictions about the impact of future environmental change on galago species difficult. In regard to *G. moholi*, the species' nocturnal lifestyle along with high levels of behavioural and physiological plasticity may allow adaptation to changing conditions: Selective torpor use as an energy- and water-saving adaptation may well act as a buffer against elevated temperatures. Furthermore, the ability to use various food sources means that the species is able to adapt to periods of limited naturally occurring food sources due to climate change or urbanisation. Additional research is needed to determine what the effect of long-term consumption of anthropogenic food sources, the possible shift in reproductive timing, along with various novel threats present in the urban environment, such as novel pathogens, predators and linear infrastructure will be, and how these might drive population dynamics and survival rates.

Although this review suggests possible outcomes for the species under current climate change predictions and urbanisation, it also highlights the need to conduct long-term research on galagos to better understand their response to human induced environmental change.

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Data Availability The datasets analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

Inclusion and Diversity Statement While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

The author list includes contributors from the location where the research was conducted, who participated in study conception, study design, data collection, analysis, and/or interpretation of the findings.

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