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Life on the ground: The behavioural ecology of risk and terrestriality in primates

A thesis submitted for the degree of

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by

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Abstract

The spread of predation risk across an environment creates a “landscape of fear” that acts as a significant driver of behaviour and evolution in prey species. This thesis explores primates’ landscapes of fear, with a particular focus on the relationship between perceived risk, substrate use, and the evolution of primate – including human – locomotion. Chapter One provides an introduction and overview of the landscape of fear concept, how it might have featured in the paleoenvironments of early hominins, and how it is studied in extant primates. Chapter Two presents a quasi-experimental study of risk perception in baboons in Gorongosa, Mozambique. In this study, habituation by human observers is used to document relationships between perceived risk of humans, mediating environmental variables, and behavioural correlates in two baboon troops. The results demonstrate that behaviours indicative of perceived risk – vocalisations and vigilance – decline throughout habituation and are mediated by habitat structure and time of day. There is also a negative relationship between these behaviours and baboons’ use of the ground. Chapters Three and Four explore this relationship between risk and ground-use at broader scales and using the presence of carnivores, rather than humans, as indicators of risk. In Chapter Three, camera trap data provides insight into the effects of ecology, season, and risk on the terrestrial activity patterns of two neighbouring baboon populations in Mozambique. The results illustrate that seasonality influences baboons’ use of the ground, and suggest that circadian patterns in terrestrial activity are sensitive to predator abundance or species in a landscape. Chapter Four investigates these dynamics at an even broader scale, comparing carnivore and baboon activity across 10 different sites in eastern and southern Africa. Results from this chapter indicate that loss of carnivore diversity – and particularly the absence of leopards – releases restrictions on baboon terrestriality, facilitating their use of the

ground during crepuscular and nocturnal hours. Finally, Chapter Five returns to an evolutionary perspective with a review of the origins of hominin locomotion and the emergence of primate terrestriality. This chapter emphasises the value of integrating paleontological research with insights from behavioural ecology to generate more nuanced understandings and hypotheses about the environments that have shaped human evolution.

Statement of authorship

This document follows the integrated thesis format. Chapter Two was published in the *American Journal of Biological Anthropology* in June 2022. Chapters Three, Four, and Five are all in preparation for submission to peer-reviewed journals. All of these chapters are the product of collaborations with my supervisors, colleagues, and external researchers who have contributed to the development and execution of the studies. I am responsible for the majority of work presented in each chapter in terms of conceptualisation, methodological design, data collation and analysis, interpretation and visualisation of results, and writing up. For Chapter Two, I shared responsibility for primary data collection during fieldwork with my colleague Lynn Lewis-Bevan. For Chapters Three and Four, primary data was collected and managed by a vast array of researchers, including but not limited to Kaitlyn Gaynor, Tara Easter, Meredith Palmer, Kristen Snyder, Noel Mbise, Ernest Eblate Mjingo, Lindsey Rich, and other contributors to the Snapshot Safari camera trap research network. For all chapters I benefited from computational support and revision by co-authors of the manuscripts. Note that these chapters have been written in the first-person plural in preparation for their submission to journals as collaborative pieces of research. The published version of Chapter Two can be found in the appendices of this thesis (Appendix E), included under the terms of a Creative Commons Attribution License.

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Chapter One
Introduction

Predator-prey dynamics create "evolutionary arms races" that significantly shape animal morphology, behaviour, and dispersal patterns due to their direct and severe impact on the inclusive fitness of both predators and prey (Davies, Krebs, & West, 2012). Operating within equally-dynamic ecosystems, these arms races are likely to have contributed to faunal extinction and speciation events across evolutionary history and may have influenced some of the key transitions in primate evolution – including within our own human lineage. But to what extent? What were the ecological relationships between prehistoric predators and our early human ancestors? Which behavioural adaptations in hominins might have been most heavily influenced by these relationships, and by what proximate mechanisms? And how do we study the roots of behaviours that evolved millions of years ago? Through a series of empirical studies of behavioural ecology, combined with a review of evidence from African primate and carnivoran fossil records, this thesis explores the role of predation risk in shaping primate behavioural evolution.

Recent paleontological advances afford us increasingly detailed snapshots of events in the fossil record that may be pertinent to understanding human evolution. One such event is a noticeable drop in the abundance and diversity of carnivore species that occurred between 2 and 1.5 Ma (Lewis & Werdelin, 2007; Werdelin & Lewis, 2005, 2013a) and coincides with a critical period for hominin evolution. Three hominin species – *Homo habilis*, *Paranthropus boisei*, and *Paranthropus robustus* – went extinct around this time, whilst a single lineage – *Homo ergaster/erectus* – successfully dispersed across and out of Africa, ancestors to modern *Homo sapiens* (Behrensmeyer, 2006; Bobe & Behrensmeyer, 2004; deMenocal, 2004; Potts, 2013; Wood & Boyle, 2016). Establishing

ecological and possibly causal relationships between these significant events in the fossil record is difficult. Was the apparent drop in carnivore abundance a direct result of dispersal and technological advances in *Homo* that allowed them to hunt or outcompete carnivores (Werdelin & Lewis, 2005)? Or conversely, could a drastic decline in predation pressure on hominins have facilitated certain behavioural adaptations that contributed to the unique flexibility and "success" of *H. erectus*?

Fossil and archaeological records provide us with increasingly accurate timelines for shifts in the parameters of carnivore and hominin communities as well as shifts in hominin technological complexity. Precisely detecting the timing and order of these shifts will provide insights into if, when, and where, hominins' status changed from prey species to serious competitors in the carnivorous niche. This is a contentious topic in the study of human evolution that has largely focussed on the emergence of lithic technology and meat-eating, probably because stone tools and evidence of butchery are the most tangible records of hominin behaviour available to us from that time (Domínguez-Rodrigo, 2010; Stanford & Bunn, 2001; Thompson, Carvalho, Marean, & Alemseged, 2019). However, these innovations likely did not stand alone, and should be considered in the context of other behavioural, social, and cognitive changes that might have been significant precursory or parallel adaptations for their emergence.

Exploration of such nuances using just the carnivoran, hominin, and archaeological records is limited by several factors. Firstly, both hominins and carnivores are rare amongst paleontological collections, restricting the temporal and geographic resolution with which hominin-carnivore dynamics can be explored. For this reason, it is important to examine not only hominin, but also other primate fossil records to document broader trends in anti-predation adaptations such as body size or substrate-use (Cheney & Wrangham, 1987; Clutton-Brock & Harvey, 2009; Willems & Hill, 2009). A further limitation is that behaviour does not fossilise. Paleontological data does little to

reveal the proximate mechanisms involved in the dynamic relationship between hominins' ecology and their behavioural repertoire. For this reason, research into the behavioural ecology of extant primates is key to a fuller understanding of both the proximate and ultimate effects of predation pressure on primate evolution (Elton, 2006; Hart & Sussman, 2008; Isbell, Bidner, Van Cleave, Matsumoto-Oda, & Crofoot, 2018).

Indeed, from studies of extant primate species that share homologous or homoplastic traits with hominins, it has been hypothesised that shifts in predation pressure might have given rise to novel or more diverse behavioural strategies in hominins. These include reducing constraints on primate sleeping patterns and sleep site choice (e.g. Coolidge & Wynn, 2006; Markham, Alberts, & Altmann, 2016), facilitating dispersals over novel or broader home ranges (Isbell, 1994), and possibly facilitating greater allocation of time and energy to technological and social behaviours (Samson & Nunn, 2015; Willems & Hill, 2009). These proximate behavioural changes, along with the direct effects of reduced extrinsic mortality from diminished predator populations, might in turn have prolonged hominin maturation processes, ultimately shaping modern human life history strategy, sociality, and intelligence (Coolidge & Wynn, 2006; Kuzawa & Bragg, 2012; Potts, 2012; Samson & Nunn, 2015).

This thesis presents a series of empirical studies of extant baboons (genus *Papio*) – a highly terrestrial and behaviourally flexible primate living in varied habitats across Africa, some of which are indicatively similar to well-studied hominin paleoenvironments (Bobe, 2018). These studies investigate the proximate effects of predation risk – both real and perceived – on primate behaviour at various geographic and temporal scales. With a focus on substrate-use and diel patterns in baboon activity, insights from these field studies shed light on mechanisms that might have contributed to key transitions in the behavioural evolution of African primates – including hominins – since the

Miocene.

1.1 Introduction to “the landscape of fear”

Both morphological and behavioural traits in animals adapt to a conglomeration of environmental factors, some of which have greater effects on the survival and reproductivity of a species than others. The risk of predation is thought to be a highly influential factor, imposing two types of costs on prey. The first is the obvious direct and severe cost of mortality, which alters features like prey survival rates, population sizes, and demographics. The second are the “chronic indirect costs” incurred by any species avoiding predation whilst trying to balance biological requirements (J. M. McNamara & Houston, 1987; Port et al., 2020; Shultz, Noë, Mcgraw, & Dunbar, 2004).

By one definition, the “landscape of fear” for an animal is a representation of how predation risk varies across its environment (Laundré, Hernández, & Ripple, 2010). This can be used in conjunction with models of resource variation across the same environment to explore how fear, and the consequent trade-offs with activities like foraging, affects the animal’s spatial and temporal use of the habitat (Brown, 1999; Laundré et al., 2010; Searle, Stokes, & Gordon, 2008). Although the landscape of fear concept has been widely adopted in predator-prey research, its definition remains ambiguous, as discussed further in Chapter Two. This ambiguity results in the use of unsuitable proxies and circular reasoning about risk and response, and inhibits nuanced exploration of mechanisms linking the two (Gaynor, Brown, Middleton, Power, & Brashares, 2019). Landscapes of fear have been defined variously as (1) the mapped physical environment, (2) the geographical spread of actual predation risk, and (3) spatial patterns in antipredator behaviours. Using the framework outlined by Gaynor et al. (2019), in my research I recognise these as three distinct and measurable landscapes, each with a non-linear relationship to one-another, as well as to a fourth distinct layer of *spatial variation in perceived risk* which is “the landscape of fear”.

The landscape of fear is likely to have had a significant influence on the evolution of anti-predation behaviours and adaptations in primates. Behavioural flexibility facilitates response not only to *actual risk*, but also – and perhaps predominantly – to *perceived risk* of predation in the environment (Willems & Hill, 2009). All prey species are constrained in their knowledge about the habitat around them, including about the actual risk of predation within it. However, the severity of any predation event is so great that it creates a selective pressure for animals to have an underlying fear of predation that allows them to modify their behaviour to the level of perceived risk around them (Brown, 1999).

Studies of responses to both actual and perceived risk, conducted across the primate order, are thus useful for demonstrating if and how these effects vary across species and environments, and they also yield primate models that serve as analogues for hominin behaviour (e.g. Isbell, Bidner, & Van Cleave, 2018; Samson & Shumaker, 2015). Some such studies pertaining to the effects of landscapes of fear on primate ranging, sleeping, and social behaviours are detailed in Section 1.3. But first, Section 1.2 outlines the paleoecological, paleontological, and archaeological evidence that provide us with broad estimates about the spread of risk across hominin landscapes.

1.2 Landscapes of fear for early hominins

Molecular and fossil evidence indicates that the last common ancestor (LCA) of all extant primates lived between 80 and 55 Ma (Steiper & Young, 2006; Tavaré, Marshall, Will, Soligo, & Martin, 2002). Platyrrhine and catarrhine primates diverged around 43 Ma, apes and cercopithecoid monkeys from hominoids around 31 Ma, and African and Asian great apes around 18 Ma (Steiper & Young, 2006). This situates the emergence and evolution of African great apes in the Miocene (23 Ma – 5.3 Ma) (Gradstein, Ogg, Schmitz, & Ogg, 2012), an epoch marked by the highest known level of hominoid diversity (Casanovas-Vilar, Alba, Garcés, Robles, & Moyà-Solà, 2011). Chapter Five

provides a review of some key transitions in hominid and hominin evolution from the late Miocene through to the Pleistocene, with a particular focus on locomotion and substrate-use. This period includes evidence of the diversification of hominins in Africa, as well as significant shifts in terrestrial carnivoran fossil records, which are summarised in Figure 1.1 and will be outlined and situated within the context of broader climatic and ecological trends in the sections below.

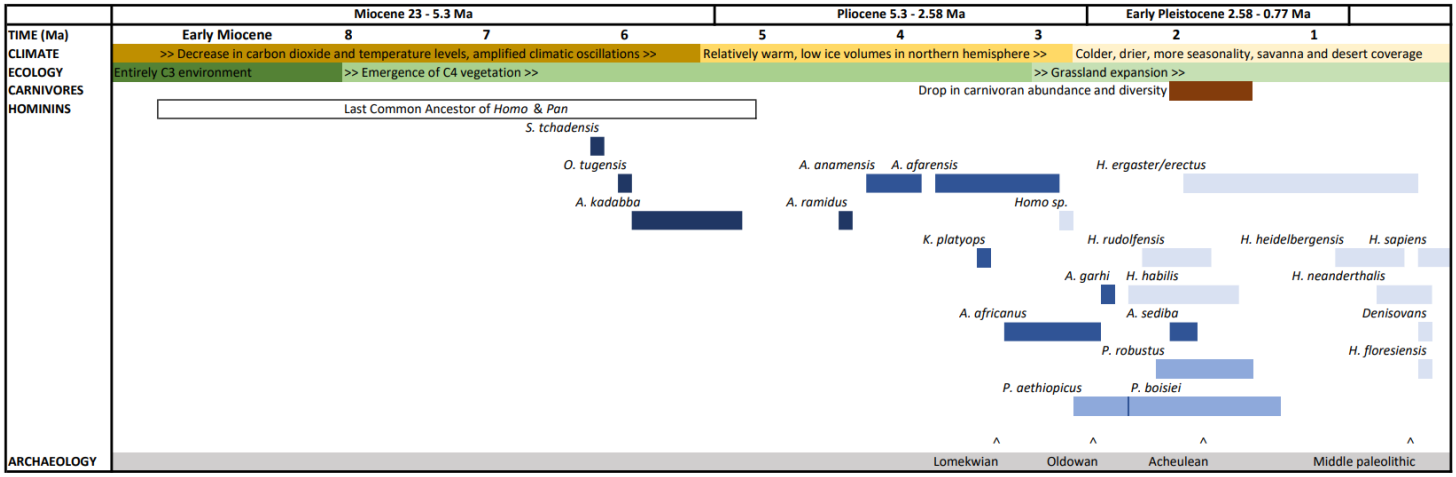


Figure 1.1. *A timeline of African hominin evolution alongside ecological and archaeological trends (adapted from Bobe, 2017). The proposed drop in carnivore abundance and diversity is also highlighted (data from Werdelin and Lewis, 2012).*

1.2.1 Miocene paleoenvironments

Climatic events are clearly marked in the geological record, are examples of directional forces of selection, and often underlie changes in other selective forces acting upon a species, including their habitat quality, resource availability, and exposure to predatory or competitor species. Thus, paleoclimatic data allows scientists to track the effects of climate on the turnover, dispersal, demographics, and species-level traits of hominins and other fauna across time (Basell, 2008; Eriksson et al., 2012; Potts & Faith, 2015). The fossil records of certain taxa can also be useful "tools" to complement stratigraphic and climatic data on paleoenvironments. For example, isotopic

and morphological features of fossilised ungulate teeth provide valuable information on the vegetation available in eastern African landscapes across time (Bobe & Behrensmeyer, 2004; Bobe, 2011), and have even been used to estimate temperature and precipitation levels in these paleoenvironments (Fortelius et al., 2016).

The latter half of the Miocene is characterised by two major climatic trends that are likely to have had an impact on faunal evolution in eastern Africa; paleoclimatic data indicate an overall decrease in carbon dioxide and temperature levels, and an amplification in climatic oscillations (Bobe & Behrensmeyer, 2004; deMenocal, 2014; Maslin et al., 2014). Decreasing levels of CO_2 in the atmosphere are thought to have had global effects on vegetation features; by about 8 Ma, C_4 plants had evolved from what had previously all been C_3 vegetation in Asia, Africa, North America, and South America (Cerling, Harris, MacFadden, & Leakey, 1997). Although not absolute, C_3 and C_4 isotopic signatures have been associated with woodland and grassland vegetation respectively (Cerling et al., 2015, 1997). Carbon isotope ratios, measured from fossil soils or tooth enamel, can thus indicate the types and proportions of plant-types present in fossilised animals' immediate environments and/or in their diets. Indeed, the emergence of C_4 signatures in fossilised plants coincides with the appearance of C_4 isotopes in the teeth of fossilised mammals, demonstrating which species were exploiting these foods newly-present in their environment (Cerling et al., 2015, 1997).

1.2.2 The Miocene-Pliocene transition and the emergence of hominins

The LCA of modern humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), and bonobos (*Pan paniscus*) is thought to have lived around the time of these climatic shifts in the late Miocene; molecular and fossil evidence indicate a divergence between the *Pan* and *Homo* lineages between 10 and 6 million years ago (Ma) (Moorjani, Amorim, Arndt, & Przeworski, 2016; Prado-Martinez et al.,

2013; Wilkinson et al., 2011). There is no clear candidate for this LCA in the fossil record, and the identity of the first members of the hominin clade are still a matter of debate. *Sahelanthropus tchadensis*, *Orrorin tugenensis*, *Ardipithecus kadabba*, and *Ardipithecus ramidus* are included in the clade based on evidence of reduced canine size and honing compared to extant non-human apes, and morphological indicators of bipedal locomotion, but the first genus considered indisputably hominin is *Australopithecus*, present in the fossil record from 4.2 Ma (Boyle & Wood, 2017).

Regardless of their specific identity, an emergence date in the late Miocene suggests that the earliest hominins lived in an environment where C_4 plants were emerging and becoming increasingly available. However, isotopic evidence from fossilised hominin teeth shows that in the early Pliocene (4.4 Ma) *Ardipithecus* was still eating a fully C_3 diet (White et al., 2009). Evidence from *Australopithecus* fossils indicates that early specimens, dated at 4.2 Ma old (Cerling, Manthi, et al., 2013), also consumed predominantly C_3 foods, but that by 3.7 Ma australopithecines were incorporating C_4 resources into their diet (Sponheimer et al., 2013). Studies linking the known spread of australopithecine fossils and surrounding contextual vegetation data suggest that these animals had a preference for mosaic habitats – areas composed of patches of woodland and grassland – even before they began incorporating C_4 resources into their diet (Bobe, Manthi, Ward, Plavcan, & Carvalho, 2020; Reynolds, Bailey, & King, 2011).

1.2.3 The Pleistocene and the emergence of *Homo*

The Early Pleistocene (2.59 to 0.78 Ma) appears to have been a crucial interval for hominin evolution. The fossil record indicates the presence of at least three hominin genera in eastern Africa at the start of the Pleistocene – *Australopithecus, Paranthropus,* and *Homo* – but this diverse clade was pruned down by the disappearance of *Australopithecus* and *Paranthropus* by 1 Ma. Meanwhile, a single species of *Homo* – *H. erectus* – appears to have flourished both within Africa and in its

dispersal out of Africa and across Eurasia about 1.8 Ma (Behrensmeyer, 2006; Potts, 2013; Rito et al., 2013; Stringer, 2002; Wood & Boyle, 2016). To understand the evolutionary success of *H. erectus*, and the subsequent ecological hegemony of *H. sapiens*, we must examine in detail the events of the Pleistocene. What happened to affect such drastic changes within the hominin clade? What forces influenced the evolution and extinction of *Australopithecus* and *Paranthropus*? And what were the key selection pressures that ultimately shaped modern human morphology and behaviour?

Advances in paleo-ecological techniques, combined with ever-growing fossil data sets, are facilitating increasingly accurate and detailed studies of environmental change and evolutionary trends in the Pleistocene (Cerling et al., 2013, 2015; Fortelius et al., 2016; Fortelius, Geritz, Gyllenberg, Raia, & Toivonen, 2015; Tryon, Faith, Peppe, & Beverly, 2016). Paleoclimatic data indicates a major global transition from a relatively warm climate during the early Pliocene, likely characterised by low volumes of ice in the Northern Hemisphere, to a generally colder, but cyclic climate during the Pleistocene, characterised by fluctuating volumes of ice (deMenocal, 2004; Levin, 2015). These global climatic changes appear to have affected African environments by making them colder, drier, and more seasonal, and facilitating increased savannah and desert coverage of areas in northern, eastern, and southern Africa (Antón et al., 2014; Bobe & Behrensmeyer, 2004; Bobe, 2011; deMenocal, 2004; Fernández & Vrba, 2006).

Isotope analyses of plant lipids retrieved from aeolian dust in ocean sediments show that eastern African grasslands expanded by as much as 50% between 3 and 2 Ma (deMenocal, 2014). Other dust samples, from terrestrial and lacustrine deposits, confirm that the period between 1.9 and 1.5 Ma was a time of extreme climatic variability, cycling between wet periods and droughts and contributing to the fluctuating presence of a multitude of large lakes that developed in eastern Africa around 3 Ma (deMenocal, 2004; Maslin et al., 2014; Trauth, Maslin, Deino, & Junginger, 2010; Trauth, Maslin,

Deino, & Strecker, 2007). These lakes are predominant features of the eastern African landscapes inhabited by early hominins, and have been described as "amplifier lake systems" as they are thought to have increased the sensitivity of the proximate environment to climate change, compared to surrounding African habitats (Trauth et al., 2010).

Matching the isotopic signatures indicated by oceanic sediments, terrestrial samples from eastern African paleontological sites also demonstrate an increase in the presence of C_4 vegetation during the Pleistocene, signalling the expansion of grasslands (Cerling, 2014; Feakins, Levin, Liddy, & Sieracki, 2013; Levin, Quade, Simpson, & Semaw, 2004; Maslin et al., 2014; Ségalen, Lee-Thorp, & Cerling, 2007). Furthermore, isotopic evidence from fossilised teeth demonstrate that herbivore diets included more C_4 material from about 3 Ma, a shift that became more pronounced closer to 2 Ma (Lee-Thorp, Sponheimer, & Luyt, 2007). Functional analyses of such teeth indicate that hypsodont morphology, specialised for processing grassland plants, also became increasingly common, along with other morphological traits demonstrative of grassland-adaptation (Bobe & Behrensmeyer, 2004). Tracking these so-called "grassland indicators" in the fossil record shows that grasslands formed an increasingly large portion of eastern African landscapes from about 2.5 Ma, and particularly after 1.8 Ma. Indeed, the period from 2 to 1.8 Ma marks a notable bout of extinctions of animals that had been adapted to closed and arboreal habitats, alongside an origination pulse in grassland-adapted fauna (Bobe & Behrensmeyer, 2004).

There is some debate over the impact of these climatic changes on both ecological turnover and hominin evolution. For example, the "Turnover Pulse Hypothesis" postulates significant bouts of speciation and extinction tied to climatic shifts (Vrba, 1993, 1995), whilst other studies suggest a more continuous rate of change in faunal abundance and diversity (Bibi & Kiessling, 2015; Frost, 2007; Werdelin & Lewis, 2005), perhaps with distinct periods of fluctuation, for example in repeated

100ky cycles of faunal change in the Mid-Pleistocene (Bobe & Behrensmeyer, 2004). Other hypotheses suggest that ecological shifts were more nuanced, with underlying fluctuations of moisture and aridity creating variable and spatially heterogeneous habitats for Pleistocene hominins to deal with. According to the "Variability Selection Hypothesis", this constant variability might have been the crucial selective pressure for the behavioural flexibility observed in modern humans (Antón et al., 2014; Maslin et al., 2014; Maslin, Shultz, & Trauth, 2015; Potts, 1998; Potts et al., 2020).

Another historically prominent theory in human evolution, "The Savannah Hypothesis", interprets the significantly expanding grasslands as the primary driver of human traits like bipedalism and hunting in the open savannah (Dart, 1925). *Australopithecus* is the first hominin genus in which bipedal locomotion is undisputed (Potts, 2013), but it does not necessarily mark a transition to exclusive terrestriality. Emerging ecological data indicate that hominin environments likely had higher tree coverage than previously assumed (Negash, Wynn, & Bobe, 2019), and increasingly detailed evidence of hominin limb morphology depicts a complex and varied relationship between bipedality and arboreality across time and hominin species, which will be discussed in further detail in Chapter Five (Dunmore et al., 2020; Prang, Ramirez, Grabowski, & Williams, 2021; Richmond et al., 2020; Ruff, 2009; Senut et al., 2001; Ward, Leakey, & Walker, 2001).

Australopithecines disappear from both the eastern and southern African fossil records during the Early Pleistocene; the most recent specimen demonstrates that *A. sediba* was present in South Africa less than 2 Ma (Dirks et al., 2010), and other members of the genus were spread over eastern and southern Africa until ~2.5 Ma (Wood & Boyle, 2016). Evidence shows that *Australopithecus* overlapped both temporally and geographically with two other hominin genera; the megadont, *Paranthropus*, and early species of our own genus, *Homo* (Herries et al., 2020; NG Jablonski,

Leakey, Ward, & Antón, 2008; Potts, 2013; Wood & Boyle, 2016).

Paranthropus appears in the eastern and southern African fossil records ~2.7 Ma and 2 Ma respectively, and disappears from both around 1.2 Ma (Potts, 2013; Wood & Boyle, 2016). Carbon isotope analyses of teeth from *P. boisei*, present in eastern Africa from 2.3 Ma until 1.2 Ma, suggest that the species was a C_4 specialist (Sponheimer et al., 2013). The earliest evidence of the genus *Homo* is a little older than *Paranthropus* and just pre-dates the start of the Pleistocene; one specimen identified as a *Homo* mandible is thought to be about 2.8 million years old (Villmoare et al., 2015). Named species, *H. habilis* and *H. rudolfensis,* appear in the fossil record between 2.5 and 2 Ma, and disappear between 1.8 and 1.6 Ma, whilst the first clearly "premodern human", *H. erectus*, originated at least 1.89 Ma and only went extinct about 200 000 years ago (Wood & Collard, 1999).

Compared to the C_4 specialisation indicated by *P. boisei* fossils, *Homo* teeth indicate a mixed diet, composed of both C_3 and C_4 resources (Sponheimer et al., 2013). This suggests that, although *Paranthropus* and *Homo* species were at times sharing relatively small habitats (Bobe & Carvalho, 2019) and dealing with the same climatic shifts – increasing aridity, seasonality, and mosaic habitats – they were utilising the environment differently. It seems that perhaps *Paranthropus* lived and foraged predominantly in the more open C_4 areas, whilst *Homo* inhabited a wider range of environments (Cerling, Manthi, et al., 2013). Both genera appear to have been bipedal, but morphological evidence suggests that this mode of locomotion was less specialised in *Paranthropus* than in *Homo* species (Harcourt-Smith & Aiello, 2004; Richmond et al., 2020).

The brains of *Homo* and *Paranthropus* also display significant differences; the skulls and endocasts of the latter are not distinct from those of *Australopithecus*, and are possibly even less developed, whilst the size and shape of the *Homo* brain are two of the most distinguishing features of the genus

(Falk et al., 2000). This difference suggests that the larger brains observed in *Homo* species cannot be attributed only to environmental shifts, as evidenced by the fact that smaller-brained *Paranthropus* hominins successfully existed through at least a million years of climatically variable Pleistocene, as well as at least half a million years of co-existence with *Homo.* It is thus useful to consider how niche-partitioning by these genera likely shaped their divergent adaptations. For example, different dietary strategies and preferred habitats might also have exposed them to different types of competition or predation pressure even within the same broader environment, perhaps significantly impacting their respective morphologies and behaviours.

1.2.4 Predation pressure on hominins

Based on the knowledge that extant terrestrial and semi-terrestrial primates often face predation from multiple sources (discussed further in Section 1.3), it is likely that early hominins had a variety of predators including raptors, reptiles, and terrestrial carnivorans. Direct evidence of their interactions with these predators is limited, but we can use proxies from the fossil record to estimate the risk imposed upon hominins by predators. Hominin fossils can be analysed for evidence of predation like tooth or claw marks on the bones (Berger & Clarke, 1995; DeSilva, Steininger, & Patel, 2013; Fourvel, Thackeray, Brink, O'Regan, & Braga, 2018; Gommery, Pickford, & Senut, 2007; Hart & Sussman, 2011; Margvelashvili, Tappen, Rightmire, Tsikaridze, & Lordkipanidze, 2022; McGraw, Cooke, & Shultz, 2006; Njau & Blumenschine, 2012; Pickering, Clarke, & Moggi-Cecchi, 2004; Val, Taru, & Steininger, 2014; Woldegabriel et al., 1994). However, the low number of hominin fossils in the record limits the chances of finding a sizeable set of marked bones for analysis. A more feasible option is to document the abundance and dispersal of specimens of potential predators in relation to hominin specimens, providing a proxy for levels of predation risk across hominin environments.

However, absolute numbers of predators in an environment are not the only consideration when quantifying risk in the environment. As outlined in Section 1.1, the *actual risk* posed by predator presence does not necessarily translate exactly to the *perceived risk* experienced by prey. Each has differing effects on primate behaviour and evolution, which are further mediated by predator-specific traits and hunting techniques, as well as intraguild dynamics (Hayward & Slotow, 2009; Searle, Smit, Cusack, et al., 2021; Willems & Hill, 2009). It is thus necessary to understand the separate effects and relationship between actual and perceived risk for primates, as well as the influence of predator diversity and density in an environment. Such dynamics will be discussed further in Section 1.3 and are the subject of the empirical chapters of this thesis.

The focus of hominin-predator dynamics has been mainly on large terrestrial carnivores such as the Canidae, Felidae, and Hyaenidae families (Lewis, 2017; Werdelin & Lewis, 2005). This is partly due to a historical bias towards mammalian fauna in paleontological research, despite the collection of numerous and well-preserved specimens from the crocodilian order (Storrs, 2003). Additionally, an historically hominin-centric approach has focussed on the entrance of hominins into the carnivorous niche and the resulting competition between them and terrestrial carnivores, whilst relatively little attention has been paid to hominins as prey species (Hart & Sussman, 2008; Hopwood, 2014; Werdelin & Lewis, 2013b).

Analyses of the Carnivora fossil record indicate that there was a global faunal turnover event around the Miocene-Pliocene transition (~5.3 Ma) that appears to have been relatively abrupt in Asia and more drawn out in Africa, resulting in an increase in carnivoran abundance and diversity in eastern Africa that peaked around 3.5 Ma, and was followed by a clear decline towards the present (Lewis & Werdelin, 2007; Werdelin & Lewis, 2005, 2013a). Based on climatic data, some authors have hypothesised a turnover pulse in Carnivora around 2.5 Ma (Turner, 1990), but closer analyses reveal

that the carnivoran species origination rate between 3 and 2.4 Ma in Africa was in fact zero, ruling out a pulse at this time (Werdelin & Lewis, 2005). There may be a small peak in origination rate around 2.1 to 1.8 Ma, but at higher resolution this is thought to be a sampling effect, and in any case it is smaller than the 3.5 Ma origination rate peak (Werdelin & Lewis, 2005). Carnivore extinction rates appear to have been relatively constant until about 1.8Ma, after which there is a dramatic drop in both the abundance and diversity of species in African records (Lewis & Werdelin, 2007; Werdelin & Lewis, 2005, 2013a).

It has been argued that this drop in carnivoran richness in eastern Africa cannot simply be due to climatic changes, but must have been caused, at least in part, by "fierce interference competition" from hominins (Willems & Van Schaik, 2017). According to such hypotheses, dietary and behavioural innovations of Pleistocene hominins must have contributed significantly to the wave of carnivore extinctions around 1.8 Ma as hominins changed their status from prey species to serious competitors within the predator guild, capable of pushing other carnivores to extinction (Lewis & Werdelin, 2007; Ripple & Van Valkenburgh, 2010; Werdelin & Lewis, 2013a).

There has been limited acknowledgement that the opposite causal relationship could be possible. If climatic or ecological shifts in the Pleistocene removed or reduced certain species or types of predator from the environment, this drop in predation pressure might have facilitated some of the dietary and behavioural innovations that solidified the hominin position in the carnivore guild (Hopwood, 2014). This is a hypothesis that needs more detailed and nuanced exploration, both to understand the potential selective effects of predation pressure and to track exactly when, where, and how hominins became competitive enough within the carnivorous niche to cause mass extinctions.

1.2.5 Hominin technology and the "human predatory pattern"

At the peak of carnivoran species richness, the only hominins known to be inhabiting eastern African environments were australopithecines, already living in somewhat mosaic habitats and consuming a mix of C_3 and C_4 resources by 3.7 Ma. The earliest possible evidence of butchery and the earliest stone tools appear in the archaeological record around this time, but there is broad debate over what they can tell us about the carnivorous behaviours of these hominins. Dated at ~3.4 Ma, two marked ungulate bones found in the Sidi Hakoma Member of the Hadar Formation, in Dikkika, Ethiopia, have been attributed to hominin processing of animal tissue (McPherron et al., 2010). Some argue that the marks could be the result of trampling (Domínguez-Rodrigo, Pickering, & Bunn, 2012) or crocodile predation (Sahle, Zaatari, & White, 2017), but taphonomic analyses indicate that these explanations are unlikely (Thompson et al., 2015).

The earliest known tools are the "Lomekwian tools", dated at ~3.3 Ma, found in the Nachukui Formation in West Turkana, Kenya (Harmand et al., 2015). These indicate that australopithecines engaged in "core reduction and battering activities" (Harmand et al., 2015) of some food items, perhaps similar to nut-cracking behaviours seen in modern chimpanzees (Caruana et al., 2014; Carvalho, Matsuzawa, & McGrew, 2013), and perhaps including the extraction of bone marrow or brain tissue from scavenged carcasses (Plummer, 2004; Thompson et al., 2019; Toth, 1997). The archaeological record, combined with an understanding of tool use in extant non-human primates, indicates that hominin tool-use arose prior to the emergence of our genus, and parsimony would suggest that these earliest technologies consisted largely of percussive and perishable technology (Carvalho & Beardmore-Herd, 2019). Although this evidence indicates an early date of emergence for tool-use in hominins, it is contextualised by evidence that they were small-bodied apes living in relatively small groups without any obvious signs of cooperation at this time. It is thus unlikely that

the earliest lithic tools would have provided significant protection against the large-bodied, abundant, and diverse carnivore populations of the time, nor that they would have introduced high competitive interference for access to prey.

Following the contentious evidence of butchery ~3.4 Ma, the next earliest signs of animal processing by hominins are 2.6 million-year-old cut-marked bones from Gona, Ethiopia (Domínguez-Rodrigo, Pickering, Semaw, & Rogers, 2005). This coincides with the emergence of bifacial lithic technology, "Oldowan tools", which many have used as a proxy for increased meat consumption by hominins (Ferraro et al., 2013). However, the earliest evidence of persistent carnivory comes from Kanjera South, in Kenya, dated at 2 Ma, where large assemblages of fauna demonstrate that hominins were regularly processing small ungulate carcasses, and even some larger mammal carcasses (Ferraro et al., 2013). Most assessments of hominin predatory behaviours thus focus on evidence from post-2 Ma sites, usually placing emphasis on the emergence of "hunting" and "meat-eating" behaviours around this time, and arguing for their central role in the evolutionary success of *Homo* (Thompson et al., 2019). However, it is a matter of debate whether Pleistocene hominins entered the carnivorous niche through active hunting or passive or confrontational scavenging, and it is not clear whether they were primarily accessing meat or inside-bone tissues (Blumenschine, 1986; Domínguez-Rodrigo & Pickering, 2003; Pickering & Bunn, 2007; Pobiner, 2020; Shipman, 1986; Thompson et al., 2019). For example, butchery assemblages like those at Kanjera might be the product of hominins using rocks as percussive technology for passive scavenging of tissues like bone marrow or brain matter from carcasses killed by other predators (Thompson et al., 2019). Additionally, recent analyses of cut-marked bones suggest that changes interpreted as an increase in butchery 2 Ma might in fact be a sampling artefact (Barr, Pobiner, Rowan, Du, & Faith, 2022).

Thus, whilst most researchers agree that the regular acquisition of animal tissues by hominins proved

to be a highly successful adaptive dietary strategy that significantly influenced various life history and social traits of *H. erectus* (Antón et al., 2014; Stanford & Bunn, 2001; Thompson et al., 2019), there has been a call for more careful investigation of the nature and initial emergence of the "human predatory pattern". This is defined as the regular consumption of tissues extracted from animals the same size or larger than humans themselves and is a trait that separates humans from the various primate species known to be opportunistically omnivorous (Thompson et al., 2019).

The traditional assumption has been that the earliest hominins, like extant chimpanzees, were actively and cooperatively hunting small animals by hand and then transitioned to similar but enhanced hunting of larger animals through the use of stone tools and persistence hunting (Stanford & Bunn, 2001). Recent research on percussive technology and its potential role in scavenging activity calls this into doubt and highlights a different potential route into active hunting (Thompson et al., 2019). Some argue that any procurement of animal tissues by hominins – even through scavenging – would have required strategies for resisting kleptoparasitism by carnivores. It is argued that these strategies, combined with anti-predation behaviours like mobbing (seen in extant chimpanzees and baboons), would provide the necessary behavioural foundations for active procurement of meat (Lewis & Werdelin, 2007). However, such strategies might not have been essential if scavenging in closed woodland environments reduced the chances of hominins being detected by competing scavengers and other predators. Sabertooth cats are thought to have hunted in closed woodland environments, and display specialised morphological traits for ripping meat off carcasses but not for crunching bones, possibly creating a marrow-scavenging niche for hominins living in closed woodlands during the Plio-Pleistocene (Marean, 1989). The subsequent shift to more open landscapes and the consequent extinction of sabertooth cats might have spurred hominins from passive to more confrontational scavenging by interactions with the new carnivore guild (Marean,

1989).

These various hypotheses highlight the necessity of understanding the behavioural ecology, not only of the various hominin species, but also of the different types of predators with which hominins might have interacted. Investigation of fossilised morphological traits, combined with an understanding of modern behavioural analogues will help us build and test hypotheses about the evolution of anti-predation, scavenging, and hunting strategies in primates such as early hominins.

It should also be noted that not all Pleistocene hominins were necessarily practising carnivory. The C_4-heavy diet of *Paranthropus boisei* is thought to have been drawn predominantly from open grasslands (Cerling, Manthi, et al., 2013), supported by morphological indicators of a robust chewing anatomy in the genus. Their large, thickly-enamelled teeth and heavy jaws were first thought to be specialised for eating tough fruits and nuts (Wood & Strait, 2004), but microwear analyses suggest that *Paranthropus* was more likely processing large quantities of fibrous vegetation like grasses and/or sedges (Cerling et al., 2013; Lee-Thorp, 2011; Ungar, Grine, & Teaford, 2008). This, and the fact that no lithic technology has been specifically attributed to the genus (Rogers, Harris, & Feibel, 1994; but see Elton, Bishop, & Wood, 2001), suggests that *Paranthropus* was not a serious competitor within the hominin predatory niche.

Homo specimens, on the other hand, are increasingly found in proximity to archaeological indications of butchery across the Pleistocene (Stanford & Bunn, 2001), making them the real focus of the emergence and adaptive consequences of the human predatory pattern. Various *Homo* traits have been attributed to the adoption of a consistently omnivorous diet. For example, there appears to have been a significant increase in *Homo* body and brain size about 1.8 Ma (Grabowski, 2016; Wood & Boyle, 2016), arguably indicating consistent access to higher-value foods. Both of these traits have

implications for hominin-predator interactions; bigger bodies likely deterred attack from smaller and aerial predators, and bigger brains might have facilitated more complex antipredation and carnivorous behaviours (Milton, 1988; Treves & Palmqvist, 2007).

Low temporal resolution linking *Homo* trait shifts with the drop in carnivoran species richness make it difficult to attribute causality in either direction. At 1.8 Ma we see the earliest evidence of *H. erectus* dispersal out of Africa (Potts, 2013) and at 1.76 Ma a rise in technological complexity with the appearance of "Acheulean tools" (Potts, 2013). At 1.7 Ma we see a significant reduction in *Homo* tooth size, and by 1.5 Ma the modern body form emerges in *H. erectus* (Gowlett & Wrangham, 2013). It is only at 1 Ma that we see evidence of significantly reduced sexual dimorphism, followed by a rapid increase in cranial capacity, slower dental development, and longer life history (Gowlett & Wrangham, 2013; Potts, 2013). These changes, indicative of reduced mortality and extended maturation processes, emerge well after the drop in carnivoran species richness, demonstrating that at least some of the more complex adaptations seen in *H. erectus* appeared after the onset of the decline in the African carnivore population.

A reduction in predation pressure during the Pleistocene, regardless of its initial cause and combined with other changing features of hominin habitats, could have acted as a catalyst for certain facets of *H. erectus* evolution. These might include intensified carnivory and the cumulative complexity of hominin technology and culture. Unpicking the direction of causality in such trends is dependent on a broad and integrated understanding of prehistoric records, as well as the study of extant primate and carnivore behavioural ecology. Chapter Five of this thesis returns to a paleontological exploration of primate-predator dynamics, whilst the preceding chapters focus on behavioural ecology in modern African ecosystems.

1.3 Landscapes of fear for extant African primates

The influence of predation pressure on human evolution cannot be understood in a vacuum; it requires understanding the effects of predation on behaviour across the primate order, and particularly on species that share homologous or homoplastic features with hominins (Isbell, 1994; Willems & Van Schaik, 2017). Models of hominin behaviours often focus on chimpanzees (genus *Pan*) due to their close phylogenetic relatedness to humans, relatively large brains, cultural behaviours, and use of tools (Carvalho et al., 2012; Elton, 2006; Rolian & Carvalho, 2017). Extant chimpanzees face their biggest threat of predation from humans (Lindshield, Danielson, Rothman, & Pruetz, 2017), but their low densities, large body size, and preference for closed habitats is thought to limit their vulnerability to non-human predators (Stewart & Pruetz, 2013). Chimpanzees do fall into the preferred prey-size for leopards (*Panthera pardus*), which are reportedly their main non-human predators (Hayward et al., 2006; Stewart & Pruetz, 2013). There have been rare reports of lion (*Panthera leo*) predation on chimpanzees, but most research into the dietary preferences of lions, hyenas *(Crocuta crocuta, Hyaena brunnea, H. hyaena),* and wild dogs *(Lycaon pictus)* has focussed on open savannah environments currently uninhabited by chimpanzees (Stewart & Pruetz, 2013). Despite the relatively low actual risk of non-human predation faced by chimpanzees, they are known to display proximate behaviours demonstrative of perceived risk. These include alarm calls and vigilance (which are common across the primate order), mobbing of predators (also seen in baboons) (Willems & Van Schaik, 2017), and nest-sleeping (also seen in other great apes), which is a behaviour likely shaped by predator-avoidance amongst other factors including parasite-avoidance and increased comfort (Hernandez-Aguilar & Reitan, 2020; Koops, Mcgrew, De Vries, & Matsuzawa, 2012; Samson & Nunn, 2015; Sept, 1998; Stewart & Pruetz, 2013).

Whilst chimpanzees might provide good analogues for certain aspects of hominin evolution, there

are several dimensions along which other primate models might be better (Bandini, Harrison, & Motes-Rodrigo, 2022; Elton, 2006). Chimpanzees rely on a relatively specialised diet of ripe fruits and their dispersal appears to be heavily constrained by the availability of forested habitats. This lies in stark contrast to the hominin lineage, which is thought to have moved towards a generalist diet and increased exploitation of mosaic habitats during the Plio-Pleistocene (see Section 1.2). Thus, insight into the behavioural ecology of hominins might be better accessed through the study of a primate species with a more generalist diet and the behavioural flexibility to thrive in variable environments. The cercopithecoid monkeys diverged from apes between 31 and 25 Ma (Byrne, 2001; Steiper & Young, 2006) but share many features with the hominin clade. For example, genera like *Theropithecus* and *Papio* are often used in comparative research of hominin evolution because they have evolved in parallel with humans, inhabiting similar environments, going through similar diversification patterns, and successfully dispersing across Africa as relatively large-bodied terrestrial primates (Foley, 1993; Gilbert, Frost, Pugh, Anderson, & Delson, 2018; Hughes, Elton, & O'Regan, 2008; Jolly, 2001; Strum & Mitchell, 1987; Swedell & Plummer, 2012). Extant baboons (genus *Papio)* are the most widespread non-human primates in Africa, occupying a range of habitats across the continent, as shown in Figure 1.2 below.

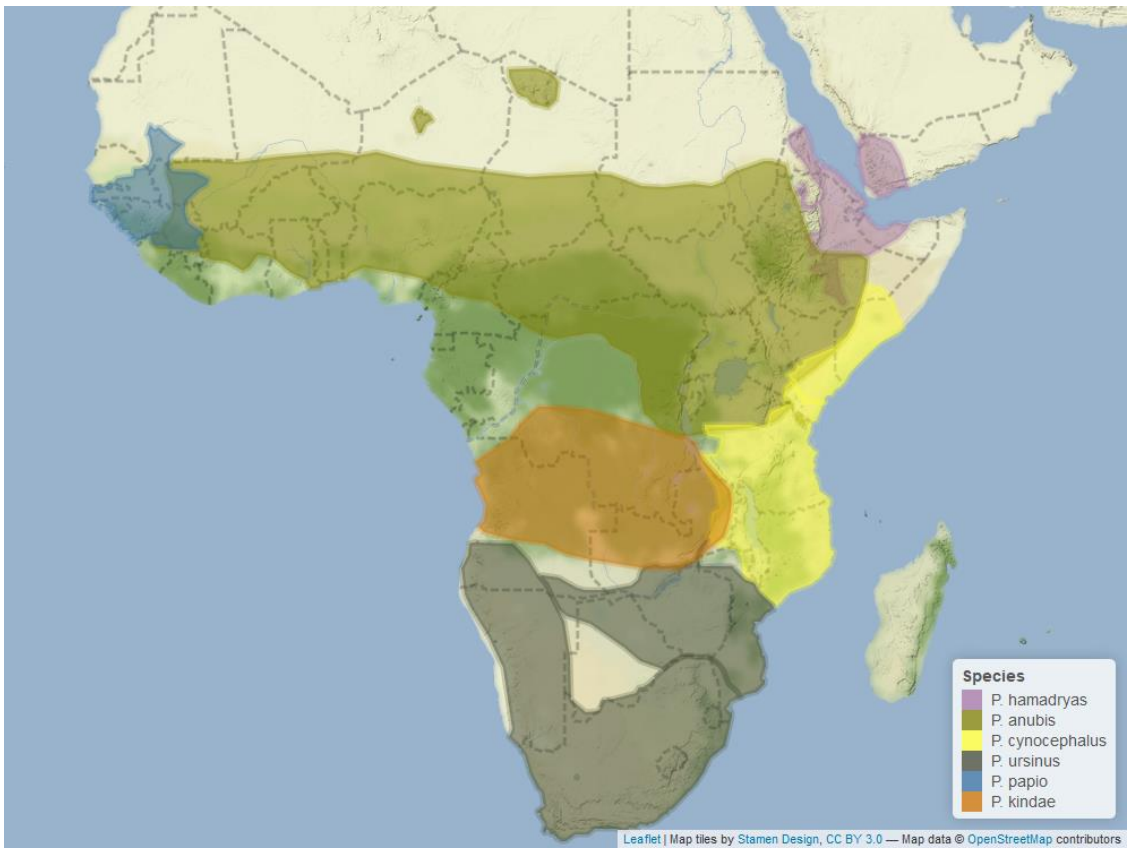


Figure 1.2. *Map showing the IUCN (2021) distribution of Papio species across Africa.*

Papio exhibit several traits thought to make them good models for understanding hominin ecology. Although quadrupedal rather than bipedal, they have a largely terrestrial lifestyle and inhabit a broad range of habitats, living in cohesive, stable, multi-male multi-female groups that vary in size from below 10 to over 200 individuals (Bettridge & Dunbar, 2012), with social features like alloparenting, paternal care, and male-female friendships (Alberts, 2019; Altmann & Alberts, 2003; Altmann & Altmann, 1970; Elton, 2006; Elton & Dunn, 2020; Fischer et al., 2019; Hrdy, 2011; Zinner, Groeneveld, Keller, & Roos, 2009). Whilst most extant primates rely heavily on C_3 resources, Cercopithecoids incorporate high levels of C_4 foods like grasses into their diet, particularly as "fall-back foods" in response to extreme seasonality (Alberts et al., 2005; Altmann, 2009). The terrestrial lifestyle and generalist diet of *Papio* species also allows them to exploit valuable food sources like

underground storage organs and small vertebrates in grasslands and woodlands (Noser & Byrne, 2007a, 2007b). Unlike chimpanzees, who depend on regular exploitation of ripe fruit patches, baboons are able to optimise opportunistic behaviour, allowing them to inhabit a wide and varied range of vegetation types (Alberts, 2019; Winder, 2014).

Compared to extant apes, baboons' inhabitation of a range of variable and more open habitats also exposes them to a range of predators that is arguably more analogous to those sharing Pleistocene environments with hominins (Stewart & Pruetz, 2013). Bettridge and Dunbar (2013) identify eight potential terrestrial predator species of baboons: leopards *(Panthera pardus)*, lions *(Panthera leo)*, hyaenas *(Crocuta crocuta, Hyaena brunnea, H. hyaena)*, chimpanzees *(Pan troglodytes)*, cheetahs *(Acononyx jubatus)*, wild dogs *(Lycaon pictus)* and black-backed and side-striped jackals *(Canis mesomelas* and *C. adustus)*. The first four listed are considered the main predators of baboons, based on attack and predation rates (Cowlishaw, 1994). Whilst the other four evoke behaviours demonstrative of perceived risk (such as vigilance and vocalisations), none have been reported to actually kill baboons except in a single recent report documenting the emergence of regular hunting of baboons by wild dogs in the Zambezi Valley, Zimbabwe (Dyer, 2018).

Leopards and lions are the most-documented predators of baboons; posited as the primary cause of death for juvenile and adult baboons at a study site in Botswana, and often held responsible for the decimation of troops across African parks and research sites, despite a paucity of directly observed events (Cheney et al., 2004; Isbell et al., 2018). Leopards in particular are considered the primary predators of baboons; they were held accountable for over 77% of baboon kills in a study in Kruger, South Africa (Pienaar, 1969), their diets have been estimated to include up to 10% terrestrial primates (Isbell, 1994), and they are known to actively target baboon sleep sites at night or in the early morning (Altmann & Altmann, 1970; Busse, 1980; Cheney, 2004; Cowlishaw, 1994; Isbell,

1990, 2009, 2018). Baboons also fall within the preferred prey size of leopards – between 10 and 40 kg (Hayward et al., 2006) – whilst lions preferentially hunt prey between 190 and 550 kg (Hayward & Kerley, 2005). Lions are thus thought to pose less of a threat to baboons than leopards, with baboons composing only 1% of their estimated diet (Isbell, 1994), although some baboon populations are reportedly exposed to a low but consistent rate of lion predation (Busse, 1980; Pienaar, 1969). A greater understanding of these dynamics is key for elucidating the effects of predation pressure on prey. For example, how abundant does a carnivore species need to be in an environment to heighten perceived risk across the landscape? And how often must primates encounter or experience predation events by a certain carnivore species before they exhibit responses indicative of perceived risk?

Other contributors to primate landscapes of fear also need further exploration. For example, systematic studies of the dynamics between baboons and reptilian or avian predators are very limited. One study of baboon vocalisations found that they make distinct alarm calls in response to mammalian carnivores and crocodiles, but never in response to raptors – at least during that study (Fischer, Hammerschmidt, Cheney, & Seyfarth, 2001). This is in contrast to the behaviour of vervet monkeys (*Chlorocebus aethiops*), who have a specific call in response to the presence of raptors (Seyfarth, Cheney, & Marler, 1980). This difference in response might be due to vervets' greater risk of predation because of their smaller body size compared to baboons. The examples above highlight how the specific behavioural ecology of different predators might influence the risk perceived by primates and their subsequent behaviours.

One of the convoluting features of research on landscapes of fear is that predation pressure is often treated as "a homogenous evolutionary force", despite the fact that predators vary hugely in their ecologies and hunting behaviours, and can impose very different forces of selection upon their prey

(Zuberbühler & Jenny, 2002). For example, a study of vervet monkeys demonstrated that whilst they responded to risk from certain predators (leopards and baboons) through avoidance on a horizontal spatial plane, they responded to risk from avian predators (eagles) through vertical adjustments of their substrate use (Willems & Hill, 2009). Another example shows how the diel patterns in predators' activities can alter landscapes of fear; a recent study used GPS-tracking collars to find that baboons are actually avoided by leopards during the day, but are more vulnerable to leopard-attack at night than other sympatric primate species (Isbell et al., 2018). Such findings, combined with previous evidence of leopards targeting baboon sleep sites, indicates that perceived risk of leopards might be a strong driver of baboon behaviours – particularly around sleep sites. Indeed, there have been reports of baboons abandoning or departing later from sleep sites after predation events or attempts by leopards, and perceived risk has also been proposed as the explanation for why male baboons often descend from sites first (Anderson, 1986; Bidner, Matsumoto-Oda, & Isbell, 2018; Loftus, Harel, Núñez, & Crofoot, 2022). Additionally, mobbing behaviour – another antipredation strategy seen in baboons – is predominantly targeted at leopards (Cowlishaw, 1994; Isbell et al., 2018).

Predation has been reported as the primary cause of infant and adult mortality in some baboon populations (Alberts, 2019; Busse, 1980) and has been described as "the most important single factor in the interpretation of baboon ecology and social behaviour" (DeVore & Hall, 1965). But other researchers argue that predation might not be such a central tenet of primate evolution, often highlighting low predation rates and the rarity of encounters with predators in studied primate populations (Anderson, 1986; Cheney & Wrangham, 1987; Isbell, 1994). For example, a study conducted across 24 primate populations estimated a median annual predation rate of 3% (range: 0 – 15%) (Cheney & Wrangham, 1987). However, there are several factors that should be taken into

consideration here. Many predators hunt at night when researchers are not present, and during hours when researchers *are* present they can actively deter predators from their study populations if the carnivore is afraid of humans (Nowak, le Roux, Richards, Scheijen, & Hill, 2014). A study of vervet monkeys showed that predation by leopards was significantly higher when there were no researchers in the study area compared to times when they were present (Isbell & Young, 1993). Another factor to consider is that modern predation rates might be relatively low for extant primate populations because carnivore populations have diminished globally, largely due to recent anthropogenic influence (Werdelin & Lewis, 2013b). However, even if predation pressure might not appear to be the primary proximate driver of behaviours in modern primates, it does not follow that predation has not been an influential selective force on the evolution of said behaviours. For example, even "low" rates of predation could be impactful on primate behaviour, especially if infants and juveniles are more vulnerable to predation, and especially in species with slower life histories. This proximate-ultimate distinction should be kept in mind during the design and analysis of studies exploring the effects of predation pressure. Finally, if predation has played a significant role in primate evolution and led to successful antipredation strategies, these adaptations would allow them to thrive, even in environments where they face risk, and would limit the rates of successful predation events. The sections below review the key primate traits that are thought to have been heavily influenced by predation pressure and are pertinent to models of hominin landscapes of fear.

1.3.1 Demographic and social adaptations to predation pressure

Group-living in primates and other animals has regularly been attributed to selection by predation pressure; groups both dilute the risk of predation to individuals, and heighten the chances of detecting risk in the environment (Alexander, 1974; Caro, 2005; Clutton-Brock & Harvey, 1977; Hamilton, 1971; Isbell, Bidner, & Van Cleave, 2018; Van Schaik, 1983; Wrangham, 1980).

However, empirical studies yield mixed results. A set of correlational analyses at both species and population levels show great variation in the relationship between predation risk and group size (Anderson, 1986). And multiple studies have found no, or negative, relationships between bigger groups and lower predation rates (Isbell & Young, 1993; Zuberbühler & Jenny, 2002).

There are many possible explanations for such results. Firstly, in areas with small or non-existent predator populations, low predation rates might facilitate high levels of primate reproduction and therefore bigger groups, potentially concealing positive relationships between predator-presence and group size in comparisons made across populations or species. Secondly, even if bigger groups do increase the chances of detecting certain predators as suggested by the "more-eyes hypothesis", this advantage might not reduce predation by carnivores who, for example, use ambush tactics when hunting, resulting in equal predation rates by such carnivores across group sizes (Isbell et al., 2018). This highlights the importance of accounting for the behavioural ecology of different predators in the study of prey behaviours, and researchers should also consider how the combined effects of a range of predators, mediated by habitat type, affect behaviours (Shultz et al., 2004; Willems & Hill, 2009). Finally, studies measuring predation *rate* might find no relationship with group size if predation rate reflects the "residual mortality" of primates after their anti-predator defences have been evoked by predation *risk* (Dunbar & Hill, 1998; Isbell et al., 2018; Shultz et al., 2004). This highlights a common conflation made in predation research, between the selective roles of *predation rate* and *predation risk.* This is another important distinction that should be kept in mind and explicitly defined when exploring their effects on primate behaviour (Dunbar & Hill, 1998).

Another widely-reported impact of predation pressure on primate demographics is its selection for higher male: female ratios in groups, especially in species where males engage in active defence of the group (e.g. *Pan* and *Papio*) (Hill & Lee, 1998; Willems & Van Schaik, 2017). However, analyses

conducted both across and within primate species highlight the complexity of this relationship; sex ratio, as well as group size, is mediated by substrate use. Thus, terrestrial primate groups are larger and include more males than those that travel arboreally. Furthermore, across 16 primate species of 13 genera, counterattacks against predators occurred most frequently in terrestrial species living in open habitats, with *Pan* and *Papio* accounting for over half of the reported events (Willems & Van Schaik, 2017). This demonstrates how features like the substrate and openness of an environment, which affect primate visibility and access to refuge, can mediate the effects of predation pressure on primate behaviours. Furthermore, habitat features and resource distribution underly primate social structure itself. Baboons, like many cercopithecids, are matrilocal; females are born into stable dominance hierarchies and remain in their natal groups for life, whilst males usually disperse out of the group around sexual maturity (Cheney et al., 2004; Silk, Seyfarth, & Cheney, 1999). In such primate societies, female distribution is primarily dictated by resource distribution and male distribution then maps onto that of females (Hill & Lee, 1998; Wrangham, 1980).

Social behaviours like grooming are central to the maintenance of kin-networks, reproductive consortships, male-female friendships, and same sex alliances in baboons (Strum & Mitchell, 1987; Washburn & DeVore, 1961). Maintenance of such bonds appears to enhance fitness (Alberts, 2019; McFarland et al., 2017; Silk, Alberts, & Altmann, 2003), but does require time and energy that could be spent on behaviours like resource-acquisition or predator-avoidance, which appear more obviously fitness-enhancing. It is thus informative to explore the ecological factors that promote or reduce time allocated to affiliative behaviours like play or grooming. For example, behavioural research suggests that cercopithecine monkeys are rarely vigilant whilst grooming (Cords, 1990; Gaynor & Cords, 2012), perhaps indicative of a trade-off between social and anti-predation behaviours dependent on the level of perceivefd risk in an environment.

1.3.2 Primate ranging patterns and behaviours

A central tenet of the behavioural ecology of any animal is how it exploits its environment over time and space. The "home range" of a primate group denotes the area covered during their normal daily foraging and social behaviours and can be quantitively expressed as the intensity of space-use within a defined area (Willems & Hill, 2009). Daily Path Lengths (DPLs) are useful for constructing the home range of a group, and for comparisons of the ecological determinants of primate movements (Johnson, Piel, Forman, Stewart, & King, 2015). A study conducted across 47 troops of baboons from 23 populations demonstrated that, at a continental level, troops adapt their ranging behaviours to a number of ecological variables; high monthly rainfall and high anthropogenic influence both predict shorter DPLs, whilst high average annual temperatures predict longer DPLs (Johnson et al., 2015). At a troop level, DPLs are longer when food quality is low and are influenced by the location of key resources like water sources and sleep sites. DPLs are also longer for larger groups – although this effect is reduced by evenly-distributed and homogenous food sources – and are influenced by the avoidance of conspecific groups and predators (Isbell et al., 2018; Johnson et al., 2015; Markham, Gesquiere, Alberts, & Altmann, 2015). In seasonal environments, studies have recorded flexible ranging behaviours that allow baboon troops to switch from broadly "searching strategies" in the wet season to more conservative strategies that reduce heat-exposure, energy expenditure, and water requirements in the dry season (Gesquire et al., 2008; Hill, 2006). These findings highlight some of the variables that must be integrated into an understanding of the role of predation pressure on movement within primate habitats.

Whilst geographic and temporal distribution of resources are relatively easy to record, monitoring predation risk in an environment is significantly harder for reasons already described above; primarily the occurrence of nocturnal predation and the deterring effects of human observation on

carnivores (Isbell & Young, 1993; Nowak et al., 2014). However, the advent of remote sensing studies allows researchers to use GPS-tracking collars on primates and their predators to follow their diel ranging patterns in high resolution without the potential bias of human presence (Isbell et al., 2018). Recent studies using these methods have revealed complex interactions between predator and primate movements. Leopards, for example, appear to actively avoid baboon troops but not vervet troops during the day, whilst preferentially targeting baboons over the smaller-bodied vervet monkeys at night. These findings suggest that leopards might be deterred by the risk of baboon mobbing behaviours during the day, but take advantage of baboons' poor nocturnal vision to target the larger prey at night (Isbell et al., 2018).

Similar collaring methods have also been used to monitor how different baboon troops move within a shared environment. Baboons are not particularly territorial animals; troops rarely actively exclude conspecifics from areas within their home range. However, their ranging patterns demonstrate that they do avoid contact with one another. Analysis of collar data at monthly, biweekly, and weekly time scales revealed that these avoidance behaviours are mediated by seasonality; troops overlapped more with each other when dry periods made them reliant upon evenly-distributed, low-quality fall-back foods like grass corms (Markham et al., 2013). Collaring studies are also set to provide us with insights beyond the spatio-temporal ranging habits of primates. "Bio-logging" refers to the remote monitoring of animal movement, behaviour, or physiology through animal-attached devices (Fehlmann & King, 2016). Accelerometers attached to collars have been used to collect data on the activities of baboons, even resulting in a machine-learning "acceleration ethogram" which can distinguish between walking, running, resting, and foraging behaviours in baboons (Fehlmann et al., 2017).

Group cohesivity is another behaviour that is purportedly influenced by predation pressure. For

example, a study in South Africa found that baboon troops became more cohesive in areas of higher risk, as measured by leopard-presence (Bidner, 2009). In this study, cohesivity was the only antipredator behaviour that seemed to emerge in these higher risk areas; rates of vigilance and alarm calling did not correspond with variation in leopard presence. This indicates that different antipredation strategies might be employed for different types of predator, or in different habitats or contexts. It also demonstrates that the employment of one antipredation strategy might reduce the need for others; for example, perhaps alarm calling is unnecessary when the troop is more compact. The cohesivity of a group as it moves through its environment is likely to have downstream effects on the fitness of group members. If higher predation pressure forces groups to travel more compactly, they might suffer from greater competition over food patches, or have reduced chances of discovering novel resources or extensions to their home range. Conversely, lower predation pressure might allow primate groups to spread over and explore larger areas, perhaps contributing to successful dispersal strategies at broader scales.

Travel on the ground is an additional ranging behaviour with links to predation pressure. Terrestriality is rare in primates (Galán-Acedo, Arroyo-Rodríguez, Andresen, & Arasa-Gisbert, 2019). It correlates with both large body size and large group size, as well as with cooperative antipredation strategies like counterattacks and mobbing of predators (Willems & van Schaik, 2017), perhaps indicating that the sacrifice of arboreal refuge requires compensatory antipredation adaptations. Terrestrial primates were long assumed to be exposed to greater predation risk than arboreal primates, but empirical work suggests they do not suffer higher predation rates (Cheney & Wrangham, 1987; Isbell, 1994). This is another case where it is important not to conflate predation risk and rate. It is possible that historic predation risk was higher for terrestrial than arboreal primates, but that this risk selected for the antipredation strategies mentioned above, thus moderating

predation rate in terrestrial populations. It is also possible that terrestrial behaviours evolved in areas of lowered risk, or areas – like open savannahs – where the ecology of local predators meant that they had access to a wider range of preferred prey than terrestrial primates (Cheney & Wrangham, 1987; Isbell, 1994). There has been limited research into the proximate effects of predation pressure on terrestriality, but further exploration of the relationship is pertinent to understanding how locomotion and substrate-use shifted during the Pleistocene, not only in hominins but across primate taxa inhabiting the landscapes of that time. Several approaches to monitoring proximate effects of risk on primate terrestriality will be explored in Chapters Two to Four and are then discussed in relation to the evolution of hominin locomotion and terrestriality in Chapter Five.

1.3.3 Primate sleeping patterns and nocturnal behaviours

Sleep is a multi-faceted neurological state displayed in various forms across the animal kingdom. It is thought to be fundamental for the restoration and consolidation of various metabolic, immune, cognitive, and emotional processes, as well as "niche-specific predation avoidance" (Samson & Shumaker, 2015). However, the ultimate functions of sleep are still poorly understood and, due to anthropocentric bias and the logistical constraints of gathering non-human sleep data, evolutionary and comparative research on the topic is limited (Anderson, 1998; Miller & Rucas, 2012; Nunn, Samson, & Krystal, 2016). Phylogenetic research indicates that mammalian sleep durations are primarily shaped by ecology; each species sleeps enough to balance its costs and benefits of predation, foraging, and social interactions; predators at higher trophic levels get more sleep than their prey, and animals with higher energetic demands sleep less than those with slower metabolisms or shorter gestation lengths (Lesku, Roth, Amlaner, & Lima, 2006; McNamara et al., 2008; Nunn et al., 2016).

Not only must all animals balance trade-offs between waking activities and sleep, but also between

the amounts of slow-wave and rapid eye movement (REM) sleep they invest in. Mammalian relative brain mass does not correlate with sleep duration, but it does correlate positively with REM investment (Lesku et al., 2006). In primates for example, humans have the shortest average sleep cycles, but with the highest proportion of REM sleep (Lesku et al., 2006; Nunn & Samson, 2018; Nunn et al., 2016). REM sleep provides potentially greater cognitive benefits than slow-wave sleep, but due to its higher thresholds for arousal, it is thought to be the riskier sleep state (S. L. Lima, Rattenborg, Lesku, & Amlaner, 2005). This is likely what makes it the sleep variable most heavily influenced by predation pressure; across mammals, higher risk predicts lower REM levels (Lesku et al., 2006), and experimental studies in rats show that REM is significantly reduced after exposure to incontrollable stressors in the environment (Sanford et al., 2010). Exposure to predators has also been shown to increase sleep-interruptions in birds, a negative effect that is reduced by sleeping in a group (Lima et al., 2005). "Huddling" in sleep sites by primates might serve a similar function (Stewart & Pruetz, 2013).

The findings above indicate significant effects of predation pressure both on sleep quality and quantity, but the longer-term consequences of sleep reduction are less clear, particularly in wild animals (Lima et al., 2005). This is largely due to the practical difficulties of tracking sleep and nocturnal behaviours in ecologically realistic settings (Lima et al., 2005). However, advances in methods such as bio-logging (e.g. Fehlmann et al., 2017) and camera-trapping (which will be discussed further in Section 1.4) make it possible to collect remotely-sensed data on the movements and activities of wild animals, opening new avenues for high resolution and broader-scale monitoring of nocturnal activity and sleeping patterns. With these advances, and the extent of data being collected on human sleep patterns – also from bio-logging devices – comparative analyses of primates are likely to become increasingly informative about the evolutionary functions and drivers

of sleep.

According to the “Sleep Quality Hypothesis”, the cognitive development and behavioural flexibility exhibited by modern humans might have been shaped by “a unique sleep architecture promoting information consolidation”, only possible in secure and comfortable locations and perhaps instigated by a shift to terrestrial sleeping (Coolidge & Wynn, 2006; Samson & Nunn, 2015). Most primate species are arboreal and the earliest ancestral primates were nocturnal species who, similar to extant galagos, likely established “fixed point” sleep sites in tree-holes, protecting them from predators and parasites and providing thermoregulatory benefits for sleeping during the day (Nunn et al., 2016; Samson & Nunn, 2015). Most extant primates – both nocturnal and diurnal, and including those that are predominantly terrestrial – still sleep in trees, although some species like baboons have also been known to use cliffs or caves as sleep sites (Fruth, Tagg, & Stewart, 2018). In fact, baboons appear to favour cliffs over trees in environments with higher predation risk, especially from leopards (Anderson, 1998; Hamilton, 1982). The location and quality of sleep sites thus become a central determinant of primate ranging pattern. Baboons are selective about their sleep sites (Hamilton, 1982), resulting in troop-level dominance hierarchies amongst baboon populations competing for preferred sites (Markham et al., 2016). They will also alter or abandon sleep sites after predation events, sometimes shifting their entire home range (Altmann & Altmann, 1970; Bidner et al., 2018; Matsumoto-Oda, 2015).

Whilst large-bodied cercopithecids like baboons sleep in upright guarded positions in their elevated sleep sites, all apes sleep horizontally in constructed “nests” (Fruth et al., 2018; Samson & Shumaker, 2015). Nest-building is thought to have emerged in the ape clade between 18 and 14 Ma, coinciding with an increase in body mass to about 30kg (Nunn et al., 2016). Because muscle relaxation is induced by the onset of sleep, ape nests are thought to be “behavioural facilitators” of

greater comfort and protection from falling out of sleep sites, as well as providing thermoregulatory benefits (Coolidge & Wynn, 2006; Samson & Nunn, 2015; Stewart & Pruetz, 2013). Comparative infrared videography of orangutans and baboons in captivity demonstrated that the relaxed positions and constructed platforms of orangutans promoted deeper, less fragmented sleep than that experienced by the baboons (Samson & Shumaker, 2015).

Although uncommon, terrestrial sleeping has been recorded in apes other than humans; large-bodied gorillas build their nests on the ground, but females occasionally nest in trees (Coolidge & Wynn, 2006). And terrestrial nests have been reported in several chimpanzee populations, representing between 6.1% and 14% of nests surveyed at different sites, with evidence suggesting that these are predominantly built by males (Koops, McGrew, Matsuzawa, & Knapp, 2012). Predation pressure was reportedly low at most of these sites and terrestrial nesting has been reported as less common in areas with higher predation risk (Hernandez-Aguilar & Reitan, 2020), although there are some possible exceptions (Hicks, 2010). This variation in extant ape populations' sleeping behaviours indicates how a trend towards terrestrial sleeping might have started before moving to fixation in early hominins.

It has been suggested that nest-building facilitated a "great leap forward" in ape cognition (Fruth & Hohmann, 1996), and that this was amplified by a transition to regular terrestrial sleeping at some point in hominin evolution, increasing the efficiency of sleep. The modern human average is 420 minutes of sleep, compared to the 720 minutes of "obligate inactivity of arboreal sleep sites" for other apes (Samson & Nunn, 2015). This shift is postulated to have occurred in *H. erectus* because, whilst the morphological adaptations of early *Homo* fossil specimens do not necessitate terrestriality, *H. erectus* specimens suggest that by ~1.5 Ma the species was no longer adapted to frequent arboreal climbing (Coolidge & Wynn, 2006; Wood & Collard, 1999). Further discussion around the fossil

evidence for hominin terrestriality will be presented in Chapter Five. Some have argued that a transition to terrestrial sleeping would have relied upon the controlled use of fire to avoid predation (Samson & Nunn, 2015; Wrangham & Carmody, 2010). There is possible evidence of fire usage in the archaeological record at 1.5 Ma (Hlubik, Berna, Feibel, Braun, & Harris, 2017) but with the earliest definite evidence only at 800 Ka (Gowlett & Wrangham, 2013; Potts, 2013), it is not yet clear if or when the regular use of fire became a strategy available to *H. erectus*.

The timing of ascent into sleep sites is also thought to be strongly dictated by risk of predation, with downstream effects on primates' access to resources and activity budgets (reviewed by Nunn et al, 2016). Baboons, for example, are reportedly in their sleep sites and inactive from about 1800 until 0600 (Isbell et al., 2018; Markham et al., 2016), with one remote sensing study reporting an average of only 17 minutes of activity between the hours of 1900 and 0600 (Markham et al., 2016), and another highlighting that baboons left their sleep sites significantly later in the morning after nights when a leopard had visited the site (Bidner et al., 2018). Recent studies of chimpanzees' nocturnal behaviour suggest that the length and nature of chimpanzee sleep periods also vary by site, moon phase, seasonality, daily temperature, and levels of human activity (Pruetz, 2018; Tagg et al., 2018). Activity at night, especially during fuller moon phases of the dry season, indicates that chimpanzees might combat thermoregulatory stress by performing some of their travel and foraging behaviours nocturnally (Pruetz, 2018). This highlights the benefits that might be gained by engaging in nocturnal behaviour, especially in hotter geographic regions or seasons, but it is unclear whether – or how frequently – other primate species are using strategies like those recently observed amongst chimpanzee populations.

Logistical constraints on night-time observation of primates have limited research on this topic thus far, but it is likely that environments with lower risk offer the potential for extra foraging and

socializing time if early ascent into sites is not necessary. This might be combined with benefits of more efficient and better-quality sleep if site-choice is less restricted by predation risk, and if sleep is not interrupted by predator presence or the need for vigilance. These nutritional, social, and restorative benefits might in turn reduce chronic stress, lengthen lifespans, and facilitate higher reproductive rates in the population, with implications for both the adaptiveness of the species, and the ecosystem in which it lives (Bettridge, Lehmann, & Dunbar, 2010; Hill & Dunbar, 2002). Methods like camera trapping and bio-logging are now making it possible to start testing such hypotheses by facilitating remote and broader spatial and temporal monitoring of animal activity patterns. The following section introduces and discusses the use of remote sensing methods in the study of primate behavioural ecology.

1.4 Remote sensing and landscape-scale methods in primatology

As discussed in the sections above, the study of landscapes of fear involves theoretical issues such as avoiding conflation of actual and perceived risk, as well as of predation risk and rate. It also poses many logistical challenges. One is that direct observation of encounter-rates and interactions between predators and prey is uncommon in natural environments, especially as fieldwork is often conducted during daylight hours, whilst many mammalian carnivores are predominantly nocturnal (Dröge, Creel, Becker, & M'soka, 2017; Hayward & Slotow, 2009; Searle, Smit, Cusack, et al., 2021). Additionally, when humans are present, they can deter or change the behaviour of either predator and/or prey species under observation (Isbell & Young, 1993; Nowak, le Roux, Richards, Scheijen, & Hill, 2014). Traditional, or direct observational methods are also limited by the fact that researchers following focal individuals or groups usually cannot observe the simultaneous activity of other animals in the landscape, reducing the extent to which dynamics between predator and competitor species can be measured. This highlights the point that the landscape of fear is not a static

representation of risk. Spatial variation in perceived risk is dynamic, not only because animals move around, but also because of changes that occur with seasonality or time of day (Gaynor et al., 2019; Isbell et al., 2018; Palmer, Fieberg, Swanson, Kosmala, & Packer, 2017; Palmer, Gaynor, et al., 2022). Furthermore, prey species do not exhibit the same responses to all potential predators (Coleman & Hill, 2014; Willems & Hill, 2009), indicating that their perceived risk and resultant behaviours depend on the species, hunting styles, hunting frequency, and diversity of predators that are encountered within an environment.

Interactions between all these variables are thought to influence individuals' landscapes of fear, altering their behaviour both spatially and temporally, with implications for evolutionary patterns in species' landscape use, dispersal, energetic trade-offs, diel activity, and sleep behaviours (Havmøller, Jacobsen, Scharff, Rovero, & Zimmermann, 2020; S. L. Lima et al., 2005; Mekonnen et al., 2021; Palmer et al., 2017; Palmer & Packer, 2021). However, collection and quantification of the relevant data have been logistically difficult. Only with recent advances in remote sensing methods has it become possible to simultaneously monitor both predator and prey activity alongside several variables that might mediate perceived risk, all with minimal human interference. Such methods include camera trapping (McCarthy et al., 2019; Palencia, Vicente, Soriguer, & Acevedo, 2022; Rowcliffe, 2017), bio-logging (Fehlmann & King, 2016; Tomkiewicz, Fuller, Kie, & Bates, 2010), and extracting ecological variables from satellite imagery (Hanan, Prihodko, Ross, Bucini, & Tredennick, 2020; Rose et al., 2015). An added advantage of remote sensing methods is that both their deployment and data output can be standardised across studies and sites to a much greater extent than observational methods (Rowcliffe, 2017). This makes it possible to study species' use of the environment – alongside their competitors and predators – at much broader spatio-temporal scales than previously possible (e.g. Pardo et al., 2021). This broadening of methods beyond site-specific case studies is particularly useful for applying behavioural ecology insights to our

interpretations of data from the fossil record – which generally represent spatio-temporal trends on a grand scale. Although landscape-scale collection of behavioural ecology data narrows the gap between understanding extant and extinct fauna, it is important to note that there is still a significant amount of both time and space-averaging inherent to paleontological research (Faith et al., 2021).

There are, of course, also limitations that come with broadscale remote sensing methods. For example, the sheer volume of data produced by camera trapping or bio-logging studies can be difficult to manage, and must be analysed with great care to avoid conflation of effects caused by true ecological variables with those caused by methodological features of the research (Palencia et al., 2022). Remote sensing methods also should not entirely replace *in situ* observation and data collection at field sites. Rather, these methods should complement one another, with on-the-ground data collection used to ground truth remotely sensed information. Furthermore, interpretation of data from technologies like accelerometer devices and camera traps requires an understanding of the behaviours of study species that can only be gained through immersive research. In this thesis, Chapter Two presents analyses of data collected through behavioural observation of two baboon troops in Gorongosa National Park, Mozambique. Questions generated by this *in situ* research are then explored at broader spatio-temporal scales in Chapters Three and Four, which draw upon data collected from camera trap grids established across several study sites in Africa. The sections below provide an introduction to camera trapping methodology.

1.4.1 An introduction to camera trapping methodology

Autonomously-triggered cameras – "camera traps" – are providing new ways for researchers to study the occurrence, richness, abundance, and even behaviours of various animal species. They provide relatively non-invasive ways of detecting and tracking rare and elusive species, and they broaden the spatial and temporal extent over which animal species, populations, and communities can be

monitored (Palencia et al., 2022; Rowcliffe, 2017). Camera trapping methods have been used to develop and deploy photographic, video, and audio technologies to suit different research needs (Boyer-Ontl & Pruetz, 2014; McCarthy et al., 2019; Palmer, Wang, Plucinski, & Pringle, 2022; Tagg et al., 2018). These deployment methods are accompanied by a fast-developing range of data processing techniques – including the use of artificial intelligence to identify animal species and even behaviour (Bain et al., 2021; Miao et al., 2021; Schneider, Taylor, Linquist, & Kremer, 2019; Schofield et al., 2019) – as well as increasingly sophisticated analytical techniques that include occupancy models, capture-recapture models, abundance estimation methods, and activity overlap analyses to draw meaningful ecological insights from the data captured by camera traps (Frey, Fisher, Burton, & Volpe, 2017; Sollmann, 2018).

A common method of deployment of camera traps across a landscape uses each camera station as a point-based sampling unit, for example within a grid-based format. Cameras are triggered by movement to capture a pre-defined number of photos, or length of video footage, which is then used for species identification and the collection of other relevant variables. The spatial mapping of such data provides information on how species utilise their environment, and the timestamps on photos or videos provide insights into species' temporal activity patterns. Metadata about the habitat in which each station is situated, such as tree coverage or its distance from water, can also be used to explore how such ecological variables influence species' activity in different parts of a landscape (L. Rich et al., 2017). Such metadata can be collected manually on the ground or extracted from sources such as satellite imagery (Hanan et al., 2020; Rose et al., 2015).

Analyses of camera trap data often rely on assumptions that must be considered when setting up camera traps. For example, the spacing of camera stations should provide spatial independence between sampling points, and camera settings or post-collection data cleaning should be used to

achieve temporal independence between detections of the same species at each station. This is to avoid multiple captures of the same individual(s) inflating detection rates of a species. Establishing the parameters to best meet these assumptions requires knowledge of target species' ecology and ethology, for example by spacing cameras according to the size of the species' home range and determining temporal thresholds for independent detections based on the species' general speed of travel (Sollmann, 2018).

The sheer number of photographs taken by camera traps, especially over long-term study periods, provides huge amounts of data which must be consolidated to perform meaningful analyses on them. The species detected in photographs have often been manually classified by researchers, but innovative uses of citizen science and now machine learning are speeding up the rate at which camera trap data can be processed (Miao et al., 2021). The output of such processing provides geo-tagged and time-stamped instances of species detections which can then be analysed in several ways.

There are further assumptions that must be taken into consideration at this stage. The number of independent detections of a species at a station, divided by operating time, provides the photographic rate of that species. However, photographic rate should not be taken as a proxy for the *abundance* of a species, but as an indicator of the *relative activity* of the species in that area, which is also influenced by factors such as the species' movement patterns and the habitat structure (Henrich et al., 2022; Sollmann, 2018), as well as factors like camera trap model, settings, and placement – all of which can affect the detectability of different animal species (Palencia et al., 2022).

This is an important point for consideration when studying primates. Camera trapping has often been used to monitor terrestrial animal communities (Rowcliffe, 2017), with cameras placed relatively close to the ground to maximise detection of medium to large mammalian species. Under such

conditions, arboreal species – including most primates – often go undetected (Moore et al., 2020). For semi-terrestrial primates like baboons or vervet monkeys, terrestrial camera trap studies provide an insight into their rates of activity on the ground, but the species' vertical use of space creates an extra dimension along which they are likely to be missed by camera trap point sampling. Thus, periods of non-detection at any given terrestrial station could signify either that the species is not using that area, or that they preferentially travel through the area arboreally, above the camera trap. As camera trapping methods develop, arboreal camera trapping is likely to become more common and better integrated with terrestrial monitoring methods (Moore et al., 2021).

1.4.1.1 Data collection and processing

Chapters Three and Four present analyses of data from camera trap grids generating still images. Over months – or even years – of data collection, such grids can generate millions of images which then need to be processed. Historically, this has been a case of researchers manually labelling images, although citizen science platforms like "Zooniverse" (www.zooniverse.org) have made the process more efficient by using consensus classification from volunteers' labelling efforts to extract species identification with 97% accuracy (Pardo et al., 2021). Additionally, machine learning algorithms are improving the process further, classifying images with 90% accuracy using only 20% of the human annotation previously required (Miao et al., 2021).

Once images have been classified using the methods described above, the output datasets contain time-stamped records of every capture event, tagged with the species detected in the image and, in some cases, additional information about the number of individuals and types of behaviour detected in the photo. Metadata for the camera grid are also collected, including the GPS point for each camera station, and its distance to landscape features such as rivers or roads, as well as the type of habitat in which it is located. In this way, detections captured across the grid can be geo-tagged to

document the presence, distribution, diversity, and relative activity of each species within the camera-trapped landscape. Time-stamped detections of different species can also be used to document temporal distributions of their activity, for example across 24-hour cycles, or between seasons. These are the types of data that will be used in Chapters Three and Four to explore the spatio-temporal activity patterns of terrestrial baboons and their predators.

1.5 Research questions and structure of thesis

Sections 1.1 to 1.3 of this chapter provide an overview of the many aspects of primate social structure and behaviour that are thought to be adaptations to predation pressure. A focus on baboons highlights how these adaptations manifest in a broadly dispersed, behaviourally flexible, large-bodied, terrestrial African primate, providing reference and insight for interpreting the fossil records of similar primates, including hominins. The review above also introduces the complexity of relationships between predation rate and prey adaptations, between actual and perceived risk, and between carnivore behavioural ecology and primate landscapes of fear. The nuances of these relationships must be better understood in modern landscapes before they can be used to interpret and infer the dynamics that might have existed amongst fauna that lived across Africa millions of years ago. Key to generating insights into these relationships is the integration of research findings across multiple levels – from individual or group-level behaviours (as will be explored in Chapter Two of this thesis) to landscape-scale trends (as will be explored in Chapters Three and Four, using the methods introduced in Section 1.4 above) – which can then be used to aid our interpretation of data collected from the fossil record (as will be discussed in Chapter Five). The research questions and objectives of each chapter of this thesis are outlined below.

In Chapter Two, habituation is used as a quasi-experimental setting through which to investigate the proximate effects of perceived risk on primate behaviour. For this chapter, behavioural data were

collected from two troops of previously unhabituated chacma baboons in Gorongosa National Park, Mozambique. The data were analysed to test for mediating effects of habitat structure and diel variables on perceived risk, and to explore the relationship between risk perception and terrestriality. The chapter explores:

(1) whether habituation progress can be quantitatively tracked using behaviours indicative of perceived risk of humans, namely vocalisations and observer-directed vigilance,
(2) how levels of perceived risk, as measured by these indicators, vary by vegetation structure and time of day, and
(3) how levels of perceived risk are related to terrestriality in baboons.

Thus, Chapter Two uses human presence as a proxy for predation risk, generating insights into potential mediating factors and consequential effects of baboons' landscapes of fear more generally. Chapters Three and Four explore how such landscapes of fear manifest at broader ecological scales, first in a case-study of neighbouring baboon populations in Mozambique and then at a continental scale. These chapters investigate the effects of predator presence, type, and diversity on baboon behaviour, with a focus on terrestriality and diel activity patterns.

Chapter Three presents analyses of data from two camera trap grids – one inside Gorongosa National Park, established in an area inhabited by a small population of lions, and the other just outside the park's boundaries in an area inhabited by leopards. This chapter explores:

(1) spatial patterns in baboon terrestrial activity and whether they are affected by localised variation in predator presence, as well as tree coverage, water availability, seasonality, and anthropogenic features of the environment; and
(2) temporal patterns in baboon terrestrial activity and the extent to which they demonstrate (a) temporal partitioning with the apex predators in each landscape, (b) different activity patterns by the neighbouring baboon populations, and (c) an effect of predator species on the times of day when baboons are most active on the ground.

Chapter Four presents a broader scale comparison of circadian patterns in baboons' terrestrial activity across 10 sites in Africa. Across the 10 sites, this chapter investigates:

(1) how much variation exists in the diel activity patterns of baboons,
(2) the extent of and variation in temporal partitioning between baboons and their potential predators, and
(3) the relationship between carnivore diversity and baboons' use of the ground during nocturnal and crepuscular hours.

Finally, the discussion in Chapter Five provides a review of the evolution of human terrestrial bipedalism in the context of the findings from previous chapters and their implications for primate behavioural evolution. It explores the origins of hominid and hominin locomotion, as well as the emergence of terrestriality in primates more broadly. The chapter integrates fossil evidence with discussion from the findings presented in previous chapters of the thesis, using a behavioural ecology lens to evaluate:

(1) morphological evidence from Miocene ape fossils that pre-date the emergence of hominins,

(2) the evidence for a diversity of locomotive styles and continued arboreality across several hominin taxa in the Plio-Pleistocene, and

(3) the potential impact of prehistoric predators on primate behaviour and evolution.

This chapter also discusses issues, methods, and potential case studies for studying landscapes of fear from the fossil record and emphasises the value of integrating paleontological research with insights from behavioural ecology to generate more nuanced understandings and hypotheses about the environments that have shaped human evolution.

Chapter Two

Risk perception and terrestriality in primates: a quasi-experiment through habituation of chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique

Habituation is a common pre-requisite for studying non-captive primates. Details and quantitative reporting on this process are often overlooked but are useful for measuring human impact on animal behaviour, especially when comparing studies across time or sites. During habituation, perceived risk of a stimulus – human observers – is assumed to decline with repeated exposure to that stimulus. In this study, we use habituation as a quasi-experiment to study the landscape of fear, exploring relationships between actual risk, perceived risk, mediating environmental variables, and behavioural correlates. We recorded vocalisations and observer-directed vigilance as indicators of perceived risk during habituation of two troops of chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique. Here, we model changes in these variables as a function of habituation time, troop, time of day, and habitat features. We also model the relationship between each of the anti-predator behaviours and ground-use, exploring whether they predict greater terrestriality in the baboons. In both troops, vocalisation rates and observer-directed vigilance declined with cumulative exposure to observers, but were heightened later in the day and in denser habitat types. We found that terrestrial activity was negatively related to levels of both vocalisations and observer-directed vigilance. This study provides a quantitative assessment of the impact of human observation on primate behaviour and highlights environmental variables that influence anti-predator behaviours, perhaps indicating heightened perception of risk. The relationship between perceived risk and terrestriality is significant for understanding the evolution of this rare trait in primates.

2.1 Introduction

Habituation is the period and process by which researchers accustom focal individuals or groups of wild animals to their presence, until the animals treat the observers as neutral stimuli in their habitat (Tutin & Fernandez, 1991). Although common practice in ethology, habituation is often viewed simply as a means to an end; namely, the collection of naturalistic data. Details about the process are thus underreported and studies rarely quantify the time taken for specific effects of observer presence on animal behaviour to either plateau or disappear (Allan, Bailey, & Hill, 2020; Samuni, Mundry, Terkel, Zuberbühler, & Hobaiter, 2014; Williamson & Feistner, 2003).

Amongst primates, common initial reactions to the presence of humans include vocalisations, vigilance, threatening displays, and retreat, but the intensity of such responses decreases across repeated encounters with observers (Jack et al., 2008; Johns, 1996; McLennan & Hill, 2010; Schaller, 1962; Williamson & Feistner, 2003). The few published accounts of habituation indicate that great apes take at least two to five years to habituate to human presence (Williamson & Feistner, 2003), whilst "opportunistic" generalist taxa, such as *Papio* and *Macaca,* are thought to habituate to researchers comparatively quickly. However, even within the *Papio* genus there have been a range of habituation times reported – from five months to two years (Barton & Whiten, 1993; Cowlishaw, 1997b; Kummer, 1997; Noser & Byrne, 2007b). This is convoluted further by the lack of a clear working definition for "habituated" primates, and the range in strategies and intensity of habituation efforts. Additionally, a recent study highlights that habituation does not occur at the same rate across groups but is influenced by each individual's tolerance of human presence (Allan et al., 2020).

Greater use of quantitative measures of habituation is thus needed to account for potential observer effects in behavioural studies, and to facilitate standardised comparison of behavioural and fitness data across studies and field sites. This is because animals may forego fitness-enhancing activities

such as foraging, mate-seeking, or grooming to engage in observer-directed behaviours such as vocalisation or vigilance (Frid & Dill, 2002).

Human presence has also been linked to both proximate and more long-lasting changes in primates' substrate use. Unhabituated primates often retreat from terrestrial observers into – or higher into – trees (Johns, 1996; Carel P. van Schaik, van Noordwijk, Warsono, & Sutriono, 1983), and comparisons across field studies demonstrate longer-term effects: habituated groups of primates exhibit more frequent and varied use of the ground than less habituated groups of the same species (*Ateles* spp.: Campbell et al., 2005; *Brachyteles hypoxanthus*: Mourthé et al., 2007). At its extreme, habituation shields primates from exposure to predators who avoid humans (for example, leopards: Isbell & Young, 1993), which can inflate primate activity on or near the ground when humans are present (*Cercopithecus mitis erythrarcus:* Nowak, le Roux, Richards, Scheijen, & Hill, 2014). These examples highlight why observer-effects – on unhabituated through to well-habituated animals – must be understood, quantified, and incorporated into analyses of naturalistic behaviour.

Quantitative monitoring of habituation also sheds light on adaptations to risk more generally. This is because predators evoke responses, trade-offs, and changes to substrate-use in primates, similar to those described above (Campbell et al., 2005; Cowlishaw, 1997b; S. Lima, 1998; Mourthé et al., 2007; Souza-Alves et al., 2019). The term "landscape of fear" (J. W. Laundré, Hernández, & Altendorf, 2001) has been widely adopted in the study of predator-prey dynamics but its definition has remained ambiguous, largely due to conflation of patterns of actual risk, perceived risk, and behavioural responses to perceived risk. This ambiguity results in the use of unsuitable proxies and circular inferences about risk and response, and inhibits nuanced exploration of the mechanisms linking the two (Gaynor et al., 2019). Landscapes of fear have been defined variously as (1) the mapped physical environment, (2) spatial variation in actual predation risk, or (3) spatial patterns in

anti-predator behaviours. Gaynor et al. (2019) propose a framework in which these are three distinct, measurable landscapes, related in nonlinear ways and linked by the true landscape of fear: a fourth distinct layer representing *spatial variation in risk perception*.

These are important distinctions for exploring how ecological factors mediate predator-prey dynamics. For instance, habitat structure is reported to affect risk-invoked behaviours in many prey species (Atuo & O'Connell, 2017; Gorini et al., 2011), including primates (Coleman & Hill, 2014; Enstam & Isbell, 2002, 2004; Hill & Weingrill, 2007). However, habitat could influence the cognitive experience of risk perception in several different ways. Firstly, due to predators' habitat preferences or hunting techniques (ambush or cursorial), encounters between predators and prey are more likely in certain habitats and at certain times. Thus, prey might perceive greater risk in these areas and times, based on past experience. Secondly, habitat features such as low visibility reduce the probability of detecting predators, perhaps heightening perceived risk in certain habitats *regardless* of actual predator presence. And thirdly, habitat features such as tree density might either aid or prevent primates escaping from predators, with these opportunities for risk mitigation altering the level of perceived risk that they experience (Hill & Weingrill, 2007).

For example, baboons' reported avoidance of areas with denser vegetation (Cowlishaw, 1997b; Hill & Weingrill, 2007; Rasmussen, 1983) might demonstrate a straightforward relationship between actual predation risk and prey response if predators are more prevalent or likely to attack in such habitats. However, even if predators are not actually present or concentrated in tall grass or wooded vegetation, it is argued that primates display heightened anti-predator behaviours in such areas because reduced visibility increases the perception of risk in denser habitats (Altmann & Altmann, 1970; Cowlishaw, 1997b; Hill & Weingrill, 2007; Rasmussen, 1983). On the other hand, trees can provide refuge from predation and vantage points from which to detect terrestrial predators. Patas

monkeys (*Erythrocebus patas*) were found to use taller-than-average trees to scan their surroundings and, despite predators being present across the landscape, made most successful predator detections from within these "tall habitats" (Enstam & Isbell, 2004).

Furthermore, the same risk stimulus – a mammalian predator alarm call – has been shown to evoke different anti-predator responses depending on the habitat structure in which it is heard during playback experiments. Vervet monkeys (*Chlorocebus pygerythrus*) switched between arboreal and terrestrial escape strategies when they heard the same call in different environments (Enstam & Isbell, 2002). This behavioural flexibility is also demonstrated in a study where vervet monkeys reduced their levels of vigilance in areas that became more open after a fire (Jaffe & Isbell, 2009). These examples highlight the varied and non-linear effects that vegetation might have on risk perception, and demonstrate that primates employ a range of flexible and compensatory behaviours to minimise their exposure to risk in the environment.

Measuring variation in actual predation risk across an environment is difficult, due to the elusiveness of carnivores, and the fact that their distribution and density across the landscape changes with time of day, season, and availability of prey and water. This makes it hard to untangle the contributing roles of actual risk and external ecological factors to prey animals' perception of risk. Habituation provides a quasi-experimental setting in which focal animals are repeatedly exposed to the same risk stimulus (the presence of human observers) across time and habitat types. This provides an opportunity to elucidate the proximate effects of risk on behaviour, as well as mediating effects of temporal and ecological factors on this relationship (Cowlishaw, 1997a; Frid & Dill, 2002; Carel P. van Schaik et al., 1983).

Based on the assumption that perceived risk of humans declines with habituation, our study measures

changes in (a) vocalisation rates and (b) observer-directed vigilance during primate habituation, and tests how each of these response variables is affected by ecological and temporal factors. We also test whether prevalence of these anti-predator behaviours predicts levels of terrestrial behaviour in baboons.

2.2 Methods

2.2.1 Study site and species

Gorongosa National Park (-18.96°, 34.36°), Mozambique, lies at the southern end of the East African Rift System (EARS). It is composed of approximately 4,000 km^2 of heterogeneous habitats (Bouley, Poulos, Branco, & Carter, 2018; Stalmans & Beilfuss, 2008; Tinley, 1977) and is inhabited by over 200 troops of chacma baboons (Stalmans, Peel, & Gonçalves, 2018). Two focal troops were followed during this study: the Woodland Troop (WT) and the Floodplain Troop (FT), composed of 88 and 37 individuals respectively, based on counts at the end of the study period. As the names suggest, WT ranges predominantly in an *Acacia-Combretum* savannah woodland, whilst FT ranges predominantly in floodplain grasslands, although they return to riverine sleep sites with more tree coverage. The baboons forage on a range of fruits, seeds, and foliage, as well as grass, rhizomes, and insects. Occasionally, individuals in both troops were also observed hunting and eating small vertebrates such as young antelope, warthogs, and ducklings.

Civil war in Mozambique between 1977 and 1992 decimated wildlife in the park; populations of large herbivorous mammals declined by > 90%, and apex predators were almost completely lost from the landscape (Daskin, Stalmans, & Pringle, 2016). Before the war, leopard (*Panthera pardus*) and lion (*Panthera leo*) were abundant in the park, and wild dog (*Lycaon pictus*) and spotted hyena (*Crocuta crocuta*) were present in smaller numbers (Tinley, 1977). A small and slowly growing lion

population survived the war (Bouley et al., 2018) but the other three carnivore species were not seen in the park until a single leopard sighting in April 2018, and the reintroduction of a pack of wild dogs to the park in June 2018 (Atkins et al., 2019).

Reduced predation pressure since the war has facilitated rapid growth of several mammal populations, including baboons (Atkins et al., 2019), and the troops in this study have had limited exposure to large mammalian carnivores. As this study marks the first primatological research in the park, the troops had also experienced minimal exposure to humans – especially humans on foot and off-road – prior to the start of our data collection.

2.2.2 Data collection

We collected data during day follows in which each focal troop was followed by one researcher and one park ranger between the hours of 06:00 and 18:00 (although logistical constraints often limited this period to between 07:00 and 17:00, especially for FT). These follows began in April 2018 for WT and May 2018 for FT, and ended in November 2018 for both troops due to park closure in the wet season. Throughout follows, we attempted to remain as close to the troops as possible without eliciting obvious fleeing behaviour. We used handheld GPS devices (Garmin Oregon 700 and Garmin Map64) to record tracks of the daily follow routes, and customised applications on Apple iPads to collect time-stamped activity and habitat data.

The Animal Behaviour Pro application (University of Kent, 2012) was used to conduct all-occurrence vocalisation sampling for five minutes every 30 minutes throughout the day. We logged every vocalisation heard during the sample as a “Bark”, “Grunt”, “Copulation Call”, or “Contact Call”. As the clearest indicators of external risk (Fischer et al., 2001), only barks are included in the analyses below. There is a risk that some contact calls might have been included in the “bark”

category, as they are not always easy to distinguish from one another, and acoustic analyses suggest there is a graded variation of vocalisations between tonal contact calls and harsher alarm barks (Fischer et al., 2001). Whilst we expect human presence to have an effect on alarm barks over time (declining with habituation), we would not expect it to influence the frequency of contact calls between baboons. However, potential impacts of both habitat and time of day on contact calls will be addressed in the discussion. To account for troop size, vocalisation data from WT and FT were divided by 80 and 30 respectively, producing troop-adjusted vocalisation rates.

The Animal Observer application (Dian Fossey Gorilla Fund International, 2012) was used to conduct activity scan samples every 30 minutes during follows until the 14th September 2018 and every 15 minutes after that date. As our analyses examine the probability of a behaviour occurring per scan, this change in frequency should not affect our results. Scans were always conducted from left to right to minimise the chances of bias towards attention-catching behaviours, and were conducted within a five-minute limit. During scans, we logged the activity, vigilance-state, and position (on or above the ground) of every monkey in view of the observer. Defining vigilance has proved problematic in primatology (Allan & Hill, 2018). To reduce ambiguity, vigilance was coded at the individual level as "looking directly at the observer during scan", or "not looking directly at the observer during scan". Individuals for whom vigilance-state was unknown were excluded from the analyses below. Terrestriality was coded according to the position of each individual baboon during scans; those on the ground were coded as "terrestrial", and those positioned on raised objects (such as rocks or fallen logs) or in trees were coded as "not terrestrial".

Habitat type and average height of ground cover were also recorded at the start of each scan, using the same application. For the analyses below, habitat type is coded as "More than 10% tree coverage", "Less than 10% tree coverage", or "Water". The 10% tree coverage threshold was chosen

to distinguish habitats in which the lack of trees is likely to dictate terrestriality. “Water” includes large pans or riverbanks and was included as a separate habitat type due to increased vulnerability of baboons whilst drinking and the potential risks of encountering other animals at major water sources. Estimations of the height of ground cover were coded as “Low” (under 0.5 m tall) or “High” (over 0.5 m tall), based on the approximate shoulder height of a female chacma baboon, to account for potential effects of ground cover on visibility. Examples of habitat type combinations are shown in Figure 2.1. Time-stamped data were coded categorically as “AM” (06:00 – 09:59), “MID” (10:00 – 13:59), or “PM” (14:00 – 17:59).

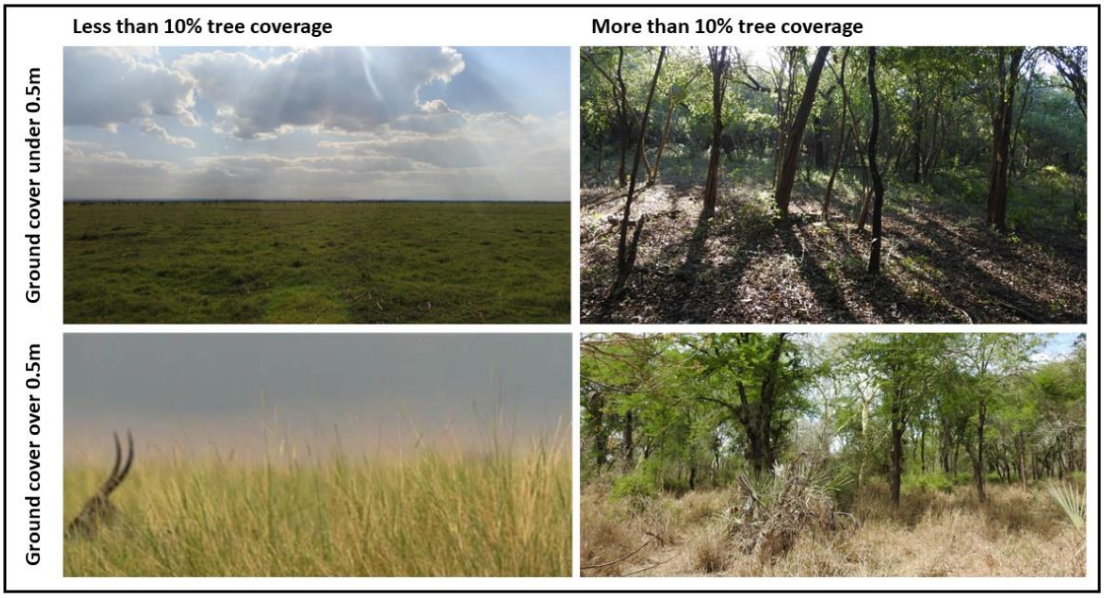


Figure 2.1. *Examples of habitat type combinations in the home ranges of the focal baboon troops.*

2.2.3 Statistical analyses

We began by running generalised linear models (GLMs) to determine whether (a) vocalisation rates and (b) the probability of observer-directed vigilance changed over cumulative habituation time, measured in full follow days (> 6hrs data collection). We then tested whether these anti-predator behaviours were significantly related to substrate-use by baboons. All models were fitted in R v4.0.2

and we used likelihood ratio tests (LRTs) and the drop1 function from the "stats" package to select models (R Core Team, 2020). Maps and graphs were produced using the "sf" (Pebesma, 2018), "ggmap" (Kahle & Wickham, 2013), and "ggplot2" (Wickham, 2009) packages in R.

2.2.3.1. Vocalisations and Vigilance models

2.2.3.1(a) Vocalisations

Due to zero-inflation in the vocalisation data we used a hurdle model to explore changes in vocalisation rates over habituation time. First, we fitted a GLM with a binomial error distribution and a logit link function to model binary data, classified as "at least one bark" (1) or "no barks" (0) during a scan. Then we fitted a GLM with a gamma distribution and a log link function to all non-zero data to model bark rate as a continuous response. Predictions from each model were multiplied together to fit the final model.

2.2.3.1(b) Observer-directed vigilance

We used a binomial GLM with a logit link function to model the occurrence of observer-directed vigilance over habituation time. As described above, this was coded as a binary variable, with individuals classified as "looking directly at the observer during scan" (1), or "not looking directly at the observer during scan" (0).

2.2.3.2. Terrestriality models

Using the response variables from the models described above, we ran binomial GLMs with logit link functions to model the effects of (a) vocalisation rates and (b) the likelihood of observer-directed vigilance, on occurrence of terrestrial behaviour. Terrestriality was coded as a binary variable at the individual level; "terrestrial" (1) or "not terrestrial" (0).

2.2.3.3. Fixed effects

To account for potential inter-troop differences, we included "Troop" as a fixed variable in all models described above. We also included time of day ("Diel"), habitat type ("Habitat"), and height of ground cover ("Cover") as fixed explanatory variables, with an interaction between Habitat and Cover as both are vegetation features. All were chosen for their ecological significance in mediating anti-predator responses.

2.2.4 Ethical note

This work was carried out with ethical clearance from Oxford University (APA/1/5/ACER/23Jan2018) and from the Ministry of Tourism and the Gorongosa Restoration Project in Mozambique (permit numbers PNG/DSCi/C114/2018 and PNG/DSCi/C93/2018). All data collection was observational in the troops' natural habitats and researchers did not come into contact with any of the animals.

2.3 Results

Between April and November 2018, WT was followed for a total of 921 hours, distributed over 106 full follow days (average length: 8.64 hours) and 14 partial follow days (< 6 hours). FT was followed for a total of 576.5 hours, distributed over 63 full follow days (average length: 7.98 hours) and 22 partial follow days. The mean break between follows was 2.47 days for WT (range: 1 – 19 days) and 3.26 days for FT (range: 1 – 29 days). WT ranged within a total area of 8.7km^2, predominantly in areas habitats with high tree coverage (72% of scans were conducted in habitats with more than 10% tree coverage, 9% in areas with less than 10% tree coverage, and 19% at major water sources). FT ranged within a total of 15.6km^2, predominantly within open habitats (67% of scans were conducted in habitats with less than 10% tree coverage, 24% in habitats with more than 10% tree coverage, and

9% at major water sources). It should be noted that FT significantly shifted their ranging patterns halfway through the field season, accounting for the greater overall size of their range. The reasons for this shift are currently under investigation. The troops' home ranges are shown in Figure 2.2.

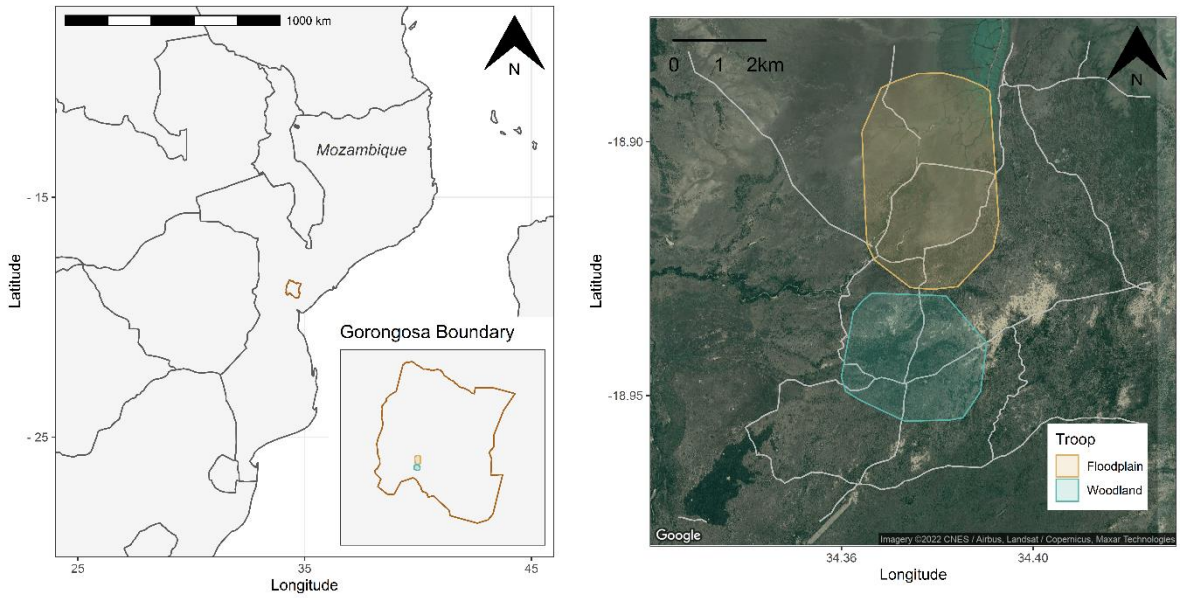


Figure 2.2. *Map showing the location of Gorongosa National Park in Mozambique (left) with home ranges of the two focal troops highlighted within the park (inset). Home ranges are shown as 95% minimum convex polygons overlaid upon roads (grey lines) and satellite imagery of vegetation within the park (right).*

2.3.1 Results from vocalisations and vigilance models

Likelihood Ratio Tests provide very strong evidence that Habituation time (Day Number) was a significant predictor of both the probability and rate of vocalisations, and of the probability of observer-directed vigilance during this study. Of the fixed variables, there is strong evidence that Troop and Diel affected response variables across all three models, and that an interaction between the vegetation variables Habitat and Cover affected the probability of vocalisations and vigilance, but

not the rate of vocalisations. These results are summarised in Table 2.1.

Table 2.1. *Results of Likelihood Ratio Tests for GLMs modelling A. vocalisation (i) probability and (ii) rates, and B. observer-directed vigilance probability over habituation time, and across troops, habitat types, and times of day. Asterisks indicate statistical significance of p-values (* = < 0.05, ** = < 0.01, *** = < 0.001).*

	A. Vocalisation Models				**B. Vigilance Model**	
	(i) Binomial		(ii) Gamma		Binomial	
	LRT	**p**	**AIC scaled dev.**	**p**	**LRT**	**p**
Day Number	65.97	< 0.001***	128.13	< 0.001***	680.70	< 0.001***
Troop	412.30	< 0.001***	7.34	0.01**	540.12	< 0.001***
Diel	21.18	< 0.001***	9.93	0.01**	27.30	< 0.001***
Habitat*Cover	8.31	0.02*	1.14	0.57	52.51	< 0.001***

2.3.1.1 Results from vocalisation hurdle model

The results from the vocalisation hurdle model, listed in Table 2.2, provide very strong evidence that both the probability and rate of vocalisations during scans decreased over habituation time, and were significantly lower in FT than WT. The binomial model results (Table 2.2: A.(i)) demonstrate that vocalisations were more likely to occur later in the afternoon (PM) than at any other time of day and were less likely in habitats with less than 10% tree coverage than the other two habitat types. High ground cover increased the likelihood of vocalisations occurring, particularly in habitats with less than 10% tree coverage. The gamma model results (Table 2.2: A. (ii)) show that vocalisation rates decreased significantly over habituation time and were consistently lower in FT, but there is no evidence that any of the other fixed effects influenced vocalisation rates. Vocalisation data and results from the hurdle model are plotted in Figure 2.3.

2.3.1.2 Results from observer-directed vigilance model

The vigilance model results, also listed in Table 2.2 above (model B), demonstrate very strong evidence that the probability of observer-directed vigilance occurring during a scan decreased over habituation time and, as with vocalisations, was lower in FT than WT. The results provide strong evidence that observer-directed vigilance was more likely to occur in the late afternoon and in habitats with more than 10% tree coverage than the other two habitat types. High ground cover increased the likelihood of observer-directed vigilance. An interaction effect between habitat variables suggests that vigilance was most likely at water sources with high ground cover, and least likely in habitats with less than 10% tree coverage but high ground cover, compared to other habitat combinations. Vigilance data and results from this model are plotted in Figure 2.4.

2.3.2 Results from terrestriality models

Table 2.3 summarises the results from two GLMs, run with (A) vocalisation rate and (B) likelihood of observer-directed vigilance as predictors of terrestriality. Both higher vocalisation rates and levels of observer-directed vigilance predict a lower likelihood of baboons being on the ground during a scan. Inclusion of fixed variables in the models highlights that FT was more terrestrial than WT, that terrestriality was highest in late afternoon, and that baboons were more terrestrial in habitats with less than 10% tree coverage and at water sources than in habitats with more than 10% tree coverage. High ground cover significantly reduced terrestriality, particularly at water sources and areas with less than 10% tree coverage.

Table 2.2. *Results from GLMs showing the effects of habituation time and fixed variables on A.(i) probability of vocalisations, (ii) rates of vocalisations, and B. probability of observer-directed vigilance by baboons. Asterisks indicate statistical significance of p-values (* = < 0.05, ** = < 0.01, *** = < 0.001).*

GLM	Estimate	Std. Error	p
A. (i) Vocalisations: Binomial			
(Intercept)	1.81	0.17	< 0.001***
Day Number	-0.01	0.00	< 0.001***
Troop: Floodplain	-2.62	0.14	< 0.001***
Diel: MID	-0.18	0.12	0.13
Diel: PM	0.30	0.13	0.02*
Habitat: Open	-0.75	0.15	< 0.001***
Habitat: Water	-0.18	0.14	0.19
Cover: High	0.41	0.14	< 0.003**
Habitat: Open*Cover: High	0.73	0.25	< 0.004**
Habitat: Water*Cover: High	0.15	0.39	0.70
A. (ii) Vocalisations: Gamma			
(Intercept)	1.12	0.11	< 0.001***
Day Number	-0.01	0.00	< 0.001***
Troop: Floodplain	-0.34	0.12	< 0.001***
Diel: MID	-0.15	0.09	0.09
Diel: PM	0.08	0.09	0.37
Habitat: Open	0.00	0.12	0.98
Habitat: Water	0.18	0.10	0.07
Cover: High	0.06	0.09	0.53
Habitat: Open*Cover: High	0.17	0.21	0.42
Habitat: Water*Cover: High	-0.23	0.38	0.54
B. Vigilance			
(Intercept)	0.01	0.09	0.93
Day Number	-0.03	0.00	< 0.001***
Troop: Floodplain	-1.82	0.08	< 0.001***
Diel: MID	-0.06	0.07	0.35
Diel: PM	0.24	0.07	< 0.001***
Habitat: Open	-0.76	0.09	< 0.001***
Habitat: Water	-0.64	0.07	< 0.001***
Cover: High	0.23	0.08	0.004**
Habitat: Open*Cover: High	-0.56	0.21	0.01**
Habitat: Water*Cover: High	1.46	0.21	< 0.001***

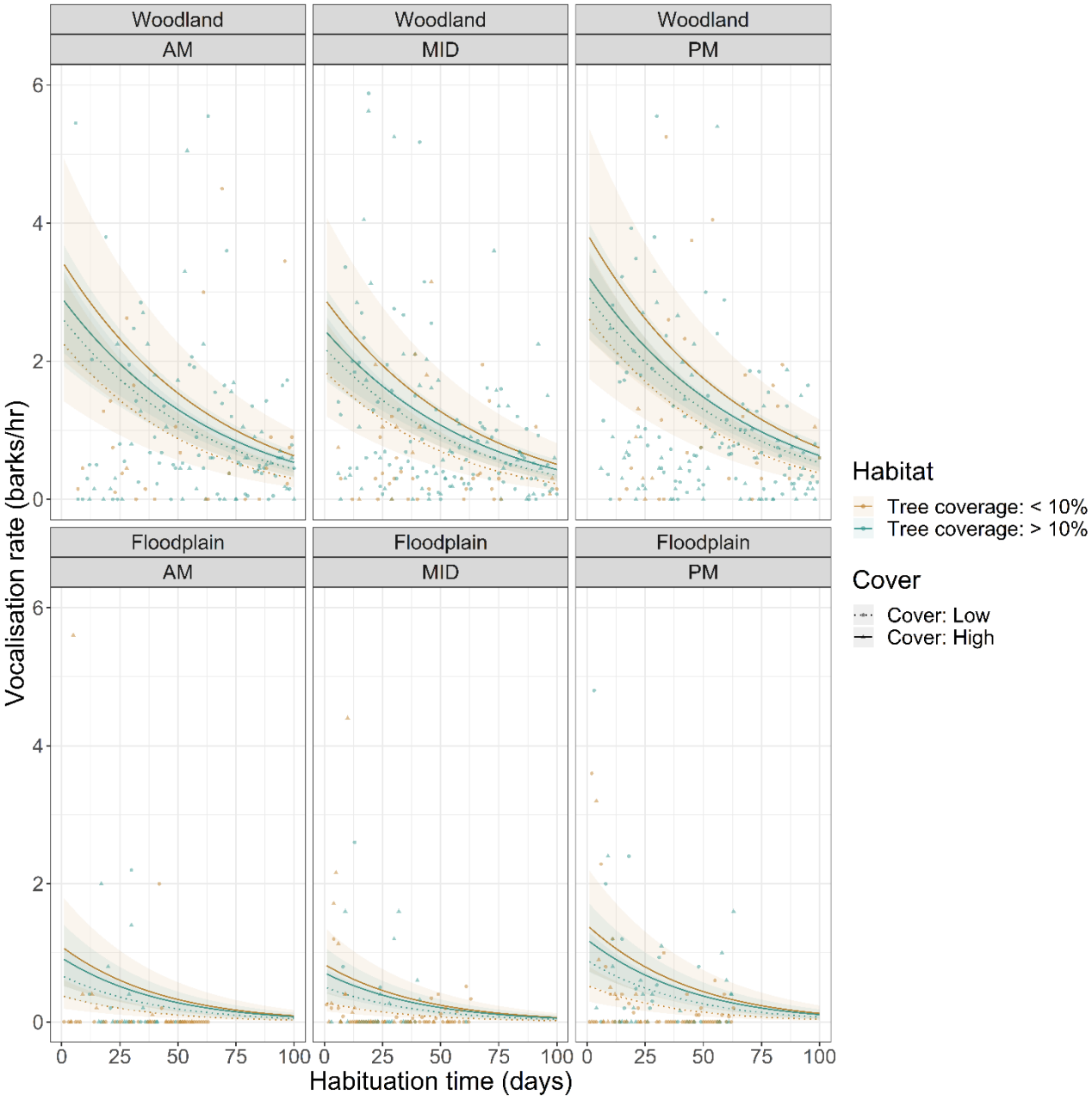


Figure 2.3. *Changes in baboon vocalisation rates over habituation time (measured in number of full day follows) for the Woodland Troop (top row) and Floodplain Troop (bottom row), grouped by time of day. Habitat types are differentiated by colour, and ground cover by differently shaped data points and line types.*

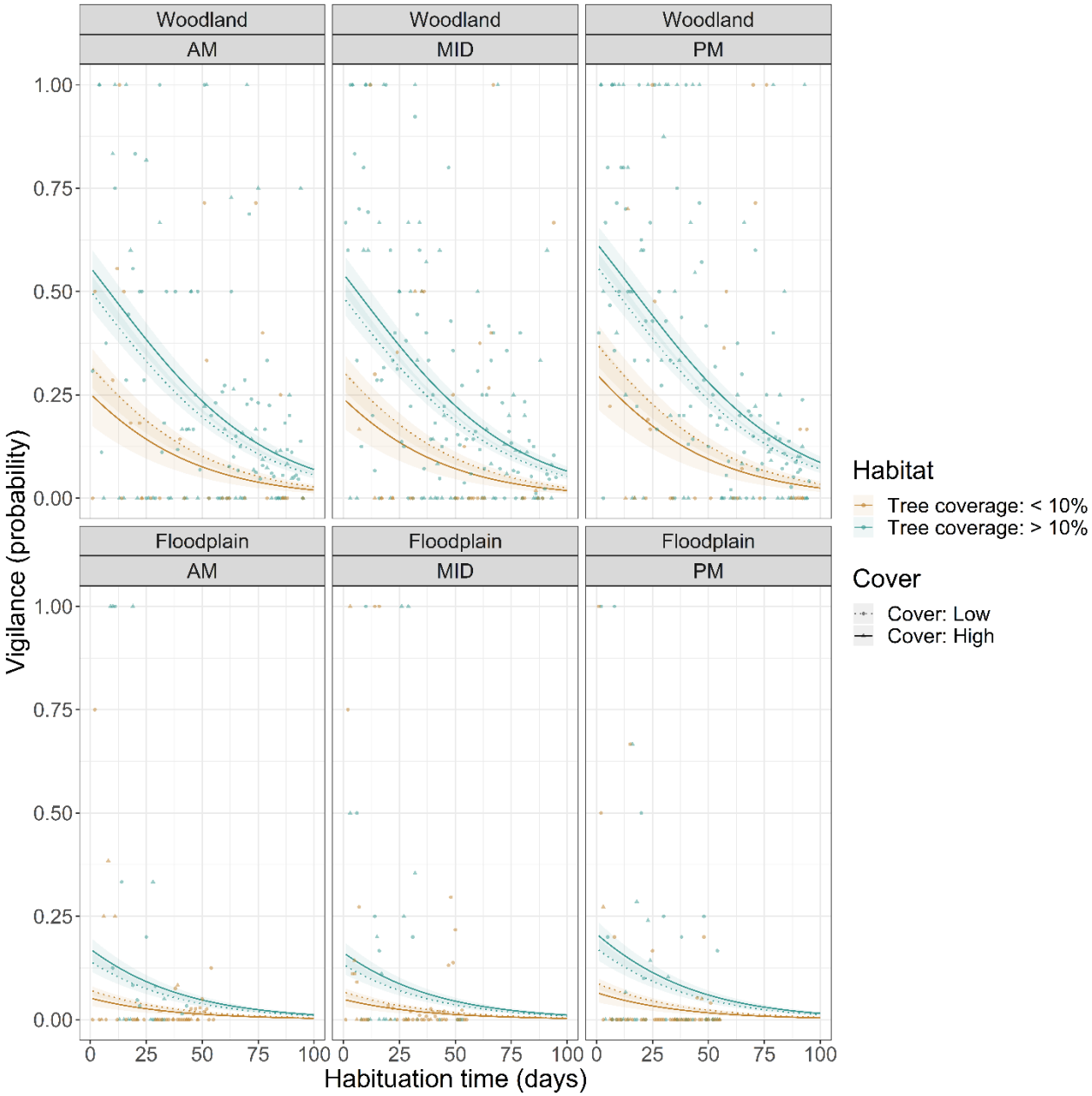


Figure 2.4. *Changes in the probability of observer-directed vigilance over habituation time (measured in number of full day follows) for the Woodland Troop (top row) and Floodplain Troop (bottom row), grouped by time of day. Habitat types are differentiated by colour, and ground cover by differently shaped data points and line types.*

Table 2.3. *Results from GLMs using A. vocalisation rate, and B. the likelihood of observer-directed vigilance as predictors for the occurrence of terrestrial behaviour in baboons during habituation. Asterisks indicate statistical significance of p-values (* = < 0.05, ** = < 0.01, *** = < 0.001).*

GLM	**Estimate**	**Std. Error**	**p value**
A. Vocalisation rate as predictor			
(Intercept)	0.68	0.06	< 0.001***
Vocalisation rate	-0.17	0.05	< 0.001***
Troop: Floodplain	0.66	0.07	< 0.001***
Diel: MID	-0.01	0.05	0.88
Diel: PM	0.43	0.06	< 0.001***
Habitat: Open	2.21	0.09	< 0.001***
Habitat: Water	2.00	0.06	< 0.001***
Cover: High	-0.85	0.06	< 0.001***
Habitat: Open*Cover: High	-0.72	0.13	< 0.001***
Habitat: Water*Cover: High	-2.13	0.17	< 0.001***
B. Vigilance as predictor	Estimate	Std. Error	p
(Intercept)	0.60	0.06	< 0.001***
Vigilance	-0.51	0.24	0.03*
Troop: Floodplain	0.72	0.06	< 0.001***
Diel: MID	0.01	0.05	0.82
Diel: PM	0.41	0.06	< 0.001***
Habitat: Open	2.21	0.09	< 0.001***
Habitat: Water	1.96	0.07	< 0.001***
Cover: High	-0.87	0.06	< 0.001***
Habitat: Open*Cover: High	-0.77	0.13	< 0.001***
Habitat: Water*Cover: High	-2.04	0.18	< 0.001***

2.4 Discussion

We modelled the change in vocalisation rates and levels of observer-directed vigilance over several months of habituation of two troops of chacma baboons, demonstrating that both measures declined with cumulative exposure to observers. Both measures also varied predictably by troop, time of day, the openness of the environment and ground cover. Both vocalisation rates and observer-directed

vigilance had a negative relationship with the likelihood of ground-use by the baboons.

Such models can be used to explore whether, or when, habituation achieves its purpose of allowing focal animals to treat observers as neutral stimuli in their environment. For example, based on daily means from our study, the likelihood of observer-directed vigilance dropped below 5% after 95 days in WT and after 44 days in FT. Although this threshold is somewhat arbitrary, recording and reporting such measures provides a standardised method for accounting for observer presence. By measuring the extent to which observers might be interfering with focal animals' normal activity patterns these indicators can be incorporated into analyses of behavioural data collected from different stages of habituation and from different study troops or sites. Such measurements could also serve as a reminder that observers might never be neutral features in study animals' environments. The growing use of remote sensing tools such as camera traps and activity loggers will shed light on the extent to which animals considered habituated to human observers are exhibiting "natural" behaviours.

Our results also highlight that, even between the two troops in this study, habituation appears to have occurred at quite different rates; both vocalisation rates and observer-directed vigilance were consistently lower in FT than WT throughout the study. There are several factors that might be at play here. WT is double the size of FT and it might have taken longer for all individuals in the bigger troop to be exposed to the observers. Furthermore, this study does not account for individual differences in tolerance to humans or risk, which could account for different rates of habituation both within and between troops (Allan et al., 2020). Alternatively, or additionally, difference in vocalisations and vigilance across the troops might reflect how habitat features in their respective home ranges influence their perceived risk of observers. Our results suggest that lower visibility in the predominantly closed habitats of WT increased anti-predator behaviours in response to humans

amongst these woodland-dwelling baboons compared to those ranging on the floodplain.

This pattern is also reflected *within* the home range of each troop, with both vocalisations and vigilance more likely to occur in areas where vegetation structure – greater tree density or taller ground cover – reduces visibility. Compared with other vegetation combinations, areas with tree density less than 10% but high ground cover predicted a greater likelihood of vocalisations but lower levels of vigilance, perhaps highlighting how vegetation structure determines the most appropriate responses to perceived risk. When available, trees might serve as lookout points from which to detect and be vigilant of risk, but when they are unavailable, vocalisations might be used to alert others to risk or to prevent separation of the troop in areas of high ground cover (Byrne, 1981).

Our results show that temporal as well as spatial factors mediate risk responses. Across habitat types, baboon vocalisations and vigilance were more likely in the late afternoon than earlier in the day, suggesting that the perceived risk of observers was heightened at this time of day. This might signal an adaptation to avoiding risk from predominantly nocturnal predators. The extant carnivore guild (with the exception of cheetahs) hunt most successfully at night and in crepuscular hours (Treves & Palmqvist, 2007), and many baboon predation events occur at their sleeping sites, to which they would be travelling in the late afternoon (Cowlishaw, 1994; Isbell, Bidner, Van Cleave, Matsumoto-Oda, & Crofoot, 2018). The reduction of visibility in twilight hours might also contribute to increases in vocalisations and vigilance towards the end of the day.

It should also be noted that some of the vocalisations recorded in our "bark" sample might in fact have been contact calls rather than alarm barks, as these two types of vocalisation are not always clearly distinguishable (Fischer et al., 2001). Whilst we attribute the clear decline in bark rates over habituation time to a reduction in baboons' perceived risk of researcher presence, it is possible that

the influence of both habitat type and time of day on vocalisation rates might be capturing some effects of those variables on contact calls. For example, baboons may need to make contact calls more frequently in closed environments or towards the evening as they congregate at their sleep sites, and this increase in vocalisations might have been recorded in our counts of barks. However, the fact that observer-directed vigilance is similarly influenced by these variables provides an independent source of evidence for the effects of habitat and diel periods on anti-predator behaviours.

Finally, we consider the relationship between anti-predator behaviours and terrestriality. Baboons are a highly terrestrial species but – like most primates – rely on trees for refuge, for example by seeking out trees and cliffs as sleeping sites. Threat from large mammalian carnivores (or perceived threat from human observers) might therefore reduce baboons' time spent on the ground. Terrestriality is of course inextricably linked to habitat structure, and this is clear in the results from our analyses. The Floodplain Troop were found to be significantly more terrestrial than the Woodland Troop, and within each troop's home range the baboons were more likely to be on the ground in areas with minimal tree coverage and lower ground cover. They were also found to be more terrestrial in the late afternoon. This might be explained by baboons' tendency to forage for depletable resources, such as arboreal fruits, in the morning before feeding on less desirable but more abundant foods, such as seeds and grasses, later in the day (Noser & Byrne, 2007b).

Beyond these predictable effects of habitat structure and possible consequences of daily routine, our analyses demonstrate that higher levels of anti-predator behaviours – vocalisations and vigilance – predict lower occurrence of terrestriality in baboons. These results have implications for the study of both extant and extinct primate species. Firstly, they imply that researchers may perceive a study group to be more arboreal than they really are before the effects of observer-induced fear wear off.

And at the other extreme, when primates are well-habituated and observer presence keeps carnivores at bay, this shift in the landscape of fear might inflate the time focal primates spend on the ground. This again questions whether researchers can ever be considered neutral stimuli in their study animals' environments and emphasises the need for incorporating quantified effects of observer-presence into behavioural studies.

The second set of implications of these results concerns the evolution of terrestriality in certain primate species, including baboons and humanAlthough it is common for primates to occasionally come to the ground, particularly during travel, very few non-human species are considered terrestrial or even semi-terrestrial (Galán-Acedo et al., 2019). Modern humans are unique amongst primates in both their obligate terrestriality and bipedalism. There has been more focus on the evolution of bipedality than terrestriality in our lineage, but their origins are not necessarily linked (Harcourt-Smith, 2010; Richmond, Begun, & Strait, 2001).

Broad shifts in habitat structure from closed to more open environments have often been postulated as the primary driver of increasingly terrestrial adaptations in hominins and other African terrestrial primates (Dart, 1925, 1949; Foley, 1993; Harcourt-Smith, 2010; NG Jablonski, 1993b; Senut, Pickford, Gommery, & Ségalen, 2018). In the case of hominins, this "Savannah Hypothesis" has become more nuanced as evidence has emerged that the earliest hominins inhabited areas with relatively high tree coverage (Bobe et al., 2020; White et al., 2009) and that adaptations to arboreality are retained in species of the *Australopithecus*, *Paranthropus*, and *Homo* lineages (Dunmore et al., 2020; Feuerriegel et al., 2017; Richmond et al., 2020; Ruff, 2009; Stern & Susman, 1983; Ward, 2002). Some researchers have suggested that modern human locomotion emerged in a series of distinct shifts from "occasional" to "facultative", and then to "obligate" terrestrial bipedalism, each occurring in different ecological contexts and therefore influenced by separate

selective forces (Harcourt-Smith, 2010; NG Jablonski, 1993b). Our study indicates that the landscape of fear should be considered amongst such forces. Alongside changing habitat structure, turnovers in the African carnivore guild would have altered the amount and distribution of risk across certain habitats, particularly as the abundance and diversity of carnivores declined from the Pliocene to the modern day (Treves & Palmqvist, 2007). Our results indicate that reduced risk from terrestrial predators and a consequent rise in time spent on the ground might have helped drive terrestrial traits to fixation in African terrestrial primates, including hominins.

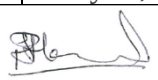
2.5 Conclusion

In this study, we recorded chacma baboons' vocalisations and observer-directed vigilance over several months to monitor changes in the frequency of their anti-predator responses to humans during habituation, and possible effects on their terrestriality. Our results suggest that vegetation structures which reduce visibility increase perceived risk, and that baboons experience heightened perception of risk later in the day, which might be an adaptive response to avoiding predominantly nocturnal predators. Our results also indicate that, across habitats and times of day, higher levels of anti-predator behaviours predict lower chances of baboons spending time on the ground, suggesting that perceived risk reduces terrestriality in baboons. A better understanding of the extent to which substrate-use is determined by risk perception will be significant for incorporating the effects of human presence into studies of primate behaviour, and for understanding the origins and evolution of terrestriality – a rare trait amongst primates.

Statement of Authorship for Chapter Two

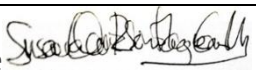
Title of paper	Risk perception and terrestriality in primates: A quasi-experiment through habituation of chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique
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Student Confirmation

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Supervisor Confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor name and title: Susana Carvalho, Professor		
Supervisor comments: I confirm the information provided is accurate		
Signature 	Date	30/08/2022

Chapter Three

Primate terrestriality: Using camera trap data to explore the effects of ecology, season, diel cycles, and risk on activity patterns in chacma baboons (*Papio ursinus*)

Terrestrial activity is rare in primates, but is associated with a variety of morphological, behavioural, and cognitive traits across the order, and is a defining feature of our own human lineage. With the exception of humans, primates who engage in terrestrial behaviours rarely do so outside of daylight hours. Predation pressure is thought to have played a significant role in shaping primate behaviours like the selection of arboreal sleep sites, but little is known – particularly at the landscape scale – about how risk interacts with other ecological and seasonal variables to drive terrestrial activity in primates. This chapter uses camera trap data to investigate both spatial and temporal patterns in the terrestrial activity of two neighbouring populations of chacma baboons (*Papio ursinus*) in Gorongosa, Mozambique. We explore how these patterns vary with tree coverage, proximity to water, season, anthropogenic variables, and the prevalence and type of apex predators in the landscape. We find evidence that baboon terrestrial activity increases in the late dry season and differs across the two populations. Differences in the diel activity patterns seen across the two grids indicate that baboons might be particularly sensitive to leopard activity, avoiding terrestrial activity during crepuscular and nocturnal hours when this predator is present in the landscape. We discuss these findings in relation to the evolution of terrestriality in human and non-human primates.

3.1 Introduction

Most primate species spend their time almost exclusively in the trees. Amongst the few species that do utilise the ground, terrestrial behaviour is associated with a variety of morphological and behavioural traits such as larger body sizes, joints built for speed over rotational movements, larger group sizes and home ranges, use of open habitats, a shift in diet, and the use of tools (Bandini et al., 2022; Clutton-Brock & Harvey, 1977; Fleagle, 2013; Heldstab et al., 2016; McCrossin, Benefit, Gitau, Palmer, & Blue, 1998; Wright et al., 2019). By one estimate, terrestriality is seen in less than 6% of extant primate species, with semi-terrestriality reported in an additional 9% of species (Galán-Acedo et al., 2019). However, there are no clear definitions, nor standardised methods for classifying "terrestrial" and "semi-terrestrial" primates. For example, the estimates above are taken from a database where species described as "carrying out most of their daily activity on the ground" were labelled as terrestrial, and those "commonly active on both substrates" were labelled as "both terrestrial and arboreal", but the data come from studies and sites across the world that all use different metrics. The classification might also depend upon researchers' behaviours of interest. Chimpanzees (*Pan troglodytes*), for example, often travel on the ground but do much of their feeding in trees (Hunt, 2016), and even the "most terrestrial" of non-human primates still sleep in trees (Anderson, 1998).

This is exemplified in baboons (genus *Papio*), whose time spent on the ground is thought to be amongst the highest of non-human primates, but is still confined almost entirely to daylight hours as they reliably return to trees or cliffs to sleep every night (Altmann & Altmann, 1970; Bidner et al., 2018; Cowlishaw, 1994; Hamilton, 1982; Markham et al., 2016). Both their diurnal activity patterns and sleep site preferences have been attributed to a strong selective force of predation risk, which is highest at night when large terrestrial carnivores are more active and when the probabilities of

detecting and escaping predators are lower due to reduced visibility – primates' primary sensory modality (Altmann & Altmann, 1970; Anderson, 1986; Bidner et al., 2018; Cowlishaw, 1994; Hamilton, 1982). Whilst sleeping above the ground appears to be a fixed trait in baboons, even amongst those in captivity who are safe from predation (Samson & Shumaker, 2015), there is evidence from several primate species that frequency of diurnal terrestrial behaviour is affected by the level of risk perceived in the environment (see Chapter Two of this thesis, as well as Campbell et al., 2005; Mourthé et al., 2007; Nowak, le Roux, Richards, Scheijen, & Hill, 2014; Souza-Alves et al., 2019). Many of these studies focus on primate species who rarely descend to the ground, and most explore immediate effects of perceived risk on substrate choice or types of terrestrial behaviour. However, the longer-term effects of risk on terrestriality are less clear, particularly in relation to other ecological variables such as the availability of trees, the prevalence and distribution of water, and anthropogenic disturbance in the environment, all of which are likely to be key drivers of ground-use in primate species. This study provides a systematic landscape-scale investigation of the effects of these variables on baboons' terrestrial activity patterns.

There is growing recognition that "the landscape of fear" – perceived spatial variation in predation risk across a landscape – is not a static representation held by animals, but varies with factors like habitat-structure, season, and time of day, as well as the diversity and hunting styles of all predators in the environment (Gaynor et al., 2019; Kohl et al., 2018; Palmer et al., 2017; Palmer, Gaynor, et al., 2022). Interactions between these dynamic variables are thought to shift animals' perceptions of risk across both space and time, influencing a range of their behaviours, from immediate reactive anti-predation strategies such as vigilance, to adaptions such as diurnal activity patterns or group-living (Palmer et al., 2017; Palmer & Packer, 2021; Tambling et al., 2015; Willems & Hill, 2009; Winnie & Creel, 2017). Monitoring these dynamics at a landscape scale is now possible thanks to

developments in remote sensing methods such as bio-logging, camera trapping, and extraction of ecological data from satellite imagery (see Chapter One, section 1.4, for details about these methods). Remote sensing technologies facilitate synchronous monitoring of multiple species within an environment, alongside the collection of relevant ecological variables, all whilst minimising human interference and improving opportunities for standardisation across long-term and cross-site studies (Pardo et al., 2021; Rowcliffe, 2017).

Remote sensing methods are increasingly being adopted in primatology, which has long relied on observational studies where researchers follow one or several primate groups within a landscape, recording the behaviours of individuals within each group (Janson, 2012). Whilst this immersive strategy has provided great insights into primate behaviours and social interactions, it is difficult and costly to simultaneously monitor more than a handful of neighbouring primate troops at best. Additionally, the suitability of observational methods varies by topic of investigation. For example, data on predation risk have often been derived from primate-predator encounters that occur whilst researchers are in the field. Such encounters are limited, both by the fact that many large carnivores are most active at night when researchers are usually not present, and because human presence can actually deter predators from the primates under observation (Isbell & Young, 1993b; Nowak et al., 2014).

Recent remote sensing studies provide insights into the nuanced effects of predation risk on primate behaviour. For example, a study that used GPS-collars to simultaneously track leopards (*Panthera pardus*), vervet monkeys (*Chlorocebus pygerythrus*), and olive baboons (*Papio anubis*) found that the leopards appeared to target the two primate species at different times of day. Leopards preferentially hunted the smaller-bodied vervets during the day whilst actively avoiding baboons, who are known to attack and even kill leopards. However, the leopards then targeted the larger-

bodied baboons (whose size falls within leopards' preferred prey size) at night, when detection and pre-emptive attack by the baboons were less likely (Isbell et al., 2018). This highlights how risk from a particular predator can change across the diel period, and why baboons' nocturnal activities might be particularly affected by the presence of leopards. Indeed, collar data from the same field site showed that only 5% of all baboon departures from sleep sites occurred before sunrise and there was evidence that they left their riverine sleep sites significantly later on mornings after a leopard had visited the site (Bidner et al., 2018). At a broader scale, a camera trapping study found temporal partitioning between leopards and several of their prey species, with yellow baboon (*Papio cynocephalus*) activity showing the least degree of overlap with leopard activity (Havmøller et al., 2020). It is perhaps because primates can evade predation along two dimensions that terrestrial camera traps capture this signal of clearer temporal partitioning by baboons than all the ungulate prey species at the site.

The research findings described above not only highlight the temporal dynamics of landscapes of fear, but also the potential significance of predator species and hunting style. Leopards, whose preferred prey size ranges between 10 and 40 kgs, are considered baboons' primary predator in areas where they occur (Hayward et al., 2006; Zuberbühler & Jenny, 2002), whilst lions, for example, generally prefer larger bodied prey – between 190 and 550 kgs – although they do sometimes kill baboons (Busse, 1980; Hayward & Kerley, 2005). In this study, we investigate the effects of spatial variation in predator presence on baboons' terrestrial activity and explore whether baboons are more likely to avoid leopards than lions, based on the hypothesis that leopards pose the greater risk to them.

To explore these questions, we use terrestrial camera trap data from two neighbouring populations of chacma baboons (*Papio ursinus*) in Mozambique, one of which is exposed to the risk of predation by

lions (*Panthera leo*), and the other by leopards (*Panthera pardus*). First, we test whether spatial variation in predator presence affects terrestrial activity levels in baboons, hypothesising that baboons are less active on the ground in areas where predators are most active. Alongside this spatial measure of localised risk, we test how baboon activity varies with tree coverage, water availability, seasonality, and anthropogenic features of the environment. We assume that the availability of trees in an area is a fundamental driver of terrestrial activity in baboons, and that the proximity of water on the ground (in rivers, lakes, or pans) might increase ground-use. We predict that seasonality also affects terrestrial activity, with baboons descending to the ground more frequently in the dry season to travel to scarce water sources, or to utilise fall-back foods like grasses and tubers when arboreal fruits are less abundant. Anthropogenic features of the environment might also impact detection of baboon activity. For example, baboons might be attracted to human settlements for foraging opportunities, or they might avoid human disturbance if they are unhabituated to people. Research from other study sites also indicates that baboons preferentially utilise roads for travel (Kiffner et al., 2022; Strandburg-Peshkin, Farine, Crofoot, & Couzin, 2017), which might lead to higher detection rates of the species closer to roads.

As well as exploring how baboon activity varies spatially and seasonally, we compare the daily activity patterns of baboons across each of the camera trap grids to investigate their temporal partitioning with two different apex predators. Based on the hypothesis that baboons perceive a higher risk of leopards than lions, and that crepuscular and nocturnal hours are "riskier" times of day than daylight hours, we test (a) the extent to which the two baboon populations show temporal partitioning with their respective predator species, (b) the extent to which the two baboon populations' activity patterns overlap, and (c) whether predator species affects the times of day during which baboons are most active on the ground in the neighbouring landscapes.

3.2 Methods

3.2.1 Study site

Gorongosa National Park, Mozambique (-18.96°, 34.36°), is composed of ca. 4,000 km^2 of heterogeneous habitats and is inhabited by over 200 troops of chacma baboons, amongst many other species (Stalmans et al., 2018). Whilst apex predators including lions, leopards, wild dogs (*Lycaon pictus*) and spotted hyenas (*Crocuta crocuta*) used to be widespread in the park (Tinley, 1977), civil war in Mozambique between 1977 and 1992 decimated wildlife in the park and apex predators were almost completely lost from the landscape (Daskin et al., 2016; Stalmans, Massad, Peel, Tarnita, & Pringle, 2019), except for a small but now growing lion population (Bouley et al., 2018). Since 2018, both wild dogs and leopards have been successfully reintroduced to the park (Bouley, Paulo, Angela, Plessis, & Marneweck, 2021), but these reintroductions occurred after the data collection period for this study.

Situated at the southern end of the East African Rift System, a 40-km-wide valley runs through Gorongosa National Park, with a grassland floodplain and Lake Urema at its centre. Woodland savannahs surround the floodplain, predominantly composed of *Acacia-Combretum* assemblages, with some palmveld and closed-canopy forest. The area has a sub-tropical climate, with the majority of rainfall occurring between December and March. In the valley, typical annual rainfall is 700 – 900 mm, but it is higher on the surrounding plateaus. South of Lake Urema there is a road network used by a small but growing tourist operation, as well as researchers and rangers (Gaynor, Daskin, Rich, & Brashares, 2021; Stalmans & Beilfuss, 2008).

A 5333 km^2 buffer zone surrounds Gorongosa National Park and is designated as a mixed-use area, inhabited by 200 000 subsistence farmers. To the east of Gorongosa's park boundaries and buffer

zone lies a 460 km^2 forestry concession, certified by the Forest Stewardship Council for low intensity, rotational timber harvesting (Easter, Bouley, & Carter, 2019). The area is composed of predominantly tall miombo woodlands, with some variation in vegetation density between more open grasslands and closed-canopy riparian areas, but generally tree coverage is more homogenous than within the park's boundaries. The concession is inhabited by several mammalian species, with leopards as the only known apex predator in the area. The concession partly contains a human settlement, as well as several households and a sawmill. There is a simple road network within the concession, used mainly for harvesting timber, and to connect the sawmill and community with main roads (Easter et al., 2019).

3.2.2 Camera trap grids

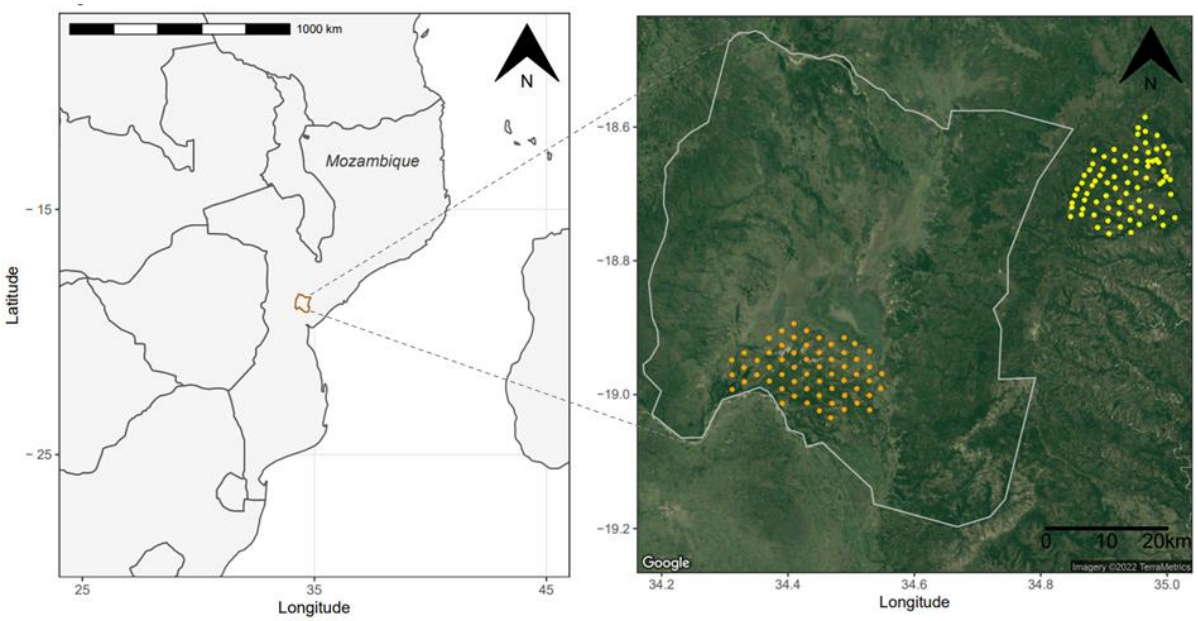


Figure 3.1. *Map showing the position of Gorongosa National Park (GNP) in Mozambique (on left), and the locations of two camera trap grids in relation to the park's boundaries (on right). The position of each camera station is marked in orange for the GNP grid and in yellow for the Forestry Concession (FC) grid.*

This study draws on data collected from two camera trap grids, mapped in Figure 3.1. The Gorongosa National Park (GNP) grid was established in 2016 by Kaitlyn Gaynor, covering approximately 300 km^2 within the park's main boundaries (Gaynor et al., 2021). The grid is still running today, but the data included in this study were collected between June 2016 – September 2018. Tree coverage and habitat type vary considerably across the GNP grid area, as does each camera's distance from roads and water sources. Thus, the grid facilitates exploration of how baboon activity varies with these ecological variables, as well as by season. Lions were the only apex predator inhabiting the gridded area during the study period.

The second camera trap grid was established by Tara Easter in the sustainable-use forestry concession east of the park's boundaries (Easter et al., 2019). The forestry concession grid (hereafter "FC grid") operated between June and October 2017 and had a slightly different format than the GNP grid (see Table 3.1). The area covered by the FC grid is characterised by denser and more homogenous tree coverage than the area covered by the GNP grid, and the only known apex predators in the area are leopards.

Both grids were established with camera trap stations placed roughly at the centre of evenly spaced hexagonal grid cells, although the FC grid also included some cameras specifically placed along roads. The GNP grid used a single camera trap at each station, whilst most FC sites had paired cameras (to aid in identifying individual leopards). This difference in setup is not expected to influence results, given that baboons' large group sizes give them a high probability of detection (Gaynor et al., 2021). Cameras were mounted on trees, approximately a metre off the ground, and were motion-triggered to take two photographs, classified as a single detection. For paired-camera stations, animals captured by both cameras at the same time were also classified as a single detection. The grids' features and operating procedures are summarised in Table 3.1 below.

Table 3.1. Operating period, procedures, and features of the GNP and FC camera trap grids.

	Gorongosa grid	FC grid
Operating period	June 2016 – Sept 2018	June – Oct 2017
Cameras	Bushnell Trophy Cam	Bushnell Trophy Cam
Total area monitored by grid	300 km^2	320 km^2
Total camera trap stations	60	75
Hexagonal grid cell size	5 km^2	4 km^2
Operating procedure	Single camera per station, mounted throughout operating period. All cameras placed roughly at centre of grid cell.	Paired cameras at most stations, rotated in four successive blocks. Some cameras specifically placed along roads.
Photo capture procedure	Bursts of two with 30s delay, independent detections classified using 30min interval.	Bursts of two with 2s delay, independent detections classified using 30min interval.

3.2.3 Data processing

The species captured in images across both grids were identified and labelled manually by researchers and assistants. The R package "camtrapR" (Niedballa, Sollmann, Courtiol, & Wilting, 2016) was used to generate a timestamped record of all species detections across both grids. The records from each grid were then cleaned to generate data sets of independent species detections, classified using a 30-minute interval between detections of the same species at the same station. Whilst somewhat arbitrary, this is a standard independence time interval used in camera trapping research, and we consider it long enough to account for baboons' average group size and travel speed (Sollmann, 2018).

The GPS coordinates for each camera station in each grid were recorded alongside several ecological variables when the grids were first established. These include each camera's distance from the nearest river, nearest road, and nearest human settlement. For the GNP grid, there is also a measure of each camera's distance from Lake Urema as it is the largest permanent water source in the park.

To these variables we added an estimate of tree coverage at each camera station, under the assumption that the availability of trees would explain some variation in baboons' terrestrial activity. Using the cameras' GPS points, we extracted an estimate of woody (tree and shrub) cover from an existing database of woody cover across Sub-Saharan Africa at a resolution of 1 km (Hanan et al., 2020).

Whilst the FC grid only operated during the dry season, the GNP grid captured data across the annual cycle and all species detections were therefore classified as "Wet" (December – March), "Early dry" (April – July), or "Late dry" season (August – November). For analyses of activity across different diel periods, species detections were classified as "Dawn" (the 120 minutes around sunrise), "Dusk" (the 120 minutes around sunset), "Day" (the time between dawn and dusk periods), and "Night" (the time between dusk and dawn periods). Sunrise and sunset times for Gorongosa were identified using the website: https://www.timeanddate.com/sun/ and all timestamped images were classified according to the diel period in which they were captured. Predator presence across each grid was classified using a binary system; camera sites at which lions or leopards were detected at least once during the study period were labelled as having localised predator activity ("Predators"), whilst all other cameras were labelled as having no localised predator activity ("No predators"). Of course, the absence of predator detections at a camera trap site does not mean that there are no predators active in that area of the landscape. However, this binary classification system serves as a proxy that aims to capture the areas in which predators are most active.

3.2.4 Statistical analyses

3.2.4.1 Spatial and seasonal variation in baboon activity: Does terrestrial activity vary with localised predator activity, ecological, seasonal, and anthropogenic variables?

We ran two sets of analyses to explore how baboons' terrestrial activity levels are influenced by spatial variation in predator activity, as well as other ecological and seasonal variables. For both sets of analyses, baboon activity was quantified using a Relative Activity Index (RAI), which represents the number of independent baboon detections captured per 100 operating hours at each camera station. In the first set of analyses, we ran generalised linear mixed effects models (GLMMs), using only data from the GNP grid so that seasonality could be included in the model. Camera station was thus included as a random variable to account for repeated sampling of each station across seasons. The ecological variables included in the models were woody cover, distance from the nearest river, distance from Lake Urema, season, and predator presence. Under the assumption that anthropogenic activity in the environment might also have some effect on baboon activity, we ran a second model that included all ecological variables plus distance from nearest road and distance from nearest human settlement. All continuous covariates were centred and scaled prior to modelling, and the log-transformed value of operating hours per camera per season was included as an offset term. We calculated and compared the Akaike information criterion (AIC) scores for each of these two models, taking the model with the lowest AIC score as the model that provides the best explanation of the variation in the data.

For the second set of analyses, we included data from both the GNP and FC grids, limiting our analysis to a single dry season period when both grids were active. For these analyses we fitted negative binomial generalised linear models to the data, to account for zero inflation in the data. The

ecological fixed variables included in the model were woody cover, distance from nearest water source (lake for GNP cameras and river for FC cameras), and predator presence. Location ("GNP" or "FC") was also included as a fixed variable. Again, the log-transformed value of operating hours per camera was included as an offset term in the models. As in the first set of analyses, we used AIC scores to compare the relative explanatory power of a model that included just the ecological variables to one that also included distance from nearest road and distance from nearest human settlement.

3.2.4.2 Diel variation in baboon activity: how is terrestrial activity distributed across the diel cycle, do these patterns vary across the two grids, and to what extent do the two baboon populations show temporal partitioning with their respective predator species?

To explore daily temporal patterns in baboons' terrestrial activity, we used data from both camera trap grids. First, we investigated when baboons were most active on the ground during the circadian cycle and whether this varied across grids. For this, we fitted a negative binomial GLMM to the camera trap data to test whether baboon RAI varied significantly by diel period (dawn, day, dusk, or night). We included an interaction term between diel period and location (GNP or FC), based on the hypothesis that baboons' diel activity patterns would be different in a landscape inhabited by lions compared to a landscape inhabited by leopards. Woody cover, distance from water, and localised risk were included as fixed variables, based on results from the spatial models (described in section 3.2.4.1), and camera station was included as a random variable to account for repeated sampling across diel periods. The log-transformed value of total operating hours per camera per diel period was included as an offset term. All models were fitted using functions from the "lme4" package in R (Bates, Mächler, Bolker, & Walker, 2015).

Next, we used temporal overlap analyses to further explore possible differences in the terrestrial activity patterns of GNP and FC baboons, and to test the extent to which baboon activity overlapped with predator activity across each grid. For these analyses, we calculated a coefficient of temporal overlap, d-hat, for each pair of diel activity distributions, where 0 represents no temporal overlap and 1 represents complete overlap. We used the d-hat1 formula for sample sizes under 50 independent detections and the d-hat4 formula for those over 50. We used bootstrapping with 10,000 resamples to estimate 95% confidence intervals for each overlap estimate. These analyses were performed using the "overlap" package in R (Ridout & Linkie, 2009). We also used the compareCkern function in the "activity" package in R (Rowcliffe, 2022) to estimate the probability that the activity patterns in each pair came from the same distribution. All analyses were conducted in R v4.1.1 (R Core Team, 2021).

3.3 Results

Table 3.2 summarises the camera metadata, operating periods, and image data collected across the GNP and FC grids. There was a broad range of woody cover values across the GNP cameras (mean: 52%, range: 20 – 71%) compared to the higher and more homogenous tree coverage across the FC grid (mean: 67%, range: 58 – 78%). On average, GNP cameras were further from water and settlements but closer to roads than FC cameras. Overall, more animal activity was captured across the GNP grid (approximately 3.4 independent detections per operating day) than the FC grid (approximately 0.9 independent detections per operating day). Baboons accounted for 15% of all detections across the GNP grid, compared to only 8% of those across the FC grid. Across the GNP grid, lions accounted for 0.05% of detections. Across the FC grid, leopards accounted for 0.04% of detections. No other large carnivores were detected across either grid. Human activity was much higher across the FC grid (18% of detections) than the GNP grid (0.03% of detections). Appendix A contains a summary of all the species detected across each camera trap grid.

Table 3.2. *Summary of operating days and image data collected across GNP and FC grids. All detections were classified using a 30-minute independence interval.*

	GNP grid	**FC grid**
Camera metadata: mean (range)		
Woody cover (%)	52 (20 – 71)	67 (58 – 78)
Distance from lake (km)	9 (1.3 – 19.4)	NA
Distance from river (km)	3.8 (0.1 – 8.7)	1.8 (0 – 5.7)
Distance road (km)	0.6 (0 – 2.3)	2.1 (0 – 6.3)
Distance from settlement (km)	10.7 (1.1 – 20.7)	8.3 (0.5 – 19.4)
Operating days:		
Total	26,523	2,090
Mean per camera site	442	28
Independent species detections:		
Total	89,349	1,800
Baboon	13,659 (15%)	147 (8%)
Lion	54 (0.05%)	0 (0%)
Leopard	0 (0%)	8 (0.04%)
Human/ vehicle	30 (0.03%)	319 (21.62%)
Sites with detections of:		
Baboon	60 (100%)	56 (75%)
Lion	19 (32%)	0 (0%)
Leopard	0 (0%)	6 (8%)

3.3.1 Spatial and seasonal variation in baboon activity

3.3.1.1 GLMM results from seasonal data (GNP grid only)

Of the two GLMMs fitted to the seasonal GNP grid data, the model with only ecological and seasonal variables had a lower AIC score (AIC = 2988.6) than the model which also included anthropogenic variables (AIC = 2991.5). We therefore consider it the better model for explaining variation in these data. Table 3.3 summarises the associations of each of the chosen model's fixed variables with baboon RAI (see Appendix B(1) for results from alternate model). These results suggest that baboon terrestrial activity does not vary consistently with tree coverage, distance from water, nor the localised presence of predators. There is strong evidence ($p < 0.001$) that across the

grid, baboon terrestrial activity is higher in the late dry season than at other times of year. These seasonal differences are shown in Figure 3.2 below.

Table 3.3. *Ecological and seasonal factors associated with baboon activity across the GNP grid. Asterisks indicate statistical significance* of *p-values (* = < 0.05, ** = < 0.01, *** = < 0.001).*

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-4.29	0.11	-40.00	< 0.001***
Woody cover	0.00	0.09	0.04	0.97
Lake distance	-0.11	0.10	-1.18	0.24
River distance	0.03	0.09	0.36	0.72
Risk: Predator	0.29	0.22	1.32	0.19
Season: Late dry	0.27	0.02	12.65	< 0.001***
Season: Wet	-0.01	0.03	-0.50	0.62

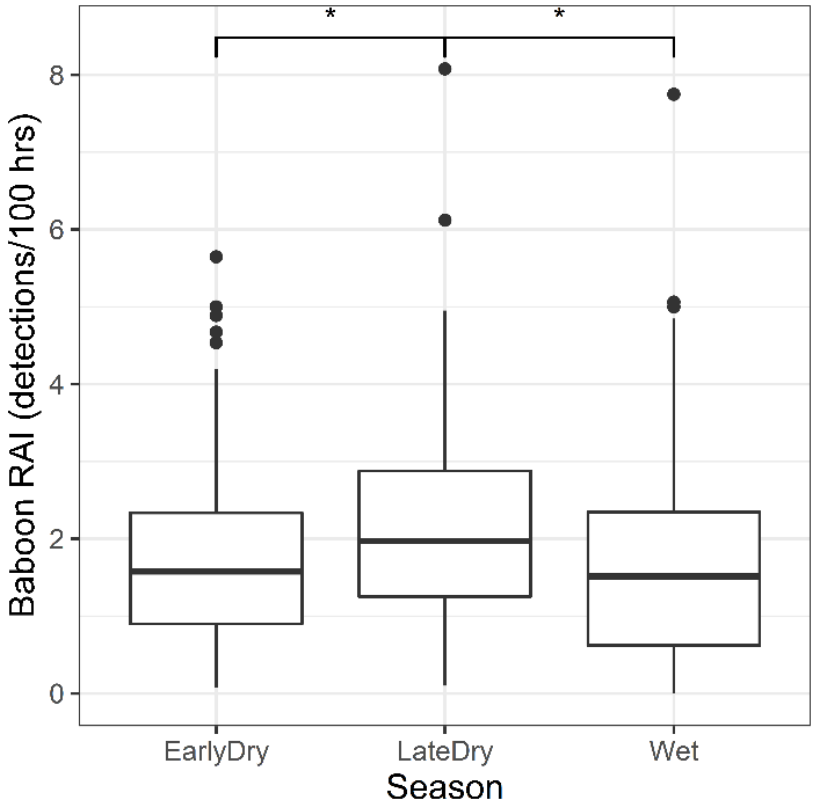


Figure 3.2. *Seasonal differences in the relative activity indices (detections per 100 operating hours) of GNP baboons. Asterisks indicate statistically significant differences between pairs.*

3.3.1.2 GLM results from data collected across both grids

Of the two GLMs fitted to the dry season data collected across both camera trap grids, it was again the model with only ecological variables that had the lower AIC score (807.53) than the model that included anthropogenic variables (811.2). Table 3.4 summarises the associations of each of this model's fixed variables with baboon RAI (see Appendix B(2) for results from alternate model). Again, these results indicate that baboon terrestrial activity does not vary consistently with tree coverage, distance from water, nor the localised presence of predators. There is strong evidence ($p < 0.001$) that baboon activity is higher across the GNP grid than across the FC grid (see Figure 3.3 below).

Table 3.4. *Ecological factors associated with baboon activity across the GNP and FC grids. Asterisks indicate statistical significance* of *p-values (* = < 0.05, ** = < 0.01, *** = < 0.001).*

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-5.01	0.55	-9.16	< 0.001***
Woody cover	-0.01	0.01	-1.43	0.15
Water distance	-0.01	0.03	-0.39	0.70
Risk: Predator	-0.11	0.23	-0.50	0.62
Location: GNP	2.11	0.29	7.17	< 0.001***

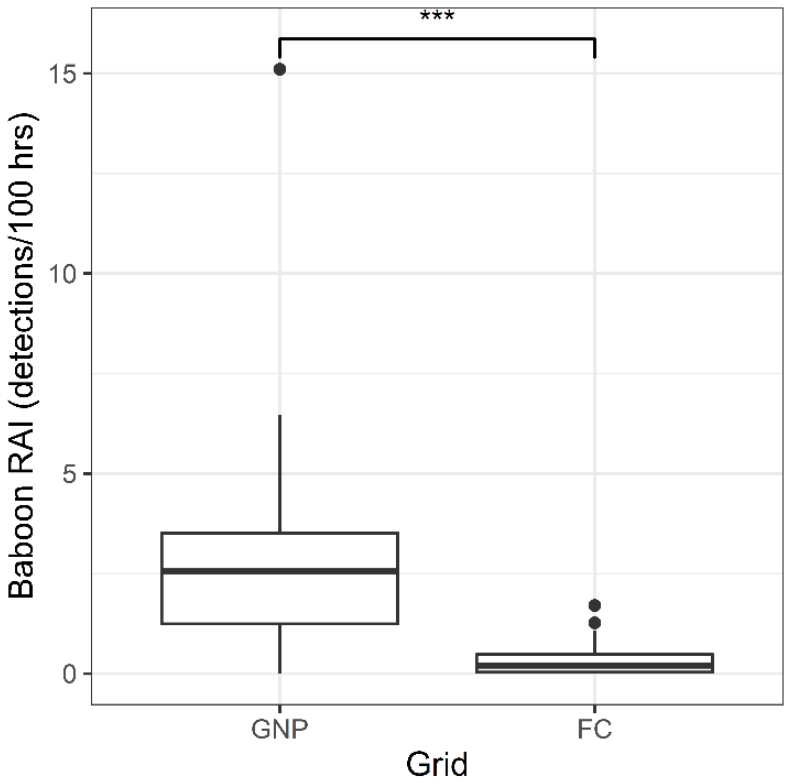


Figure 3.3. *Differences in the relative activity indices (detections per 100 operating hours) of baboons across the GNP and FC grids. Asterisks indicate statistically significant differences between pairs.*

3.3.2 Diel variation in baboon activity

3.3.2.1 GLMM results from diel data (both grids)

Table 3.5 summarises the output from the GLMM that was fitted to diel data from both the GNP and FC grids. Once again, these results provide no evidence of woody cover, distance from water, or localised risk predicting terrestrial baboon activity. However, there is a statistically significant interaction between diel period and location, indicating that baboon activity varies by time of day, and that this variation is different across the grids. The distribution of baboon detections across diel

periods for each grid is depicted in Figure 3.4 below.

Table 3.5. *Ecological and diel factors associated with baboon activity across the GNP and FC grids. Asterisks indicate statistical significance* of *p-values (* = < 0.05, ** = < 0.01, *** = < 0.001).*

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-6.83	0.50	-13.75	< 0.001***
Woody cover	-0.13	0.10	-1.27	0.21
Water distance	0.13	0.10	1.36	0.17
Risk: Predator	0.10	0.22	0.44	0.66
Location: GNP	3.28	0.54	6.04	< 0.001***
Diel: Day	1.72	0.50	3.45	< 0.001***
Diel: Dusk	0.81	0.58	1.38	0.17
Diel: Night	-19.16	2974.64	-0.01	0.99
GNP*Day	-1.51	0.52	-2.92	0.004**
GNP*Dusk	-1.71	0.61	-2.83	0.005**
GNP*Night	12.46	2974.64	0.00	0.99

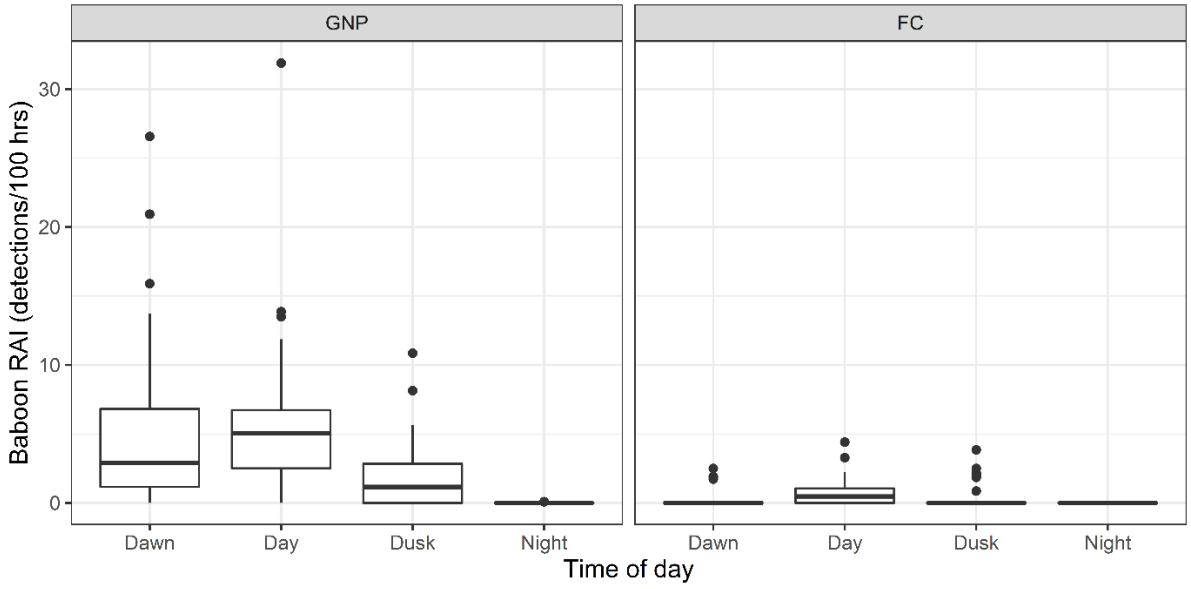


Figure 3.4. *Differences in the relative activity indices (detections per 100 operating hours) of baboons across diel periods for each camera trap grid.*

3.3.2.2 Coefficients of overlap

Table 3.6 summarises the results from the activity overlap analyses between baboons and their predators, and between the GNP and FC baboons. The coefficient of overlap between the GNP and FC baboons is 0.84, likely reflecting the fact that both populations are almost entirely diurnal. However, the probability that their activity patterns come from the same distribution is 0.02, suggesting that there are some significant differences in how their terrestrial activity is spread across the day. The coefficient of overlap between baboons and lions is greater than that between baboons and leopards, suggesting that baboons might exhibit greater temporal partitioning with the latter predator species. However, the large confidence interval around the baboon-leopard d-hat value highlights that there are too few leopard detections to get a precise portrayal of their activity patterns in the FC area. Figure 3.5 shows the kernel density distributions for baboon and apex predator detections across the Gorongosa and FC grids, where the area under each curve is equal to 1 and times are scaled to sunrise and sunset.

Table 3.6. *Coefficients of overlap between baboon populations and between the baboons and predators at each site. Confidence intervals were estimated using bootstrapping with 10,000 resamples and p-values represent the probability that the two activity patterns come from the same distribution.*

	Overlap coefficient (d-hat)	**Confidence interval**	**p-value**
GNP & FC baboons	0.84	0.79 – 0.89	0.02*
GNP baboons & lions	0.32	0.21 – 0.42	< 0.001***
FC baboons & leopards	0.16	0.00 – 0.42	< 0.001***

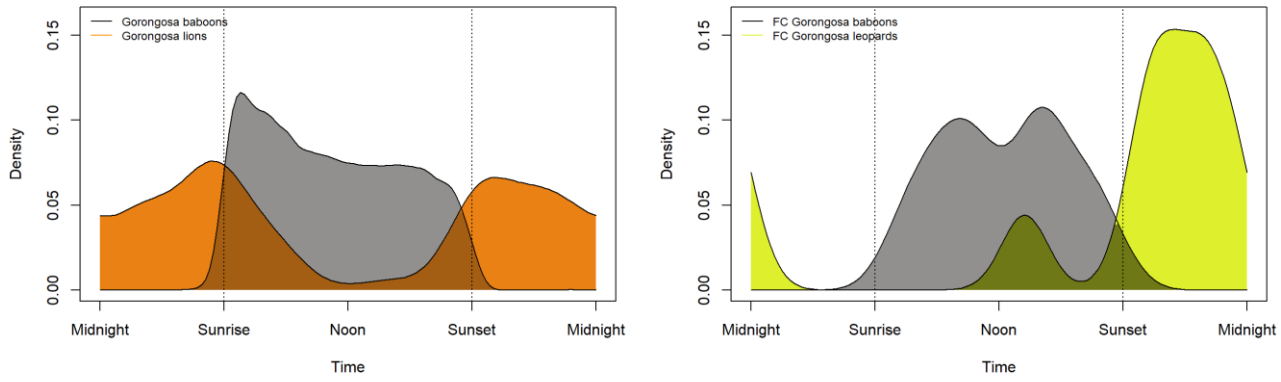


Figure 3.5 *Graphs depicting the temporal overlap between detections of baboons (grey) and apex predators at each site (GNP lions in orange and FC leopards in yellow). Dotted vertical lines represent sunrise and sunset, standardised across sites and seasons.*

3.4 Discussion

In this study we used terrestrial camera trap data to explore how ground-based baboon activity varies with risk and other ecological variables. We explored both spatial variation in predator activity and hypothesised differences in the level of perceived risk across the 24-hour cycle and of different predator species. We first tested whether localised predator presence affects baboons' terrestrial activity levels, hypothesising that baboons may avoid or be more arboreal in areas where predators are more active. In these analyses we also included tree coverage, proximity to water, proximity to roads and human settlements, and seasonality as other potential explanatory variables of baboon terrestrial activity. Contrary to our hypothesis, we found no evidence that baboons were less active in the localised areas where lions or leopards were detected. Whilst this might suggest that baboons are not spatially avoiding these predators, the results could instead reflect that our measure of predator activity is too coarse to detect fine-scaled avoidance strategies in the landscape. Baboons may be

avoiding predators in real-time as they detect them in certain locations, but our results suggest that they either do not avoid predator-occupied areas over longer time scales, or that our methods did not accurately identify the riskiest areas in the landscape.

Our results also indicate that terrestrial baboon activity is not strongly associated with any of the ecological variables we measured, except for season. We found no evidence that baboons' terrestrial activity varied reliably with tree coverage, proximity to water, or proximity to anthropogenic features in the environment. Across the GNP camera trap grid, we did find season to be a significant predictor of baboon terrestrial activity, with baboons more active on the ground during the late dry season than at other times of year. In the analysis of data from both grids, baboon activity was found to be significantly higher across the GNP grid than the FC grid.

Interpretations of these results must include the consideration that stations with low detection rates of baboons could indicate that they are not using an area at all, or that they engage in more arboreal rather than terrestrial activity in that area and therefore are not captured by cameras close to the ground. For example, the effect of season on baboon activity has multiple interpretations. Baboon detections across the grid might be lower in the wet season because baboons do not need to move around as much to find food or water, and therefore visit certain areas less frequently. Alternatively – or perhaps as an additional factor – the wet season likely coincides with greater availability of arboreal resources like fruit, whilst the dry season requires baboons to spend more time on the ground travelling to scarce water sources or foraging for resources like grasses or underground storage organs. As the FC grid was only deployed during the dry season, we cannot explore whether FC baboons show the same seasonal shift in activity patterns as seen in GNP baboons.

We found strong evidence that terrestrial activity levels across the GNP grid were much higher than

across the FC grid. The size of this difference suggests that it likely captures several effects that cannot be identified with the available data. As seen in Table 3.2, the percentage of woody cover is higher and more homogenous across the FC grid than the GNP grid, and it might seem parsimonious to assume that baboons living in an area with more trees simply spend less time on the ground. However, our results indicate no significant effect of woody cover on baboon activity within GNP (where tree coverage ranges from 20% to 71%), nor across grids. This suggests that the number of trees available to baboons is not the primary predictor of their terrestriality, and perhaps only becomes significant across large changes in tree coverage, or when it interacts with other variables (like risk perception) to influence whether or not baboons frequently use the trees available to them.

Another key reason why baboons might be detected at higher rates across the GNP grid than the FC grid is population size. Whilst we have an estimate from aerial surveys that approximately 60 troops of baboons range across the GNP grid, we do not know how many troops live in the FC area, nor do we have an estimate of average troop sizes in either area. It is likely that a higher density of baboons in the GNP area accounts for higher detection rates across this grid. Additionally, the presence of different apex predators across the grids might be a contributing factor to terrestrial baboon activity. As previously noted, leopards are thought to be baboons' top predator, whilst lions generally target larger animals. If predation of baboons is higher by leopards in FC than by lions in GNP, this might contribute to a lower population density of baboons across the FC grid. Furthermore, if baboons *perceive* a higher threat from leopards than they do from lions, they might be avoiding the FC area altogether and/or spending less time on the ground there to avoid terrestrial encounters with leopards.

Because we do not have estimates of the different population densities and predation rates across the two grids, it is valuable to look at other more comparable patterns in the baboons' terrestrial activity to determine how they respond to different apex predators in their respective environments. In our

second set of analyses, we explored variation in baboon activity over the 24-hour cycle, how this pattern differs across the two grids, and the extent to which the baboons demonstrate temporal partitioning with apex predators in their environments.

First, we found that baboons across both grids were clearly diurnal, as can be seen in Figure 3.5. This is reflected in the fact that significantly more baboon detections were recorded during the day than during crepuscular and nocturnal periods, and that there was an 84% overlap in the patterns of terrestrial baboon activity detected across each grid. Despite this high overlap, we found a low probability that the two baboon activity patterns came from the same underlying distribution, which indicates that the two baboon populations have distinct patterns within the diurnality observed across each grid. Indeed, the distribution of detections across diel periods demonstrates that in FC, baboon activity was high during the day compared to dawn and dusk periods, and no terrestrial baboon activity was detected at night. In Gorongosa, however, baboon activity was high during both dawn and day periods, only declining slightly at dusk, and there were even a few (n = 20) detections of baboons on the ground at night. Figure 3.5 visualises the difference in baboon activity patterns across sites, clearly showing a peak in terrestrial activity detection soon after sunrise in GNP, whilst the FC distribution is centred more around the middle of the day.

Our results indicate that this difference in timing of terrestrial activity across the two grids might be due to the presence of different apex predators in each landscape. Figure 3.5 demonstrates that the apex predators across both habitats are predominantly nocturnal and that baboons show significant temporal partitioning with both lions and leopards in their respective environments. However, the overlap in activity patterns between FC baboons and leopards was smaller than that between GNP baboons and lions, suggesting baboons might exhibit greater temporal partitioning with leopards. It should be noted that the number of leopard detections across the FC grid is low, making it difficult to

get a precise indication of their activity patterns. However, our results suggest that baboons living in an environment with leopards might confine much of their terrestrial activity to the middle of the day, when the crepuscular predator is less active. Baboons in GNP, on the other hand, perhaps feel safer to venture to the ground very early in the morning and even sometimes at night, despite overlapping with lions' hunting periods.

There are two clear research avenues to explore these diel patterns further. First, Gorongosa provides an ideal setting for a longitudinal natural experiment. Whilst this study documents baboon activity in an environment without leopards and with minimal predation risk from the few lions in the park, Gorongosa baboons' landscape of fear is likely changing. Since 2018, two packs of wild dogs have been released and have successfully reproduced within the park, and six leopards have been reintroduced to the area. Ongoing camera trap data collection will thus provide valuable insights into how baboon terrestriality and diel activity patterns change with increasing risk. A second research path involves cross-site comparisons to determine whether certain predator species and/or the carnivore diversity within different landscapes evoke similar trends to those seen in this study. This approach will be explored in Chapter Four.

Terrestriality in primates is rare, but across the order it correlates with a variety of morphological and behavioural traits, including larger body sizes, group sizes, and home ranges, as well as longer day ranges (Clutton-Brock & Harvey, 1977). These traits facilitate easier and broader dispersal across a range of terrains, resulting in the occupation of a greater variety of habitat types by terrestrial primates (see Chapter Five and Galán-Acedo et al., 2019). Furthermore, studies have found that even a partly terrestrial lifestyle has a positive relationship with tool-use and manipulation complexity in primates, as well as birds (Bandini et al., 2022; Falótico & Ottoni, 2022; Heldstab et al., 2016; Meulman, Sanz, Visalberghi, & van Schaik, 2012; Ottoni & Izar, 2008; Wright et al., 2019). We see

many of these traits in humans – the most terrestrial of primates – and our hominin lineage is largely defined by a locomotive shift to obligate terrestrial bipedalism. The origins and drivers of primate terrestriality are therefore of key interest for understanding human behavioural evolution.

This study highlights the potential impact of variation in risk on primate terrestriality at a landscape scale, with a particular emphasis on temporal dynamics and predator species. To build a fuller picture of the effects of dynamic landscapes of fear on primate behaviour, it will be necessary to tease apart the effects and interactions of many spatial and temporal variables. For instance, whilst we find no effect of woody cover on baboon terrestriality in this study, it is likely that there are thresholds above and below which tree coverage drastically alters baboons' spatial activity patterns. And whilst each of the landscapes included in this research was only inhabited by one apex predator, ecosystems with several carnivores will have more complex dynamics of spatial and temporal partitioning amongst members of the guild with different consequences for prey behaviour. Remote sensing methodologies are improving our abilities to monitor community ecology at broad scales and with unprecedented scope for longitudinal and simultaneous monitoring of species. These technologies, combined with more traditional *in situ* observational research, will facilitate more accurate and nuanced models of how risk impacts behavioural ecology and evolution in primates and other taxa.

3.5 Conclusion

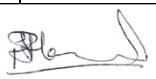
Primate terrestriality is rare and most species have fairly constrained diel activity patterns. Predation pressure is often implicated in the evolution of such behaviours, but it has been hard to study – particularly at broad scales and before the advent of remote sensing technologies. This study investigates how the terrestrial activity patterns of baboons are affected by risk, as well as ecological, seasonal, and temporal variables. We find no effects of localised spatial variation in predator

presence, nor tree coverage, water availability, or anthropogenic variables on baboon activity. We do find that baboons are more active on the ground in the late dry season and that their use of the ground varies across the two populations studied here. These differences might be attributable to the presence of leopards in one of the landscapes limiting baboon terrestriality to "safer" periods of the day. Whilst further research is needed, these results indicate that predator species is a key contributor to baboons' landscapes of fear, and that risk might have a greater impact on their temporal rather than spatial partitioning behaviours. These insights contribute to our growing understanding of complex community ecology dynamics as well as the emergence and evolution of behaviours.

Statement of Authorship for Chapter Three

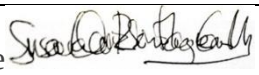
Title of paper	Primate terrestriality: Using camera trap data to explore the effects of ecology, season, diel cycles, and risk on activity patterns in chacma baboons (*Papio ursinus*).
Publication status	Unpublished and unsubmitted work written in a manuscript style
Publication details	Hammond, P., Gaynor, K., Easter, T., Biro, D., & Carvalho, S. (In Preparation). Primate terrestriality: Using camera trap data to explore the effects of ecology, season, diel cycles, and risk on activity patterns in chacma baboons (*Papio ursinus*).

Student Confirmation

Student name	Philippa Hammond		
Contribution to the paper	Philippa Hammond: conceptualization, methodology, data collation and management, formal analysis, data visualization, interpretation, write-up. Kaitlyn Gaynor: data collection and sharing, support with methodology, review, and editing. Tara Easter: data collection and sharing, support with methodology, review, and editing. Dora Biro: support with conceptualization, methodology, formal analysis, review, and, editing. Susana Carvalho: support with conceptualization, methodology, formal analysis, review, and editing.		
Signature 		Date	29/08/2022

Supervisor Confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor name and title: Susana Carvalho, Professor		
Supervisor comments: I confirm the information provided is accurate		
Signature 	Date	30/08/2022

Chapter Four

The influence of carnivore diversity on baboon terrestriality and diel activity patterns across eastern and southern Africa

Prey species can use spatial and temporal partitioning to avoid predators in a landscape. Arboreality in primates adds an extra dimension to their predator avoidance strategy, providing a spatial refuge during time periods of higher risk. For example, all primates sleep in trees or elevated sites at night and some will delay their descent to the ground in the morning when carnivores have been active nearby. In this study, we use camera trap data to explore circadian patterns in baboon terrestriality across 10 sites in southern and eastern Africa. We investigate variation in these patterns across the different populations and in relation to predator prevalence and diversity at each site. We find that there is a high degree of overlap in the activity patterns of baboons across sites, driven largely by their diurnality. However, our findings indicate that a reduced carnivore guild – and particularly the absence of leopards – might release restrictions on baboon terrestriality, facilitating greater use of the ground during crepuscular and nocturnal hours. Our study highlights some of the limitations and considerations that must be incorporated into multi-site camera trap studies and opens new avenues for site-specific and longitudinal research into the effects of predation risk on primate terrestriality.

4.1 Introduction

In any ecosystem, partitioning along various niche axes provides a mechanism for species to minimise the costs of competition and predation (Carothers, Jaksić, & Jaksic, 1984; Macandza, Owen-Smith, & Cain, 2012; Schoener, 1974). Spatial partitioning strategies include herbivores spreading out over a landscape to maximize foraging opportunities (e.g. Macandza et al., 2012) or prey species avoiding carnivores (e.g. Owen-Smith, 2019). However, because spatial segregation can incur the loss of valuable resources, animal species may also utilise temporal partitioning (e.g. Searle et al., 2021). For instance, many large African carnivores are nocturnal or crepuscular, maximising their hunting efficiency by exploiting reduced visibility for prey species during these hours (Hayward & Slotow, 2009), but they must also balance this with avoiding competition and kleptoparasitism from other predators (Havmøller et al., 2020; Searle, Smit, Strampelli, et al., 2021). Meanwhile, many prey species attempt to minimise their overlap with predator activity by confining their foraging and travelling to daylight hours and sleeping in burrows to avoid detection, although these behaviours vary by taxa and are influenced by other factors such as habitat type, lunar cycles, and visual acuity (Anderson, 1998; Caro, 2005; Palmer et al., 2017; Palmer, Gaynor, et al., 2022; Prugh & Golden, 2014). These strategies can be explored within a "dynamic landscape of fear" framework in which predator behaviour interacts with ecological variables to create spatial hotspots of perceived risk that vary across temporal cycles and influence prey behaviour (Palmer, Gaynor, et al., 2022).

Across primate species, many behaviours are thought to be driven by risk of predation, including diurnal activity patterns (Hill, 2006b), arboreal sleep sites (Anderson, 1998; Bidner et al., 2018), and limited use of the ground even during daylight hours (Campbell et al., 2005; Hammond, Lewis-Bevan, Dora Biro, & Carvalho, 2022; Mourthé et al., 2007; Nowak et al., 2014; Souza-Alves et al., 2019). Trees act as refugia from most large predators, even those with some arboreal capabilities.

This is because primates can both evade detection amongst their leaves and also use terminal branches and gaps between trees as escape routes (Cant, 1992). Using arboreal and other elevated sleep sites, such as cliffs, appears to be a highly conserved trait amongst primates, with the notable exception of humans and occasional instances of terrestrial nest-building in gorillas and chimpanzees (Coolidge & Wynn, 2006; Hernandez-Aguilar & Reitan, 2020; Koops, McGrew, Matsuzawa, & Knapp, 2012). Diurnal arboreality, however, is a more flexible behaviour, with levels of actual and perceived risk – amongst other ecological factors – influencing both the frequency and type of activities that occur on the ground (Campbell et al., 2005; Hammond et al., 2022; Monteza-Moreno, Crofoot, Grote, & Jansen, 2020).

Baboons (genus *Papio*) are some of the most terrestrial non-human primates, although their terrestrial activity is almost entirely confined to daylight hours (Bidner et al., 2018; Fischer et al., 2019; Markham et al., 2016). Baboons' use of the ground likely facilitates longer distance travel and access to a broader range of foraging opportunities than if they remained in the trees, although both the consequences and ecological drivers of terrestriality have been underexplored. Studies of baboon behaviour have typically been carried out at the troop level. This has largely been due to a focus on behavioural research, as well as the time, labour, and logistical constraints involved in habituating and studying troops of wild primates (see Chapter Two for further discussion). Such methods have produced detailed and often longitudinal data on the ecology, activity budgets, social dynamics, and genetics of troops from sites across Africa (Alberts et al., 2012; Cheney et al., 2004; Fischer et al., 2019).

There are six phylogenetic baboon species; chacma (*P. ursinus*), yellow (*P. cynocephalus*), kinda (*P. kindae*), olive (*P. anubis*), Guinea (*P. papio*), and hamadryas (*P. hamadryas*). Extensive observation of multiple troops across all six species has revealed systematic differences in their social structures.

A key difference is the male philopatry of the hamadryas and Guinea baboons compared to the female philopatry of the "COKY" baboons (chacma, olive, kinda, and yellow). A recent hypothesis suggests that the male philopatry of hamadryas and Guinea baboons might be due to their common ancestor's adaptations to being at the frontier of a rapidly expanding African population (Jolly, 2020). It will take continued behavioural research and collaboration across sites to test and advance such hypotheses. All baboon populations included in this paper come from the female-philopatric "COKY" group of species in which stable female hierarchies form the core of each baboon troop. Long-term studies at multiple sites have demonstrated that the strength of female-female bonds impact both adult females' fitness and that of their offspring (Alberts et al., 2012; Silk et al., 2009; Silk et al., 2010). Whilst the matrilineal structure remains constant, behavioural research has documented social differences both between and within COKY baboon species. For example, recent research indicates that kinda baboons have different sexual signals and behaviours than the other three species; the males engage in less direct and more indirect competition to mate with females, and females have stronger grooming partnerships with males than seen in other COKY baboons (Petersdorf, Weyher, Kamilar, Dubuc, & Higham, 2019). There is also variation in male social behaviours such as age of dispersal from their natal troop as well as levels of aggressiveness and infanticide (Fischer et al., 2019). It will be essential to integrate ecological, behavioural, and genetic data to further explore the underpinnings of these differences in behaviour and their evolutionary roots.

Baboons live in groups that range from tens to hundreds of individuals and they occupy a wide range of habitat types including semi-deserts, grasslands, woodland savannas, humid forests, and Afroalpine grasslands over 3,000 meters above sea level (Fischer et al., 2019). Baboon troops travel between one and ten kilometres a day and spend approximately a third of their time feeding (range:

20.3% - 59.3%), a quarter of their time moving (range: 17.6% - 33.1%), and spread the rest of their time across the broad categories of resting and socialising, dependent on their ecological niche, seasonal changes, and the constraints of time (Dunbar, 1992) Activity budgets are flexible and time alone might not capture the efficiency of baboons' activities. For example, one study that explored variation in activity budgets across groups of different sizes found that a small baboon troop spent much less time feeding than larger troops, but did not have lower efficiency in terms of nutritional uptake because they simply ate faster. This might have been due to higher demands on the smaller group to be vigilant for predators (Stacey, 1986). This highlights how baboon behaviour is influenced by a complex array of factors – some sociological and some ecological – and it is thus important to collect data at multiple scales to understand their behavioural ecology.

Whilst time spent engaged in different activities has been monitored and reported across many baboon troops and subspecies, there has been less standardised collection of data on the proportion of these activities carried out on the ground versus in the trees. This makes it difficult to explore the variation in terrestrial activity within and between baboon subspecies, and how it is affected by variation in predation pressure at broad scales. There is some evidence from observational research that smaller groups of baboons tend to stay closer to trees during the day, whilst larger groups venture into more exposed areas. In the same study, smaller groups were also found to spend more time in elevated positions whilst larger groups spent more time on the ground (Stacey, 1986). These patterns in substrate use are perhaps related to heightened perceived risk in smaller groups, and fall in line with the results presented in Chapter Two of this thesis where heightened perceived risk of humans reduced baboons terrestriality during habituation. Furthermore, as discussed in Chapters Two and Three, there is also evidence of a link between perceived risk, baboon terrestriality, and diel activity patterns, as exemplified by the delayed descent of baboons from riverine sleep sites on

mornings after leopard presence at the site (Bidner et al., 2018). However, such evidence is often limited to observation of immediate effects, and/or behaviours recorded in just a single troop or a few individuals. It is less clear if or how this behaviour manifests at a landscape scale across baboon populations. Researchers have also been methodologically constrained in their ability to explore variation in circadian activity patterns between and within baboon species, as well as how they are influenced by predator species, abundance, and diversity in different landscapes.

These methodological constraints are being lifted by recent and rapid expansion of remote monitoring technologies, such as the use of camera traps to monitor landscapes. For example, one camera trap study has found that capuchins on predator-free islands spend more time on the ground – particularly in the morning and evening – than populations in environments with predators (Monteza-Moreno et al., 2020). This study also indicates that lack of predation pressure encourages larger groups to descend to the ground, particularly including more vulnerable individuals such as juveniles and females, and that capuchins engage in a broader range of activities once on the ground. In this study, we use camera trap data from ten sites across eastern and southern Africa to explore variation in baboon terrestriality in different environments, particularly in relation to the presence and diversity of large carnivore species at each site.

4.1.1 Potential predators of baboons

Several large mammalian carnivores have been identified as potential predators of baboons. Four are identified as baboons' main predators, based on attack and predation rates: leopards *(Panthera pardus)*, lions *(Panthera leo)*, hyenas *(Crocuta crocuta, Hyaena brunnea, H. hyaena)*, and chimpanzees *(Pan troglodytes)* (Cowlishaw, 1994). Four other species evoke baboon behaviours demonstrative of perceived risk (such as vigilance and vocalisations): cheetahs *(Acononyx jubatus)*, wild dogs *(Lycaon pictus)* and black-backed and side-striped jackals *(Canis mesomelas* and *C.*

adustus) (Bettridge & Dunbar, 2012). However, none of the latter group have been reported to actually kill baboons except one population of wild dogs in the Zambezi Valley, Zimbabwe (Dyer, 2018).

Lions and leopards are the best-known predators of baboons, posited as the primary cause of death for juvenile and adult baboons at some study sites and held responsible for the decimation of troops at others, despite a paucity of directly observed events (Busse, 1980; Cheney et al., 2004; Isbell et al., 2018; Pienaar, 1969). Leopards in particular are considered baboons' primary predators and baboons fall comfortably within their preferred prey size of 10 – 40 kg, compared to lions' preference for prey between 190 – 550 kg (Hayward et al., 2006; Hayward & Kerley, 2005). By one estimate, terrestrial primates make up approximately 10% of leopards' diets, compared to just 1% of lions' diets (Isbell, 1994). There is also a growing body of evidence that leopards actively target baboon sleep sites at night or in the early morning (Altmann & Altmann, 1970; Busse, 1980; Cheney, 2004; Cowlishaw, 1994; Isbell, 1990, 2009, 2018), and that baboon behaviour is particularly responsive to leopard activity. For example, baboon mobbing behaviour is usually directed at leopards (Cowlishaw, 1994; Isbell et al., 2018) and one study found that baboons showed strong temporal partitioning with leopards – more so than any other prey species in that landscape (Havmøller et al., 2020). Activities such as baboons' choice, abandonment, and departure time from sleep sites are also significantly affected by leopard activity (Altmann & Altmann, 1970; Bidner et al., 2018; Hamilton, 1982; Matsumoto-Oda, 2015).

To understand the effects of predation pressure on baboons' circadian activity patterns, it is thus important to consider the behavioural ecology and hunting styles of all their potential predators and to evaluate the effects of particular species – for example, leopards – as well as the cumulative impact of multi-predator presence in a landscape. Of the sites included in this study, none are

inhabited by chimpanzees, but they are home to members of Africa's large carnivore guild – lion, leopard, spotted hyaena, cheetah, and African wild dog. Because these species overlap both geographically and dietarily, the completeness and diversity of the carnivore guild at a particular site is expected to affect predators' activity patterns. When sharing a landscape, subordinate predators (for example, cheetahs and wild dogs) are thought to minimise their spatial and temporal overlap with more competitively dominant and kleptoparasitic carnivores (for example, lions and spotted hyenas), resulting in shortened and more flexible periods of activity than the longer continuous activity periods of top predators in the landscape (Durant, 1998; Hayward & Slotow, 2009; Linnell & Strand, 2000; Schoener, 1974; Searle, Smit, Cusack, et al., 2021). Although there is variation across ecosystems and with the lunar cycle, subordinate predators are generally more diurnal than dominant members of the guild but do much of their hunting either at dawn or dusk when it is cooler and visibility is reduced for prey. Top predators are more nocturnal, but they also show peaks of activity around dawn and dusk (Cozzi et al., 2012; Dröge et al., 2017; Hayward & Slotow, 2009). Thus, crepuscular activity is common across the guild, making it an especially risky time for prey species.

4.1.2 Exploring the effects of predator diversity on baboon activity

In this study, we investigate diel patterns in baboon terrestriality, and how they relate to carnivore activity patterns. Using camera trap data from 10 sites across eastern and southern Africa, we explore the extent to which baboon activity differs from site to site, and we analyse the temporal partitioning between baboons and members of the large carnivore guild – spotted hyenas, lions, leopards, cheetahs, and wild dogs – at each site. There is evidence that time spent by baboons' on their core activities – foraging, travelling, socialising, and resting – is constrained by the daylight hours available to them and that predation risk is likely the key factor limiting their temporal flexibility (Hill, 2006b; Hill et al., 2003). We therefore expect baboon activity to follow a relatively conserved

diurnal pattern across sites, but hypothesise that sites with a lower abundance and/or diversity of predators will release some restrictions on baboons' crepuscular and nocturnal activity, allowing them to descend from sleep sites earlier in the morning and/or stay out on the ground later into the evening. As leopards are baboons' primary predator and are known to influence their behaviour around sleep sites, we predict that the absence of leopards from sites will have a particularly strong effect on baboons' terrestrial activity patterns.

4.2 Methods

4.2.1 Camera trap grids

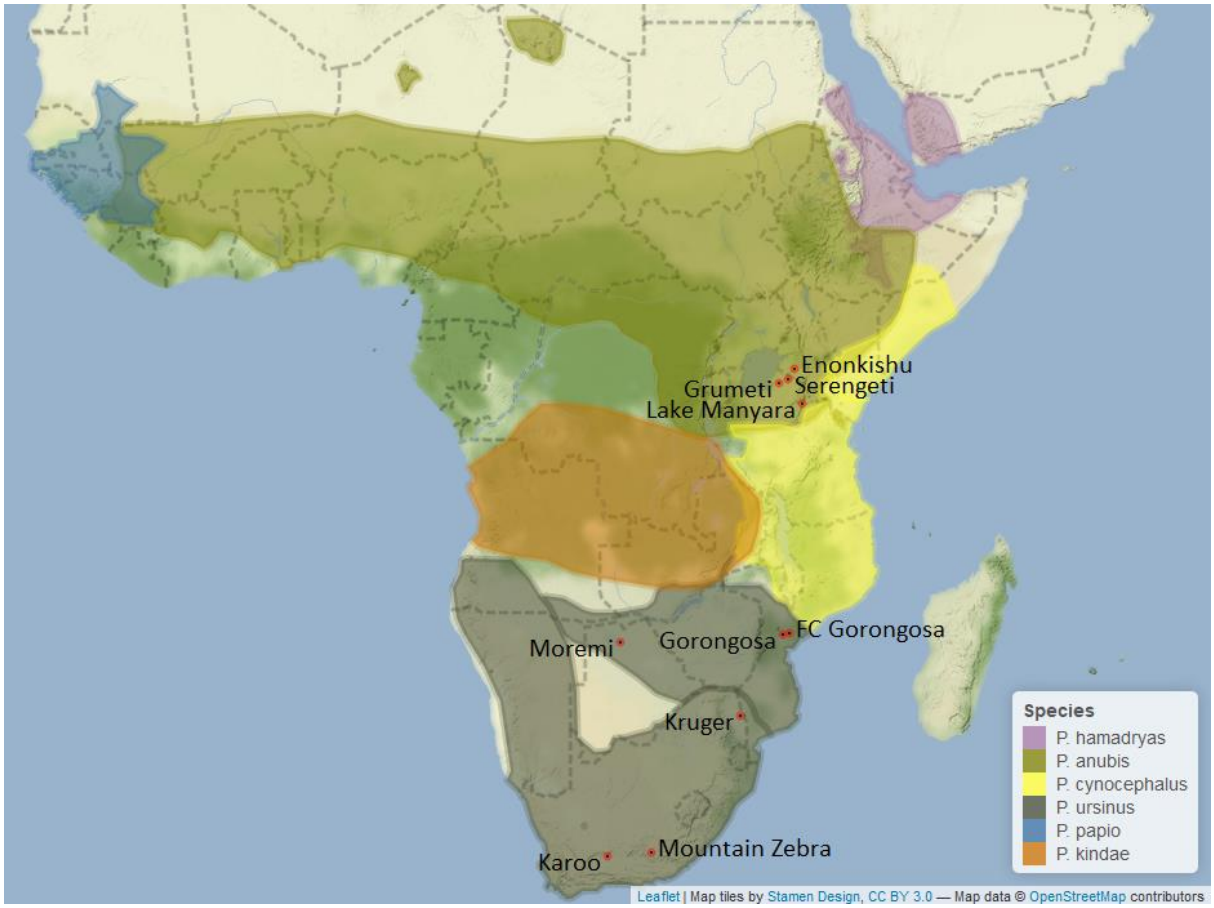


Figure 4.1. *Map showing the locations of the 10 camera trap grid sites included in this study (red dots) overlaid upon the IUCN (2021) distribution of Papio species across Africa.*

Table 4.1. *Details of grid set-up at each of the 10 camera trap grid sites included in this study.*

Site	Grid (km^2)	Camera stations	Study (days)	Habitat description	Baboon species	Carnivores present
†**Enonkishu, KE (Eno)**	~80	16	89	Community conservancy with a structured grazing regime	*P. anubis*	Hyena, lion, leopard, cheetah
†**Serengeti, TZ (Ser)**	1,125	225	1146	Game reserve; open plains and savannah woodlands.	*P. anubis*	Hyena, lion, leopard, cheetah
Grumeti, TZ (Gru)	~1,390	278	386	Game concession; open plains and savannah woodlands.	*P. anubis*	Hyena, lion, leopard, cheetah
‡**Lake Manyara, TZ (Man)**	168	46	~281*	National Park; lakeside alkaline grasslands and Acacia and escarpment woodlands.	*P. anubis*	Hyena, lion, leopard
FC Gorongosa, MZ (FCG)	320	75	129	Sustainable use forestry-concession (rotational harvesting); tall miombo woodlands.	*P. ursinus*	Leopard
Gorongosa, MZ (Gor)	300	60	814	National Park; floodplain and savannah woodlands.	*P. ursinus*	Lion
Moremi, BW (Mor)	550	223	288	Multi-habitat: reserve, wildlife management, grazing. Note: cameras along roads.	*P. ursinus*	Hyena, lion, leopard, cheetah, wild dog
†**Kruger, ZA (Kru)**	~185	37	49	National Park; lowveld savannah. Note: artificial waterholes.	*P. ursinus*	Hyena, lion, leopard, cheetah, wild dog
†**Mt Zebra, ZA (MZ)**	~95	19	213	National Park; Nama-Karoo	*P. ursinus*	Lion, leopard, cheetah
†**Karoo, ZA (Kar)**	~75	15	126	National Park; Nama-Karoo	*P. ursinus*	Lion

**Operating days within each data collection period are calculated based on periods of time where at least one camera was active within a 5-day period. Where equivalent data were unavailable, operating days were estimated from published information. †Data gathered from LILA BC. ‡Data published in Clauss et al. (2021). All other data sets provided by researchers at each site.*

Data for this study were compiled from 10 different camera trap grids (henceforth, "sites") located across five African countries; Kenya, Tanzania, Mozambique, Botswana, and South Africa (see Figure 4.1 above). The grids were established to monitor terrestrial activity across faunal communities, with all cameras placed approximately 0.5 – 1m above the ground. Thus, all baboon activity captured across the grids represents terrestrial activity. Grids were established by different teams of researchers and over different time periods, although all Snapshot Safari sites were set up

according to the same methodology and the Gorongosa grid is also closely based on the original Snapshot Safari set-up (Pardo et al., 2021). Several factors vary from site to site, including baboon species, the broader faunal community in which baboons and carnivores reside, habitat, seasonality, duration of data collection, and grid features. Table 4.1 summarises the set-up details for each grid included in the study and further information can be found in Appendix C. For the five sites that are part of the "Snapshot Safari" network, data were gathered from the Labelled Information Library of Alexandria: Biology and Conservation (LILA BC, https://lila.science/datasets). Data from Lake Manyara are publicly available from a previous publication (Clauss, Scriba, Kioko, Ganzhorn, & Kiffner, 2021). All other data sets were gathered from researchers working at sites.

4.2.2 Data cleaning and analyses

The images collected at each site were classified by researchers and citizen scientists, and in some cases through a combination of AI and citizen science (Miao et al., 2021; Pardo et al., 2021; Swanson et al., 2015). The classifications were compiled into raw data sets of time-stamped species detections from every image captured at every site. Variation in camera settings across sites included the number of photos taken per motion-trigger, and the length of forced delay between capture events. We thus cleaned the data using a 30-minute interval to define independent detections of species at each camera station. This standardises the formatting of the data and avoids inflated detection rates of species based on captures of the same individuals or large groups in short periods of time (Sollmann, 2018).

4.2.2.1 Relative abundance and distribution of species at each site

To get a sense of the relative abundance of baboons and their predators at each site, we first looked at the total number of species detected at each site, and their proportional representation in the camera

trap detections. We then calculated the proportion of total detections represented by baboons and large carnivores (spotted hyenas, lions, leopards, cheetahs, and wild dogs) amongst the faunal community at each site. We also calculated the proportion of camera trap stations at which each of these species was detected, providing a measure of their distribution across each grid.

4.2.2.2 Assessing variation in baboon terrestrial activity across sites

To explore how similar baboon activity patterns were across different sites, we used the "overlap" package in R (Ridout & Linkie, 2009). For every paired combination of baboon sites, we calculated a coefficient of temporal overlap, d-hat, where 0 represents no temporal overlap and 1 represents complete overlap.

4.2.2.3 Temporal overlap between activity of baboons and large carnivores

To explore the extent of temporal overlap between baboon terrestrial activity and that of large carnivores, we again used the "overlap" package in R (Ridout & Linkie, 2009). We calculated the d-hat value for overlap between baboons and each large carnivore species present at a given site, as well as for the combined set of large carnivore detections at the site.

For all overlap analyses, we used the d-hat1 formula for sample sizes under 50 independent detections and the d-hat4 formula for those over 50. We used bootstrapping with 10,000 resamples to estimate 95% confidence intervals for each overlap estimate and we used the *compareCkern* function in the "activity" package in R (Rowcliffe, 2022) to estimate the probability that the activity patterns in each pair came from the same distribution. This p-value was only calculated for sites where both sets of detections had $n > 30$.

4.2.2.4 Plotting species' diel terrestrial activity patterns

To visualise the diel terrestrial activity patterns of baboons and large carnivores, we plotted the kernel density of detections across the 24-hour cycle. To account for the cyclical nature of time and variation in sunrise and sunset times across sites and seasons, all times were scaled to radians so that $\pi/2$ corresponds to sunrise and $3\pi/2$ to sunset.

4.2.2.5 Baboon terrestriality during crepuscular hours

Finally, to explore baboon terrestriality in relation to sunrise and sunset, we analysed the first and last daily detections of baboons across each grid. Sunrise and sunset times for each site were identified using the website https://www.timeanddate.com/sun/ so that timestamped images could be classified in terms of minutes after sunrise or before sunset. We then ran an ANOVA to explore how first and last daily baboon detections varied by site. All analyses were conducted in R v4.1.1 (R Core Team, 2021).

4.3 Results

4.3.1 Relative abundance and distribution of species at each site

In total, our data set was collected from 994 camera stations established at 10 sites across five African countries. Table 4.2 below summarises the number of detections and the composition of mammal communities monitored at each grid site. It includes numbers of detections of humans as an indicator of relative levels of anthropogenic activity at each site. Moremi, for example, has a high number of human detections, likely due to the placement of cameras along roads at this site. Table 4.3 highlights the proportional representation of baboons and large carnivores at each site, as well as the percentage of camera trap stations at which they were detected during each study period.

Table 4.2. *Species detections across each camera grid, as well as a summary of the number of mammalian species and the five most prevalent non-human mammals detected at each site. "UNK" refers to unknown, where data are not available. Asterisks reference cases where only independent detections, rather than total detections, are known from the available data.*

Site	**Detections:**		**Non-human mammals:**					
	Humans	**Animals**	**N**	**Five most prevalent species (% of non-human detections)**				
Eno	332	4,597	34	Impala (17%)	Zebra (15%)	Warthog (13%)	Wildebeest (10%)	Domestic (9%)
Ser	12,237	417,502	42	Wildebeest (28%)	Zebra (21%)	T. gazelle (16%)	Buffalo (4%)	Hartebeest (4%)
Gru	3,925	172,441	52	Wildebeest (20%)	Zebra (15%)	Buffalo (7%)	Impala (7%)	Baboon (4%)
Man	UNK	13,800*	29	Baboon (16%)	Impala (15%)	Vervet (9%)	Elephant (8%)	Wildebeest (7%)
FCG	320	1,480*	33	Duiker (18%)	Mongoose (11%)	Genet (10%)	Baboon (10%)	Civet (8%)
Gor	49	210,964	37	Waterbuck (26%)	Baboon (21%)	Warthog (16%)	Impala (11%)	Bushbuck (9%)
Mor	35,704	26,912	57	Elephant (13%)	Impala (9%)	Hyena (7%)	Giraffe (4%)	Steenbok (3%)
Kru	175	1,591	40	Impala (36%)	Elephant (12%)	Zebra (7%)	Buffalo (6%)	Giraffe (6%)
MZ	510	5,622	42	Zebra (32%)	Kudu (9%)	Springbok (8%)	Wildebeest (6%)	Hartebeest (6%)
Kar	83	2,511	29	Gemsbok (26%)	Kudu (15%)	Hartebeest (14%)	Eland (12%)	Baboon (7%)

Table 4.3. *Percentage of detections in which baboons and large carnivore species were captured at each site (white rows) and percentage of cameras across each grid where each species was detected (grey rows). "UNK" refers to unknown, where data are not available. Asterisks reference cases where only independent detections, rather than total detections, are known from the available data.*

Site	**Total:** Detections Stations	**Baboon** (%) (%)	**Hyena** (%) (%)	**Lion** (%) (%)	**Leopard** (%) (%)	**Cheetah** (%) (%)	**Wild dog** (%) (%)
Eno	**4,597**	3.20	6.37	0.13	0.28	0.02	0.00
	16	69	69	31	31	6	0
Ser	**417,502**	0.48	1.68	1.24	0.07	0.40	0.00
	225	44	98	88	36	62	0
Gru	**172,441**	4.42	0.93	1.07	0.15	0.15	0.00
	278	59	78	77	45	42	0
Man	**13,800***	15.92	2.57	0.34	0.36	0.00	0.00
	46	UNK	UNK	UNK	UNK	UNK	UNK
FCG	**1,480***	9.93	0.00	0.00	0.54	0.00	0.00
	75	75	0	0	8	0	0
Gor	**210,964**	21.03	0.00	0.04	0.00	0.00	0.00
	60	100	0	32	0	0	0
Mor	**26,912**	0.30	7.18	1.43	2.27	0.02	2.59
	223	16	93	34	73	2	49
Kru	**1,591**	2.39	4.65	0.50	0.50	0.06	0.13
	37	24	49	11	14	3	5
MZ	**5,622**	5.23	0.00	0.84	0.02	0.05	0.00
	19	79	0	32	5	5	0
Kar	**2,511**	7.09	0.00	0.28	0.00	0.00	0.00
	15	87	0	27	0	0	0

On average, baboons made up 7% of camera trap detections, but this ranged from 0.30% in Moremi to 21.03% in Gorongosa. There was also a broad range in the percentage of camera stations at which baboons were detected (mean ± SD: 61.44 ± 26.80%). In Moremi, they were only captured at 16% of stations, whilst in Gorngosa they were detected at 100% of stations.

Large carnivores represented, on average, 3.69 ± 3.94% of non-human detections across all grids.

This ranged from 0.04% of detections in Gorongosa to 13.49% in Moremi, with hyenas generally representing the majority of carnivore detections at sites where they occur. Despite making up small percentages of overall species detections at each site, large carnivores were often detected across broad portions of the camera grids. The average distribution of hyena detections, for example, was across 77.4 ± 17.58% of camera trap stations (range: 49% in Kruger – 98% in Serengeti) and the average distribution of leopard detections was across 30.29 ± 22.28% of stations (range: 5% in Mt Zebra – 73% in Moremi).

4.3.2 Variation in baboons' terrestrial activity patterns between sites

Table 4.4 shows the coefficients of overlap for baboon activity between each pair of grid sites. There were high degrees of overlap across most pairings. In most cases, baboon activity at any given site overlapped more than 80% with the activity patterns at other sites. Baboon activity at Moremi and Karoo showed the least overlap with other sites. The average degree of overlap between baboon activity at Moremi and other sites was 0.68, and for Karoo it was 0.72.

Table 4.4. *Overlap coefficients (d-hat) between baboon populations at each site (where 0 represents no temporal overlap and 1 represents complete overlap). Confidence intervals are shown in parentheses, estimated using smoothed bootstrapping with 10,000 resamples. Highlighted cells indicate significant differences in activity patterns: light blue represents a probability < 0.05 and dark blue represents a probability < 0.001 that patterns came from the same distribution. Cells highlighted in grey had too few detections (<30) to calculate a p-value.*

	Kenya	*Tanzania*			*Mozambique*		*Botswana*	*South Africa*		
Site	**Eno**	**Ser**	**Gru**	**Man**	**FCG**	**Gor**	**Mor**	**Kru**	**MZ**	**Kar**
Eno	-	0.84 (0.75 - 0.92)	0.87 (0.77 - 0.94)	0.84 (0.74 - 0.92)	0.81 (0.70 - 0.90)	0.78 (0.64 - 0.92)	0.64 (0.49 - 0.77)	0.85 (0.69 - 0.96)	0.88 (0.77 - 0.97)	0.74 (0.63 - 0.83)
Ser			0.89 (0.87 - 0.91)	0.91 (0.88 - 0.94)	0.92 (0.86 - 0.97)	0.81 (0.72 - 0.90)	0.66 (0.57 - 0.76)	0.83 (0.69 - 0.93)	0.91 (0.85 - 0.96)	0.71 (0.63 - 0.79)
Gru				0.89 (0.86 - 0.91)	0.88 (0.82 - 0.94)	0.85 (0.84 - 0.87)	0.71 (0.62 - 0.80)	0.84 (0.70 - 0.94)	0.85 (0.78 - 0.91)	0.80 (0.72 - 0.87)
Man					0.96 (0.90 - 0.99)	0.82 (0.80 - 0.84)	0.69 (0.60 - 0.79)	0.87 (0.73 - 0.96)	0.88 (0.82 - 0.94)	0.73 (0.66 - 0.81)
FCG						0.84 (0.79-0.89)	0.71 (0.60 - 0.81)	0.84 (0.70 - 0.95)	0.86 (0.78 - 0.94)	0.75 (0.66 - 0.83)
Gor							0.86 (0.77 - 0.93)	0.80 (0.65 - 0.90)	0.74 (0.68 - 0.81)	0.75 (0.68 - 0.81)
Mor								0.67 (0.49 - 0.81)	0.59 (0.48 - 0.71)	0.62 (0.52 - 0.71)
Kru									0.85 (0.70 - 0.96)	0.69 (0.55 - 0.81)
MZ										0.70 (0.60 - 0.79)
Kar										-
Mean	**0.81**	**0.83**	**0.84**	**0.84**	**0.84**	**0.81**	**0.68**	**0.80**	**0.81**	**0.72**

4.3.3 Temporal overlap between activity of baboons and large carnivores

Table 4.5 shows the overlap coefficients between baboon activity and large carnivore activity at each site. These results demonstrate significant temporal partitioning between baboons and carnivores, particularly in the cases of the three more nocturnal carnivores (spotted hyena, lion, and leopard). Baboons show the least temporal overlap with spotted hyenas (mean = 0.22) and the most with wild

dogs (mean = 0.58).

Table 4.5. *Overlap coefficients (d-hat) between baboons and large carnivores at each site (where 0 represents no temporal overlap and 1 represents complete overlap). Confidence intervals are shown in parentheses, estimated using smoothed bootstrapping with 10,000 resamples. Highlighted cells indicate significant differences in activity patterns: light blue represents a probability < 0.05 and dark blue represents a probability < 0.001 that patterns came from the same distribution. Cells highlighted in grey had too few detections (<30) to calculate a p-value.*

	Spotted hyena	**Lion**	**Leopard**	**Cheetah**	**Wild dog**	**All carnivores**
Eno	0.14 (0.07 - 0.22)	0.24 (0.03 - 0.48)	0.28 (0.10 - 0.48)	(1 detection)	-	0.15 (0.08 - 0.23)
Ser	0.28 (0.26 - 0.30)	0.69 (0.67 - 0.71)	0.24 (0.19 - 0.29)	0.53 (0.50 - 0.56)	-	0.41 (0.40 - 0.43)
Gru	0.35 (0.33 - 0.38)	0.71 (0.69 - 0.74)	0.39 (0.33 - 0.44)	0.54 (0.48 - 0.59)	-	0.51 (0.49 - 0.53)
Man	0.08 (0.05 - 0.10)	0.12 (0.05 - 0.20)	0.30 (0.19 - 0.40)	-	-	0.11 (0.08 - 0.12)
FCG	-	-	0.19 (0.00 - 0.42)	-	-	0.19 (0.00 - 0.42)
Gor	-	0.32 (0.21 - 0.42)	-	-	-	0.32 (0.21 - 0.42)
Mor	0.16 (0.11 - 0.21)	0.20 (0.13 - 0.27)	0.30 (0.24 - 0.36)	(4 detections)	0.44 (0.36 - 0.52)	0.22 (0.17 - 0.28)
Kru	0.28 (0.16 - 0.41)	0.21 (0.00 - 0.49)	0.35 (0.10 - 0.62)	-	-	0.30 (0.18 - 0.42)
MZ	-	0.50 (0.34 - 0.65)	(1 detection)	(3 detections)	-	0.47 (0.32 - 0.61)
Kar	-	0.53 (0.27 - 0.79)	-	-	-	0.53 (0.27 - 0.79)
Mean	**0.22**	**0.39**	**0.29**	**0.53**	**0.44**	**0.32**

4.3.4 Diel terrestrial activity patterns

Figure 4.2 shows the diel activity patterns of baboons in relation to each of the large carnivore species present at each site (see Appendix D for a comparison with combined carnivore activity at

each site). As can be seen in the figure, baboons across all sites are almost entirely diurnal. Their terrestrial activity patterns are generally unimodal, and most populations are most active on the ground around midday, with declines towards sunrise and sunset. Notable exceptions are (a) Gorongosa, where baboon activity peaks soon after sunrise, (b) Moremi, where baboons show a bimodal terrestrial activity pattern with the greatest peak in activity soon after sunrise, and (c) Karoo, where there is more nocturnal terrestrial activity than detected at any other site.

The figure also demonstrates that spotted hyenas, lions, and leopards are predominantly nocturnal at most sites (except for Serengeti and Grumeti lions), whilst cheetahs and wild dogs are more active during daylight hours. The activity patterns of several carnivores across the sites demonstrate a peak in activity shortly before sunrise or after sunset. This results in a combined peak of activity around these times at sites with multiple large carnivore species. The figure also highlights that a full large carnivore guild was only detected at three sites (Grumeti, Moremi, and Kruger), whilst four sites were home to either three or four carnivore species. Sites where only one large carnivore species was detected were Gorongosa (lion), Forestry Concession Gorongosa (leopard), and Karoo (lion).

4.3.5 Baboon terrestriality during crepuscular hours

Figure 4.3 plots the first and last daily detections of baboons across each grid, in relation to sunrise and sunset. There are two sites at which baboons are detected significantly earlier on the ground than across other sites; on average, Grumeti baboons first appear on the grid 53 minutes after sunrise, and Gorongosa baboons 38 minutes after sunrise, compared to a group mean of approximately 240 minutes after sunrise. Similarly, Grumeti baboons are last detected on the ground 69 minutes before sunset and Gorongosa baboons 84 minutes before sunset, compared to a group average of approximately 280 minutes before sunset.

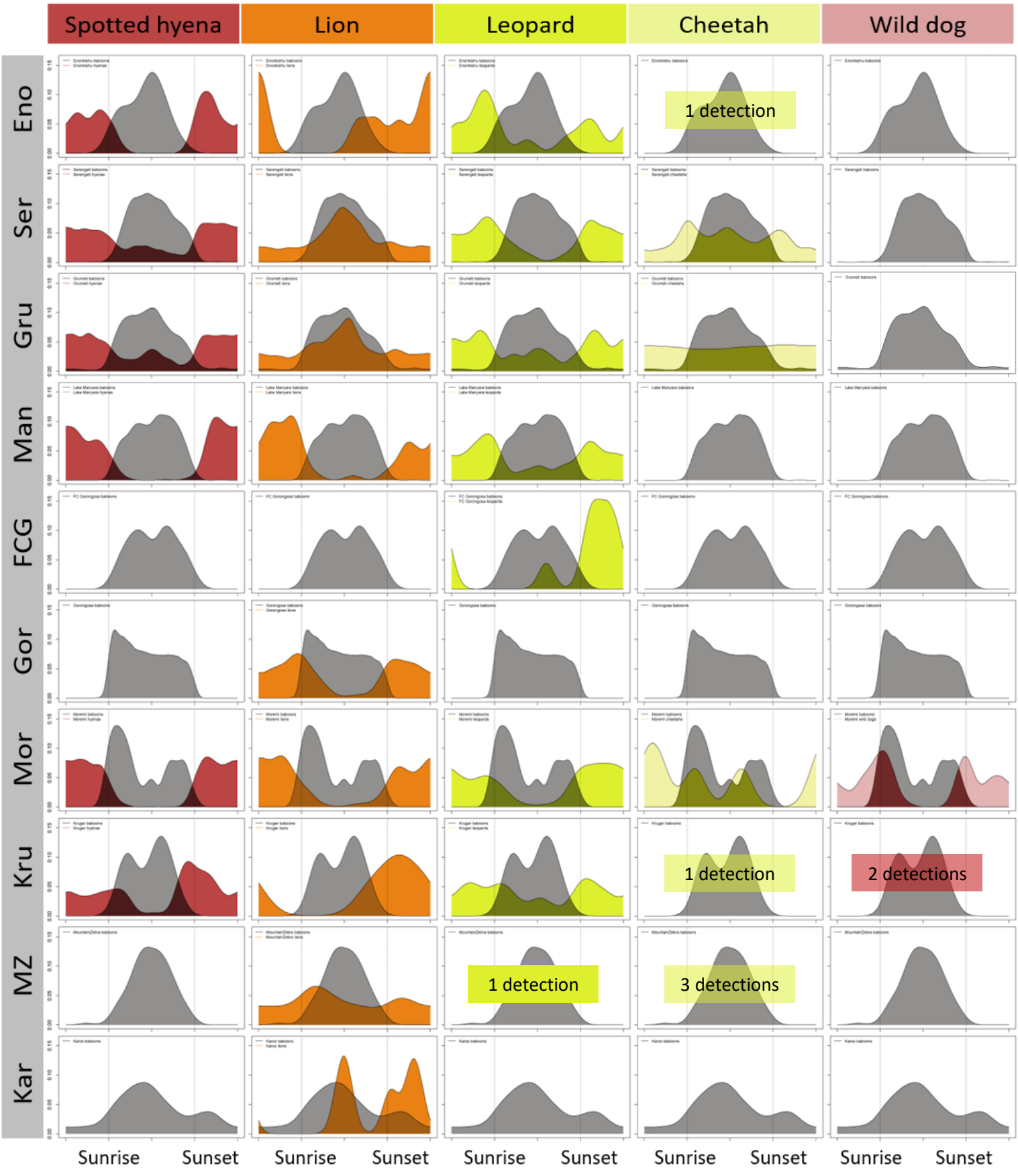


Figure 4.2. *Graphs depicting the temporal overlap between detections of baboons (grey) and spotted hyenas (red), lions (orange), leopards (yellow), cheetahs (light yellow) and wild dogs (light red) at each camera grid site. Dotted vertical lines represent sunrise and sunset, standardised across sites and seasons.*

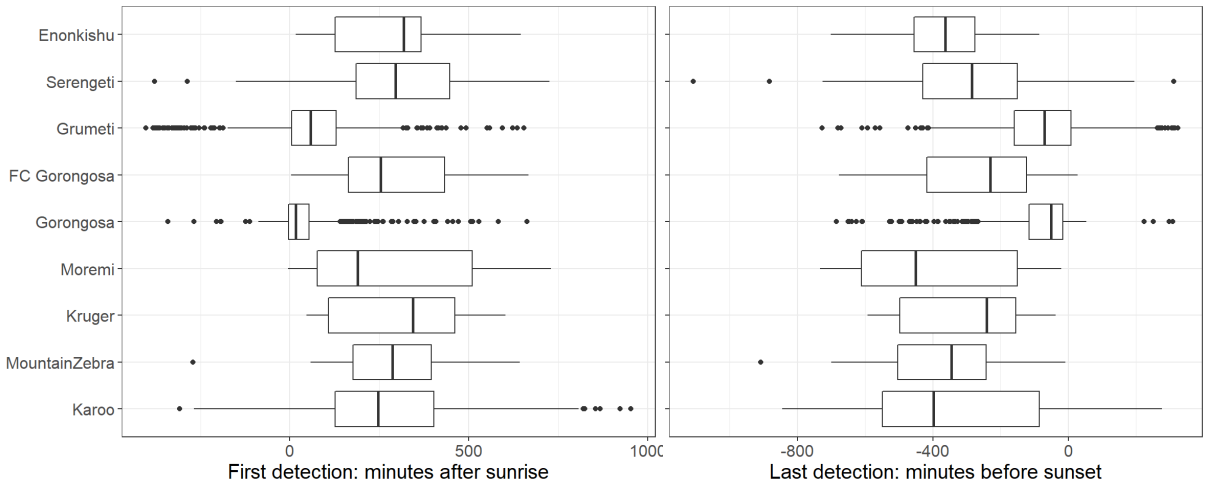


Figure 4.3. *Graph showing the distribution of first and last daily detections of baboons at each site, in relation to sunrise and sunset. Lake Manyara is not included as timestamped data were unavailable.*

4.4 Discussion

In this study we explored variation in circadian patterns of baboon terrestriality and its relationship to large carnivore activity, using camera trap data from 10 sites in eastern and southern Africa. It should be noted that many factors affect the likelihood and rate of species detections across camera grids. Beyond its abundance in a landscape, a species is more likely to be detected by cameras if it is large bodied and/or group-living rather than solitary (Palencia et al., 2022; Treves, Mwima, Plumptre, & Isoke, 2010; Wong et al., 2019). Furthermore, species detections across a grid will depend upon the habitat in which it has been established, as well as set-up details such as whether cameras have been placed at random points in the environment or along specific landscape features, as well as camera height and the camera models used (Palencia et al., 2022). Additionally, for grids with fewer stations, each camera has more of an influential effect on the overall activity patterns captured across the grid, creating potentially misleading patterns in the data (Searle, Smit, Strampelli, et al., 2021). These

factors are taken into consideration in our interpretation of results below.

Baboons were present at all 10 sites included in this study, making up an average of 7% of non-human terrestrial activity captured across grids, with a range from 0.3% of detections in Moremi to 21% of detections in Gorongosa. The high level of baboon activity captured in Gorongosa was also widely distributed across the grid, with baboons detected at 100% of camera stations. At most other sites, baboons were detected at well over 50% of stations, but they were only detected at 24% of Kruger stations and 16% of Moremi stations.

These detection and distribution figures indicate that Gorongosa holds a relatively large and widespread population of baboons, and/or that Gorongosa baboons live in larger groups or spend more time on the ground than those at other sites. However, grid features are likely to have been influential on species detection rates, particularly the low representation of baboons across the Moremi grid. In Moremi, all cameras were placed along sandy roads, and the high level of human (including vehicle) detections suggests that the roads were often busy during the day. Whilst there is evidence from other studies that baboons preferentially utilise roads for travel (Kiffner et al., 2022; Strandburg-Peshkin et al., 2017), it seems that anthropogenic activity might have restricted baboons' use of roads in Moremi.

Road-based camera placement might also explain the higher rates of large carnivore detections in Moremi than at other sites (13.5% compared to a mean of 3.7% of detections across all sites). Because most human traffic in Moremi is diurnal (see Appendix D), nocturnal species are likely disproportionately represented amongst Moremi grid detections compared to other sites. Whilst carnivores make up relatively small portions of the detections across each grid, these detections are generally widespread across the stations at each site. Gorongosa, for example, had the lowest

proportional representation of large carnivores (0.04% of all detections), but these were spread out over almost a third of the camera stations in the landscape. The most widely distributed carnivore at a given site was the spotted hyena in Serengeti, where hyenas were detected at 98% of all stations, despite representing only 1.63% of all activity detected across the grid.

There are many factors to be considered when inferring carnivore activity from camera trap data. For example, there is evidence that larger mammals are easier to detect, but that detection probabilities are lower for species that are predominantly nocturnal or solitary, and that different camera models perform differently across these metrics (Palencia et al., 2022; Treves et al., 2010; Wong et al., 2019). It is thus possible that carnivore activity is underrepresented at some – or all – of the grids in this study. However, patterns of low relative activity but broad distribution of carnivores across each grid serve as a reminder that species at the top of the trophic guild often represent a small fraction of mammalian biomass in any ecosystem but can have large home ranges and a broad impact on prey species across the landscape. Indeed, certain carnivore species were only captured by single camera detections at some sites (see Figure 4.2), but just confirming their presence in the landscape implies that they could have a significant influence on prey species' behaviour at that site.

It is also important to consider the completeness of the carnivore guild and intraguild competition at each site. When there are multiple large carnivore species in an environment, complex and dynamic rules of avoidance and attraction might alter their activity patterns, with downstream consequences for prey species. For example, in Ruaha-Rungwa, Tanzania, camera trap data suggest that leopards avoid lions whilst spotted hyena appear to follow both leopards and lions (Searle, Smit, Strampelli, et al., 2021). Elsewhere in Tanzania, evidence suggests that leopards might use temporal partitioning to avoid kleptoparisitism from spotted hyenas (Havmøller et al., 2020). These dynamics are further impacted by carnivore avoidance of humans in increasingly anthropogenic environments. For

example, in the Ruaha-Rungwa study, leopards in more human-impacted areas were most active in the hours after midnight, compared to leopards in the acacia and miombo woodlands whose activity peaked between 21:00 – 22:00 and 04:00 – 05:00 (Searle, Smit, Strampelli, et al., 2021). These complex interactions must be taken into consideration when evaluating the effects of risk on particular prey species.

So, how does baboon terrestriality vary in relation to carnivore activity at the sites included in this study? Across most sites, terrestrial detections of baboons occurred almost entirely during the day and followed a unimodal pattern with a peak around midday (see Figure 4.2). These commonalities result in a high degree of temporal overlap between baboon activity when compared across most sites. The two exceptions are Moremi and Karoo, where the average degree of overlap with other sites is 0.68 and 0.72 respectively. Possible drivers of these activity patterns are discussed below.

As can be seen in the visualisation of their activity pattern (see Figure 4.2), Moremi baboon detections follow an unusual bimodal pattern with a peak around sunrise and another smaller peak in the late afternoon. This pattern – particularly the high proportion of baboon detections occurring around sunrise – is unexpected in a landscape with a complete large carnivore guild and strong leopard presence. The Moremi baboon activity seemingly falls within a peak period of carnivore activity. However, as was highlighted above, baboons represent a very small proportion of the overall animal activity detected in Moremi (0.3% of detections) compared to other sites (mean = 7%) and they are detected across a much smaller portion of the Moremi grid (16% of camera stations) than others (mean = 61%). This might indicate that baboons in Moremi are using more spatial partitioning with leopards than at other sites, perhaps only travelling terrestrially in certain areas, and only when necessary. It is also possible that these results are dictated by the placement of cameras along roads and high levels of human activity deterring diurnal species from these areas, as discussed

previously. These possibilities require further site-specific research.

In Karoo, baboon activity patterns are more nocturnal than those at other sites. Compared to less than 1% of baboon detections at all other sites, 11% of Karoo baboon detections were captured between the end of dusk and the onset of dawn. This increase in nocturnal activity might be due to the fact that lions are the only large carnivore detected at Karoo, and only in very low numbers. Furthermore, Karoo is one of only two sites at which no leopards were detected. Perhaps the absence of baboons' primary predator reduces the overall perceived risk in this landscape, facilitating more nocturnal terrestriality in baboons than at other sites. Further study of the nocturnal images from Karoo might provide insights into the behaviours occurring during these periods, and whether they are driven by seasonality, temperature, lunar cycle, or other ecological features in the landscape.

Gorongosa is the other site at which no leopards were detected. Although Gorongosa baboon activity overlapped greatly with the baboon activity seen at other sites, its distribution is unusual in that it peaks soon after sunrise, rather than around midday like most other sites (see Figure 4.2). It is also clear from the analysis of daily detections that Gorongosa baboons are detected on the ground much earlier in the morning (38 minutes after sunrise) than baboons at other sites (mean = 240 minutes). Perhaps the absence of leopards (or the generally low presence of predators) allows baboons to descend from their sleep sites earlier in the morning and to be more active on the ground throughout the day compared to baboons at other sites. The fact that baboons make up more than 21% of camera trap detections in Gorongosa suggests that the landscape either hosts a larger population and/or facilitates more terrestrial travel in baboons than at other sites, both of which are likely consequences of reduced predation pressure in the environment.

Whilst a comparative study like this one is inherently limited by differences in the ecology and grid

set-up across sites, Gorongosa provides an opportunity for longitudinal analysis of the impact of leopards and a more diverse carnivore guild on baboon behaviour. Since data were collected for this study, wild dogs, leopards, and hyenas have been reintroduced to the Gorongosa ecosystem. Ongoing data collection from the camera trap grid will provide unique insights into the changing behaviours of baboons – amongst other prey species – as each of these apex predators enters and alters the landscape. Future questions – for both longitudinal and comparative research – include exploring the impact of predator diversity on group size and cohesion, variation in the types of behaviours that occur on the ground in lower risk landscapes, and other selection pressures driving terrestriality earlier in the morning and/or later at night.

Traditional observational studies have collected data on baboon activities throughout daily follows, but have often focussed on the proportion of time dedicated to these activities (categorised as feeding, moving, resting, and socialising), rather than circadian patterns in their distribution (Dunbar, 1992; Eley et al., 1989; Post, 1981). Some general patterns that have been reported include an increasing or sustained high level of feeding throughout the day until mid-afternoon, after which feeding rates taper off slightly (Davidge, 1977; Post, 1981), although some studies also report a mid-day "resting" period during which feeding behaviour dips (Forthman-Quick, 1986; Stoltz & Saayman, 1970). Many emphasise that foraging requirements are the primary driver of the relative time and dispersal of non-foraging activities throughout the day. Foraging requirements are driven by seasonal factors and the types and homogeneity of habitats from which baboons are accessing their resources, and then dictate the time available for other activities such as resting and socialising (Altmann & Muruthi, 1988; Dunbar, 1992; Hill et al., 2003; Post, 1981). Whilst camera traps do not provide high resolution data on the types of activities occurring across the day, they do offer an opportunity to look at seasonal differences in activity patterns, and how these might vary with

resource homogeneity and risk prevalence across different sites. Whilst this chapter provides a first look at risk, finding some evidence of circadian shifts in activity with lowered predation pressure, future analyses will benefit from integration of ecological data across sites to explore additional or interactive effects of habitat productivity and homogeneity on baboon activity. Advancing methods in AI classification of images might also facilitate data collection on the types of behaviours occurring across time and space, perhaps allowing for exploration of variation in social behaviours under different ecological conditions.

Under traditional observational methods, many studies highlight the importance of sleep sites as refuge from nocturnal predation (Cowlishaw, 1994; DeVore & Hall, 1965; Hamilton, 1982), but few explicitly measure how risk affects variation in departure from and arrival at sites, nor the onset and distribution of diurnal activity in baboons. One study of chacma baboons reported a mean departure time of 18 minutes after sunrise (range: -20 to +104 minutes) (Noser & Byrne, 2007), and another of Guinea baboons reported a mean time of first exit as 45 minutes before sunrise in the wet season (range: -28 to +208 minutes) and 11 minutes before sunrise in the dry season (range: -18 to -5 minutes) (Anderson & McGrew, 1984). These results suggest earlier activity than recorded across all sites examined in this chapter, although a distinction should be made between first exit of sleep sites and first detection of baboons across camera grids. As noted by Anderson and McGrew (1984) and others (Altmann & Altmann, 1970; Davidge, 1977; Forthman-Quick, 1986), baboons will often rest in close proximity to their sleep tree or cliff for periods that last between a few minutes and three hours before they move off and start foraging. Both departure time and this resting period reportedly vary with season and lunar phase (Anderson & McGrew, 1984; Davidge, 1977; Forthman-Quick, 1986), indicating that light levels might be influencing baboon troops' departure from the safety of their sleep site. However, the studies discussed here do not explore whether variation in this resting

period was related to perceived risk in the area, or by other factors such as temperature. Recent methodological developments, such as the use of collars on both baboons and their predators, indicate that day-to-day departure times from sleep sites are influenced by leopard activity (Bidner et al., 2018). The results presented in this chapter add to this evidence, indicating that a reduced perception of risk across a landscape might facilitate earlier terrestrial activity in baboons.

Again, it will be important to integrate more variables into future cross-site comparisons of camera trap data to account for factors like foraging requirements on variation in the onset of baboon activity across sites. For example, there is evidence that baboon troops ranging in more anthropogenic environments depart later from their sleep sites than wild-ranging troops in the same population (Altmann & Muruthi, 1988). This appears to be explained by the fact that the semi-provisioned troops face lower foraging pressures and can spend more of the day resting and socialising than wild-ranging troops (Altmann & Muruthi, 1988; Forthman-Quick, 1986). Additionally, at a site where baboons left their sleeping cliffs later in the winter, it was found that the overall proportion of rest did not vary seasonally; the troop simply dispersed their rest in shorter bouts throughout the day during summer, compared to a longer morning rest near the sleep site in winter (Davidge, 1977). This suggests that the troop had certain foraging requirements that had to be met each day, throughout the year, and that other pressures were acting upon when they took their rest. Another relevant finding is evidence that baboons depart earlier from their sleep sites when travelling to scarce and clumped resources than when travelling to more abundant homogenous resources (Noser & Byrne, 2007), again highlighting effects of foraging pressures on circadian activity patterns. With all these considerations in mind, the early morning activity of baboons recorded on the Gorongosa camera traps might be explained as a response to high inter-troop competition for access to specific resources. Further work is needed to integrate risk, ecological, and demographic factors into

comparative camera trap analyses to explore such possibilities. The increasing standardisation of camera trapping methods and the availability of ecological data from satellite imagery will help with the development of more holistic comparative analyses.

Whilst this chapter provides initial insights into baboon activity patterns and predator-prey dynamics, they exist at a very broad scale – both geographically and in terms of the data that can be captured by camera trap grids. Remote monitoring methods provide tools for studying primate populations in ways that were logistically impossible before, but they cannot replace observational research conducted at the troop and individual level. Indeed, interpretations of camera trap data in this study rely heavily upon information collected over years of observation of baboon troops. We know from such studies that predation can be the main cause of mortality in adult females and juvenile baboons in some troops, that leopards are a primary predator of baboons and are particularly dangerous to the primate species at night, dawn, and dusk, and that baboons respond to such risks with vocalisations and mobbing behaviours (Busse, 1980; Cheney et al., 2004; Cowlishaw, 1994; DeVore & Hall, 1965; Fischer et al., 2001). Whilst observational studies have provided foundational data on predator-related behaviours in baboons, they have also highlighted the issues inherent in trying to study the rates and effects of predation on baboon groups, namely the facts that most predation happens at night and that humans can reduce predator-prey encounters (Cheney et al., 2004; Nowak et al., 2014). Camera trap studies serve to counteract some of these limitations and to expand the focus beyond the troop level to explore population dynamics and their interaction with broader faunal communities. This can be seen in the demonstration of landscape-scale shifts in circadian activity patterns in this paper. But whilst camera traps currently only document broad fluctuations in "activity" we must return to observational data, collected over decades of research, to integrate the knowledge that *types* of activity – both of primates and their predators – are also affected by

circadian rhythms. For example, because baboons mob leopards during the day, leopards are more avoidant of baboons in the daytime and use a different hunting style – caching carcasses in trees – when they make a kill during daylight hours (Bidner, Isbell, & Matsumoto-Oda, 2016; Cheney et al., 2004). There is also evidence that predation of baboons in some environments might vary seasonally or with particular ecological factors such as flooding (Cheney et al., 2004). On the ground research is needed to record predation events and rates, but remote monitoring could help explain such patterns, for example by demonstrating shifts in occupancy of the landscape during flooding or across seasonal cycles. Going forward, efforts should be made to integrate observational and remote monitoring of baboon populations and to standardise and share methods and data across sites. This will provide a fuller picture of baboons' landscapes of fear and how these contribute to their broader behavioural and evolutionary ecology.

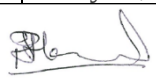
4.5 Conclusion

In this study, we used camera trap data to explore variation in risk and primate terrestriality across 10 African sites. Whilst there are methodological limitations to a continental-scale survey, the data indicate that circadian patterns in baboon terrestriality are affected by predator diversity. Baboons are more active on the ground during crepuscular and nocturnal hours in landscapes with low carnivore diversity, particularly those without leopards. Future site-specific research is needed to further explore population size, group cohesion, and the types of behaviours occurring on the ground at these sites, as well as the impact of other ecological variables on baboons' temporal and terrestrial activities.

Statement of Authorship for Chapter Four

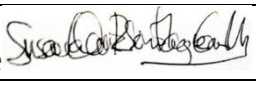
Title of paper	The influence of carnivore diversity on baboon terrestriality and diel activity patterns across eastern and southern Africa
Publication status	Unpublished and unsubmitted work written in a manuscript style
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Student Confirmation

Student name	Philippa Hammond		
Contribution to the paper	Philippa Hammond: conceptualization, methodology, data collation and management, formal analysis, data visualization, interpretation, write-up. Kaitlyn Gaynor: data collection and sharing, support with methodology, analysis, visualization, review, and editing. Meredith Palmer: data collection and sharing, support with methodology, analysis, review, and editing. Tara Easter: data collection and sharing, support with review, and editing. Kristen Snyder: data collection and sharing, support with review, and editing. Noel Mbise: data collection and sharing, support with review, and editing. Ernest Mjingo: data collection and sharing, support with review, and editing. Dora Biro: support with conceptualization, methodology, formal analysis, review, and, editing. Susana Carvalho: support with conceptualization, methodology, formal analysis, review, and editing.		
Signature 		Date	29/08/2022

Supervisor Confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor name and title: Susana Carvalho, Professor		
Supervisor comments: I confirm the information provided is accurate		
Signature 	Date	30/08/2022

Chapter Five

Discussion: Exploring the origins of hominin locomotion and drivers of primate terrestriality

A defining feature of the hominin clade is bipedality, often parcelled together with terrestriality. However, there is increasing evidence of locomotive diversity, both within the hominin clade and amongst the Miocene apes that came before them. There is also growing recognition that bipedalism might have arboreal origins and that arboreality persisted in several hominin taxa, including our own genus *Homo*. Combining fossil and palaeoecological evidence with insights from behavioural ecology facilitates new interpretations of evolutionary pathways and highlights the importance of considering homoplasy as well as homology in the emergence of locomotive traits. Taking such an approach also moves away from assumptions of a straight-line trajectory towards modern human locomotion and explores the likelihood that independent forms of bipedality and terrestriality arose at different times and in different combinations with other features of ape locomotion. Evidence from extant species can broaden our understanding of the correlates, causes, and consequences of increased primate terrestriality and can be used to generate hypotheses which are then explored further using paleontological methods. Here, I review the fossil evidence for the evolution of hominid and hominin locomotion through the Miocene and Plio-Pleistocene. I combine this with discussion of the evolution of terrestriality in primates more broadly and use a behavioural ecology lens to apply insights from previous chapters of this thesis to my interpretation and hypothesis generation about primate locomotion.

5.1 Introduction

Philosophers and scientists have a long history of trying to pinpoint just what makes humans a "uniquely unique species" amongst animals (R. Alexander, 1990). It is still a matter of debate whether or not it is valid – or morally appropriate – to distinguish humans from all other animals in this way, especially when the distinction is accompanied by an assumption of human superiority (Chapman & Huffman, 2018). Regardless of whether we should be classified as *uniquely unique*, it is fascinating to consider the origins of traits that define us.

Traits that "make us human" have been explored both through delving into the past and analysing modern human behaviour. In the paleoanthropological world, fossils are classified as hominins i.e., more related to humans than to chimpanzees, based on two key features; reduced canine size with loss of the canine honing complex, and morphological adaptations suggestive of habitual bipedal locomotion (Almécija et al., 2021; Harcourt-Smith, 2010). When modern humans are compared to other extant animal species, it has been argued that our cognition, cooperation, culture and/or social structure set us apart from the rest of the animal kingdom (DeVore & Tooby, 1987; Foley & Gamble, 2009; Hill, Barton, & Magdalena Hurtado, 2009; Tomasello & Vaish, 2013). However, the evolution of these complex adaptations is attributed to a set of key "pre-adaptations" that include the emergence of bipedality facilitating broader dispersal, social changes, and manual dexterity, and therefore a dietary shift towards hunting and extractive foraging. It has been hypothesised that this change in diet coevolved with provisioning and task specialisation, along with cognitive skills like imitation and shared intentionality which underlie human culture and cooperation (Hill et al., 2009).

From both the past and the present, evidence appears to converge on the emergence of bipedality as fundamental to what makes us human. Built into our understanding of human bipedality is that it is a terrestrial locomotion, making us the only primate species to live almost exclusively on the ground.

However, it is possible that bipedality and terrestriality emerged at different times and under separate selection pressures (Richmond et al., 2001; Takemoto, 2004), and it is thus important to explore the roots of both behaviours. This chapter reviews prominent theories and evidence concerning the evolution of human locomotion, its roots in the Miocene and Plio-Pleistocene, and the evolution of terrestriality in primates. Beyond using the morphology and context of hominin fossils themselves, this chapter emphasises consideration of species beyond our direct lineage. It also includes discussion and application of insights from the research presented in previous chapters of this thesis, using a behavioural ecology lens to broaden our understanding of primate adaptations.

5.2 The evolution of hominin locomotion

As stated above, bipedal morphology is one of the defining features of the hominin clade, emerging after we shared a last common ancestor (LCA) with chimpanzees and bonobos, between 10 and 6 million years ago (Ma) (Moorjani et al., 2016; Prado-Martinez et al., 2013; Wilkinson et al., 2011). For many years, the prevailing questions were about when and why hominins stood up from all-fours to walk on two legs, under the assumption that locomotive traits like quadrupedalism and knuckle-walking – which are shared amongst non-human African great apes – were present in our LCA (Richmond et al., 2001). However, the use of extant great apes to deduce LCA morphology and behaviour assumes that their modern-day similarities are homology rather than homoplasy, and that extant apes inhabit environments so similar to those of the LCA that they have not faced new selection pressures resulting in significant evolutionary change since the LCA (Sayers, Raghanti, & Lovejoy, 2012). Contrary to such assumptions, there is some evidence that variation in hand and wrist morphologies of modern apes is more suggestive of independent evolution of knuckle-walking in the *Pan* and *Gorilla* lineages (Dainton & Macho, 1999; Kivell & Schmitt, 2009). To get a fuller picture, these top-down explorations of ape evolution must be complemented by bottom-up

explorations of the ape fossil record (Almécija et al., 2021).

5.2.1 Miocene apes and the origins of hominid locomotion

The Miocene (~23 – 5.3 Ma) has been dubbed "the real planet of the apes" (Begun, 2015) and is therefore a critical period for exploring the deep roots of locomotion in hominoids (all apes), hominids (the great apes), and hominins (the human lineage) (Almécija et al., 2021). Unfortunately, the African ape record is sparse between ~14 and 10 Ma but rare exceptions, such as the discovery of an infant ape cranium in Kenya, *Nyanzapithecus alesi* (~13 Ma), provide insights into potential stem hominoids. Nyanzapithecines share similarities with extant hylobatids (gibbons) in their relatively small bodies and arboreality, but the inner ear of the *N. alesi* cranium suggests that their movements were probably less acrobatic than modern-day gibbons (Nengo et al., 2017).

Ongoing debate about where and when the earliest hominids emerged will likely remain unresolved whilst this critical gap in the African fossil record persists. One possibility is an "out of Africa" and then "back-to-Africa" sequence of events. The first fossil evidence of apes outside of Africa comes from Europe in the middle Miocene (~16.5 – 14 Ma) and many of the most recent Miocene apes for which we have postcranial remains have been found in Europe. These include *Pierolapithecus catalaunicus* (~11.9 Ma) (Hammond, Alba, Almécija, & Moyà-Solà, 2013; McNutt, Zipfel, & DeSilva, 2018), *Danuvius guggenmosi* (~11.6 Ma) (Böhme et al., 2019), and *Rudapithecus hungaricus* (~10 Ma) (Begun, Nargolwalla, & Kordos, 2012).

The foot, hand, and pelvic morphologies of *Pierolapithecus* suggest that it lived a fully arboreal lifestyle, did not engage in suspensory locomotion, and was more frequently engaged in orthograde behaviours than earlier hominoids, but not as frequently as extant great apes (Hammond et al., 2013). In contrast, *Rudapithecus* and *Danuvius* show adaptations to suspensory locomotion and there has

even been an argument for evidence of above-branch bipedalism in the latter (Böhme et al., 2019), although this is contested (Williams, Prang, Meyer, Russo, & Shapiro, 2020).

These Miocene apes provide a diverse set of possibilities for the roots of hominid locomotion. Amongst this diversity, the three genera described above share certain characteristics that could be inferred to have been present in the LCA of African hominids. For example, at approximately 30 kg in body mass, these apes were all smaller than extant great apes (perhaps with the exception of bonobos) (*Pierolapithecus*: Moyà-Solà, Köhler, Alba, Casanovas-Vilar, & Galindo, 2004; *Rudapithecus*: T. M. Smith, Tafforeau, Pouech, & Begun, 2019; *Danuvius*: Böhme et al., 2019). They show adaptations to an arboreal lifestyle and indicate early origins of an orthograde body plan that could then have been co-opted for behaviours including below-branch suspension, knuckle-walking, and/or terrestrial bipedalism in different hominid taxa. Both this upright posture and an increase in brain size – traits that are central to discussions about human evolution – are in fact rooted in evolutionary trends seen in the Miocene (Alba, 2010; Almécija et al., 2021; Moyà-Solà et al., 2004).

Whilst the traits discussed above might describe the LCA of African hominids, it is difficult to plot out their diverging evolutionary trajectories after this point, due to the scarcity of fossils from the extant African ape clades. Other than a few teeth and a possible proximal femur, we have no fossil evidence for the chimpanzee or gorilla lineages (Cote, 2004; DeSilva, Shoreman, & MacLatchy, 2006; McBrearty & Jablonski, 2005; Pickford & Senut, 2004). There is fossil evidence of three ape genera from northern and eastern Africa in the late Miocene, all of which have been putatively assigned to the hominin lineage: *Sahelanthropus*, *Orrorin*, and *Ardipithecus*. The traits of these genera are discussed below, with a focus on their inferred styles of locomotion.

At 7 million years old, *Sahelanthropus tchadensis* fossils from Chad represent the oldest possible hominin, classified as such on the basis of small canines and the position of its foramen magnum, which might indicate bipedal locomotion (Brunet, Guy, Pilbeam, Mackaye, & Likius, 2002). However, this ape retains many primitive features similar to earlier apes like *Pierolapithecus*, and the foramen magnum positioning may simply indicate its orthograde posture (Andrews, 2020).

Orrorin tugenensis fossils discovered in Kenya and dated to ~6 Ma have also been given hominin status by some, based largely on an initial proposal that its femur morphology was more similar to modern humans than other extant apes or australopithecines, indicating that it was adapted to terrestrial bipedalism of some sort, whilst retaining good climbing adaptations (Senut et al., 2001). More recent interpretations of femoral evidence highlight that *Orrorin* shares many features with earlier Miocene apes and later hominins, and likely represents an "intermediate" morphology between them (Almécija et al., 2013; Richmond & Jungers, 2008).

At the very end of the Miocene (~5.8 – 5.2 Ma) evidence of *Ardipithecus kadabba* from the Middle Awash, Ethiopia, has also been attributed to "the first hominin", due to the possible absence of a functional canine honing complex, and some indicators of "an early form of terrestrial bipedality" (Haile-Selassie, 2001). However, depending on how morphological comparisons are made, different conclusions can and have been reached about *Ardipithecus*. These range from it being assigned the status of the first hominin, the *Homo-Pan* LCA, or as a genus more related to chimpanzees than to the hominin lineage (Haile-Selassie, 2001; Sayers et al., 2012; Senut et al., 2001). As mentioned before, some of these interpretations rely on an assumption that the LCA was essentially chimpanzee-like, and therefore use chimpanzee morphology as a reference point to assess how "hominin-like" a fossil is, rather than acknowledging that both later hominins and chimpanzees are likely to display very different, derived features from their LCA. Researchers trying to move away

from an over-reliance on the "Chimpanzee Referential Doctrine" have highlighted that because *Ardipithecus* does not exhibit clear adaptations to below-branch suspension, knuckle-walking, or vertical climbing, it should not be assumed that these locomotive traits existed in the LCA of *Homo* and *Pan* (Sayers et al., 2012).

5.2.2 Plio-Pleistocene apes and the origins of hominin locomotion

The Plio-Pleistocene represents a key period for understanding the origins of hominin locomotion, as it encompasses the emergence of the first undisputed hominins, the existence and even co-existence of a diverse array of hominin species and morphology, and then the extinction of all hominin genera except *Homo*, the ancestor of modern humans. It also marks a period of climatic and ecological change that resulted in the expansion of grasslands across Africa. It is this shift towards more open environments that laid the foundations for the "Savannah Hypothesis" – the idea that human bipedality is an adaptation to receding forests (Dart, 1925, 1949; Harcourt-Smith, 2010; Senut et al., 2018). This hypothesis gained and retained a lot of attention in popular understandings of human evolution, but several lines of evidence suggest that bipedality was not driven solely by expanding savannahs. These will be discussed further below.

Following the first appearance of the *Ardipithecus* genus in the Miocene, it is represented in the Pliocene by the species *Ardipithecus ramidus*, a "primitive" bipedal ape that ranged in wooded habitats in the area now known as Ethiopia, approximately 4.4 Ma (Semaw et al., 2005; White et al., 2009). Initial interpretations of *Ardipithecus* postcranial material posit that the ape combined some form of terrestrial bipedality with arboreal clambering, which involved weight-bearing in the palms and was unlikely to include knuckle-walking. However, this locomotive style was not well-adapted to long bouts of terrestrial bipedalism, nor to the levels of suspensory arboreal locomotion seen in the African apes of today (White et al., 2009; White, Lovejoy, Asfaw, Carlson, & Suwa, 2015). Recent

analyses of *Ardipithecus* fossils have prompted some researchers to say that it did in fact engage in suspensory locomotion and maybe even knuckle-walking, because its hand morphology is closer to extant apes than more generalised quadruped primates (Prang et al., 2021). A similar argument has been used to propose that its feet were also more similar to those of extant African apes than previously thought (Prang, 2019, 2022). Other researchers disagree that these similarities warrant the conclusion that *Ardipithecus'* locomotion was anything like that seen in modern African apes, and highlight that comparisons using extant primate data continue to be limited whilst we have almost no fossil record for *Pan* or *Gorilla* (Chaney, Ruiz, Meindl, & Lovejoy, 2022).

Separating homologous and homoplastic traits amongst extant apes will certainly be made easier through the discovery of more fossils, but it can also be aided by considerations of selection pressures that shaped the behavioural ecology of these ape lineages. For example, the LCA of all extant African apes is often assumed to have been at least semiterrestrial, because terrestriality is seen in gorillas, chimpanzees, bonobos, and humans. However, several Miocene ape fossils (discussed above) appear to be smaller, arboreal creatures, and some interpretations of the *Ardipithecus* evidence indicate that the LCA of *Homo*, *Pan*, and *Gorilla* was likely an above-branch clambering quadruped from whom the extant apes independently acquired their specialisations for suspension, vertical climbing, and knuckle-walking (Dainton & Macho, 1999; Kivell, 2019; Lovejoy, Suwa, Simpson, Matternes, & White, 2009). It is thus worth considering the ecological factors that might have selected for increased terrestriality across all these ape lineages, rather than assuming the shared trait existed in their LCA.

Whilst debate about the positional behaviour of *Ardipithecus* is ongoing, evidence suggests that it lived in woodland and forested habitats, and had a C_3-heavy diet, indicating that its locomotive adaptations were not driven by a move onto the savannah (White et al., 2009). The influence of

expanding grasslands has most often been discussed in relation to the emergence of australopithecines – the first apes considered indisputably hominin and often referred to as "committed", "obligate", or at least "habitual" bipeds (Anaya, Patel, Orr, Ward, & Almécija, 2021; Bobe et al., 2020; Harcourt-Smith, 2010; White et al., 2009). However, as this range of descriptive terms might suggest, there is still much debate around the exact nature of australopithecine locomotion, and it is likely that there was locomotive diversity within the genus (Senut et al., 2018). *Australopithecus* was at first contrasted with the "more primitive" *Ardipithecus*, and researchers suggested that australopithecines' derived postcranial features showed that they "had largely abandoned locomotion in the arboreal canopy" (White et al., 2009). However, there is increasing evidence that the morphology, paleoecology, and diet of australopithecines was more adapted to woodland-living than initially thought, especially when the genus first emerged (Bobe et al., 2020; Cerling, Manthi, et al., 2013; Sponheimer et al., 2013).

Au. anamensis first appears in the Kenyan and Ethiopian fossil records from about 4.2 Ma (Ward, Leakey, & Walker, 1999; Ward et al., 2001; White et al., 2006). Similarities in the paleoecology and faunal records at Kanapoi in the Turkana Basin, Kenya, and Asa Issie in the Afar, Ethiopia, highlight the biogeographic connections that must have existed between these sites, and suggest that *Au. anamensis* thrived in habitats with a mix of C_3 and C_4 vegetation, although they still showed a dietary preference for C_3 foods at this time (Bobe et al., 2020). Their probable descendants, *Au. afarensis*, were the first hominins to begin incorporating C_4 foods into their diets approximately 3.7 Ma, whilst still living in relatively wooded environments (Sponheimer et al., 2013). *Au. afarensis* is probably also the hominin species around which bipedality has been most discussed, famous for both the "Lucy" skeleton and the Laetoli footprints that have been attributed to the species (Kimbel & Delezene, 2009; Leakey & Hay, 1979; Raichlen, Pontzer, & Sockol, 2008). These footprints are

strong evidence that hominins did travel on the ground with a bipedal gait, but could have been made by a stride very different to modern human locomotion (Raichlen et al., 2008). Recent analyses of additional trackways indicate that there may even have been more than one species of "small, cross-stepping bipedal hominin" traversing the Laetoli landscape over 3.5 Ma (McNutt et al., 2021). If so, this evidence would suggest that the emergence of bipedality was not necessarily rare or unique, but an adaptive response by several ape species to shared selection pressures. Indeed, analyses of hominin foot morphologies indicate a diversity at the base of the lineage suggestive of different locomotive styles and "experimentation in bipedalism" (DeSilva, McNutt, Benoit, & Zipfel, 2019).

Alongside evidence of some form of terrestrial bipedality from footprints and the derived foot morphology of *Au. afarensis* (Ward, Kimbel, & Johanson, 2011), the species retains some adaptations for arboreal locomotion (Stern & Susman, 1983; Ward, 2002). Signs of arboreality are also seen in several other hominin species that both pre and postdate *Au. afarensis*. There has been heated debate about whether such morphological traits are simply a retention of a "primitive" ancestral adaptation, no longer in use nor adaptive in hominins, or if they serve as evidence for continued arboreality in multiple hominin genera (Anaya et al., 2021; Kimbel & Delezene, 2009; Ward, 2002). Several lines of evidence suggest that these signals should not be dismissed as primitive relics from pre-hominin ancestors. The first comes from hominin fossils themselves, and further evidence can be found in paleoecological data and applied insights from primate behavioural ecology.

5.2.3 Signals of arboreality in a range of hominin fossils

The first line of evidence is the diversity of hominin taxa in which indicators of arboreality exist. Described above is the postcranial evidence from the eastern African Pliocene species, *Au. anamensis* and *Au. afarensis* (Kimbel & Delezene, 2009; Ward, 2002; Ward et al., 2001). Arboreal

morphology is seen in southern African species of the genus too. *Au. africanus* appears in the fossil record ~3 Ma, which is later than *Au. AfarensisAlt*hough there is some evidence of reduced arboreality in this species (at least in comparison to extant great apes) (Georgiou et al., 2020), its morphology has generally been interpreted as being better adapted to climbing than the eastern African australopithecine (Green, Gordon, & Richmond, 2007). This has prompted researchers to question whether the climbing adaptations of *Au. Africanus* were "secondarily derived" after arboreality declined in the ancestral *Au. AfarensisAlt*ernatively, both *Au. afarensis* and *Au. africanus* might have inherited their arboreal adaptations from a primitive ancestor. However, if *Homo* is a descendant of *Au. africanus* (as has been proposed), this scenario would suggest that derived terrestrial bipedality evolved independently in the *Au. afarensis* and *Homo* lineages at different times (Green et al., 2007; Prabhat et al., 2021). Again, such a scenario would suggest that mosaic styles of ape locomotion represent sensitive adaptions to ecological pressures, and we should not assume that modern human bipedality evolved along a steady linear path.

In *Au. sediba*, a southern African australopithecine that lived more recently than 2 Ma, internal finger bone structure demonstrates in vivo power grasping, showing that their postcranial morphology was more than just a primitive relic of arboreality. This proven climbing ability existed alongside knee, ankle, and lower back morphology suggestive of bipedalism (Dunmore et al., 2020; Williams et al., 2021). Recent dating of South African fossil sites indicates that this australopithecine existed contemporaneously and within a 250 km^2 area inhabited by both *Paranthropus robustus* and *Homo* aff. *erectus* (Herries et al., 2020). Not only does this evidence highlight the diversity of the Pleistocene hominin family tree, but it too brings up questions about the role of homology and homoplasy in shaping "unique" features of human morphology. Whilst *Au. sediba* has often been considered to sit between *Au. Africanus* and *Homo* in the ancestral tree, the discovery of their

contemporaneity suggests that it may not be ancestral to *Homo*, in which case their shared features are homoplastic rather than homologous (Herries et al., 2020).

Evidence of arboreality persists beyond the australopithecines. There are now analyses of the upper limb of *Paranthropus boisei* suggesting that this species was regularly climbing trees in eastern Africa approximately 1.5 Ma (Richmond et al., 2020). And a study of the trabecular structure of southern African hominin femurs indicates regular climbing behaviours in a specimen attributed to either *Paranthropus robustus* or *Homo* (Georgiou et al., 2020). Within the genus *Homo*, it appears that 1.8 million-year-old *H. habilis* had forelimbs that were conducive to climbing (Ruff, 2009), a feature that also seems to have been present in *H. naledi*, a southern African hominin that lived as recently as 200 to 400 ka (Dirks et al., 2017; Feuerriegel et al., 2017). Even within the past 100 ka, we have postcranial evidence from *H. floresiensis* fossils that suggest the small-bodied hominin had a very different gait to its contemporaneous *Homo* species (Harcourt-Smith & Aiello, 2004b; Jungers et al., 2009; Larson et al., 2009). Whilst an interpretation of the locomotor style of *H. floresiensis* remains elusive, analyses of hominin limb joint proportions place *H. floresiensis* in a group with *Au. africanus*, *Au. sediba*, *P. robustus*, *P. boisei*, and *H. habilis*, all of which have more "ape-like" proportions than those of *Au. afarensis*, *H. erectus*, and *H. naledi* which more closely resemble those of modern humans (Prabhat et al., 2021).

Analyses like the one mentioned above can be criticised for their dichotomous comparison of "ape-like" and "human-like" traits and an over-reliance on extant ape locomotion as a model for extinct species. Furthermore, different methods and interpretations of evidence lead researchers to different and even contradictory conclusions (e.g. Chaney et al., 2022; Prang, 2019). However, there is much to learn from this accumulation of fossil evidence. Not only does it highlight that arboreality was likely present in a diverse range of hominin taxa and across multiple geographic regions and time

periods, but it also demonstrates that terrestrial bipedality emerged in different forms, at different times, and in varied combinations with other traits such as larger brains – all contributing to the mosaic nature of evolution seen in hominins (Foley, 2016). *Au. Afarensis*, for example, demonstrates a combination of some form of terrestrial bipedality with a small endocranial volume and ape-like brain organisation (Gunz et al., 2020), whilst *H. habilis* combines the "typical" larger brain of *Homo* with signals of continued arboreality (Ruff, 2009; Spoor et al., 2015), and *H. naledi* is a relatively recent species of *Homo* but with both a smaller brain and adaptations for climbing (Feuerriegel et al., 2017). Evidence of this diversity and mosaic nature of locomotive traits calls attention to the many selective pressures that act on behaviour and morphology. What were the biotic and abiotic variables that released some primate species from the ancestral state of arboreality? And what dictated the locomotive style in which this transition to the ground was made by different taxa? These are questions that can be answered by studying the interactions between primate morphology, behaviour, substrate-use, and ecology in past and present ecosystems.

5.2.4 Paleoecological evidence and insights from behavioural ecology

The second reason why signals of arboreality across the hominin tree should not be overlooked is the palaeoecological evidence suggesting that many hominin species lived in and utilised environments with more woody cover than previously thought. Evidence suggests that grasslands began emerging in eastern Africa approximately 10 Ma, with an increase in the rate of this expansion around 4 Ma that can be seen in a significant shift in herbivores' diets by 2 Ma (Cerling et al., 2015; Uno, Polissar, Jackson, & Demenocal, 2016). Whilst hominins emerged alongside expanding grasslands, their habitats had more tree cover than previously thought (Negash et al., 2019) and the composition of their diets suggests that they were still utilising these more wooded environments even as grasslands expanded (Cerling, Manthi, et al., 2013; Manthi, Cerling, Chritz, & Blumenthal, 2020; Senut et al.,

2018; Uno et al., 2016). This not only dispels the savannah hypothesis but is also a strong indication that the prevalence of trees would have continued to act as a positive selection pressure for climbing adaptations in primates descended from an arboreal ancestral state. The evidence suggests that it is probably only sometime after 2 Ma that the thinning out of trees might have driven increased terrestriality in some primate lineages, including the hominin taxa *Paranthropus* and *Homo* (Levin, 2015; Negash et al., *under review*; Quinn et al., 2013; Wynn et al., 2020).

Tree availability and its selection in favour of primate arboreality highlights a third important set of evidence that should be considered when assessing hominin morphology: behavioural ecology. It is useful to hypothesise and test the relationships between ecological factors, behaviour, and morphology, and to use insights from extant animal species to interpret what is seen in the fossil record. For example, we know from the study of extant primates that the vast majority of species are arboreal (Galán-Acedo et al., 2019) and are thus very sensitive to fragmentation of their habitats (Marsh, 2013; Pozo-Montuy, Serio-Silva, & Bonilla-Sánchez, 2011). For species described as "terrestrial" or "semi-terrestrial" – terms that are not well-defined – there are likely to be multiple ecological factors that select for and against time spent on the ground, beyond simply the availability of trees.

For example, the previous chapters of this thesis explore the effects of risk on the terrestrial behaviours of baboons, a "highly terrestrial" non-human primate. Chapter Two reports on baboon behaviour during habituation, adding to a body of evidence demonstrating that primates spend more time on the ground when perceived risk in the environment is low (Campbell et al., 2005; Hammond et al., 2022; Isbell & Young, 1993b; Monteza-Moreno et al., 2020; Mourthé et al., 2007; Nowak et al., 2014). The chapter also provides evidence that risk perception is mediated by habitat structure and temporal variables, and that different strategies – for example, vocalisations or vigilance – might

be deployed in different habitats or contexts. This kind of behavioural flexibility and responses tuned to microhabitat variability demonstrates how primate groups exposed to slightly different environments and levels of risk could adopt different behavioural repertoires over time, with longer-term consequences including speciation or morphological change.

Camera trap research presented in Chapters Three and Four of this thesis explores the drivers of baboon terrestriality at broader scales, with the data suggesting that it is not simply dictated by tree coverage, but also by factors such as seasonality and risk. Baboons spend more time on the ground in the dry season, perhaps having to travel further for scarce water resources, or perhaps due to a reliance on fall-back foods like grass or tubers when fruit is less available. This highlights the need to study hominin fossils and behaviour in the context of the environments in which they lived. For example, the availability and distance between water sources could have been a selective pressure for increased terrestriality and/or or a limiting factor on the extent of hominin dispersals (Foley, 2018). The more data we can collect on the seasonality and water availability in their landscapes, the better we can understand how and why different hominin taxa might have had to spend more time on the ground than others. The evidence from Chapters Three and Four also demonstrates how the types, prevalence, and diversity of predators in a landscape might shift terrestrial behaviour, particularly at "riskier" times of day. These findings are discussed further in Section 5.4. Insights from this and other behavioural ecology research can and should be combined with evidence from the fossil record to aid our interpretation of primate – including human – evolution. The evolution of primate terrestriality is discussed further in the sections below.

5.3 The evolution of terrestriality in primates

In the hunt to find what makes humans unique, terrestrial bipedalism has received a lot of attention as a seemingly obvious trait that sets us apart from extant and extinct apes (Almécija et al., 2021). As

described previously, researchers have often attributed a degree of bipedality to hominin fossils, with australopithecines described variously as “committed”, “obligate”, or “habitual” bipeds (Anaya et al., 2021; Bobe et al., 2020; Harcourt-Smith, 2010; White et al., 2009), and with *Homo* fossils as different as *H. habilis* and *H. erectus* classified as “obligate” bipeds, albeit with the latter species distinguished as a “fully committed” biped (Harcourt-Smith, 2016; Ruff, 2009). The difference between these terms is not clearly defined and is usually dictated by the level of bipedality inferred from fossil features, rather than what each type of behaviour would entail in vivo. This issue is compounded when interpretations of hominin morphology are based on comparisons with extant primate bones belonging to species classified as “arboreal”, “semi-terrestrial”, or “terrestrial” – another set of terms with no clear definitions. These terms also overlook the fact that even the most terrestrial of non-human primates engage in relatively frequent arboreal activity, at least ascending into trees for some foraging and to trees or cliffs to sleep at night. This shines a spotlight on the role behavioural ecology can play in aiding interpretations of the fossil record. It is essential to understand how extant primate morphology relates to proportional substrate-use by different species and what factors drive these behaviours. It is also important to disentangle bipedality and terrestriality. The traits have been bundled together in hominin-related research but deserve more exploration as independent features of locomotion with independent ecological drivers.

For example, a reliance on extant African great apes as referential models has often led to the assumption that their LCA was at least semi-terrestrial, and questions were therefore formed around how and when hominins “stood up” from knuckle-walking to bipedal locomotion (Richmond & Strait, 2000; Sayers et al., 2012). However, there is evidence that knuckle-walking in non-human apes might be homoplasy rather than homology (Dainton & Macho, 1999; Kivell & Schmitt, 2009), and some argue for an arboreal origin of bipedalism in the hominin lineage, highlighting that this

would provide a relatively secure food supply and security from predators, and fits better with the palaeoecological evidence that hominins emerged in wooded environments (Crompton, Sellers, & Thorpe, 2010; Senut et al., 2018; Thorpe, Holder, & Crompton, 2007). By considering extant orangutan behaviour in interpretations of the ape fossil record, an argument has been made that arboreal bipedalism might have conferred advantages for locomotion on flexible branches in the LCA of extant apes. This would explain apes' shared adaptations to orthogrady, as well as the fossil evidence that many early and possible hominins display hindlimb adaptations to bipedalism whilst retaining forelimb adaptations for arboreality (Thorpe et al., 2007). Furthermore, an arboreal origin of ape bipedalism might be linked to growing competition from monkey species during the middle Miocene. Monkeys' abilities to eat increasingly less-ripe fruits in the centre of trees could have forced apes to compete by using more suspensory and clambering behaviours to reach riper fruits at the end of branches (Hunt, 2016). This highlights faunal context as another driver of behaviour and an important consideration when evaluating species' behavioural ecology.

5.3.1 Correlates, causes, and consequences of primate terrestriality

To understand the origins of hominin locomotion, it is thus important to examine the timing and drivers of terrestrial behaviours, not just amongst hominins, but also other primate species. As discussed above, some level of terrestriality has often been assumed to have existed in the LCA of all great apes, based on the fact that it exists across the extant taxa. But terrestriality is a rare trait amongst primates, and the fossil record increasingly points towards arboreal origins for the hominid LCA (Andrews, 2020), so it is likely that terrestriality is more common across all the extant African great apes than it was in their LCA. Until we have a more extensive fossil record for *Gorilla* and *Pan*, we can only hypothesise about the locomotion and postcranial morphology of their ancestors, but there are some indicators that the extant species are more terrestrial than earlier species. For

example, we know from extant apes that there is a trade-off between the amount of time that can be spent in arboreal travel and body size. Gorillas – the largest of the non-human apes – are the most terrestrial, male chimpanzees and orangutans are more likely to travel terrestriality than females, and there is some evidence that smaller-bodied bonobos travel arboreally more often than chimpanzees (Doran, 1993). All extant African great apes are larger-bodied than the hypothesised 30 kg of their Miocene LCA (Almécija et al., 2021) (body masses summarised in Table 5.1 below), suggesting that they might all be more terrestrial than their shared ancestor, but with different locomotor styles that have evolved to fit their substrate-use and the different three-dimensional features of their respective environments.

Table 5.1. *Summary of the male and female body masses of all extant African great ape species.*

Extant African Great Apes	Males (kg)	Females (kg)	Reference
Bonobos	45	33.2	(R. Smith & Jungers, 1997)
	37.7	33	(Yapuncich, Bowie, Belais, Churchill, & Walker, 2020)
Chimpanzees	60	47.4	(Galán-Acedo et al., 2019)
P. t. schweinfurthii	42.7	33.7	(R. Smith & Jungers, 1997)
P. t. troglodytes	59.7	45.8	
P. t. verus	46.3	41.6	
Gorillas			(R. Smith & Jungers, 1997)
***G. g. gorilla* (Western lowland)**	170.4	71.5	
***G. g. beringei* (Mountain)**	162.5	97.5	
***G. g. graueri* (Eastern lowland)**	175.2	71.0	
Humans (averages from several populations worldwide)	63.4	54.9	(R. Smith & Jungers, 1997) and (Ruff, Scott, & Liu, 1991)

Body size is just one of several factors thought to be associated with primate terrestriality. Others include bigger home ranges and social groups, higher male: female ratios, the use of open habitats, a shift to a broader diet, and the use of tools (Bandini et al., 2022; Clutton-Brock & Harvey, 1977; Fleagle, 2013; Heldstab et al., 2016; Kim, McQueen, & Hawkes, 2019; McCrossin et al., 1998; Meulman & van Schaik, 2013; Willems & Van Schaik, 2017; Wright et al., 2019). Many of these

traits have been central to the study of what makes humans “unique”. However, it is difficult to disentangle which, if any, of the factors *cause* an increase in primate terrestriality, and which are *consequences* of more time spent on the ground (McCrossin et al., 1998). Evidence, both from the fossil record and living primates suggests that many of these traits fall in the latter category.

As discussed previously in this chapter, there is growing evidence that hominins were engaging in some form of terrestrial bipedalism whilst still living in relatively wooded habitats. And beyond the hominin lineage, the earliest evidence of terrestriality in Old World primates comes from the Kenyan fossil record at Maboko Island 15 Ma, in both a cercopithecoid, *Victoriapithecus*, and a hominoid, *Equatorius* (formerly known as *Kenyapithecus*). There is no evidence that this shift was preceded by an increase in their body sizes or an opening up of habitats, but the fact that adaptations to terrestriality emerged in two separate clades at the same time suggests there was some environmental factor(s) driving a change in their substrate-use (McCrossin et al., 1998). This evidence not only highlights that primate terrestriality emerged as early as the Miocene and was independent from bipedality, but it also provides an example of a time period and fossil site ripe for further examination of the biotic and abiotic variables that might have driven primates to spend more time on the ground. A similar example exists at Koobi Fora and surrounding deposits in the Omo-Turkana Basin, also in Kenya, where the fossil record captures an increase in terrestriality in both hominins and the cercopithecid genus, *Theropithecus*, over millions of years (Bobe, Coelho J, Carvalho, & Leakey, 2022; Cerling, Chritz, Jablonski, Leakey, & Manthi, 2013; NG Jablonski, 1993b). These sites will be discussed further in the section below.

Amongst extant primate species, there are clear associations between locomotion style and body mass, home range size, and the number of habitat types inhabited by different species. Table 5.2 and Figure 5.1 below summarise these relationships using data from the “Ecological traits of the world's

primates" database, a compilation of data on 504 primate species collected from a review of 1,216 studies published between 1941 and 2018 (Galán-Acedo et al., 2019). As can be seen below, species that spend some time on the ground (classified as either "terrestrial", or "both") have larger home ranges and inhabit a greater number of habitat types than arboreal species. An interaction between locomotion style and body mass indicates that for terrestrial primates, there is a strong positive relationship between body mass and home range size. Whilst there are limitations in such broad classifications of "locomotion styles", and clearer demonstrations of the directions of causality are needed, the relationships depicted below demonstrate how a shift to spending more time on the ground might allow a species to disperse further and exploit novel and more diverse environments.

Table 5.2. *Results from general linear models (GLMs) showing the predictive effects and interactions between locomotion and body mass on (A) home range size and (B) number of habitat types inhabited by species across the Primate Order. Data from "Ecological traits of the world's primates" database* (Galán-Acedo et al., 2019).

GLMs	**A. Home range size**			**B. Habitat types**		
	Estimate	Std. Error	p-value	Estimate	Std. Error	p-value
(Intercept)	52.513	49.885	0.293	0.201	0.041	< 0.001***
Locomotion: Both	648.948	139.983	< 0.001***	0.317	0.105	0.003**
Locomotion: Terrestrial	-961.488	293.847	0.001**	0.417	0.194	0.031*
Body mass (BM)	13.255	7.236	0.067	-0.002	0.007	0.774
Both * BM	2.118	8.343	0.800	0.000	0.007	0.989
Terrestrial * BM	185.134	23.092	< 0.001***	0.014	0.016	0.365

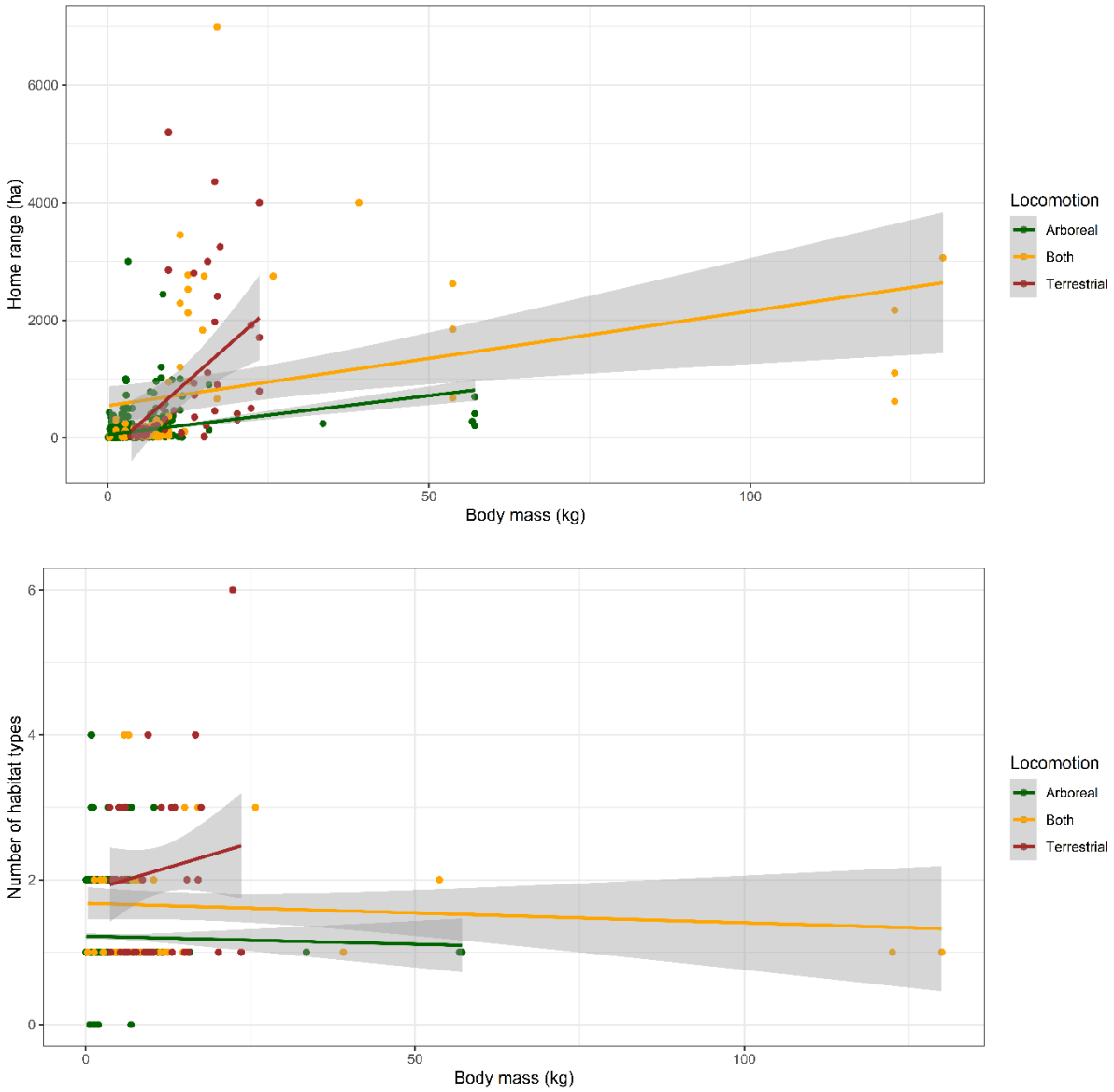


Figure 5.1. *Visualisations of the relationships between body mass, locomotion, and (A) home range size (top graph) and (B) number of habitat types (bottom graph) for species across the Primate Order. Data from "Ecological traits of the world's primates" database* (Galán-Acedo et al., 2019).

Of key interest from an evolutionary perspective is the relationship between terrestriality and technology in extant primates, which indicates that tool-use is likely a consequence of spending more time on the ground (Falótico & Ottoni, 2022; Meulman et al., 2012; Ottoni & Izar, 2008). Once thought to be unique to humans, and specifically to the genus *Homo* (Kivell, 2015; le Gros Clark,

1966), tool-use is now studied in several species across the animal kingdom, and several lines of evidence link it with terrestriality. Tool-use is most prolific amongst primate and bird species that spend a significant amount of time foraging on the ground (Heldstab et al., 2016) and is more common and complex in terrestrial than arboreal settings (Meulman et al., 2012; Visalberghi, Sirianni, Fragaszy, & Boesch, 2015). Terrestriality is also positively associated with technological diversity, as reflected in variation amongst capuchin populations (Falótico & Ottoni, 2022) and perhaps explaining the higher rates and types of tool-use displayed by chimpanzees compared to more arboreal bonobos (Doran, 1993; Samuni, Lemieux, Lamb, Galdino, & Surbeck, 2022). It is thought that terrestriality facilitates more frequent and complex use of technology by increasing individuals' exposure to a greater range of food and raw materials, as well as providing better opportunities for social learning. The stability of the ground frees up primates' hands, acts as a more reliable substrate than tree branches for activities like nut cracking, and provides space for juveniles to observe and scrounge from more proficient tool users. Furthermore, the accumulation of materials at specific sites increases encounter rates with the materials and settings needed for primates to engage in tool-use, learning, and innovation (Meulman et al., 2012; Ottoni & Izar, 2008; Visalberghi et al., 2015). Orangutans, the most arboreal of the extant great apes, very rarely make complex tools in the wild, but are able to do so in captivity where they lead more terrestrial lives. This suggests that they are not limited by cognitive factors but by their ecological setting (Meulman & van Schaik, 2013).

Baboons are another primate species that use tools in captivity, but not in the wild (Laidre, 2008). This is somewhat surprising given their degree of terrestriality but serves as a reminder of the complex web of relationships that link ecology with behaviour. The broad-scale comparisons of baboon populations presented in Chapters Three and Four identify environments in which baboons

are more terrestrial than others. Future research could use these populations for comparative analyses of how terrestriality influences object manipulation and extractive foraging. Whilst tool-use might be absent across all the populations, they provide an opportunity to test whether baboons who spend more time on the ground engage in more frequent or complex object manipulation than those that spend more time in trees.

Exploring the drivers of terrestriality could enhance our understanding of the roots of technology, amongst other behaviours fundamental to primate, including human, evolution. The "landscape of fear" – the spatial distribution of perceived risk in an environment (Gaynor et al., 2019; Palmer, Gaynor, et al., 2022) – has been widely studied in modern ecological settings, and is increasingly recognised as having both immediate and long-term effects on the amount of time primates spend on the ground (Campbell et al., 2005; Hammond et al., 2022; Isbell & Young, 1993b; Monteza-Moreno et al., 2020; Mourthé et al., 2007; Nowak et al., 2014). Fear of predators is also thought to be the primary driver of one of the most conserved traits across the primate family: ascending from the ground to sleep at night (Anderson, 1998; Bidner et al., 2018). With the risk of predation acting as a powerful selection pressure *against* engaging in ground-based behaviour, especially at night, it is worth exploring the evolutionary relationships between prehistoric predators and the emergence of terrestriality across various primate taxa. It is also worth considering when and how hominins overcame the fear of predators to the extent that they no longer needed to climb to safety at night, as this would surely mark the true point of transition to a "fully committed" terrestrial biped. The section below discusses methods for and issues with studying terrestriality and landscapes of fear in the fossil record.

5.4 Primate terrestriality and landscapes of fear in the fossil record

A major issue with searching for and interpreting trends in fossil and palaeoecological data is the

extreme spatial and temporal averaging that must be done due to low resolution of the data. We see this in the exploration of palaeoenvironments and hominin bipedality; the savannah hypothesis was built and survived on the detection of a general trend towards expanding grasslands that happened over millions of years, in combination with very few and geographically sparse hominin fossils. It has taken finer-scale examination of the environments at each fossil site to highlight that the earliest hominins arose in wooded habitats. Similarly, due to the relative rarity of both hominin and carnivoran fossils, our understanding of the dynamics between hominins and predators is built on general and long-term trends. As discussed in Chapter One, portrayal of hominin-predator dynamics has predominantly focused on the entrance of hominins to the carnivorous niche rather than their vulnerability to predation by the various large terrestrial carnivores roaming the landscape, as well as other predators such as crocodiles or raptors (Hopwood, 2014; Werdelin & Lewis, 2013b). One trend that has been reported is that carnivoran abundance and diversity in eastern Africa peaked around 3.5 Ma, and was followed by a clear decline towards the present, with a particularly dramatic drop in both the abundance and diversity of species around 1.8 Ma (Lewis & Werdelin, 2007; Werdelin & Lewis, 2005, 2013a). This has led researchers to propose that it was hominin technology and competition that drove this wave of carnivore extinctions, broadly coincident with the emergence of *H. erectus* and a shift towards more sophisticated Acheulean technology (Lewis & Werdelin, 2007; Ripple & Van Valkenburgh, 2010; Werdelin & Lewis, 2013b; Willems & Van Schaik, 2017).

The evolution of the type and level of hominin carnivory that can be inferred from the archaeological record is still a matter of much debate. There are big questions to be answered about whether hominin meat-eating stems from hunting or scavenging origins (Blumenschine, 1986; Domínguez-Rodrigo & Pickering, 2003; Pickering & Bunn, 2007; Pobiner, 2020; Shipman, 1986; Thompson et al., 2019). Questions also remain about whether we have overestimated the importance of meat in

early hominin diets due to the longevity of stone tools compared to perishable technology and other behavioural indicators that are less-well preserved in the fossil record (Espigares et al., 2019; Pascual-Garrido & Almeida-Warren, 2021). And although there is a shift from Oldowan to more advanced Acheulean technology approximately 1.76 Ma, the tools contribute to evidence of butchery without clarifying how hominins were accessing carcasses, especially to the extent that would be necessary to outcompete other carnivores. Furthermore, recent analyses of cut-marked bones suggest that the inferred increase in meat-eating shortly after 2 Ma might in fact be a sampling artefact (Barr et al., 2022). Taken together, all this evidence indicates that hominins might not have been outcompeting carnivores and driving them to extinction by 1.8 Ma.

Whilst the timing and importance of meat-eating in hominins will continue to be a topic of much debate and research, the broad trend seen in the decline of carnivorans should also be explored from the opposite angle. What would carnivore extinctions mean for hominins and other primates? The decline from peak abundance and diversity of carnivorans 3.5 Ma, and the more rapid decline after 1.8 Ma coincides roughly with the emergence and survival of increasingly terrestrial hominins. Perhaps a reduction in predation risk eased selection pressures for arboreality, allowing hominins to spend more time on the ground? Of course, this is very hard to detect or even imagine at a continental scale and in the context of a multi-million-year decline of predation risk. Furthermore, we know from extant primate behavioural ecology that the effects of risk on terrestriality can emerge on a much smaller scale, both temporally and geographically.

For example, long-term observation of a population of northern muriquis (*Brachyteles hypoxanthus*) documented a 20-fold increase in their terrestrial activity over 23 years. This included a notable increase in nonessential terrestrial activities like resting and socialising, and a growth in group size from approximately 20 to 80 individuals. This shift in substrate-use did not appear to be driven by

availability of trees and was likely due to a shift in these monkeys' landscape of fear over the course of habituation. The presence of researchers likely reduced the monkeys' perceived risk of humans over time, and deterred their predators, possibly accompanied by a decline in the predator population over the course of the multi-decade research (Tabacow, Mendes, & Strier, 2009).

Similar insights about the localised impact of landscapes of fear can be drawn from the camera trap studies reported in Chapters Three and Four. These highlight how the loss of predators from a relatively small geographic region might alter diel patterns of terrestrial activity in a single population of baboons, perhaps resulting in different behavioural repertoires even in neighbouring primate populations. The research also highlights the significance of key predator species (leopards, in the case of baboons) whose presence or absence in a landscape can have dramatic effects on primate activity patterns. Furthermore, the findings from these chapters provide nuanced insights into *how* activity might be shaped by decreased predation pressure in a landscape. For example, if the loss of large carnivores from an ecosystem relaxes the landscape of fear and increases terrestriality, particularly around crepuscular and nocturnal hours, primates might be able to utilise these hours for extra travel, foraging, or socialising time, all during cooler parts of the day. If these activities confer advantages to groups of primates who can more flexibly utilise the ground, they could select for increasing terrestriality to an extent that drives even morphological change.

These insights generate further questions. From the behavioural ecology angle, it is necessary to unpick the consequences of terrestriality in primates, particularly around opportunities for more extensive exploration of the environment, object-manipulation, group cohesion, and social behaviours. And from the perspective of human evolution, understanding the emergence of terrestrial bipedalism will require more careful and localised investigation of predator guilds at different hominid and hominin sites through the Miocene and Plio-Pleistocene. Although methodologically

difficult, it will also be important to identify the particular carnivore species that might have been primary predators of different apes over time. Rather than trying to examine the effects of continent-wide carnivore extinction rates on human evolution, identifying these key predators and using site-specific research to pinpoint their localised extinctions will provide an avenue for exploring shifting landscapes of fear and the downstream consequences of reduced risk on primate behaviour.

5.4.1 Evidence of carnivore damage to primate fossils

One avenue for exploring which predators were the biggest threats to different primate species is to simply examine fossils for tooth or claw marks. The Taung assemblage in South Africa, which includes the skull of an *Australopithecus africanus* infant, is likely to have been accumulated by a large bird of prey approximately 2.5 Ma (Berger & Clarke, 1995; McGraw et al., 2006), which serves as a reminder that hominins faced threats beyond large terrestrial carnivores, including raptors and crocodiles (Njau & Blumenschine, 2012). Many other assemblages that contain primate fossils – particularly in South Africa – show strong signals of carnivore activity, although it is often difficult to pinpoint exactly which carnivores were responsible for the marks observed on bones (DeSilva et al., 2013; Fourvel et al., 2018; Pickering et al., 2004; Val et al., 2014). For example, the Cooper's D assemblage in South Africa contains a large proportion of large-bodied primate fossils, accumulated in a cave approximately 1.5 Ma. Fossilised primate genera include *Papio*, *Theropithecus*, *Gorgopithecus*, and *Paranthropus*, with 6.2% of the primate bones showing carnivore damage, including a mandibular fragment from *P. robustus* (Val et al., 2014). This has been attributed to leopards or hyenas based on comparisons with modern examples of bone damage, but the site was also inhabited by sabertooth cats, *Megantereon* and *Dinofelis*, whose signatures might be harder to detect due to a lack of a modern comparison (Val et al., 2014). At Swartkrans, a tooth-marked *P. robustus* cranium has also been attributed to leopard predation (Brain, 1981). However, isotopic

analyses from carnivores at the site indicate that *Megantereon* and *Crocuta* species, as well as leopards, are all possible candidates for predators of the hominins and baboons at the site (Julia Lee-Thorp, Thackeray, & Van der Merwe, 2000).

Predators appear to have been less actively involved in the accumulation of Plio-Pleistocene fossils at eastern African sites than southern African ones. However, there is still some evidence of likely carnivore damage to several hominin fossils from eastern Africa. These include signs of possible leopard predation on *Orrorin tugenensis* 6 Ma (Gommery et al., 2007), carnivore damage to *Ardipithecus ramidus* bones 4.4 Ma (Woldegabriel et al., 1994), and both crocodilian and mammalian carnivore damage to *Homo habilis* fossils 1.8 Ma (Njau & Blumenschine, 2012). Signs of fossil damage indicate that hominins continued to face threats of predation as they dispersed out of Africa (Margvelashvili et al., 2022) and through the recent past to the modern day (Camarós, Cueto, Lorenzo, Villaverde, & Rivals, 2016; Hart & Sussman, 2011). Whilst more research is needed to improve identification of specific predators from marks that they leave on bones, the presence of the marks themselves highlights the importance of considering the landscape of fear as an influential driver of behavioural evolution in hominins and other primate lineages.

5.4.2 Prehistoric carnivore behaviour

Beyond identifying key predators of different primate species, advancing methods provide insights into other aspects of prehistoric landscapes of fear. Carnivoran fossil morphology can reveal a lot about hunting styles and niche partitioning amongst members of different carnivore guilds through time. For example, sabertooth predators have evolved multiple times throughout evolutionary history, in different families. Compared to the more versatile diets of extant carnivores, sabertooths are characterised as hypercarnivores with dentition so specialised for cutting meat that they could not consume bone or other food itemAlthough often characterised as targeting megaherbivores, there is

stronger evidence to suggest that they targeted medium-sized herbivores but had adaptations to perform quicker kills and more efficient stripping of meat from carcasses than conical-toothed cats (Antón, 2013). Amongst sabertooth taxa, there appear to have evolved two general "ecomorphs", or strategies, for hypercarnivory. "Dirktooth" predators had very long sabers and a muscular build suited to a more solitary, ambush hunting strategy, likely conducted in closed environments. "Scimitar-tooths" on the other hand were more gracile with longer limbs and greater speed to pursue prey, likely hunting in more open environments and perhaps in groups (Antón, 2013). Building on this, isotopic analyses provide evidence that scimitar cats, such as the early Pleistocene *Homotherium*, were coursing predators that hunted predominantly large-bodied herbivores in open habitats. Meanwhile, dirktooth cats such as *Megantereon* were ambush hunters of browsers in closed habitats (Palmqvist, Pérez-Claros, Janis, & Gröcke, 2008). The inferred features of *Megantereon* indicate that it might once have filled a similar niche to the modern-day leopard, perhaps making it a key predator of medium to large-bodied primates – including early hominins.

Whilst informative, the examples above serve as a reminder that there are many features of prehistoric landscapes of fear that do not have modern analogues, making it difficult to do more than hypothesise about the prey preferences and hunting techniques of animals like sabertooth cats, very large hyenas, and short-faced bears (Hart & Sussman, 2011; Van Valkenburgh, Hayward, Ripple, Meloro, & Roth, 2016). Additionally, whilst Africa has the most intact and diverse predator guild in the modern-world (Cozzi et al., 2012; Dalerum, Cameron, Kunkel, & Somers, 2009), evidence from the eastern African fossil record suggests that functional richness within the guild has declined by almost 99% since 3.5 Ma (Werdelin & Lewis, 2013b). This makes it difficult to imagine the effects of far greater diversity and different intraguild dynamics on prey animals' landscapes of fear. Pleistocene ecosystems were home to many large (>100kg) hypercarnivores, several of which lived

sympatrically, but today only lions and tigers fill this niche and they do not overlap geographically. These differences in the make-up of extant and extinct carnivore guilds suggest that prey species, including primates, once inhabited more salient and complex landscapes of fear than exist today. On the other hand, predation pressure might actually be heightened in some modern ecosystems compared to prehistoric ones. This is because anthropogenically induced habitat fragmentation and restricted-size reserves (protected areas that are smaller than naturally-functioning ecosystems) might create more concentrated or "artificial" spatial overlap amongst carnivores and prey species compared to what would exist in an environment unmarred by modern human activity (Hayward & Slotow, 2009; Searle, Smit, Cusack, et al., 2021).

If fed into a cyclical feedback loop, advances in both paleontology and behavioural ecology will contribute to increasingly accurate models of past landscapes of fear. These can then be used to generate insights and further research questions about the role of risk in behavioural evolution. The collection of more fossil evidence will provide us with information on which prey species were vulnerable to certain predators, and will increase the resolution of data about presence and abundance of carnivore species through time and space. Meanwhile, advances in remote sensing and community-level ecology will expand our understanding of extant intraguild dynamics and their effects on entire ecosystems, which could perhaps then be modelled in environments without the artificial constraints of national borders or park boundaries.

5.4.3 Fossil sites for future research

Whilst it will take time to research and build increasingly accurate models of these broad environments, there are particular sites at which localised patterns of carnivore speciation, extinction, and primate substrate-use might be studied. As mentioned above, primate terrestriality emerges in two primate clades at Maboko Island, Kenya, approximately 15 Ma. The simultaneous emergence of

the trait in both the *Victoriapithecus* and *Equatorius* lineages precedes the expansion of grasslands in the region and appears to have happened when both were relatively small-bodied primate species (McCrossin et al., 1998). In the case of *Equatorius*, morphological analyses indicate that it likely engaged in palmigrade terrestrial locomotion which evolved independently to adaptations like knuckle-walking seen in living hominoids (Patel, Susman, Rossie, & Hill, 2009). Researchers have hypothesised that a shift in diet might have selected for more time spent on the ground by primates at Maboko Island (McCrossin et al., 1998). It is worth exploring this hypothesis alongside considerations of changes in pressures – including predation risk – that would have deterred them from descending to the ground. Thus, Maboko Island could be a good starting point for investigating fossil-based landscapes of fear, under the working hypothesis that the emergence of primate terrestriality might have been preceded by a drop in either the abundance or diversity of predators at the site. If temporal resolution is not high enough to explore sequential patterns at the site, the inferred landscape of fear at Maboko Island could be compared to those of other sites from a similar time period to investigate whether there were unusually low numbers of carnivores in the Maboko region around 15 Ma. It would also be a good site to study primate fossils more closely for carnivore damage, both as a proxy for predation rate amongst the sample and to identify the possible key predators of primates at the site.

It will also be valuable to explore in greater detail the relationships between primate and carnivoran fossils found in the Koobi Fora formation and surrounding sedimentary sequences that make up the Omo Group in the East African Rift System. Paleontological and archaeological research has been conducted at Koobi Fora for over 50 years, yielding vast records of paleoclimatic, fossil, and archaeological materials representative of millions of years of key ecological and technological transitions in the area (Bobe et al., 2022; Feibel, 2011). This makes it an excellent site for integrating

evidence over broad geographic and temporal scales, aided by the fact that the layers of sediments, which range from 4.3 to 0.6 Ma, are punctuated by layers of volcanic ash, making them chemically distinguishable and datable across the Plio-Pleistocene (McDougall, 1985). These also produce smaller discrete subsections that can be geochemically matched across formations, allowing researchers to analyse temporal correlations of materials found across the Omo-Turkana region (Gathogo & Brown, 2006; NG Jablonski et al., 2008; Rogers et al., 1994).

Data from the Koobi Fora formation capture several longitudinal trends. The hominin fossil record documents the presence of *Au. Anamensis* approximately 4 Ma through to a time of high hominin diversity when *H. habilis*, *H. rudolfensis*, *H. erectus*, and *P. boisei* occupied the region between 2 and 1.4 Ma (Bobe et al., 2022). Alongside this, the archaeological record demonstrates a shift from a few Oldowan sites before 1.9 Ma (Braun, Rogers, Harris, & Walker, 2010), through the transition to Acheulean technology 1.76 Ma (Lepre et al., 2011), to an abundance of many sites with large numbers of artefacts spread across the landscape by 1.5 Ma (Presnyakova et al., 2018; Rogers et al., 1994). This increase in the production of lithic technology is proof that hominins were spending a significant amount of time on the ground by 1.5 Ma. It is worth exploring whether or when their levels of terrestriality decoupled from trends seen in other primate lineages at the site. For example, Koobi Fora also documents a rise in the numbers of *Theropithecus*, a primate genus that became both increasingly terrestrial and widespread until it was the most common primate in the landscape by 1.5 Ma (Bobe et al., 2022; NG Jablonski, 1993a). On a broad scale, the timing of increased terrestriality in both the *Theropithecus* and hominin clades indicates that they might have been facing similar selection pressures. And indeed, Koobi Fora provides evidence of two possible drivers of these primate behaviours. One is the paleoecological change from wooded environments to more open grasslands, particularly after 2 Ma (Bobe et al., 2022). And the other is a decline in both the

functional and taxonomic diversity of the large carnivore guild at Koobi Fora, which occurred between 2 and 1.5 Ma (Werdelin & Lewis, 2013b, 2013a) and might have released restrictions on primate terrestriality. To examine the role of the landscape of fear in behavioural evolution at Koobi Fora, the relationships between carnivoran and primate fossils will need to be examined at higher temporal and spatial resolution. This process will likely take time but will be aided by new fossil discoveries and improved methodologies, including the incorporation of insights from modern ecosystems and behavioural ecology.

As evidenced by studies of extant primate terrestriality discussed in this thesis, a behavioural shift can arise in a relatively short period of time within a small population of animals and a localised ecological setting. Over the course of primate evolutionary history, there have likely been various spatiotemporal pockets in which the "right" ecological factors have come together to favour terrestrial behaviour in primates, sometimes lasting long enough to shift behaviour or even morphology in the species exposed to these conditions. Using this behavioural ecology lens, we can better explore how locomotive diversity arose in Miocene and Plio-Pleistocene primates, and we might be able to pinpoint the conditions or place where terrestrial bipedalism emerged in our own lineage.

5.5 Conclusion

This chapter reviews the evolution of hominin locomotion and primate terrestriality, recognising that we need to look further back than the emergence of "obligate bipedalism" in the Plio-Pleistocene to examine the primates and palaeoenvironments of the Miocene. Whilst many herbivorous taxa adapted to climate change in the Miocene with significant changes to their dentition, Miocene apes appear to have retained their diet and dentition but diversified in the ways they moved around to forage in the changing environment (Senut et al., 2018). Somewhere amongst this diversification lay

the origins of hominid and hominin locomotion, present in their respective LCAs. However, as discussed in this chapter, we should not search for "morphological intermediates" between modern great apes and humans to define these LCAs, nor should we overlook the role of homoplasy in shaping primate locomotion. There is increasing evidence that the semi-terrestrial locomotive styles of extant hominids evolved independently (Dainton & Macho, 1999; Kivell & Schmitt, 2009; Sayers et al., 2012), that hominin bipedalism might have had arboreal origins (Crompton et al., 2010; Thorpe et al., 2007), and that both terrestriality and bipedality might have arisen multiple times, in different lineages and places, and independently of one another (e.g. Hammond et al., 2020; Patel et al., 2009). Furthermore, it seems that there was great locomotive diversity amongst the hominin clade, with many species displaying mixed traits indicative of both climbing abilities and some form of terrestrial bipedalism (Dunmore et al., 2020; Prang et al., 2021; Richmond et al., 2020; Ruff, 2009; Senut et al., 2001; Ward et al., 2001). This diversity and mosaic nature of ape locomotion through time is best understood by using a behavioural ecology lens to consider the selection pressures faced by hominins and other primates.

Based on the theory and results presented in previous chapters of this thesis, I argue that the landscape of fear might be a selection pressure that has shaped primate locomotion. Rather than assuming that the shared trait of terrestriality amongst African apes indicates that it existed in their LCA, it is worth considering whether the dramatic loss in carnivore abundance and diversity over the past three million years has allowed all African apes to become more terrestrial than their LCA, albeit with different locomotive styles. It is also worth exploring further whether localised fluctuations in predator abundance or diversity facilitated the rise of terrestriality in different primate lineages at different times, ultimately explaining how one group of African apes came to spend almost all of their time on the ground. This chapter has outlined the correlates, causes, and

consequences of terrestriality, highlighting how shifts in predation pressure might have downstream consequences on primate group size, social dynamics, ranging and dispersal behaviours, and tool use. These relationships can all be explored further through future research, both in extant primate populations and from fossil sites where paleontological, paleoecological, and archaeological data provide us with details on the environments and interactions of prehistoric primates. Through the integration of these methods and iterative hypothesis generation that can be tested across different disciplines, we will better our understanding of primate evolution and of the contribution of terrestriality to our human "uniqueness".

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Student name	Philippa Hammond		
Contribution to the paper	Philippa Hammond: conceptualization, review, write-up. René Bobe: support with conceptualization, review, and editing. Susana Carvalho: support with conceptualization, review, and editing.		
Signature 		Date	29/08/2022

Supervisor Confirmation

By signing the Statement of Authorship, you are certifying that the candidate made a substantial contribution to the publication, and that the description described above is accurate.

Supervisor name and title: Susana Carvalho, Professor		
Supervisor comments: I confirm the information provided is accurate		
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Chapter Six
Conclusion

In this thesis, I have explored the behavioural ecology of primates, both past and present, with a focus on the adaptive links between predation risk and primate terrestriality. In Chapter One I introduced the concept of the "landscape of fear" and discussed the significant role that predator-prey dynamics have in shaping behavioural evolution. The chapter described the environments inhabited by early hominins and the risk that might have been present across such landscapes. It included discussion around the transition from the vulnerability of hominins as prey to the emergence of the "human predatory pattern" which sets humans apart from other primates in their ability to extract tissues from animals larger than themselves. It is this shift and the consequent hegemony of modern humans that has led many to believe that hominins were outcompeting other predators from as early as 2 Ma. However, it is still a matter of debate whether hominin hunting strategies were really the primary driver of a wave of carnivoran extinctions between 2 and 1.5 Ma. And regardless of the cause, it is worth considering what a drop in predation pressure would have meant for prehistoric primates, including hominins. This is where research from modern ecosystems can enhance our understanding of the stories told by fossil records. As described in the second half of Chapter One, there are many primate traits that are thought to be adaptations to avoiding predation. These include the demographic and social features of their troops, their ranging and dispersal patterns, and their sleeping and nocturnal behaviours. Whilst many of these behaviours have been methodologically difficult to study in the past, new methods are facilitating remote sensing and landscape-scale monitoring of primates which will help elucidate the long-term effects of risk on behaviour.

In Chapter Two I presented a quasi-experimental study of risk perception in two troops of chacma

baboons in Gorongosa National Park, Mozambique. In this study, we documented the decline of vocalisations and vigilance – behaviours indicative of perceived risk – over the course of habituation and we found mediating effects of both habitat structure and time of day on these behaviours. Both vocalisations and vigilance are higher in denser habitats and later in the day, perhaps due to reduced visibility heightening baboons' perceived risk. We also reported a negative relationship between these behaviours and baboons' use of the ground, which adds to a body of evidence suggesting that primate terrestriality increases in environments and contexts where risk is reduced.

Chapter Three zoomed out to the population level of the Gorongosa baboons and compared their ground-based activity to that of a neighbouring population of baboons. In this chapter, camera trap data provided insight into landscape-scale effects of ecology, season, and risk on primate terrestriality. Whilst we found no evidence that tree coverage predicts differences in baboons' ground-use, our results indicate that baboons spend more time on the ground in the late dry season, perhaps due to changes in their foraging behaviours or reduced water availability. We also found that overall, baboons within the park are more active on the ground than those in the neighbouring population. This result might simply reflect a larger population within the park, but it might also be explained to some extent by the different apex predators present in each landscape. Compared to the baboons exposed to lions within the park, the baboons exposed to leopards are not only generally less active on the ground, but the diel distribution of their terrestrial activity is also significantly different. These baboons are less active during nocturnal and crepuscular hours, seeming to limit their terrestrial activity to daylight hours.

Chapter Four compared circadian patterns and temporal overlap in carnivore and baboon activity across 10 sites in eastern and southern Africa. The chapter included discussion about the role of carnivore diversity and intraguild dynamics in adding complexity to dynamic landscapes of fear for

prey species. Results from this chapter suggest that baboons' circadian activity patterns overlap to a high degree across the 10 African sites. However, some variation in the distribution of these patterns does exist and might be explained by carnivore diversity at the sites. Building on the preliminary findings from Chapter Three, our results from Chapter Four provide additional evidence that leopards might have a particularly strong influence on baboon terrestriality. The absence of their primary predator from a landscape appears to facilitate baboons' use of the ground during times of day that would be perceived as "too risky" when leopards are present. Further research is needed to clearly distinguish the effects of key predator species from a more general lack of carnivore diversity at sites, and to elucidate dynamic landscapes of fear from site-specific data. For example, Gorongosa provides an ideal site for longitudinal investigation of the effects of increasing carnivore diversity on primate diversity and Karoo appears to be a good location to explore nocturnal behaviours of baboons in more detail. More detailed comparative analyses will also provide insights into the effects of other ecological variables, as well as grid features, on the detections of terrestrial baboon activity across sites.

Finally, in Chapter Five I discussed the findings from the previous chapters of this thesis, integrating behavioural ecology with fossil evidence in a review of the origins of hominin locomotion and the emergence of primate terrestriality. The chapter reviewed morphological traits of African apes from the Miocene as well as the Plio-Pleistocene, discussing historic overreliance on the "Chimpanzee Referential Doctrine" and under-appreciation of homoplasy in shaping these traits. In this discussion I emphasised the value of integrating paleontological research with insights from behavioural ecology to generate more nuanced understandings and hypotheses about the environments that have shaped human evolution. Such an approach can be used to better understand the evidence that locomotive diversity and arboreal adaptations existed across many hominin taxa. When consideration

of the landscape of fear is added to the fact that primates evolved from an arboreal ancestral state, it becomes clearer that a transition to terrestrial bipedality would not be a sudden, smooth, or obvious adaptation to emerge in an ape lineage. Understanding extant primates' responses to predation risk can add nuance and open avenues for studying predator-prey dynamics in the fossil record. An integration of these methods will help us build a clearer picture of how humans became such an unusually terrestrial primate and the extent to which living on the ground has contributed to other "unique" behaviours in our lineage.

References

Alba, D. (2010). Cognitive inferences in fossil apes (Primates, Hominoidea): does encephalization reflect intelligence. *J. Anthropol. Sci*, *88*(1).

Alberts, S. (2019). Social influences on survival and reproduction: Insights from a long-term study of wild baboons. *Journal of Animal Ecology*, *88*(1), 47–66. https://doi.org/10.1111/1365-2656.12887

Alberts, S. C., Altmann, J., Alberts, S. C., Altmann, J., Kappeler, P. M., & Watts, D. P. (2012). The Amboseli Baboon Research Project: 40 years of continuity and change. *Springer*, *9783642225147*, 261–287. https://doi.org/10.1007/978-3-642-22514-7_12

Alberts, S., Hollister-Smith, J., Mututua, R., Sayialel, S., Muruthi, P., Warutere, J., & Altmann, J. (2005). Seasonality and long-term change in a savanna environment. *Cambridge Studies in Biological and Evolutionary Anthropology*, *44*.

Alexander, R. (1990). *How did humans evolve? Reflections on the uniquely unique species.*

Alexander, R. D. (1974). The Evolution of Social Behavior. *Annual Review of Ecology and Systematics*, *5*(1), 325–383. https://doi.org/10.1146/annurev.es.05.110174.001545

Allan, A., Bailey, A., & Hill, R. (2020). Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait. *Science Advances*, *6*(28), eaaz0870. https://doi.org/10.1126/sciadv.aaz0870

Allan, A., & Hill, R. (2018). What have we been looking at? A call for consistency in studies of

primate vigilance. *American Journal of Physical Anthropology*, *165*, 4–22. Retrieved from https://onlinelibrary.wiley.com/doi/pdf/10.1002/ajpa.23381

Almécija, S., Hammond, A. S., Thompson, N. E., Pugh, K. D., Moyà-Solà, S., & Alba, D. M. (2021). Fossil apes and human evolution. *Science*, *372*(6542). https://doi.org/10.1126/SCIENCE.ABB4363/ASSET/095FDD9D-3280-4DBF-A2B2-FC05ACE166A7/ASSETS/GRAPHIC/372_ABB4363_FA.JPEG

Almécija, S., Tallman, M., Alba, D., Pina, M., Moyà-Solà, S., & Jungers, W. (2013). The femur of Orrorin tugenensis exhibits morphometric affinities with both Miocene apes and later hominins. *Nature Communications*, *4*(1), 1–12. Retrieved from https://www.nature.com/articles/ncomms3888

Altmann, J., & Alberts, S. (2003). Variability in Reproductive Success Viewed From a Life-History Perspective in Baboons. *J. Hum. Biol*, *15*, 401–409. https://doi.org/10.1002/ajhb.10157

Altmann, S. A. (2009). Fallback foods, eclectic omnivores, and the packaging problem. *American Journal of Physical Anthropology*, *140*(4), 615–629. https://doi.org/10.1002/ajpa.21097

Altmann, S., & Altmann, J. (1970). *Baboon ecology: African field research*. Chicago: University of Chicago Press.

Altmann, J., & Muruthi, P. (1988). Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology*, *15*(3), 213-221.

Anaya, A., Patel, B. A., Orr, C. M., Ward, C. V., & Almécija, S. (2021). Evolutionary trends of the lateral foot in catarrhine primates: Contextualizing the fourth metatarsal of Australopithecus afarensis. *Journal of Human Evolution*, *161*, 103078.

https://doi.org/10.1016/J.JHEVOL.2021.103078

Anderson, C. M. (1986). Predation and primate evolution. *Primates*, *27*(1), 15–39. https://doi.org/10.1007/BF02382520

Anderson, J. R. (1998). Sleep, sleeping sites, and sleep-related activities: Awakening to their significance. *American Journal of Primatology*, *46*(1), 63–75. https://doi.org/10.1002/(SICI)1098-2345(1998)46:1<63::AID-AJP5>3.0.CO;2-T

Anderson, J. R., & McGrew, W. C. (1984). Guinea baboons (Papio papio) at a sleeping site. *American Journal of Primatology*, *6*(1), 1-14.

Andrews, P. (2020). Last Common Ancestor of Apes and Humans: Morphology and Environment. *Folia Primatologica*, *91*(2), 122–148. https://doi.org/10.1159/000501557

Antón, M. (2013). *Sabertooth*. Indiana University Press.

Antón, S., Potts, R., & Aiello, L. (2014). Evolution of early Homo: an integrated biological perspective. *Science*.

Atkins, J., Long, R., Pansu, J., Daskin, J., Potter, A., Stalmans, M., … Pringle, R. (2019). Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science*. https://doi.org/10.1126/science.1205106

Atuo, F. A., & O'Connell, T. J. (2017). The landscape of fear as an emergent property of heterogeneity: Contrasting patterns of predation risk in grassland ecosystems. *Ecology and Evolution*, *7*(13), 4782–4793. https://doi.org/10.1002/ece3.3021

Bain, M., Nagrani, A., Schofield, D., Berdugo, S., Bessa, J., Owen, J., … Zisserman, A. (2021).

Automated audiovisual behavior recognition in wild primates. *Science Advances*, *7*(46). https://doi.org/10.1126/SCIADV.ABI4883

Bandini, E., Harrison, R., & Motes-Rodrigo, A. (2022). Examining the suitability of extant primates as models of hominin stone tool culture. *Humanities and Social Sciences Communications*, *9*(1), 1–18. Retrieved from https://www.nature.com/articles/s41599-022-01091-x

Barr, W. A., Pobiner, B., Rowan, J., Du, A., & Faith, J. T. (2022). No sustained increase in zooarchaeological evidence for carnivory after the appearance of Homo erectus . *Proceedings of the National Academy of Sciences*, *119*(5), e2115540119. https://doi.org/10.1073/PNAS.2115540119/-/DCSUPPLEMENTAL

Barton, R. A., & Whiten, A. (1993). Feeding competition among female olive baboons, Papio anubis. *Animal Behaviour*, *46*(4), 777–789. https://doi.org/10.1006/anbe.1993.1255

Basell, L. (2008). Middle Stone Age (MSA) site distributions in eastern Africa and their relationship to Quaternary environmental change, refugia and the evolution of Homo sapiens. *Quartenary Science Reviews*. Retrieved from https://www.sciencedirect.com/science/article/pii/S027737910800245X

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Begun, D. R. (2015). The Real Planet of the Apes. *The Real Planet of the Apes*. https://doi.org/10.1515/9781400874279/HTML

Begun, D. R., Nargolwalla, M. C., & Kordos, L. (2012). European Miocene Hominids and the Origin of the African Ape and Human Clade. *Evolutionary Anthropology*, *21*(1), 10–23.

https://doi.org/10.1002/EVAN.20329/FORMAT/PDF

Behrensmeyer, A. K. (2006). Climate Change and Human Evolution, *476*. https://doi.org/10.1126/science.1116051

Berger, L. R., & Clarke, R. J. (1995). Eagle involvement in accumulation of the Taung child fauna. *Journal of Human Evolution*, *29*(3), 275–299. https://doi.org/10.1006/JHEV.1995.1060

Bettridge, C., Lehmann, J., & Dunbar, R. I. M. (2010). Trade-offs between time, predation risk and life history, and their implications for biogeography: A systems modelling approach with a primate case study. *Ecological Modelling*, *221*(5), 777–790. https://doi.org/10.1016/J.ECOLMODEL.2009.11.017

Bettridge, C. M., & Dunbar, R. I. M. (2012). Predation as a determinant of minimum group size in baboons. *Folia Primatologica; International Journal of Primatology*, *83*(3–6), 332–352. https://doi.org/10.1159/000339808

Bibi, F., & Kiessling, W. (2015). Continuous evolutionary change in Plio-Pleistocene mammals of eastern Africa. *National Acad Sciences*. Retrieved from http://www.pnas.org/content/112/34/10623.short

Bidner, L. R. (2009). *Spatial and temporal patterns of leopard predation risk faced by chacma baboons*. Arizona State University.

Bidner, L., Isbell, L., & Matsumoto-Oda, A. (2016). Nocturnal leopard (Panthera pardus) predation risk for olive baboons (Papio anubis) in Kenya.

Bidner, L., Matsumoto-Oda, A., & Isbell, L. (2018). The role of sleeping sites in the predator-prey

dynamics of leopards and olive baboons. *American Journal of Primatology*, *80*(12), e22932. https://doi.org/10.1002/AJP.22932

Blumenschine, R. J. (1986). Carcass consumption sequences and the archaeological distinction of scavenging and hunting. *Journal of Human Evolution*, *15*(8), 639–659. https://doi.org/10.1016/S0047-2484(86)80002-1

Bobe, R. (2011). Fossil Mammals and Paleoenvironments in the Omo-Turkana Basin. *Evolutionary Anthropology: Issues, News, and Reviews*, *20*(6), 254–263. https://doi.org/10.1002/evan.20330

Bobe, R. (2018). The first three million years of human evolution: The ecology of our African ancestors. *In: Annual Meeting of the European Society for the Study of Human Evolution*.

Bobe, R., & Behrensmeyer, A. (2004). The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus Homo. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *207*(3–4), 399–420. https://doi.org/10.1016/J.PALAEO.2003.09.033

Bobe, R., & Carvalho, S. (2019). Hominin diversity and high environmental variability in the Okote Member, Koobi Fora Formation, Kenya. *Journal of Human Evolution*, *126*, 91–105. https://doi.org/10.1016/J.JHEVOL.2018.10.012

Bobe, R., Coelho J, Carvalho, S., & Leakey, M. (2022). Bobe, R., Coelho, J. D. O., Carvalho, S., & Leakey, M. (2022). Early Hominins and Paleoecology of the Koobi Fora Formation, Lake Turkana Basin, Kenya. In *African Paleoecology and Human Evolution*. Cambridge University Press.

Bobe, R., Manthi, F. K., Ward, C. V., Plavcan, J. M., & Carvalho, S. (2020). The ecology of

Australopithecus anamensis in the early Pliocene of Kanapoi, Kenya. *Journal of Human Evolution*, *140*, 102717. https://doi.org/10.1016/j.jhevol.2019.102717

Böhme, M., Spassov, N., Fuss, J., Tröscher, A., Deane, A. S., Prieto, J., … Begun, D. R. (2019). A new Miocene ape and locomotion in the ancestor of great apes and humans. *Nature 2019 575:7783*, *575*(7783), 489–493. https://doi.org/10.1038/s41586-019-1731-0

Bouley, P., Paulo, A., Angela, M., Plessis, C. Du, & Marneweck, D. G. (2021). The successful reintroduction of African wild dogs (Lycaon pictus) to Gorongosa National Park, Mozambique. *PLoS ONE*, *16*(4 April 2021), e0249860. https://doi.org/10.1371/journal.pone.0249860

Bouley, P., Poulos, M., Branco, R., & Carter, N. H. (2018). Post-war recovery of the African lion in response to large-scale ecosystem restoration. *Biological Conservation*, *227*, 233–242. https://doi.org/10.1016/J.BIOCON.2018.08.024

Boyer-Ontl, K. M., & Pruetz, J. D. (2014). Giving the Forest Eyes: The Benefits of Using Camera Traps to Study Unhabituated Chimpanzees (Pan troglodytes verus) in Southeastern Senegal. *International Journal of Primatology*, *35*(5), 881–894. https://doi.org/10.1007/s10764-014-9783-3

Braun, D. R., Rogers, M. J., Harris, J. W., & Walker, S. J. (2010). Quantifying Variation in Landscape-Scale Behaviors: The Oldowan from Koobi Fora. In *New Perspectives on Old Stones* (pp. 167–182). New York, NY: Springer New York. https://doi.org/10.1007/978-1-4419-6861-6_7

Brown, J. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research*, *1*(1), 49–71. Retrieved from http://www.evolutionary-

ecology.com/abstracts/v01/1014.html

Brunet, M., Guy, F., Pilbeam, D., Mackaye, H., & Likius, A. (2002). A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, *418*(6894), 145–151. Retrieved from https://www.nature.com/articles/nature00879

Busse, C. (1980). *Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve*. *Botswana Notes and Records*. Retrieved from https://www.jstor.org/stable/40980790

Byrne, R. (1981). Distance vocalisations of Guinea baboons (Papio papio) in Senegal: an analysis of function. *Behaviour*, *78*(3–4), 283–312. Retrieved from https://brill.com/view/journals/beh/78/3-4/article-p283_7.xml

Byrne, R. (2001). Social and technical forms of primate intelligence. In *Tree of Origin: What primate behavior can tell us about human social evolution145-172*. Harvard University Press Cambridge.

Camarós, E., Cueto, M., Lorenzo, C., Villaverde, V., & Rivals, F. (2016). Large carnivore attacks on hominins during the Pleistocene: a forensic approach with a Neanderthal example. *Archaeological and Anthropological Sciences*, *8*(3), 635–646. https://doi.org/10.1007/S12520-015-0248-1/FIGURES/4

Campbell, C. J., Aureli, F., Chapman, C. A., Ramos-Fernández Pronatura Peninsula de Yucatan, G., Matthews, K., & Behavior, T. (2005). Terrestrial Behavior of Ateles spp. *International Journal of Primatology*, *26*(5), 1039–1051. https://doi.org/10.1007/s10764-005-6457-1

Cant, J. G. H. (1992). Positional behavior and body size of arboreal primates: A theoretical framework for field studies and an illustration of its application. *American Journal of Physical*

Anthropology, *88*(3), 273–283. https://doi.org/10.1002/AJPA.1330880302

Caro, T. (2005). *Antipredator defenses in birds and mammals*. University of Chicago Press. Retrieved from https://books.google.com/books?hl=en&lr=&id=2i0tCgP_GbwC&oi=fnd&pg=PR5&ots=hf6kiQFIMP&sig=XwfVJ-UBdr11mXzlkwxCwERVf78

Carothers, J. H., Jaksić, F. M., & Jaksic, F. M. (1984). Time as a Niche Difference: The Role of Interference Competition. *Oikos*, *42*(3), 403. https://doi.org/10.2307/3544413

Caruana, M. V., Carvalho, S., Braun, D. R., Presnyakova, D., Haslam, M., Archer, W., … Harris, J. W. K. (2014). Quantifying Traces of Tool Use: A Novel Morphometric Analysis of Damage Patterns on Percussive Tools. *PLoS ONE*, *9*(11), e113856. https://doi.org/10.1371/journal.pone.0113856

Carvalho, S, Matsuzawa, T., & McGrew, W. (2013). From pounding to knapping: how chimpanzees can help us to model hominin lithics. In *Cognition and ecology* (pp. 225–241). Cambridge: Cambridge University Press.

Carvalho, Susana, & Beardmore-Herd, M. (2019). Technological Origins: Primate Perspectives and Early Hominin Tool Use in Africa. In *Oxford Research Encyclopedia of African History*. Oxford University Press. https://doi.org/10.1093/acrefore/9780190277734.013.75

Casanovas-Vilar, I., Alba, D. M., Garcés, M., Robles, J. M., & Moyà-Solà, S. (2011). Updated chronology for the Miocene hominoid radiation in Western Eurasia. *Proceedings of the National Academy of Sciences*, *108*(14), 5554–5559. https://doi.org/10.1073/PNAS.1018562108

Cerling, T. (2014). Stable Isotope Evidence for Hominin Environments in Africa. Treatise on

Geochemistry.

Cerling, T., Andanje, S., Blumenthal, S., Brown, F., Chritz, K., Harris, J., & Leakey, M. (2015). Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. *Proceedings of the National Academy of Sciences*, *112*(37), 11467–11472. Retrieved from http://www.pnas.org/content/112/37/11467.short

Cerling, T., Chritz, K. L., Jablonski, N., Leakey, M. G., & Manthi, F. K. (2013). Diet of Theropithecus from 4 to 1 Ma in Kenya. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(26), 10507–10512. https://doi.org/10.1073/PNAS.1222571110/SUPPL_FILE/PNAS.201222571SI.PDF

Cerling, T., Harris, J., MacFadden, B., & Leakey, M. (1997). Global vegetation change through the Miocene/Pliocene boundary. *Nature*. Retrieved from https://www.nature.com/articles/38229

Cerling, T., Manthi, F., Mbua, E., Leakey, L., Leakey, M., Leakey, R., & Roche, H. (2013). Stable isotope-based diet reconstructions of Turkana Basin hominins. *Proceedings of the National Academy of Sciences*, *110*(26), 10501–10506. Retrieved from http://www.pnas.org/content/early/2013/06/06/1222568110.short

Chaney, M. E., Ruiz, C. A., Meindl, R. S., & Lovejoy, C. O. (2022). The foot of the human–chimpanzee last common ancestor was not African ape-like: A response to Prang (2019). *Journal of Human Evolution*, *164*, 102940. https://doi.org/10.1016/J.JHEVOL.2020.102940

Chapman, C. A., & Huffman, M. A. (2018). Why do we want to think humans are different? *Animal Sentience*, *3*(23). https://doi.org/10.51291/2377-7478.1358

Cheney, D. L., Seyfarth, R. M., Fischer, J., Beehner, J., Bergman, T., Johnson, S. E., … Silk, J.

(2004). Factors Affecting Reproduction and Mortality Among Baboons in the Okavango Delta, Botswana. *International Journal of Primatology*, *25*(2), 401–428. https://doi.org/10.1023/B:IJOP.0000019159.75573.13

Cheney, D., & Wrangham, R. (1987). Predation. In B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, & T. Struhsaker (Eds.), *Primate Societies* (pp. 227–239). Chicago: University of Chicago PressChicago, IL.

Clauss, M., Scriba, M., Kioko, J., Ganzhorn, J. U., & Kiffner, C. (2021). Camera-trap data do not indicate scaling of diel activity and cathemerality with body mass in an East African mammal assemblage. *Ecology and Evolution*, *11*(20), 13846–13861. https://doi.org/10.1002/ECE3.8090

Clutton-Brock, T. H., & Harvey, P. H. (2009). Primate ecology and social organization. *Journal of Zoology*, *183*(1), 1–39. https://doi.org/10.1111/j.1469-7998.1977.tb04171.x

Clutton-Brock, T., & Harvey, P. (1977). Primate ecology and social organization. *Journal of Zoology*. Retrieved from https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-7998.1977.tb04171.x

Coleman, B. T., & Hill, R. (2014). Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour*, (88), 165–173. https://doi.org/10.1016/j.anbehav.2013.11.027

Coolidge, F., & Wynn, T. (2006). The effects of the tree-to-ground sleep transition in the evolution of cognition in early Homo. *Before Farming*, *2006*(4), 1–18. https://doi.org/10.3828/bfarm.2006.4.11

Cords, M. (1990). Vigilance and mixed-species association of some East African forest monkeys.

Behavioral Ecology and Sociobiology, *26*(4). https://doi.org/10.1007/BF00178323

Cote, S. (2004). Origins of the African hominoids: an assessment of the palaeobiogeographical evidence. *Comptes Rendus Palevol*, *3*(4), 323–340. Retrieved from https://www.sciencedirect.com/science/article/pii/S1631068304000855

Cowlishaw, G. (1994). Vulnerability To Predation in Baboon Populations. *Behaviour*, *131*(3), 293–304. https://doi.org/10.1163/156853994X00488

Cowlishaw, G. (1997a). Alarm Calling and Implications for Risk Perception in a Desert Baboon Population. *Ethology*, *103*(5), 384–394. https://doi.org/10.1111/j.1439-0310.1997.tb00154.x

Cowlishaw, G. (1997b). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, *53*(4), 667–686. Retrieved from https://www.sciencedirect.com/science/article/pii/S0003347296902985

Cozzi, G., Broekhuis, F., Mcnutt, J. W., Turnbull, L. A., Macdonald, D. W., & Schmid, B. (2012). *Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores*. *Ecology* (Vol. 93).

Crompton, R. H., Sellers, W. I., & Thorpe, S. K. S. (2010). Arboreality, terrestriality and bipedalism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1556), 3301–3314. https://doi.org/10.1098/rstb.2010.0035

Dainton, M., & Macho, G. (1999). Did knuckle walking evolve twice? *Journal of Human Evolution*, *36*(2), 171–194. Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248498902652

Dalerum, F., Cameron, E. Z., Kunkel, K., & Somers, M. J. (2009). Diversity and depletions in continental carnivore guilds: Implications for prioritizing global carnivore conservation. *Biology Letters*, *5*(1), 35–38. https://doi.org/10.1098/RSBL.2008.0520

Dart, R. (1925). Australopithecus africanus The Man-Ape of South Africa. *Nature*, *115*(2884), 195–199. https://doi.org/10.1038/115195a0

Dart, R. (1949). The predatory implemental technique of Australopithecus. *American Journal of Physical Anthropology*, *7*(1), 1–38. https://doi.org/10.1002/AJPA.1330070103

Daskin, J. H., Stalmans, M., & Pringle, R. M. (2016). Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *Journal of Ecology*, *104*(1), 79–89. https://doi.org/10.1111/1365-2745.12483

Davidge, C. (1978). Activity patterns of chacma baboons (Papio ursinus) at Cape Point. *African Zoology*, *13*(1), 143-155.

Davies, N., Krebs, J., & West, S. (2012). *An introduction to behavioural ecology*.

deMenocal, P. (2004). African climate change and faunal evolution during the Pliocene–Pleistocene. *Earth and Planetary Science Letters*, *220*(1–2), 3–24. https://doi.org/10.1016/S0012-821X(04)00003-2

deMenocal, P. B. (2014). Climate Shocks, *311*, 48–53. https://doi.org/10.7916/D8TQ60WN

DeSilva, J. M., McNutt, E., Benoit, J., & Zipfel, B. (2019). One small step: A review of Plio-Pleistocene hominin foot evolution. *American Journal of Physical Anthropology*, *168*, 63–140. https://doi.org/10.1002/AJPA.23750

DeSilva, J. M., Shoreman, E., & MacLatchy, L. (2006). A fossil hominoid proximal femur from Kikorongo Crater, southwestern Uganda. *Journal of Human Evolution*, *50*(6), 687–695. https://doi.org/10.1016/J.JHEVOL.2006.01.008

DeSilva, J. M., Steininger, C. M., & Patel, B. A. (2013). Cercopithecoid primate postcranial fossils from Cooper's D, South Africa. *Geobios*, *46*(5), 381–394. https://doi.org/10.1016/j.geobios.2013.07.001

DeVore, I., & Hall, K. (1965). Baboon ecology. Retrieved from https://opus4.kobv.de/opus4-Fromm/frontdoor/index/index/docId/7963

DeVore, I., & Tooby, J. (1987). The reconstruction of hominid behavioral evolution through strategic modeling. In W. Kinzey (Ed.), *The Evolution of Human Behavior: Primate Models* (pp. 183–237).

Dirks, P., Kibii, J., Kuhn, B., Steininger, C., Churchill, S., Kramers, J., & King, G. (2010). Geological setting and age of Australopithecus sediba from southern Africa. *Science*, *328*(5975), 205–208. Retrieved from http://science.sciencemag.org/content/328/5975/205.short

Dirks, P., Roberts, E. M., Hilbert-Wolf, H., Kramers, J. D., Hawks, J., Dosseto, A., … Berger, L. R. (2017). The age of homo naledi and associated sediments in the rising star cave, South Africa. *ELife*, *6*. https://doi.org/10.7554/ELIFE.24231

Domínguez-Rodrigo, M. (2010). Configurational approach to identifying the earliest hominin butchers. *Proceedings of the National Academy of Sciences*, *107*(49), 20929–20934. Retrieved from http://www.pnas.org/content/107/49/20929.short

Domínguez-Rodrigo, M., & Pickering, T. (2003). Early Hominid Hunting and Scavenging: A

Zooarcheological Review. *Evolutionary Anthropology*, *12*(6), 275–282. https://doi.org/10.1002/EVAN.10119

Domínguez-Rodrigo, M., Pickering, T., Semaw, S., & Rogers, M. (2005). Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. *Journal of Human Evolution*, *48*(2), 109–121. Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248404001411

Doran, D. M. (1993). Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. *American Journal of Physical Anthropology*, *91*(1), 83–98. https://doi.org/10.1002/AJPA.1330910106/FORMAT/PDF

Dröge, E., Creel, S., Becker, M. S., & M'soka, J. (2017). Spatial and temporal avoidance of risk within a large carnivore guild. *Ecology and Evolution*, *7*(1), 189–199. https://doi.org/10.1002/ECE3.2616

Dunbar, R., & Hill, R. (1998). An Evaluation of the Roles of Predation Rate and Predation Risk as Selective Pressures on Primate Grouping Behaviour. *Behaviour*, *135*(4), 411–430. https://doi.org/10.1163/156853998793066195

Dunbar, R. I. M. (1992). Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology*, *31*(1), 35–49. https://doi.org/10.1007/BF00167814

Dunmore, C. J., Skinner, M. M., Bardo, A., Berger, L. R., Hublin, J.-J., Pahr, D. H., … Kivell, T. L. (2020). The position of Australopithecus sediba within fossil hominin hand use diversity. *Nature Ecology & Evolution*, 1–8. https://doi.org/10.1038/s41559-020-1207-5

Durant, S. M. (1998). Competition refuges and coexistence: an example from Serengeti carnivores.

Journal of Animal Ecology, *67*(3), 370–386. https://doi.org/10.1046/J.1365-2656.1998.00202.X

Dyer, N. (2018). Painted wolves, struggling to survive, find a new food: baboons. *National Geographic*.

Easter, T., Bouley, P., & Carter, N. (2019). Opportunities for biodiversity conservation outside of Gorongosa National Park, Mozambique: A multispecies approach. *Biological Conservation*, *232*, 217–227. https://doi.org/10.1016/J.BIOCON.2019.02.007

Eley, R. M., Strum, S. C., Muchemi, G., & Reid, G. D. F. (1989). Nutrition, body condition, activity patterns, and parasitism of free-ranging troops of olive baboons (Papio anubis) in Kenya. *American Journal of Primatology*, *18*(3), 209-219.

Elton, S. (2006). Forty years on and still going strong: the use of hominin-cercopithecid comparisons in palaeoanthropology. *Journal of the Royal Anthropological Institute*, *12*(1), 19–38. https://doi.org/10.1111/j.1467-9655.2006.00279.x

Elton, S., Bishop, L., & Wood, B. (2001). Comparative context of Plio-Pleistocene hominin brain evolution. *Journal of Human Evolution*, *41*(1), 1–27. Retrieved from https://sites.google.com/site/hymsfme/eltonetal2001.pdf

Elton, S., & Dunn, J. (2020). Baboon biogeography, divergence, and evolution: Morphological and paleoecological perspectives. *Journal of Human Evolution*, *145*, 102799. https://doi.org/10.1016/j.jhevol.2020.102799

Enstam, K., & Isbell, L. (2002). Comparison of responses to alarm calls by patas (Erythrocebus patas) and vervet (Cercopithecus aethiops) monkeys in relation to habitat structure. *American Journal of Physical Anthropology*, *119*(1), 3–14. https://doi.org/10.1002/ajpa.10104

Enstam, K., & Isbell, L. (2004). Microhabitat Preference and Vertical Use of Space by Patas Monkeys (Erythrocebus patas) in Relation to Predation Risk and Habitat Structure. *Folia Primatologica*, *75*, 70–84. https://doi.org/10.1159/000076265

Eriksson, A., Betti, L., Friend, A. D., Lycett, S. J., Singarayer, J. S., Von Cramon-Taubadel, N., … Manica, A. (2012). Late Pleistocene climate change and the global expansion of anatomically modern humans. *PNAS*, *109*(40), 16089–16094. https://doi.org/10.1073/pnas.1209494109

Espigares, M. P., Palmqvist, P., Guerra-Merchán, A., Ros-Montoya, S., García-Aguilar, J. M., Rodríguez-Gómez, G., … Martínez-Navarro, B. (2019). The earliest cut marks of Europe: a discussion on hominin subsistence patterns in the Orce sites (Baza basin, SE Spain). *Scientific Reports 2019 9:1*, *9*(1), 1–13. https://doi.org/10.1038/s41598-019-51957-5

Faith, J. T., Du, A., Behrensmeyer, A. K., Davies, B., Patterson, D. B., Rowan, J., & Wood, B. (2021). Rethinking the ecological drivers of hominin evolution. *Trends in Ecology & Evolution*, *36*(9), 797–807. https://doi.org/10.1016/J.TREE.2021.04.011

Falk, D., Redmond, J., Guyer, J., Conroy, C., Recheis, W., Weber, G., & Seidler, H. (2000). Early hominid brain evolution: a new look at old endocasts. *Journal of Human Evolution*, *38*(5), 695–717. Retrieved from http://deanfalk.com/wp-content/uploads/2012/06/2000-Falk-etal-Early-hominid-brain-evolution-a-new-look-at-old-endocasts.pdf

Falótico, T., & Ottoni, E. (2022). Terrestriality is associated with tool use diversity in wild capuchin monkeys. *OSF Preprint*. Retrieved from https://osf.io/preprints/2spnx/

Feakins, S., Levin, N., Liddy, H., & Sieracki, A. (2013). Northeast African vegetation change over 12 my. *Pubs.Geoscienceworld.Org*. Retrieved from

https://pubs.geoscienceworld.org/gsa/geology/article-abstract/41/3/295/131095

Fehlmann, G., & King, A. J. (2016). Bio-logging. *Current Biology*, *26*, R830–R831. https://doi.org/10.1016/j.cub.2016.05.033

Fehlmann, G., O'Riain, M. J., Hopkins, P. W., O'Sullivan, J., Holton, M. D., Shepard, E. L. C., & King, A. J. (2017). Identification of behaviours from accelerometer data in a wild social primate. *Animal Biotelemetry*, *5*(1), 6. https://doi.org/10.1186/s40317-017-0121-3

Feibel, C. S. (2011). A Geological History of the Turkana Basin. https://doi.org/10.1002/evan.20331

Fernández, M., & Vrba, E. (2006). Plio-Pleistocene climatic change in the Turkana Basin (East Africa): evidence from large mammal faunas. *Journal of Human Evolution*. https://www.sciencedirect.com/science/article/pii/S0047248405002034

Ferraro, J. V., Plummer, T. W., Pobiner, B. L., Oliver, J. S., Bishop, L. C., Braun, D. R., … Potts, R. (2013). Earliest Archaeological Evidence of Persistent Hominin Carnivory. *PLoS ONE*, *8*(4), e62174. https://doi.org/10.1371/journal.pone.0062174

Feuerriegel, E. M., Green, D. J., Walker, C. S., Schmid, P., Hawks, J., Berger, L. R., & Churchill, S. E. (2017). The upper limb of Homo naledi. *Journal of Human Evolution*, *104*, 155–173. https://doi.org/10.1016/J.JHEVOL.2016.09.013

Fischer, J., Hammerschmidt, K., Cheney, D. L., & Seyfarth, R. M. (2001). Acoustic Features of Female Chacma Baboon Barks. *Ethology*.

Fischer, J., Higham, J. P., Alberts, S., Barrett, L., Beehner, J. C., Bergman, T. J., … Zinner, D. (2019). The Natural History of Model Organisms: Insights into the evolution of social systems

and species from baboon studies. *ELife*, *8*. https://doi.org/10.7554/eLife.50989

Fleagle, J. (2013). *Primate adaptation and evolution*. Academic Press.

Foley, R. (1993). African terrestrial primates: the comparative evolutionary biology of Theropithecus and the Hominidae. . In N Jablonski (Ed.), *Theropithecus: The Rise and Fall of a Primate Genus.* (pp. 245–270).

Foley, R. (2016). Mosaic evolution and the pattern of transitions in the hominin lineage. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1698). https://doi.org/10.1098/RSTB.2015.0244

Foley, R. (2018). Evolutionary Geography and the Afrotropical Model of Hominin Evolution. *BMSAP*, *30*, 17–31. https://doi.org/10.3166/bmsap-2018-0001

Foley, R., & Gamble, C. (2009). The ecology of social transitions in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1533), 3267–3279. https://doi.org/10.1098/RSTB.2009.0136

Fortelius, M, Žliobaitė, I., Kaya, F., Bibi, F., Bobe, R., Leakey, L., & Werdelin, L. (2016). An ecometric analysis of the fossil mammal record of the Turkana Basin. *Phil.Trans.R.Soc.B*, *371*(1698). Retrieved from http://rstb.royalsocietypublishing.org/content/371/1698/20150232.abstract

Fortelius, Mikael, Geritz, S., Gyllenberg, M., Raia, P., & Toivonen, J. (2015). Modeling the Population-Level Processes of Biodiversity Gain and Loss at Geological Timescales. *The American Naturalist*, *186*(6), 742–754. https://doi.org/10.1086/683660

Forthman-Quick, D. L. (1986). Activity budgets and the consumption of human foodsd in two troops of baboons, Papio anubis, at Gilgil, Kenya. *Primate ecology and conservation, 2*, 221-228.

Fourvel, J. B., Thackeray, J. F., Brink, J. S., O'Regan, H., & Braga, J. (2018). Taphonomic interpretations of a new Plio-Pleistocene hominin-bearing assemblage at Kromdraai (Gauteng, South Africa). *Quaternary Science Reviews*, *190*, 81–97. https://doi.org/10.1016/j.quascirev.2018.04.018

Frey, S., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sensing in Ecology and Conservation*, *3*(3), 123–132. https://doi.org/10.1002/RSE2.60

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1). Retrieved from https://www.jstor.org/stable/26271862

Frost, S. R. (2007). African Pliocene and Pleistocene cercopithecid evolution and global climatic change. In *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence* (pp. 51–76). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-1-4020-3098-7_3

Fruth, B, & Hohmann, G. (1996). *Nest building behavior in the great apes: the great leap forward? Great ape societies.*

Fruth, Barbara, Tagg, N., & Stewart, F. (2018). Sleep and nesting behavior in primates: A review. *American Journal of Physical Anthropology*, *166*(3), 499–509. https://doi.org/10.1002/ajpa.23373

Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E., & Arasa-Gisbert, R. (2019). Ecological traits

of the world's primates. *Scientific Data*, *6*(1), 55. https://doi.org/10.1038/s41597-019-0059-9

Gathogo, P., & Brown, F. (2006). Stratigraphy of the Koobi Fora Formation (Pliocene and Pleistocene) in the Ileret region of northern Kenya. *Journal of African Earth Sciences*, *45*(4–5), 369–390. Retrieved from https://www.sciencedirect.com/science/article/pii/S1464343X06000902

Gaynor, K., Brown, J., Middleton, A., Power, M., & Brashares, J. (2019). Landscapes of fear: spatial patterns of risk perception and response. *Trends in Ecology and Evolution*. Retrieved from https://www.sciencedirect.com/science/article/pii/S0169534719300199

Gaynor, K., & Cords, M. (2012). Antipredator and social monitoring functions of vigilance behaviour in blue monkeys. *Animal Behaviour*, *84*(3), 531–537. https://doi.org/10.1016/J.ANBEHAV.2012.06.003

Gaynor, K., Daskin, J. H., Rich, L. N., & Brashares, J. S. (2021). Postwar wildlife recovery in an African savanna: evaluating patterns and drivers of species occupancy and richness. *Animal Conservation*, *24*(3), 510–522. https://doi.org/10.1111/ACV.12661

Georgiou, L., Dunmore, C. J., Bardo, A., Buck, L. T., Hublin, J. J., Pahr, D. H., … Skinner, M. M. (2020). Evidence for habitual climbing in a Pleistocene hominin in South Africa. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(15), 8416–8423. https://doi.org/10.1073/PNAS.1914481117

Gesquire, L., Khan, M., Shek, L., Wango, T., Wango, E., Alberts, S., & Altmann, J. (2008). Coping with a challenging environment: Effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons. *Hormones and Behaviour*. Retrieved from

http://amboselibaboons.nd.edu/assets/81666/195.pdf

Gilbert, C. C., Frost, S. R., Pugh, K. D., Anderson, M., & Delson, E. (2018). Evolution of the modern baboon (Papio hamadryas): A reassessment of the African Plio-Pleistocene record. https://doi.org/10.1016/j.jhevol.2018.04.012

Gommery, D., Pickford, M., & Senut, B. (2007). A case of carnivore-inflicted damage to a fossil femur from Swartkrans, comparable to that on a hominid femur representing Orrorin tugenensis, BAR 1003'00 (Kenya) : scientific notes. *Annals of the Transvaal Museum*. Retrieved from https://journals.co.za/doi/abs/10.10520/EJC83650

Gorini, L., Lillell, J., May, R., Panzacchi, M., Boitani, L., Odden, M., & Nilsen, E. (2011). Habitat heterogeneity and mammalian predator-prey interactions. *Mammal Review*, *42*(1), 55–77. https://doi.org/10.1111/j.1365-2907.2011.00189.x

Gowlett, J., & Wrangham, R. (2013). Earliest fire in Africa: towards the convergence of archaeological evidence and the cooking hypothesis. *Azania: Archaeological Research in Africa*, *48*(1), 5–30. https://doi.org/10.1080/0067270X.2012.756754

Grabowski, M. (2016). Bigger Brains Led to Bigger Bodies?: The Correlated Evolution of Human Brain and Body Size. *Current Anthropology*, *57*(2), 174–196. https://doi.org/10.1086/685655

Gradstein, F., Ogg, J., Schmitz, M., & Ogg, G. (2012). *The chronostratigraphic scale*. *Elsevier*. Retrieved from https://www.sciencedirect.com/science/article/pii/B9780444594259000020

Green, D., Gordon, A., & Richmond, B. (2007). Limb-size proportions in Australopithecus afarensis and Australopithecus africanus. *Journal of Human Evolution*, *52*(2), 187–200.

Gunz, P., Neubauer, S., Falk, D., Tafforeau, P., Le Cabec, A., Smith, T. M., … Alemseged, Z. (2020). Australopithecus afarensis endocasts suggest ape-like brain organization and prolonged brain growth. *Science Advances*, *6*(14). https://doi.org/10.1126/SCIADV.AAZ4729/SUPPL_FILE/AAZ4729_SM.PDF

Haile-Selassie, Y. (2001). Late Miocene hominids from the Middle Awash, Ethiopia. *Nature* , *412*(6843), 178–181. https://doi.org/10.1038/35084063

Hamilton, W. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*. Retrieved from https://www.sciencedirect.com/science/article/pii/0022519371901895

Hamilton, W. J. (1982). Baboon sleeping site preferences and relationships to primate grouping patterns. *American Journal of Primatology*, *3*(1–4), 41–53. https://doi.org/10.1002/ajp.1350030104

Hammond, A. S., Alba, D. M., Almécija, S., & Moyà-Solà, S. (2013). Middle Miocene Pierolapithecus provides a first glimpse into early hominid pelvic morphology. *Journal of Human Evolution*, *64*(6), 658–666. https://doi.org/10.1016/J.JHEVOL.2013.03.002

Hammond, A. S., Rook, L., Anaya, A. D., Cioppi, E., Costeur, L., Moyà-Solà, S., & Almécija, S. (2020). Insights into the lower torso in late Miocene hominoid Oreopithecus bambolii. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(1), 278–284. https://doi.org/10.1073/PNAS.1911896116

Hammond, P., Lewis-Bevan, L., Dora Biro, |, & Carvalho, S. (2022). Risk perception and terrestriality in primates: A quasi-experiment through habituation of chacma baboons (Papio ursinus) in Gorongosa National Park, Mozambique. *American Journal of Biological*

Anthropology. https://doi.org/10.1002/AJPA.24567

Hanan, N., Prihodko, L., Ross, C., Bucini, G., & Tredennick, A. (2020). Gridded Estimates of Woody Cover and Biomass across Sub-Saharan Africa, 2000-2004. *Daac.Ornl.Gov*.

Harcourt-Smith, W. (2010). The First Hominins and the Origins of Bipedalism. *Evolution: Education and Outreach*, *3*(3), 333–340. https://doi.org/10.1007/s12052-010-0257-6

Harcourt-Smith, W. (2016). Early hominin diversity and the emergence of the genus Homo, *94*, 19–27. https://doi.org/10.4436/jass.94035

Harcourt-Smith, W., & Aiello, L. C. (2004a). Fossils, feet and the evolution of human bipedal locomotion. *Journal of Anatomy*, *204*(5), 403–416. https://doi.org/10.1111/j.0021-8782.2004.00296.x

Harcourt-Smith, W., & Aiello, L. C. (2004b). Fossils, feet and the evolution of human bipedal locomotion. *Journal of Anatomy*, *204*(5), 403–416. https://doi.org/10.1111/J.0021-8782.2004.00296.X

Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., … Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, *521*(7552), 310–315. https://doi.org/10.1038/nature14464

Hart, D., & Sussman, R. (2008). *Man the hunted: Primates, predators, and human evolution.* Westview Press.

Hart, D., & Sussman, R. W. (2011). The Influence of Predation on Primate and Early Human Evolution: Impetus for Cooperation. *Origins of Altruism and Cooperation*, 19–40.

https://doi.org/10.1007/978-1-4419-9520-9_3

Havmøller, R. W., Jacobsen, N. S., Scharff, N., Rovero, F., & Zimmermann, F. (2020). Assessing the activity pattern overlap among leopards (Panthera pardus), potential prey and competitors in a complex landscape in Tanzania. *Journal of Zoology, 311*(3), 175–182. https://doi.org/10.1111/JZO.12774

Hayward, M. W., Henschel, P., O'brien, J., Hofmeyr, M., Balme, G., & Kerley, G. (2006). Prey preferences of the leopard (Panthera pardus). *Journal of Zoology, 270*(2), 298–313. Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-7998.2006.00139.x

Hayward, M. W., & Kerley, G. (2005). Prey preferences of the lion (Panthera leo). *Journal of Zoology, 267*(3), 309–322.

Hayward, M. W., & Slotow, R. (2009). Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South African Journal of Wildlife Research, 39*(2), 109–125. https://doi.org/10.10520/EJC117325

Heldstab, S. A., Kosonen, Z. K., Koski, S. E., Burkart, J. M., Van Schaik, C. P., & Isler, K. (2016). Manipulation complexity in primates coevolved with brain size and terrestriality. *Scientific Reports*, *6*(1), 1–9. https://doi.org/10.1038/srep24528

Henrich, M., Hartig, F., Dormann, C. F., Kühl, H. S., Peters, W., Franke, F., … Heurich, M. (2022). Deer Behavior Affects Density Estimates With Camera Traps, but Is Outweighed by Spatial Variability. *Frontiers in Ecology and Evolution, 10*. https://doi.org/10.3389/FEVO.2022.881502

Hernandez-Aguilar, R. A., & Reitan, T. (2020). Deciding Where to Sleep: Spatial Levels of Nesting Selection in Chimpanzees (Pan troglodytes) Living in Savanna at Issa, Tanzania. *International*

Journal of Primatology, *41*(6), 870–900. https://doi.org/10.1007/s10764-020-00186-z

Herries, A. I. R., Martin, J. M., Leece, A. B., Adams, J. W., Boschian, G., Joannes-Boyau, R., … Menter, C. (2020). Contemporaneity of Australopithecus, Paranthropus, and early Homo erectus in South Africa. *Science*, *368*(6486), eaaw7293. https://doi.org/10.1126/science.aaw7293

Hicks, T. (2010). *A chimpanzee mega-culture?: exploring behavioral continuity in Pan troglodytes schweinfurthii across northern DR Congo*. Retrieved from http://dare.uva.nl/document/2/83519

Hill, K., Barton, M., & Magdalena Hurtado, A. (2009). The emergence of human uniqueness: Characters underlying behavioral modernity. *Evolutionary Anthropology*, *18*(5), 187–200. https://doi.org/10.1002/EVAN.20224/FORMAT/PDF

Hill, R. (2006a). Thermal constraints on activity scheduling and habitat choice in baboons. *American Journal of Physical Anthropology*, *129*(2), 242–249. https://doi.org/10.1002/ajpa.20264

Hill, R. (2006b). Why Be Diurnal? Or, Why Not Be Cathemeral? *Folia Primatologica*, *77*(1–2), 72–86. https://doi.org/10.1159/000089696

Hill, R., Barrett, L., Gaynor, D., Weingrill, T., Dixon, P., Payne, H., & Henzi, S. P. (2003). Day length, latitude and behavioural (in)flexibility in baboons (Papio cynocephalus ursinus). *Behavioral Ecology and Sociobiology*, *53*(5), 278–286. https://doi.org/10.1007/S00265-003-0590-7/FIGURES/2

Hill, R., & Dunbar, R. I. M. (2002). Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology*, *16*(6), 579–593. https://doi.org/10.1023/A:1021625003597

Hill, R., & Lee, P. C. (1998). Predation risk as an influence on group size in cercopithecoid primates:

implications for social structure. *The Zoological Society of London*, *245*(447-456)).

Hill, R., & Weingrill, T. (2007). Predation Risk and Habitat Use in Chacma Baboons (Papio hamadryas ursinus). In *Primate Anti-Predator Strategies* (pp. 339–354). Springer US. https://doi.org/10.1007/978-0-387-34810-0_16

Hlubik, S., Berna, F., Feibel, C., Braun, D., & Harris, J. W. K. (2017). Researching the Nature of Fire at 1.5 Mya on the Site of FxJj20 AB, Koobi Fora, Kenya, Using High-Resolution Spatial Analysis and FTIR Spectrometry. *Current Anthropology*, *58*(S16), S243–S257. https://doi.org/10.1086/692530

Hopwood, D. (2014). *Carnivorans as selective agents: Implications for the evolution of early Homo and Homo erectus behaviour*. Binghamton University.

Hrdy, S. (2011). *Mothers and others*. Harvard University Press.

Hughes, J. K., Elton, S., & O'Regan, H. J. (2008). Theropithecus and "Out of Africa" dispersal in the Plio-Pleistocene. *Journal of Human Evolution*, *54*(1), 43–77. https://doi.org/10.1016/j.jhevol.2007.06.004

Hunt, K. D. (2016). Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. *Journal of Anatomy*, *228*(4), 630–685. https://doi.org/10.1111/JOA.12454

Isbell, L. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology: Issues, News, and Reviews*, *3*(2), 61–71. https://doi.org/10.1002/evan.1360030207

Isbell, L., Bidner, L., Van Cleave, E., Matsumoto-Oda, A., & Crofoot, M. (2018). GPS-identified

vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. *Journal of Human Evolution*, (118), 1–13. Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248417304657

Isbell, L., & Young, T. (1993a). *Behavioral Ecology and Sociobiology Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living*. *Behav Ecol Sociobiol* (Vol. 32). Retrieved from https://tpyoung.ucdavis.edu/publications/1993ActivityBES.pdf

Isbell, L., & Young, T. (1993b). Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Animal Behaviour*. Retrieved from https://psycnet.apa.org/record/1993-44299-001

Jablonski, NG (Ed.). (1993). *The Rise and Fall of a Primate Genus*. Cambridge University Press.

Jablonski, NG, Leakey, M. ., Ward, C. V., & Antón, M. (2008). *Koobi Fora research project, Vol. 6: The fossil monkeys.* San Francisco .

Jack, K. M., Lenz, B. B., Healan, E., Rudman, S., Schoof, V. A. M., & Fedigan, L. (2008). The effects of observer presence on the behavior ofCebus capucinus in Costa Rica. *American Journal of Primatology*, *70*(5), 490–494. https://doi.org/10.1002/ajp.20512

Jaffe, K. E., & Isbell, L. (2009). After the Fire: Benefits of Reduced Ground Cover for Vervet Monkeys (Cercopithecus aethiops). *American Journal of Primatology*, *71*, 252–260. https://doi.org/10.1002/ajp.20644

Janson, C. H. (2012). Reconciling Rigor and Range: Observations, Experiments, and Quasi-experiments in Field Primatology. *International Journal of Primatology*, *33*(3), 520–541.

https://doi.org/10.1007/S10764-011-9550-7/FIGURES/2

Johns, B. G. (1996). Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. *Biological Conservation*, *78*(3), 257–262. https://doi.org/10.1016/S0006-3207(96)00044-4

Johnson, C., Piel, A. K., Forman, D., Stewart, F. A., & King, A. J. (2015). The ecological determinants of baboon troop movements at local and continental scales. *Movement Ecology*, *3*(1), 14. https://doi.org/10.1186/s40462-015-0040-y

Jolly, C. J. (2001). A Proper Study for Mankind: Analogies From the Papionin Monkeys and Their Implications for Human Evolution. *Yearbook of Physical Anthropology*, *44*, 177–204. https://doi.org/10.1002/ajpa.10021

Jolly, C. J. (2020). Philopatry at the frontier: A demographically driven scenario for the evolution of multilevel societies in baboons (Papio). *Journal of Human Evolution*, *146*, 102819. https://doi.org/10.1016/j.jhevol.2020.102819

Jungers, W. L., Larson, S. G., Harcourt-Smith, W., Morwood, M. J., Sutikna, T., Due Awe, R., & Djubiantono, T. (2009). Descriptions of the lower limb skeleton of Homo floresiensis. *Journal of Human Evolution*, *57*(5), 538–554. https://doi.org/10.1016/J.JHEVOL.2008.08.014

Kahle, D., & Wickham, H. (2013). ggmap: Spatial Visualization with ggplot2. *The R Journal*.

Kiffner, C., Paciência, F. M. D., Henrich, G., Kaitila, R., Chuma, I. S., Mbaryo, P., … Zinner, D. (2022). Road-based line distance surveys overestimate densities of olive baboons. *PLOS ONE*, *17*(2), e0263314. https://doi.org/10.1371/JOURNAL.PONE.0263314

Kim, P. S., McQueen, J. S., & Hawkes, K. (2019). Why does women's fertility end in mid-life? Grandmothering and age at last birth. *Journal of Theoretical Biology*, *461*, 84–91. https://doi.org/10.1016/J.JTBI.2018.10.035

Kimbel, W. H., & Delezene, L. K. (2009). "Lucy" redux: A review of research on Australopithecus afarensis. *American Journal of Physical Anthropology*, *140*(SUPPL. 49), 2–48. https://doi.org/10.1002/ajpa.21183

Kivell, T. L. (2015). Evidence in hand: Recent discoveries and the early evolution of human manual manipulation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1682). https://doi.org/10.1098/RSTB.2015.0105

Kivell, T. L. (2019, November 1). Fossil ape hints at how walking on two feet evolved. *Nature*. NLM (Medline). https://doi.org/10.1038/d41586-019-03347-0

Kivell, T. L., & Schmitt, D. (2009). Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(34), 14241–14246. https://doi.org/10.1073/PNAS.0901280106

Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., … MacNulty, D. R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs*, *88*(4), 638–652. https://doi.org/10.1002/ecm.1313

Koops, K., McGrew, W. C., Matsuzawa, T., & Knapp, L. A. (2012). Terrestrial nest-building by wild chimpanzees (Pan troglodytes): Implications for the tree-to-ground sleep transition in early hominins. *American Journal of Physical Anthropology*, *148*(3), 351–361.

https://doi.org/10.1002/ajpa.22056

Koops, K., Mcgrew, W., De Vries, H., & Matsuzawa, T. (2012). Nest-building by chimpanzees (Pan troglodytes verus) at Seringbara, Nimba Mountains: Anti-predation, thermoregulation and anti-vector hypotheses. *International Journal of Primatology*. https://doi.org/10.1007/s10764-012-9585-4

Kummer, H. (Hans). (1997). *In quest of the sacred baboon : a scientist's journey*. Princeton University Press.

Kuzawa, C. W., & Bragg, J. M. (2012). Plasticity in Human Life History Strategy. *Current Anthropology*, *53*(S6), S369–S382. https://doi.org/10.1086/667410

Laidre, M. E. (2008). Spontaneous performance of wild baboons on three novel food-access puzzles. *Animal Cognition*, *11*(2), 223–230. https://doi.org/10.1007/S10071-007-0104-5/TABLES/2

Larson, S. G., Jungers, W. L., Tocheri, M. W., Orr, C. M., Morwood, M. J., Sutikna, T., … Djubiantono, T. (2009). Descriptions of the upper limb skeleton of Homo floresiensis. *Journal of Human Evolution*, *57*(5), 555–570. https://doi.org/10.1016/J.JHEVOL.2008.06.007

Laundré, J., Hernández, L., & Ripple, W. (2010). The landscape of fear: ecological implications of being afraid. *Open Ecology Journal*, *3*, 1–7. Retrieved from http://www.academia.edu/download/44778290/The_Landscape_of_Fear_Ecological_Implica20160415-5548-9kamr3.pdf

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, *79*(8), 1401–1409. https://doi.org/10.1139/z01-094

le Gros Clark, W. (1966). *History of the Primates: An Introduction to the Study of Fossil Man*. University of Chicago Press.

Leakey, M., & Hay, R. (1979). Pliocene footprints in the Laetolil Beds at Laetoli, northern Tanzania. *Nature*, *278*(5702), 317–323. Retrieved from https://www.nature.com/articles/278317a0

Lee-Thorp, J. (2011). The demise of "Nutcracker Man." *PNAS*. Retrieved from http://www.pnas.org/content/108/23/9319.short

Lee-Thorp, JA, Sponheimer, M., & Luyt, J. (2007). Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominin sites. *Journal of Human Evolution*, *53*(5), 595–601.

Lee-Thorp, Julia, Thackeray, J. F., & Van der Merwe, N. (2000). The hunters and the hunted revisited. *Journal of Human Evolution*, *39*(6), 565–576. https://doi.org/10.1006/JHEV.2000.0436

Lepre, C. J., Roche, H., Kent, D. V., Harmand, S., Quinn, R. L., Brugal, J. P., … Feibel, C. S. (2011). An earlier origin for the Acheulian. *Nature 2011 477:7362*, *477*(7362), 82–85. https://doi.org/10.1038/nature10372

Lesku, J., Roth, T., Amlaner, C., & Lima, S. (2006). A phylogenetic analysis of sleep architecture in mammals: the integration of anatomy, physiology, and ecology. *The American Naturalist*. Retrieved from https://www.journals.uchicago.edu/doi/abs/10.1086/506973

Levin, N. E. (2015). Environment and Climate of Early Human Evolution. *Annual Review of Earth and Planetary Sciences*, *43*(1), 405–429. https://doi.org/10.1146/annurev-earth-060614-105310

Levin, N., Quade, J., Simpson, S., & Semaw, S. (2004). Isotopic evidence for Plio–Pleistocene environmental change at Gona, Ethiopia. *Earth and Planetary Science Letters*. Retrieved from https://www.sciencedirect.com/science/article/pii/S0012821X03007076

Lewis, M. (2017). Carnivore Guilds and the Impact of Hominin Dispersals. In *Human Dispersal and Species Movement: From Prehistory to the Present*.

Lewis, M., & Werdelin, L. (2007). Patterns of change in the Plio-Pleistocene carnivorans of eastern Africa. In *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence* (pp. 77–105). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-1-4020-3098-7_4

LILA BC. (n.d.). Labeled Information Library of Alexandria: Biology and Conservation. Retrieved June 30, 2022, from https://lila.science/datasets

Lima, S. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, *48*(1), 25–34. Retrieved from https://www.jstor.org/stable/1313225

Lima, S. L., Rattenborg, N. C., Lesku, J. A., & Amlaner, C. J. (2005). Sleeping under the risk of predation. *Animal Behaviour*, *70*(4), 723–736. https://doi.org/10.1016/J.ANBEHAV.2005.01.008

Lindshield, S., Danielson, B. J., Rothman, J. M., & Pruetz, J. D. (2017). Feeding in fear? How adult male western chimpanzees (P an troglodytes verus) adjust to predation and savanna habitat pressures. *American Journal of Physical Anthropology*, *163*(3), 480–496. https://doi.org/10.1002/ajpa.23221

Linnell, J. D. C., & Strand, O. (2000). Interference interactions, co-existence and conservation of

mammalian carnivores. *Diversity and Distributions*, *6*(4), 169–176. https://doi.org/10.1046/J.1472-4642.2000.00069.X

Loftus, J. C., Harel, R., Núñez, C. L., & Crofoot, M. C. (2022). Ecological and social pressures interfere with homeostatic sleep regulation in the wild. *ELife*, *11*. https://doi.org/10.7554/ELIFE.73695

Lovejoy, C. O., Suwa, G., Simpson, S. W., Matternes, J. H., & White, T. (2009). The great divides: Ardipithecus ramidus reveals the postcrania of our last common ancestors with African apes. *Science*, *326*(5949), 100–106. https://doi.org/10.1126/SCIENCE.1175833/SUPPL_FILE/LOVEJOY1175833.SOM.PDF

Macandza, V. A., Owen-Smith, N., & Cain, J. W. (2012). Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. *Oikos*, *121*(6), 891–898. https://doi.org/10.1111/J.1600-0706.2012.20250.X

Manthi, F. K., Cerling, T., Chritz, K. L., & Blumenthal, S. A. (2020). Diets of mammalian fossil fauna from Kanapoi, northwestern Kenya. *Journal of Human Evolution*, *140*, 102338. https://doi.org/10.1016/j.jhevol.2017.05.005

Marean, C. (1989). Sabertooth cats and their relevance for early hominid diet and evolution. *Journal of Human Evolution*, *18*(6), 559–582. Retrieved from https://www.sciencedirect.com/science/article/pii/0047248489900183

Margvelashvili, A., Tappen, M., Rightmire, G. P., Tsikaridze, N., & Lordkipanidze, D. (2022). An ancient cranium from Dmanisi: Evidence for interpersonal violence, disease, and possible predation by carnivores on Early Pleistocene Homo. *Journal of Human Evolution*, *166*, 103180.

https://doi.org/10.1016/J.JHEVOL.2022.103180

Markham, A. C., Alberts, S., & Altmann, J. (2016). Haven for the night: sleeping site selection in a wild primate. *Behavioral Ecology*, *27*(1), 29–35. https://doi.org/10.1093/beheco/arv118

Markham, A. C., Gesquiere, L. R., Alberts, S., & Altmann, J. (2015). Optimal group size in a highly social mammal. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(48), 14882–14887. https://doi.org/10.1073/pnas.1517794112

Marsh, L. (2013). *Primates in fragments: ecology and conservation*. *Springer*. Springer Science & Business Media. Retrieved from https://link.springer.com/content/pdf/10.1007/978-1-4614-8839-2.pdf

Maslin, M. A., Brierley, C. M., Milner, A. M., Shultz, S., Trauth, M. H., & Wilson, K. E. (2014, October 1). East african climate pulses and early human evolution. *Quaternary Science Reviews*. Pergamon. https://doi.org/10.1016/j.quascirev.2014.06.012

Maslin, M. A., Shultz, S., & Trauth, M. H. (2015). A synthesis of the theories and concepts of early human evolution. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *370*(1663), 20140064. https://doi.org/10.1098/rstb.2014.0064

Matsumoto-Oda, A. (2015). How surviving baboons behaved after leopard predation: a case report. *Anthropological Science*, *123*(1), 13–17. https://doi.org/10.1537/ase.150223

McBrearty, S., & Jablonski, N. (2005). First fossil chimpanzee. *Nature 2005 437:7055*, *437*(7055), 105–108. https://doi.org/10.1038/nature04008

McCarthy, M. S., Després-Einspenner, M. L., Farine, D. R., Samuni, L., Angedakin, S.,

Arandjelovic, M., … Kühl, H. S. (2019, November 1). Camera traps provide a robust alternative to direct observations for constructing social networks of wild chimpanzees. *Animal Behaviour*. Academic Press. https://doi.org/10.1016/j.anbehav.2019.08.008

McCrossin, M. L., Benefit, B. R., Gitau, S. N., Palmer, A. K., & Blue, K. T. (1998). Fossil Evidence for the Origins of Terrestriality among Old World Higher Primates. *Primate Locomotion*, 353–396. https://doi.org/10.1007/978-1-4899-0092-0_19

McDougall, I. (1985). K-Ar and 40Ar/39Ar dating of the hominid-bearing Pliocene-Pleistocene sequence at Koobi Fora, Lake Turkana, northern Kenya. *Geological Society of America Bulletin*, *96*(2), 159. https://doi.org/10.1130/0016-7606(1985)96<159:KAADOT>2.0.CO;2

McFarland, R., Murphy, D., Lusseau, D., Henzi, S. P., Parker, J., Pollet, T., & Barrett, L. (2017). The 'strength of weak ties' among female baboons: fitness-related benefits of social bonds. *Animal Behaviour*, *126*, 101–106. https://doi.org/10.1016/J.ANBEHAV.2017.02.002

McGraw, W. S., Cooke, C., & Shultz, S. (2006). Primate remains from African crowned eagle (Stephanoaetus coronatus) nests in Ivory Coast's Tai Forest: Implications for primate predation and early hominid taphonomy in South Africa. *American Journal of Physical Anthropology*, *131*(2), 151–165. https://doi.org/10.1002/ajpa.20420

McLennan, M. R., & Hill, C. M. (2010). Chimpanzee responses to researchers in a disturbed forest-farm mosaic at Bulindi, western Uganda. *American Journal of Primatology*, *72*(10), 907–918. https://doi.org/10.1002/ajp.20839

McNamara, J. M., & Houston, A. I. (1987). Starvation and Predation as Factors Limiting Population Size. *Ecology*, *68*(5), 1515–1519. https://doi.org/10.2307/1939235

McNamara, P., Capellini, I., Harris, E., Nunn, C. L., Barton, R. A., & Preston, B. (2008). The Phylogeny of Sleep Database: A New Resource for Sleep Scientists. *The Open Sleep Journal*, *1*, 11–14. https://doi.org/10.2174/1874620900801010011

McNutt, E. J., Hatala, K. G., Miller, C., Adams, J., Casana, J., Deane, A. S., … DeSilva, J. M. (2021). Footprint evidence of early hominin locomotor diversity at Laetoli, Tanzania. *Nature 2021*, *19*, 1–4. https://doi.org/10.1038/s41586-021-04187-7

McNutt, E. J., Zipfel, B., & DeSilva, J. M. (2018). The evolution of the human foot. *Evolutionary Anthropology: Issues, News, and Reviews*, *27*(5), 197–217. https://doi.org/10.1002/EVAN.21713

McPherron, S., Alemseged, Z., Marean, C., Wynn, J., Reed, D., Geraads, D., … Hamdallah, A. (2010). Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, *466*(7308), 857. Retrieved from https://www.nature.com/articles/nature09248

Mekonnen, A., Fashing, P. J., Venkataraman, V. V., Chapman, C. A., Stenseth, N. C., & Hernandez-Aguilar, R. A. (2021). Sleeping Site and Tree Selection by Bale Monkeys (Chlorocebus djamdjamensis) at Kokosa Forest Fragment in Southern Ethiopia. *International Journal of Primatology*, *42*(6), 915–932. https://doi.org/10.1007/S10764-021-00251-1/TABLES/6

Meulman, E., Sanz, C. M., Visalberghi, E., & van Schaik, C. P. (2012). The Role of Terrestriality in Promoting Primate Technology. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(2), 58–68. https://doi.org/10.1002/EVAN.21304

Meulman, E., & van Schaik, C. (2013). Orangutan tool use and the evolution of technology. In *Tool*

use in animals: Cognition and ecology (pp. 176–202). Cambridge University Press. https://doi.org/10.1017/CBO9780511894800.011

Miao, Z., Liu, Z., Gaynor, K., Palmer, M. S., Yu, S. X., & Getz, W. M. (2021). Iterative human and automated identification of wildlife images. *Nature Machine Intelligence 2021 3:10*, *3*(10), 885–895. https://doi.org/10.1038/s42256-021-00393-0

Miller, A. A., & Rucas, S. L. (2012). Sleep-Wake State Tradeoffs, Impulsivity and Life History Theory. *Evolutionary Psychology*, *10*(2), 147470491201000. https://doi.org/10.1177/147470491201000201

Milton, K. (1988). Foraging behaviour and the evolution of primate intelligence. Retrieved from http://psycnet.apa.org/record/1988-98392-021

Monteza-Moreno, C. M., Crofoot, M. C., Grote, M. N., & Jansen, P. A. (2020). Increased terrestriality in a Neotropical primate living on islands with reduced predation risk. *Journal of Human Evolution*, *143*, 102768. https://doi.org/10.1016/J.JHEVOL.2020.102768

Moore, J. F., Pine, W. E., Mulindahabi, F., Niyigaba, P., Gatorano, G., Masozera, M. K., & Beaudrot, L. (2020). Comparison of species richness and detection between line transects, ground camera traps, and arboreal camera traps. *Animal Conservation*, *23*(5), 561–572. https://doi.org/10.1111/ACV.12569

Moore, J. F., Soanes, K., Balbuena, D., Beirne, C., Bowler, M., Carrasco-Rueda, F., … Gregory, T. (2021). The potential and practice of arboreal camera trapping. *Methods in Ecology and Evolution*, *12*(10), 1768–1779. https://doi.org/10.1111/2041-210X.13666

Moorjani, P., Amorim, C. E. G., Arndt, P. F., & Przeworski, M. (2016). Variation in the molecular

clock of primates. *National Acad Sciences*, *113*(38), 10607–10612. https://doi.org/10.1073/pnas.1600374113

Mourthé, Í. M. C., Guedes, D., Fidelis, J., Boubli, J. P., Mendes, S. L., & Strier, K. B. (2007). Ground use by northern muriquis (Brachyteles hypoxanthus). *American Journal of Primatology*, *69*(6), 706–712. https://doi.org/10.1002/ajp.20405

Moyà-Solà, S., Köhler, M., Alba, D. M., Casanovas-Vilar, I., & Galindo, J. (2004). Pierolapithecus catalaunicus, a new Middle Miocene great ape from Spain. *Science*, *306*(5700), 1339–1344.

Negash, E., Wynn, J., & Bobe, R. (2019). Woody Cover in Modern African Ecosystems: Implications for Hominin Landscape Dynamics. Retrieved from https://search.proquest.com/openview/8e28754e6cbb74651b7ceb5d08e76913/1?pq-origsite=gscholar&cbl=18750&diss=y

Nengo, I., Tafforeau, P., Gilbert, C. C., Fleagle, J. G., Miller, E. R., Feibel, C., … Spoor, F. (2017). New infant cranium from the African Miocene sheds light on ape evolution. *Nature 2017 548:7666*, *548*(7666), 169–174. https://doi.org/10.1038/nature23456

Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, *7*(12), 1457–1462. https://doi.org/10.1111/2041-210X.12600

Njau, J. K., & Blumenschine, R. J. (2012). Crocodylian and mammalian carnivore feeding traces on hominid fossils from FLK 22 and FLK NN 3, Plio-Pleistocene, Olduvai Gorge, Tanzania. *Journal of Human Evolution*, *63*(2), 408–417. https://doi.org/10.1016/J.JHEVOL.2011.05.008

Noser, R., & Byrne, R. W. (2007a). Mental maps in chacma baboons (Papio ursinus): using inter-

group encounters as a natural experiment. *Animal Cognition*, *10*(3), 331–340. https://doi.org/10.1007/s10071-006-0068-x

Noser, R., & Byrne, R. W. (2007b). Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, Papio ursinus. *Animal Behaviour*, *73*(2), 257–266. https://doi.org/10.1016/J.ANBEHAV.2006.04.012

Nowak, K., le Roux, A., Richards, S. A., Scheijen, C. P. J., & Hill, R. (2014). Human observers impact habituated samango monkeys' perceived landscape of fear. *Behavioral Ecology*, *25*(5), 1199–1204. https://doi.org/10.1093/beheco/aru110

Nunn, C. L., & Samson, D. R. (2018). Sleep in a comparative context: Investigating how human sleep differs from sleep in other primates. *American Journal of Physical Anthropology*, *166*(3), 601–612. https://doi.org/10.1002/AJPA.23427

Nunn, C. L., Samson, D. R., & Krystal, A. D. (2016). Shining evolutionary light on human sleep and sleep disorders. *Evolution, Medicine, and Public Health*, *2016*(1), 227–243. https://doi.org/10.1093/emph/eow018

Ottoni, E. B., & Izar, P. (2008). Capuchin monkey tool use: Overview and implications. *Evolutionary Anthropology: Issues, News, and Reviews*, *17*(4), 171–178. https://doi.org/10.1002/EVAN.20185

Owen-Smith, N. (2019). Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. *Biological Conservation*, *232*, 51–58. https://doi.org/10.1016/J.BIOCON.2019.01.027

Palencia, P., Vicente, J., Soriguer, R. C., & Acevedo, P. (2022). Towards a best-practices guide for

camera trapping: assessing differences among camera trap models and settings under field conditions. *Journal of Zoology*, *316*(3), 197–208. https://doi.org/10.1111/JZO.12945

Palmer, M. S., Fieberg, J., Swanson, A., Kosmala, M., & Packer, C. (2017). A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecology Letters*, *20*(11), 1364–1373. https://doi.org/10.1111/ele.12832

Palmer, M. S., Gaynor, K. M., Becker, J. A., Abraham, J. O., Mumma, M. A., & Pringle, R. M. (2022). Dynamic landscapes of fear: understanding spatiotemporal risk. *Trends in Ecology & Evolution*. https://doi.org/10.1016/J.TREE.2022.06.007

Palmer, M. S., & Packer, C. (2021). Reactive anti-predator behavioral strategy shaped by predator characteristics. *PLOS ONE*, *16*(8), e0256147. https://doi.org/10.1371/JOURNAL.PONE.0256147

Palmer, M. S., Wang, C., Plucinski, J., & Pringle, R. M. (2022). BoomBox: An Automated Behavioural Response (ABR) camera trap module for wildlife playback experiments. *Methods in Ecology and Evolution*, *13*(3), 611–618. https://doi.org/10.1111/2041-210X.13789

Palmqvist, P., Pérez-Claros, J. A., Janis, C. M., & Gröcke, D. R. (2008). Tracing the ecophysiology of ungulates and predator–prey relationships in an early Pleistocene large mammal community. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *266*(1–2), 95–111. https://doi.org/10.1016/J.PALAEO.2008.03.015

Pardo, L. E., Bombaci, S., Huebner, S. E., Somers, M. J., Fritz, H., Downs, C., … Venter, J. A. (2021). Snapshot Safari: A large-scale collaborative to monitor Africa's remarkable biodiversity. *Sajs.Co.Za*, *117*(2), 18. https://doi.org/10.17159/sajs.2021/8134

Pascual-Garrido, A., & Almeida-Warren, K. (2021). Archaeology of the perishable ecological constraints and cultural variants in chimpanzee termite fishing. *Current Anthropology*, *62*(3), 333–362. https://doi.org/10.1086/713766/ASSET/IMAGES/LARGE/FG6.JPEG

Patel, B. A., Susman, R. L., Rossie, J. B., & Hill, A. (2009). Terrestrial adaptations in the hands of Equatorius africanus revisited. *Journal of Human Evolution*, *57*(6), 763–772. https://doi.org/10.1016/J.JHEVOL.2009.08.005

Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *R Journal*, *10*(1), 439–446. https://doi.org/10.32614/RJ-2018-009

Petersdorf, M., Weyher, A. H., Kamilar, J. M., Dubuc, C., & Higham, J. P. (2019). Sexual selection in the Kinda baboon. *Journal of Human Evolution*, *135*, 102635. https://doi.org/10.1016/J.JHEVOL.2019.06.006

Pickering, T., & Bunn, H. (2007). The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *Journal of Human Evolution*, *53*(4), 434–438. https://doi.org/10.1016/j.jhevol.2007.01.012

Pickering, T., Clarke, R. J., & Moggi-Cecchi, J. (2004). Role of carnivores in the accumulation of the Sterkfontein member 4 hominid assemblage: A taphonomic reassessment of the complete hominid fossil sample (1936-1999). *American Journal of Physical Anthropology*, *125*(1), 1–15. https://doi.org/10.1002/ajpa.10278

Pickford, M., & Senut, B. (2004). Hominoid teeth with chimpanzee-and gorilla-like features from the Miocene of Kenya: implications for the chronology of ape-human divergence and biogeography of. *Anthropological Science*, *000*, 0–000. https://doi.org/10.1537/ase.04S014

Pienaar, U. (1969). Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe*. Retrieved from https://koedoe.co.za/index.php/koedoe/article/download/753/836

Plummer, T. (2004). Flaked stones and old bones: Biological and cultural evolution at the dawn of technology. *American Journal of Physical Anthropology*, *125*(S39), 118–164. https://doi.org/10.1002/ajpa.20157

Pobiner, B. L. (2020, March 1). The zooarchaeology and paleoecology of early hominin scavenging. *Evolutionary Anthropology*. Wiley-Liss Inc. https://doi.org/10.1002/evan.21824

Port, M., Hildenbrandt, H., Pen, I., Schülke, O., Ostner, J., & Weissing, F. J. (2020). The evolution of social philopatry in female primates. *American Journal of Physical Anthropology*, *173*(3), 397–410. https://doi.org/10.1002/ajpa.24123

Post, D. G. (1981). Activity patterns of yellow baboons (Papio cynocephalus) in the Amboseli National Park, Kenya. *Animal Behaviour*, *29*(2), 357-374.

Potts, R. (1998). Variability selection in hominid evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *7*(3), 81–96. https://doi.org/10.1002/(SICI)1520-6505(1998)7:3<81::AID-EVAN3>3.0.CO;2-A

Potts, R. (2012). Environmental and Behavioral Evidence Pertaining to the Evolution of Early Homo. *Current Anthropology*, *53*(S6), S299–S317. https://doi.org/10.1086/667704

Potts, R. (2013). Hominin evolution in settings of strong environmental variability. *Quaternary Science Reviews*, *73*, 1–13. https://doi.org/10.1016/J.QUASCIREV.2013.04.003

Potts, R., Dommain, R., Moerman, J. W., Behrensmeyer, A. K., Deino, A. L., Riedl, S., … Uno, K.

(2020). Increased ecological resource variability during a critical transition in hominin evolution. *Science Advances*, *6*(43), eabc8975. https://doi.org/10.1126/sciadv.abc8975

Potts, R., & Faith, J. T. (2015). Alternating high and low climate variability: The context of natural selection and speciation in Plio-Pleistocene hominin evolution. *Journal of Human Evolution*. https://doi.org/10.1016/j.jhevol.2015.06.014

Pozo-Montuy, G., Serio-Silva, J. C., & Bonilla-Sánchez, Y. M. (2011). Influence of the landscape matrix on the abundance of arboreal primates in fragmented landscapes. *Primates*, *52*(2), 139–147. https://doi.org/10.1007/S10329-010-0231-5/TABLES/3

Prabhat, A. M., Miller, C. K., Prang, T., Spear, J., Williams, S. A., & Desilva, J. M. (2021). Homoplasy in the evolution of modern human-like joint proportions in australopithecus afarensis. *ELife*, *10*. https://doi.org/10.7554/ELIFE.65897

Prado-Martinez, J., Sudmant, P., Kidd, J., Li, H., Kelley, J., Lorente-Galdos, B., & Marques-Bonet, T. (2013). Great ape genetic diversity and population history. *Nature*, *499*(7459), 471–475. Retrieved from https://www.nature.com/articles/nature12228

Prang, T. (2019). The African ape-like foot of ardipithecus ramidus and its implications for the origin of bipedalism. *ELife*, *8*. https://doi.org/10.7554/ELIFE.44433

Prang, T. (2022). New analyses of the Ardipithecus ramidus foot provide additional evidence of its African ape–like affinities: A reply to. *Journal of Human Evolution*, *164*, 103135. https://doi.org/10.1016/J.JHEVOL.2021.103135

Prang, T., Ramirez, K., Grabowski, M., & Williams, S. A. (2021). Ardipithecus hand provides evidence that humans and chimpanzees evolved from an ancestor with suspensory adaptations.

Science Advances, *7*(9), eabf2474. https://doi.org/10.1126/sciadv.abf2474

Presnyakova, D., Braun, D. R., Conard, N. J., Feibel, C., Harris, J. W. K., Pop, C. M., … Archer, W. (2018). Site fragmentation, hominin mobility and LCT variability reflected in the early Acheulean record of the Okote Member, at Koobi Fora, Kenya. *Journal of Human Evolution*, *125*, 159–180. https://doi.org/10.1016/J.JHEVOL.2018.07.008

Pruetz, J. D. (2018). Nocturnal behavior by a diurnal ape, the West African chimpanzee (Pan troglodytes), in a savanna environment at Fongoli, Senegal. *American Journal of Physical Anthropology*, *166*(3), 541–548. https://doi.org/10.1002/ajpa.23434

Prugh, L. R., & Golden, C. D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*, *83*(2), 504–514. https://doi.org/10.1111/1365-2656.12148

Quinn, R., Lepre, C., Feibel, C., Wright, J., Mortlock, R., Harmand, S., … Roche, H. (2013). Pedogenic carbonate stable isotopic evidence for wooded habitat preference of early Pleistocene tool makers in the Turkana Basin. *Journal of Human Evolution*, *65*(1), 65–78.

R Core Team. (2020). R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.r-project.org/.

Raichlen, D. A., Pontzer, H., & Sockol, M. D. (2008). The Laetoli footprints and early hominin locomotor kinematics. *Journal of Human Evolution*, *54*(1), 112–117. https://doi.org/10.1016/J.JHEVOL.2007.07.005

Rasmussen, D. R. (1983). Correlates of patterns of range use of a troop of yellow baboons (Papio cynocephalus). II. Spatial structure, cover density, food gathering, and individual behaviour

patterns. *Animal Behaviour*, *31*(3), 834–856. https://doi.org/10.1016/S0003-3472(83)80240-1

Reynolds, S., Bailey, G., & King, G. (2011). Landscapes and their relation to hominin habitats: case studies from Australopithecus sites in eastern and southern Africa. *Journal of Human Evolution*. Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248410002058

Rich, L., Davis, C., Farris, Z., Miller, D., Tucker, J., Hamel, S., … Marcella, K. (2017). Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. *Global Ecology and Biogeography*. https://doi.org/10.1111/geb.12600

Rich, L. N., Miller, D. A. W., Robinson, H. S., McNutt, J. W., & Kelly, M. J. (2016). Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. *Journal of Applied Ecology*, *53*(4), 1225–1235. https://doi.org/10.1111/1365-2664.12650

Richmond, B., Begun, D., & Strait, D. (2001). Origin of human bipedalism: The knuckle-walking hypothesis revisited. *American Journal of Physical Anthropology*, *116*(S33), 70–105. https://doi.org/10.1002/ajpa.10019

Richmond, B., Green, D., Lague, M., Chirchir, H., Behrensmeyer, A., Bobe, R., … Braun, D. R. (2020). The upper limb of Paranthropus boisei from Ileret, Kenya. *Journal of Human Evolution*, *141*, 102727. https://doi.org/10.1016/j.jhevol.2019.102727

Richmond, B., & Jungers, W. (2008). Orrorin tugenensis femoral morphology and the evolution of hominin bipedalism. *Science*, *319*(5870), 1662–1665. https://doi.org/10.1126/SCIENCE.1154197/SUPPL_FILE/RICHMOND.SOM.PDF

Richmond, B., & Strait, D. (2000). Evidence that humans evolved from a knuckle-walking ancestor.

Nature, *404*(6776), 382–385.

Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics 2009 14:3*, *14*(3), 322–337. https://doi.org/10.1198/JABES.2009.08038

Ripple, W., & Van Valkenburgh, B. (2010). Linking top-down forces to the Pleistocene megafaunal extinctions. *BioScience*, *60*(7), 516–526. Retrieved from https://academic.oup.com/bioscience/article-abstract/60/7/516/234159

Rito, T., Richards, M. B., Fernandes, V., Alshamali, F., Cerny, V., Pereira, L., & Soares, P. (2013). The First Modern Human Dispersals across Africa. *PLoS ONE*, *8*(11), e80031. https://doi.org/10.1371/journal.pone.0080031

Rogers, M., Harris, J., & Feibel, C. (1994). Changing patterns of land use by Plio-Pleistocene hominids in the Lake Turkana Basin. *Journal of Human Evolution*, (139–158). Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248484710396

Rolian, C., & Carvalho, S. (2017). Tool use and manufacture in the last common ancestor of pan and homo. In *Chimpanzees and human evolution*.

Rose, R. A., Byler, D., Eastman, J. R., Fleishman, E., Geller, G., Goetz, S., … Wilson, C. (2015). Ten ways remote sensing can contribute to conservation. *Conservation Biology*, *29*(2), 350–359. https://doi.org/10.1111/COBI.12397

Rowcliffe, M. (2017). Key frontiers in camera trapping research. *Remote Sensing in Ecology and Conservation*, *3*(3), 107–108. https://doi.org/10.1002/rse2.65

Rowcliffe, M. (2022). Package “activity.” https://doi.org/10.6084/m9.figshare.1160536

Ruff, C. (2009). Relative limb strength and locomotion in Homo habilis. *American Journal of Physical Anthropology*, *138*(1), 90–100. https://doi.org/10.1002/AJPA.20907

Ruff, C., Scott, W. W., & Liu, A. Y. -. (1991). Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *American Journal of Physical Anthropology*, *86*(3), 397–413. https://doi.org/10.1002/AJPA.1330860306/FORMAT/PDF

Sahle, Y., Zaatari, S. El, & White, T. (2017). Hominid butchers and biting crocodiles in the African Plio–Pleistocene. *Proceedings of the National Academy of Sciences*, *114*(50), 13164–13169. Retrieved from http://www.pnas.org/content/114/50/13164.short

Samson, D. R., & Nunn, C. L. (2015). Sleep intensity and the evolution of human cognition. *Evolutionary Anthropology: Issues, News, and Reviews*, *24*(6), 225–237. https://doi.org/10.1002/evan.21464

Samson, D. R., & Shumaker, R. W. (2015). Orangutans (*Pongo spp* .) have deeper, more efficient sleep than baboons (*Papio papio*) in captivity. *American Journal of Physical Anthropology*, *157*(3), 421–427. https://doi.org/10.1002/ajpa.22733

Samuni, L., Lemieux, D., Lamb, A., Galdino, D., & Surbeck, M. (2022). Tool use behavior in three wild bonobo communities at Kokolopori. *American Journal of Primatology*, *84*(1), e23342. https://doi.org/10.1002/AJP.23342

Samuni, L., Mundry, R., Terkel, J., Zuberbühler, K., & Hobaiter, C. (2014). Socially learned habituation to human observers in wild chimpanzees. *Animal Cognition*, *17*(4), 997–1005. https://doi.org/10.1007/s10071-014-0731-6

Sanford, L., Yang, L., Wellman, L., Liu, X., Sleep, X. T.-, & 2010, U. (2010). Differential effects of controllable and uncontrollable footshock stress on sleep in mice. *Sleep*. Retrieved from https://academic.oup.com/sleep/article-abstract/33/5/621/2454542

Sayers, K., Raghanti, M. A., & Lovejoy, C. O. (2012). Human Evolution and the Chimpanzee Referential Doctrine. *Http://Dx.Doi.Org/10.1146/Annurev-Anthro-092611-145815*, *41*, 119–138. https://doi.org/10.1146/ANNUREV-ANTHRO-092611-145815

Schaller, G. (1962). *The Ecology And Behavior Of The Mountain Gorilla*. University of Wisconsin.

Schneider, S., Taylor, G. W., Linquist, S., & Kremer, S. C. (2019). Past, present and future approaches using computer vision for animal re-identification from camera trap data. *Methods in Ecology and Evolution*, *10*(4), 461–470. https://doi.org/10.1111/2041-210X.13133

Schoener, T. W. (1974). Resource Partitioning in Ecological Communities. *Science*, *185*(4145), 27–39. https://doi.org/10.1126/SCIENCE.185.4145.27

Schofield, D., Nagrani, A., Zisserman, A., Hayashi, M., Matsuzawa, T., Biro, D., & Carvalho, S. (2019). Chimpanzee face recognition from videos in the wild using deep learning. *Science Advances*, *5*(9). https://doi.org/10.1126/SCIADV.AAW0736

Searle, C. E., Smit, J. B., Cusack, J. J., Strampelli, P., Grau, A., Mkuburo, L., … Dickman, A. J. (2021). Temporal partitioning and spatiotemporal avoidance among large carnivores in a human-impacted African landscape. *PLOS ONE*, *16*(9), e0256876. https://doi.org/10.1371/JOURNAL.PONE.0256876

Searle, C. E., Smit, J., Strampelli, P., Mkuburo, L., Ikanda, D., Macdonald, D. W., … Dickman, A. J. (2021). Leopard population density varies across habitats and management strategies in a

mixed-use Tanzanian landscape. *Biological Conservation*, *257*, 109120. https://doi.org/10.1016/J.BIOCON.2021.109120

Searle, K. R., Stokes, C. J., & Gordon, I. J. (2008). When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. *Behavioral Ecology*, *19*(3), 475–482. https://doi.org/10.1093/beheco/arn004

Ségalen, L., Lee-Thorp, J., & Cerling, T. (2007). Timing of C4 grass expansion across sub-Saharan Africa. *Journal of Human Evolution*, *53*(5), 549–559. Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248407001534

Semaw, S., Simpson, S. W., Quade, J., Renne, P. R., Butter, R. F., McIntosh, W. C., … Rodgers, M. J. (2005). Early Pliocene hominids from Gona, Ethiopia. *Nature 2005 433:7023*, *433*(7023), 301–305. https://doi.org/10.1038/nature03177

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., & Coppens, Y. (2001). First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus de l'Académie Des Sciences - Series IIA - Earth and Planetary Science*, *332*(2), 137–144. https://doi.org/10.1016/S1251-8050(01)01529-4

Senut, B., Pickford, M., Gommery, D., & Ségalen, L. (2018). Palaeoenvironments and the origin of hominid bipedalism. *Historical Biology*, *30*(2), 284–296. https://doi.org/10.1080/08912963.2017.1286337

Sept, J. (1998). Shadows on a changing landscape: Comparing nesting patterns of hominids and chimpanzees since their last common ancestor. *American Journal of Primatology*, *46*(1), 85–101. https://doi.org/10.1002/(SICI)1098-2345(1998)46:1<85::AID-AJP7>3.0.CO;2-R

Seyfarth, R., Cheney, D., & Marler, P. (1980). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, *4*(1070), 1094. Retrieved from https://www.sciencedirect.com/science/article/pii/S0003347280800972

Shipman, P. (1986). Scavenging or Hunting in Early Hominids: Theoretical Framework and Tests. *American Anthropologist*, *88*(1), 27–43. https://doi.org/10.1525/AA.1986.88.1.02A00020

Shultz, S., Noë, R., Mcgraw, W. S., & Dunbar, R. I. M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. https://doi.org/10.1098/rspb.2003.2626

Silk, J., Alberts, S., & Altmann, J. (2003). Social Bonds of Female Baboons Enhance Infant Survival. *Science*, *302*(5648), 1231–1234. https://doi.org/10.1126/science.1088580

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., … Cheney, D. L. (2009). The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1670), 3099–3104. https://doi.org/10.1098/RSPB.2009.0681

Silk, J., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., … Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, *20*(15), 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067

Silk, J., Seyfarth, R., & Cheney, D. (1999). The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. *Behaviour*, *136*(6), 679–703. Retrieved from http://booksandjournals.brillonline.com/content/journals/10.1163/156853999501522

Smith, R., & Jungers, W. (1997). Body mass in comparative primatology. *Journal of Human*

Evolution. Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248496901220

Smith, T. M., Tafforeau, P., Pouech, J., & Begun, D. R. (2019). Enamel thickness and dental development in Rudapithecus hungaricus. *Journal of Human Evolution*, *136*, 102649. https://doi.org/10.1016/J.JHEVOL.2019.102649

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, *56*(4), 740–749. https://doi.org/10.1111/AJE.12557

Souza-Alves, J. P., Mourthe, I., Hilário, R. R., Bicca-Marques, J. C., Rehg, J., Gestich, C. C., … Barnett, A. A. (2019). Terrestrial Behavior in Titi Monkeys (Callicebus, Cheracebus, and Plecturocebus): Potential Correlates, Patterns, and Differences between Genera. *International Journal of Primatology*, *40*(4–5), 553–572. https://doi.org/10.1007/s10764-019-00105-x

Sponheimer, M., Alemseged, Z., Cerling, T., Grine, F., Kimbel, W., Leakey, M., & Wynn, J. (2013). Isotopic evidence of early hominin diets. *Proceedings of the National Academy Sciences*, *110*(26), 10513–10518. Retrieved from http://www.pnas.org/content/110/26/10513.short

Spoor, F., Gunz, P., Neubauer, S., Stelzer, S., Scott, N., Kwekason, A., & Dean, M. C. (2015). Reconstructed Homo habilis type OH 7 suggests deep-rooted species diversity in early Homo. *Nature 2015 519:7541*, *519*(7541), 83–86. https://doi.org/10.1038/nature14224

Stacey, P. B. (1986). Group Size and Foraging Efficiency in Yellow Baboons Behavioral Ecology Group size and foraging efficiency in yellow baboons. *Behavioral Ecology and Sociobiology Ecol Sociobiol*, *18*(18), 175–187. Retrieved from http://www.jstor.org/stable/4599878

Stalmans, M., & Beilfuss, R. (2008). *Landscapes of the Gorongosa National Park.*

Stalmans, M., Massad, T. J., Peel, M. J. S., Tarnita, C. E., & Pringle, R. M. (2019). War-induced collapse and asymmetric recovery of large-mammal populations in Gorongosa National Park, Mozambique. *PLOS ONE*, *14*(3), e0212864. doi.org/10.1371/JOURNAL.PONE.0212864

Stalmans, M., Peel, M., & Gonçalves, D. (2018). *Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, October 2018*. Retrieved from https://gorongosa.org/wp-content/uploads/2020/08/gorongosaaerialwildlifecount2018_report_december2018.pdf

Stanford, C., & Bunn, H. (2001). *Meat-eating and human evolution*. Oxford University Press.

Steiper, M. E., & Young, N. M. (2006). Primate molecular divergence dates. *Molecular Phylogenetics and Evolution*, *41*(2), 384–394. https://doi.org/10.1016/J.YMPEV.2006.05.021

Stern, J. T., & Susman, R. L. (1983). The locomotor anatomy of Australopithecus afarensis. *American Journal of Physical Anthropology*, *60*(3), 279–317. https://doi.org/10.1002/AJPA.1330600302

Stewart, F., & Pruetz, J. (2013). Do Chimpanzee Nests Serve an Anti-Predatory Function? *American Journal of Primatology*, *75*(6), 593–604. https://doi.org/10.1002/ajp.22138

Stoltz, LP & Saayman, G. (1970). Ecology and behaviour of baboons in the northern Transvaal. *Annals of the transvaal museum*, *26*(5), 99-143.

Storrs, G. (2003). Late Miocene-Early Pliocene crocodilian fauna of Lothagam, southwest Turkana Basin, Kenya. In *Lothagam: the dawn of humanity in Eastern Africa* (pp. 137–159). https://doi.org/10.7312/leak11870-008

Strandburg-Peshkin, A., Farine, D. R., Crofoot, M. C., & Couzin, I. D. (2017). Habitat and social

factors shape individual decisions and emergent group structure during baboon collective movement. *ELife*, *6*. https://doi.org/10.7554/eLife.19505

Stringer, C. (2002). Modern human origins: progress and prospects. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *357*(1420), 563–579. Retrieved from http://rstb.royalsocietypublishing.org/content/357/1420/563.short

Strum, S., & Mitchell, W. (1987). Baboon models and muddles. *The evolution of human behavior: Primate models*, 87-104.

Swanson, A., Kosmala, M., Lintott, C., Simpson, R., Smith, A., & Packer, C. (2015). Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. *Scientific Data 2015 2:1*, *2*(1), 1–14. https://doi.org/10.1038/sdata.2015.26

Swedell, L., & Plummer, T. (2012). A Papionin Multilevel Society as a Model for Hominin Social Evolution. *International Journal of Primatology*, *33*(5), 1165–1193. https://doi.org/10.1007/s10764-012-9600-9

Tabacow, F. P., Mendes, S. L., & Strier, K. B. (2009). Spread of a Terrestrial Tradition in an Arboreal Primate. *American Anthropologist*, *111*(2), 238–249. https://doi.org/10.1111/J.1548-1433.2009.01116.X

Tagg, N., McCarthy, M., Dieguez, P., Bocksberger, G., Willie, J., Mundry, R., … Boesch, C. (2018). Nocturnal activity in wild chimpanzees (Pan troglodytes): Evidence for flexible sleeping patterns and insights into human evolution. *American Journal of Physical Anthropology*, *166*(3), 510–529. https://doi.org/10.1002/ajpa.23478

Takemoto, H. (2004). Seasonal change in terrestriality of chimpanzees in relation to microclimate in

the tropical forest. *American Journal of Physical Anthropology*, *124*(1), 81–92. https://doi.org/10.1002/ajpa.10342

Tambling, C. J., Minnie, L., Meyer, J., Freeman, E. W., Santymire, R. M., Adendorff, J., & Kerley, G. I. H. (2015). Temporal shifts in activity of prey following large predator reintroductions. *Behavioral Ecology and Sociobiology 2015 69:7*, *69*(7), 1153–1161. https://doi.org/10.1007/S00265-015-1929-6

Tavaré, S., Marshall, C., Will, O., Soligo, C., & Martin, R. (2002). Using the fossil record to estimate the age of the last common ancestor of extant primates. *Nature*, *416*(6882), 726. Retrieved from https://www.nature.com/articles/416726a

Thompson, J., Carvalho, S., Marean, C., & Alemseged, Z. (2019). Origins of the Human Predatory Pattern The Transition to Large-Animal Exploitation by Early Hominins. *Ora.Ox.Ac.Uk*, *60*(1), 1–23. https://doi.org/10.1086/701477

Thompson, J., McPherron, S., Bobe, R., Reed, D., Barr, W., Wynn, J., & Alemseged, Z. (2015). Taphonomy of fossils from the hominin-bearing deposits at Dikika, Ethiopia. *Journal of Human Evolution*, *86*, 112–135. Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248415001657

Thorpe, S. K. ., Holder, R. L., & Crompton, R. H. (2007). Origin of Human Bipedalism as an Adaptation for Locomotion on Flexible Branches. *Science*. https://doi.org/10.1126/science.1138211

Tinley, K. (1977). *Framework of the Gorongosa ecosystem*. University of Pretoria. Retrieved from https://repository.up.ac.za/handle/2263/24526

Tomasello, M., & Vaish, A. (2013). Origins of Human Cooperation and Morality. *Https://Doi.Org/10.1146/Annurev-Psych-113011-143812*, *64*, 231–255.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2163–2176. https://doi.org/10.1098/rstb.2010.0090

Toth, N. (1997). The artefact assemblages in light of experimental studies. In G. Isaac (Ed.), *Koobi Fora research project: Vol.5* (pp. 364–402). Oxford.

Trauth, M., Maslin, M., Deino, A., & Junginger, A. (2010). Human evolution in a variable environment: the amplifier lakes of Eastern Africa. *Quartenary Science*. Retrieved from https://www.sciencedirect.com/science/article/pii/S0277379110002581

Trauth, M., Maslin, M., Deino, A., & Strecker, M. (2007). High-and low-latitude forcing of Plio-Pleistocene East African climate and human evolution. *Journal of Human Evolution*. Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248407001522

Treves, A., Mwima, P., Plumptre, A. J., & Isoke, S. (2010). Camera-trapping forest–woodland wildlife of western Uganda reveals how gregariousness biases estimates of relative abundance and distribution. *Biological Conservation*, *143*(2), 521–528. https://doi.org/10.1016/J.BIOCON.2009.11.025

Treves, A., & Palmqvist, P. (2007). Reconstructing Hominin Interactions with Mammalian Carnivores (6.0–1.8 Ma). In *Primate Anti-Predator Strategies* (pp. 355–381). Boston, MA: Springer US. https://doi.org/10.1007/978-0-387-34810-0_17

Tryon, C., Faith, J., Peppe, D., & Beverly, E. (2016). The Pleistocene prehistory of the Lake Victoria basin. *Quaternary International*, *404*, 100–114. Retrieved from https://www.sciencedirect.com/science/article/pii/S1040618215011994

Turner, A. (1990). The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. *Geobios*, *23*(3), 349–368.

Tutin, C. E. G., & Fernandez, M. (1991). Responses of wild chimpanzees and gorillas to the arrival of primatologists: behaviour observed during habituation. In *Primate Responses to Environmental Change* (pp. 187–197). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-94-011-3110-0_10

Ungar, P. S., Grine, F. E., & Teaford, M. F. (2008). Dental Microwear and Diet of the Plio-Pleistocene Hominin Paranthropus boisei. *PLoS ONE*, *3*(4), e2044. https://doi.org/10.1371/journal.pone.0002044

Uno, K. T., Polissar, P. J., Jackson, K. E., & Demenocal, P. B. (2016). Neogene biomarker record of vegetation change in eastern Africa. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(23), 6355–6363. https://doi.org/10.1073/PNAS.1521267113/SUPPL_FILE/PNAS.1521267113.SD07.XLSX

Val, A., Taru, P., & Steininger, C. (2014). New taphonomic analysis of large-bodied primate assemblage from Cooper's D, Bloubank Valley,South Africa. *The South African Archaeological Bulletin*, *69*(199), 49–58. Retrieved from https://about.jstor.org/terms

Van Schaik, C.P. (1983). Why Are Diurnal Primates Living in Groups? *Behaviour*, *87*(1), 120–144. https://doi.org/10.1163/156853983X00147

van Schaik, Carel P., van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in sumatran forest primates. *Primates*, *24*(2), 211–221. https://doi.org/10.1007/BF02381083

Van Valkenburgh, B., Hayward, M. W., Ripple, W. J., Meloro, C., & Roth, V. L. (2016). The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(4), 862–867. https://doi.org/10.1073/PNAS.1502554112

Villmoare, B., Kimbel, W., Seyoum, C., Campisano, C., DiMaggio, E., Rowan, J., & Reed, K. (2015). Early Homo at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science*, *347*(6228), 1352–1355. Retrieved from http://science.sciencemag.org/content/347/6228/1352.short

Visalberghi, E., Sirianni, G., Fragaszy, D., & Boesch, C. (2015). Percussive tool use by Taï Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: a comparison. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1682). https://doi.org/10.1098/RSTB.2014.0351

Vrba, E. (1993). Turnover-pulses, the Red Queen, and related topics. *American Journal of Science*, *293*, 418.

Vrba, E. (1995). On the connections between paleoclimate and evolution. In L. B. ES Vrba, GH Denton, TC Partridge (Ed.), *Paleoclimate and evolution with emphasis on human origins.* (pp. 24–45).

Ward, C. (2002). Interpreting the posture and locomotion of Australopithecus afarensis: Where do we stand? *American Journal of Physical Anthropology*, *119*(S35), 185–215.

https://doi.org/10.1002/AJPA.10185

Ward, C., Kimbel, W., & Johanson, D. (2011). Complete fourth metatarsal and arches in the foot of Australopithecus afarensis. *Science (New York, N.Y.)*, *331*(6018), 750–753. https://doi.org/10.1126/SCIENCE.1201463

Ward, C., Leakey, M., & Walker, A. (1999). The new hominid species Australopithecus anamensis. *Evolutionary Anthropology: Issues, News, and Reviews*.

Ward, C. V, Leakey, M. G., & Walker, A. (2001). Morphology of Australopithecus anamensis from Kanapoi and Allia Bay, Kenya. *Journal of Human Evolution*, *41*, 255–368. https://doi.org/10.1006/jhev.2001.0507

Washburn, S. L., & DeVore, I. (1961). The Social Life of Baboons. *Scientific American*. Scientific American, a division of Nature America, Inc. https://doi.org/10.2307/24937489

Werdelin, L., & Lewis, M. (2005). Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. *Zoological Journal of the Linnean Society*, *144*(2), 121–144. https://doi.org/10.1111/j.1096-3642.2005.00165.x

Werdelin, L., & Lewis, M. (2013a). *Koobi fora research project volume 7: The Carnivora.*

Werdelin, L., & Lewis, M. (2013b). Temporal Change in Functional Richness and Evenness in the Eastern African Plio-Pleistocene Carnivoran Guild. *PLoS ONE*, *8*(3), e57944. https://doi.org/10.1371/journal.pone.0057944

White, T., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C., Suwa, G., & WoldeGabriel, G. (2009). Ardipithecus ramidus and the paleobiology of early hominids. *Science*, *326*(5496), 64–

86. Retrieved from http://science.sciencemag.org/content/326/5949/64.short

White, T., Lovejoy, C. O., Asfaw, B., Carlson, J. P., & Suwa, G. (2015). Neither chimpanzee nor human, Ardipithecus reveals the surprising ancestry of both. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(16), 4877–4884. https://doi.org/10.1073/PNAS.1403659111/-/DCSUPPLEMENTAL

White, T., WoldeGabriel, G., Asfaw, B., Ambrose, S., Beyene, Y., Bernor, R., & Suwa, G. (2006). Asa Issie, Aramis and the origin of Australopithecus. *Nature*, *440*(7086), 883–889.

Wickham, H. (2009). ggplot2. *Ggplot2*. https://doi.org/10.1007/978-0-387-98141-3

Wilkinson, R. D., Steiper, M. E., Soligo, C., Martin, R. D., Yang, Z., & Tavaré, S. (2011). Dating Primate Divergences through an Integrated Analysis of Palaeontological and Molecular Data. *Systematic Biology*, *60*(1), 16–31. https://doi.org/10.1093/sysbio/syq054

Willems, E. P., & Hill, R. (2009). Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology*, *90*(2), 546–555. https://doi.org/10.1890/08-0765.1

Willems, E. P., & Van Schaik, C. P. (2017). The social organization of Homo ergaster: Inferences from anti-predator responses in extant primates. https://doi.org/10.1016/j.jhevol.2017.05.003

Williams, S. A., Prang, T., Meyer, M. R., Nalley, T. K., Van Der Merwe, R., Yelverton, C., … Berger, L. R. (2021). New fossils of Australopithecus sediba reveal a nearly complete lower back. *ELife*, *10*. https://doi.org/10.7554/ELIFE.70447

Williams, S. A., Prang, T., Meyer, M. R., Russo, G. A., & Shapiro, L. J. (2020). Reevaluating bipedalism in Danuvius. *Nature 2020 586:7827*, *586*(7827), E1–E3.

https://doi.org/10.1038/s41586-020-2736-4

Williamson, E., & Feistner, A. (2003). Habituating primates: processes, techniques, variables and ethics. In J. Setchell & D. Curtis (Eds.), *Field and laboratory methods in primatology: A practical guide*. Cambridge University Press.

Winder, I. C. (2014). The Biogeography of the Papio Baboons: A GIS-Based Analysis of Range Characteristics and Variability. *Folia Primatologica*, *85*(5), 292–318. https://doi.org/10.1159/000362545

Winnie, J., & Creel, S. (2017). The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs*, *12*, 88–94. https://doi.org/10.1016/J.FOOWEB.2016.09.002

Woldegabriel, G., White, T. D., Suwa, G., Renne, P., de Heinzelin, J., Har, W., & Heiken, G. (1994). Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature*, *371*(6495), 330–333.

Wong, S. T., Belant, J. L., Sollmann, R., Mohamed, A., Niedballa, J., Mathai, J., … Wilting, A. (2019). Influence of body mass, sociality, and movement behavior on improved detection probabilities when using a second camera trap. *Global Ecology and Conservation*, *20*, e00791. https://doi.org/10.1016/J.GECCO.2019.E00791

Wood, B., & Boyle, E. (2016). Hominin taxic diversity: Fact or fantasy? *American Journal of Physical Anthropology*, *159*(S61), 37–78. https://doi.org/10.1002/ajpa.22902

Wood, B., & Collard, M. (1999). The Human Genus. *Science*, *284*(65). https://doi.org/10.1126/science.284.5411.65

Wood, B., & Strait, D. (2004). Patterns of resource use in early Homo and Paranthropus. *Journal of Human Evolution*, *46*(2), 119–162. Retrieved from https://www.sciencedirect.com/science/article/pii/S0047248403001726

Wrangham, R. (1980). An Ecological Model of Female-Bonded Primate Groups. *Behaviour*, *75*(3), 262–300. https://doi.org/10.1163/156853980X00447

Wrangham, R., & Carmody, R. (2010). Human adaptation to the control of fire. *Evolutionary Anthropology*. https://doi.org/10.1002/evan.20275

Wright, K. A., Biondi, L., Visalberghi, E., Ma, Z., Izar, P., & Fragaszy, D. (2019). Positional behavior and substrate use in wild adult bearded capuchin monkeys (Sapajus libidinosus). *American Journal of Primatology*, *81*(12), e23067. https://doi.org/10.1002/AJP.23067

Wynn, J. G., Alemseged, Z., Bobe, R., Grine, F. E., Negash, E. W., & Sponheimer, M. (2020). Isotopic evidence for the timing of the dietary shift toward C4foods in eastern African Paranthropus. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(36), 21978–21984. https://doi.org/10.1073/PNAS.2006221117/-/DCSUPPLEMENTAL

Yapuncich, G. S., Bowie, A., Belais, R., Churchill, S. E., & Walker, C. S. (2020). Predicting body mass of bonobos (Pan paniscus) with human-based morphometric equations. *American Journal of Primatology*, *82*(2), e23088. https://doi.org/10.1002/AJP.23088

Zinner, D., Groeneveld, L. F., Keller, C., & Roos, C. (2009). Mitochondrial phylogeography of baboons (Papio spp.) – Indication for introgressive hybridization? *BMC Evolutionary Biology*, *9*(1), 83. https://doi.org/10.1186/1471-2148-9-83

Zuberbühler, K., & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, *43*(6), 873–886. https://doi.org/10.1006/JHEV.2002.0605

Appendices

Appendix A: Species detections across the GNP and FC camera trap grids

Camera trap grid	Species (common)	Detections	Percentage
Gorongosa National Park	Waterbuck	54074	25.63
	Baboon	44366	21.03
	Warthog	33743	15.99
	Impala	22537	10.68
	Bushbuck	18531	8.78
	Oribi	5990	2.84
	Elephant	4338	2.06
	Nyala	3926	1.86
	Genet	3474	1.65
	Civet	1773	0.84
	Vervet	1766	0.84
	Bird_other	1764	0.84
	Bushpig	1747	0.83
	Kudu	1607	0.76
	Porcupine	1573	0.75
	Wildebeest	1240	0.59
	Reedbuck	1164	0.55
	Buffalo	1139	0.54
	Mongoose	1093	0.52
	Guineafowl	908	0.43
	Unknown_antelope	858	0.41
	Duiker_red	751	0.36
	Sable_antelope	486	0.23
	Hartebeest	357	0.17
	Hare	311	0.15
	Duiker_common	260	0.12
	Honey_badger	245	0.12
	Aardvark	210	0.10
	Hornbill_ground	178	0.08
	Rodent	105	0.05
	Lion	87	0.04
	Samango	84	0.04
	Eland	57	0.03
	Serval	54	0.03

	Bushbaby	53	0.03
	Human	49	0.02
	Reptiles	49	0.02
	Hippo	33	0.02
	Pangolin	21	0.01
	Bat	4	0.00
	Duiker_unknown	3	0.00
	Insect	3	0.00
	Hippopotamus	2	0.00
	Total	**211,013**	**100**
Forestry Concession	Human	320	17.78
	Common_Duiker	267	18.04
	Bushy_Tailed_Mongoose	168	11.35
	Genet	152	10.27
	Baboon	147	9.93
	Civet	120	8.11
	Hare	106	7.16
	Suni	95	6.42
	Pouched_Rat	53	3.58
	Red_Duiker	42	2.84
	Marsh_Mongoose	40	2.70
	Guinea_Fowl	38	2.57
	Bushbuck	36	2.43
	Unknown_Ung	28	1.89
	Porcupine	27	1.82
	Samango	18	1.22
	Oribi	17	1.15
	Bushpig	12	0.81
	Serval	12	0.81
	Ground_Hornbill	10	0.68
	Warthog	10	0.68
	Squirrel	9	0.61
	Leopard	8	0.54
	Aardvark	7	0.47
	Kudu	7	0.47
	Cane_Rat	6	0.41
	Eland	6	0.41
	White_Tailed_Mongoose	6	0.41
	Honey_Badger	5	0.34
	Nyala	5	0.34
	Reedbuck	5	0.34
	Sable	5	0.34
	Gelago	4	0.27

Hartebeest	3	0.20
Monitor	3	0.20
Pangolin	2	0.14
Dog	1	0.07
Total	**1800**	**100**

Appendix B: Model selection

(1) Section 3.3.1.1 GLMM results from seasonal data (GNP grid only)

Model	Fixed effects	Random effects	AIC
Ecological	Woody cover + distance to lake + distance to river + risk + season	Camera station	2991.5
Ecological & Anthropogenic	Woody cover + distance to lake + distance to river + risk + season + distance to road + distance to settlement	Camera station	2988.6

Results from alternate model (ecological and anthropogenic). Asterisks indicate statistical significance of *p-values (* = < 0.05, ** = < 0.01, *** = < 0.001).*

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-4.29	0.11	-40.00	< 0.001***
Woody cover	0.03	0.12	0.27	0.79
Lake distance	-0.04	0.15	-0.28	0.78
River distance	0.05	0.10	0.55	0.58
Risk: Predator	0.29	0.22	1.33	0.19
Season: Late dry	0.27	0.02	12.65	< 0.001***
Season: Wet	-0.01	0.03	-0.50	0.61
Road distance	-0.07	0.08	-0.84	0.40
Settlement distance	0.08	0.15	0.51	0.61

(2) Section 3.3.1.2 GLM results from data collected across both grids

Model	Fixed effects	Random effects	AIC
Ecological	Woody cover + distance to water + risk + location	NA	807.53
Ecological & Anthropogenic	Woody cover + distance to water + risk + location + distance to road + distance to settlement	NA	811.2

Results from alternate model (ecological and anthropogenic). Asterisks indicate statistical significance of *p-values (* = < 0.05, ** = < 0.01, *** = < 0.001).*

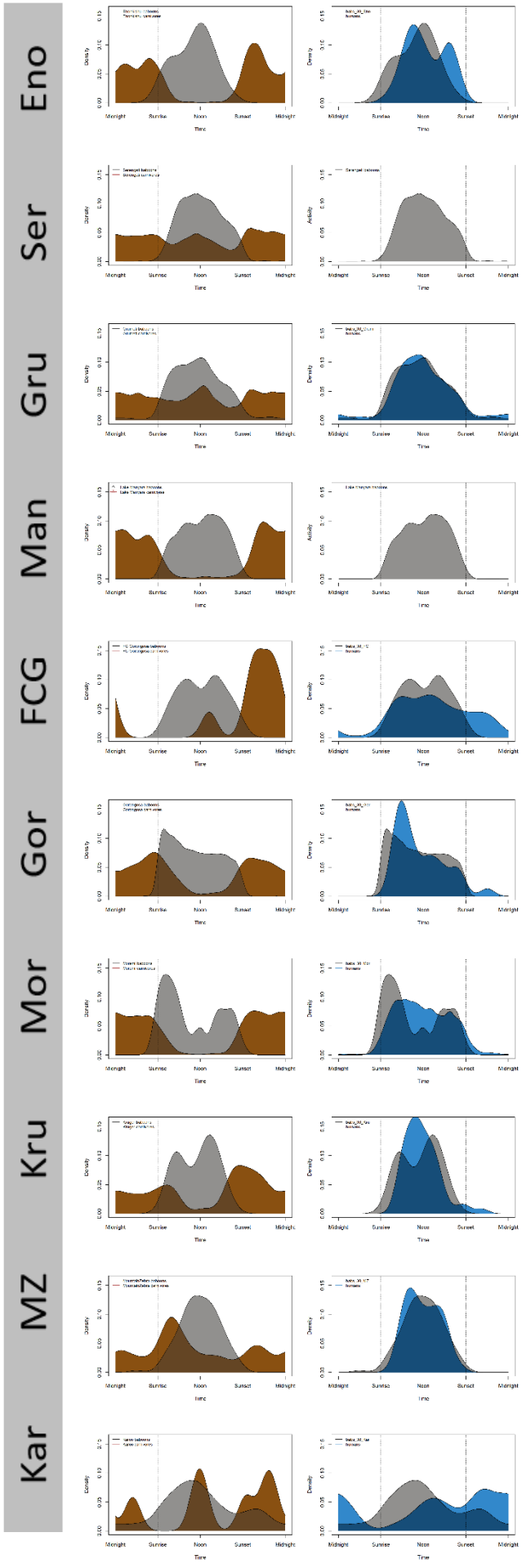
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-4.98	0.56	-8.88	< 0.001***

Woody cover	-0.01	0.01	-1.08	0.28
Water distance	-0.02	0.03	-0.52	0.60
Risk: Predator	-0.11	0.23	-0.50	0.62
Location: GNP	2.14	0.38	5.60	< 0.001***
Road distance	-0.04	0.07	-0.50	0.62
Settlement distance	-0.01	0.02	-0.28	0.78

Appendix C: Camera trap grid details

Site	Study period	Camera placement	Camera settings	Camera model	Reference
†**Enonkishu, KE (Eno)**	Apr 2018 – Dec 2018	Single cameras at centre of 5km^2 cells, ~0.5m high.	3 photos, 60s delay between triggers. For flash model: 1 photo per trigger at night.	Cuddeback	(Pardo et al., 2021)
†**Serengeti, TZ (Ser)**	Jul 2010 – Dec 2013	Single cameras at centre of 5km^2 cells, ~0.5m high.	3 photos, 60s delay between triggers. For flash model: 1 photo per trigger at night.	Scoutguard (SG565) incandescent & DLC Covert II	(Swanson et al., 2015)
Grumeti, TZ (Gru)	May 2017 – Jun 2018	Single cameras at centre of 5km^2 cells, ~0.5m high.	3 photos, 60s delay between triggers. For flash model: 1 photo per trigger at night.	Cuddeback professional color 1347 & long range IR model 1224	(Swanson et al., 2015)
‡**Lake Manyara, TZ (Man)**	Jun 2016 – Jun 2017	Single cameras at centre of 2.25km^2 cells, ~0.5m high.	1 photo, 60s delay between triggers.	LTL Acorn 5210A, infrared	(Clauss et al., 2021)
FC Gorongosa, MZ (FCG)	Jun 2017 – Oct 2017	Paired cameras at centre of 4km^2 cells, some along roads, knee-height.	2 photos, 30s delay between triggers.	Bushnell Trophy Cam	(Easter et al., 2019)
Gorongosa, MZ (Gor)	Jun 2016 – Sept 2018	Single cameras at centre of 5km^2 cells, ~1m high.	2 photos, 2s delay between triggers.	Bushnell Trophy Cam	(Gaynor et al., 2021)
Moremi, BW (Mor)	Aug 2014 – Aug 2015	Two sets of paired cameras per 5km^2 cell, all on roads, knee-height.	3 photos, 30s delay between triggers. For flash model: 1 photo per trigger at night.	Panthera v4 incandescent-flash & Bushnell Trophy Cam infrared	(Rich et al., 2016)
†**Kruger, ZA (Kru)**	May 2018 – Jul 2018	Single cameras at centre of 5km^2 cells, ~0.5m high.	3 photos, 60s delay between triggers. For flash model: 1 photo per trigger at night.	Cuddeback	(Pardo et al., 2021)
†**Mt Zebra, ZA (MZ)**	Aug 2017 – Jul 2018	Single cameras at centre of 5km^2 cells, ~0.5m high.	3 photos, 60s delay between triggers. For flash model: 1 photo per trigger at night.	Cuddeback	(Pardo et al., 2021)
†**Karoo, ZA (Kar)**	Oct 2017 – Feb 2018	Single cameras at centre of 5km^2 cells, ~0.5m high.	3 photos, 60s delay between triggers. For flash model: 1 photo per trigger at night.	Cuddeback	(Pardo et al., 2021)

Appendix D: Temporal overlap of baboons (grey) with combined large carnivore activity (brown) and with human activity (blue) across 10 African sites. Note that human data are not available for Serengeti or Lake Manyara sites.


Eno
Ser
Gru
Man
FCG
Gor
Mor
Kru
MZ
Kar
Density
Activity
Time
Midnight
Sunrise
Noon
Sunset

Appendix E: Published version of Chapter Two as it appears in the American Journal for Biological Anthropology

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RESEARCH ARTICLE

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Risk perception and terrestriality in primates: A quasi-experiment through habituation of chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique

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Abstract

Objectives: Habituation is a common pre-requisite for studying noncaptive primates. Details and quantitative reporting on this process are often overlooked but are useful for measuring human impact on animal behavior, especially when comparing studies across time or sites. During habituation, perceived risk of a stimulus—human observers—is assumed to decline with repeated exposure to that stimulus. We use habituation as a quasi-experiment to study the landscape of fear, exploring relationships between actual risk, perceived risk, mediating environmental variables, and behavioral correlates.

Materials and Methods: We recorded vocalizations and observer-directed vigilance as indicators of perceived risk during habituation of two troops of chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique. Here, we model changes in these variables as a function of habituation time, troop, time of day, and habitat features. We also model the relationship between each of the anti-predator behaviors and ground-use, exploring whether they predict greater terrestriality in the baboons.

Results: In both troops, vocalization rates and observer-directed vigilance declined with cumulative exposure to observers, but were heightened later in the day and in denser habitat types. We found that terrestrial activity was negatively related to levels of both vocalizations and observer-directed vigilance.

Discussion: This study provides a quantitative assessment of the impact of human observation on primate behavior and highlights environmental variables that influence anti-predator behaviors, perhaps indicating heightened perception of risk. The relationship between perceived risk and terrestriality is significant for understanding the evolution of this rare trait in primates.

KEYWORDS
baboons, landscape of fear, primate habituation, risk perception, terrestriality

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1 | INTRODUCTION

Habituation is the period and process by which researchers accustom focal individuals or groups of wild animals to their presence, until the animals treat the observers as neutral stimuli in their habitat (Tutin & Fernandez, 1991). Although common practice in ethology, habituation is often viewed simply as a means to an end; namely, the collection of naturalistic data. Details about the process are thus underreported and studies rarely quantify the time taken for specific effects of observer presence on animal behavior to either plateau or disappear (Allan et al., 2020; Samuni et al., 2014; Williamson & Feistner, 2003).

Amongst primates, common initial reactions to the presence of humans include vocalizations, vigilance, threatening displays, and retreat, but the intensity of such responses decreases across repeated encounters with observers (Jack et al., 2008; Johns, 1996; McLennan & Hill, 2010; Schaller, 1962; Williamson & Feistner, 2003). The few published accounts of habituation indicate that great apes take at least 2–5 years to habituate to human presence (Williamson & Feistner, 2003), whilst "opportunistic" generalist taxa, such as *Papio* and *Macaca*, are thought to habituate to researchers comparatively quickly. However, even within the *Papio* genus there have been a range of habituation times reported—from 5 months to 2 years (Barton & Whiten, 1993; Cowlishaw, 1997b; Kummer, 1997; Noser & Byrne, 2007). This is convoluted further by the lack of a clear working definition for "habituated" primates, and the range in strategies and intensity of habituation efforts. Additionally, a recent study highlights that habituation does not occur at the same rate across groups but is influenced by each individual's tolerance of human presence (Allan et al., 2020).

Greater use of quantitative measures of habituation is thus needed to account for potential observer effects in behavioral studies, and to facilitate standardized comparison of behavioral and fitness data across studies and field sites. This is because animals may forego fitness-enhancing activities such as foraging, mate-seeking, or grooming to engage in observer-directed behaviors such as vocalization or vigilance (Frid & Dill, 2002).

Human presence has also been linked to both proximate and more long-lasting changes in primates' substrate use. Unhabituated primates often retreat from terrestrial observers into—or higher into—trees (Johns, 1996; van Schaik et al., 1983), and comparisons across field studies demonstrate longer-term effects: habituated groups of primates exhibit more frequent and varied use of the ground than less habituated groups of the same species (*Ateles* spp.: Campbell et al., 2005; *Brachyteles hypoxanthus*: Mourthé et al., 2007). At its extreme, habituation shields primates from exposure to predators who avoid humans (e.g., leopards: Isbell & Young, 1993), which can inflate primate activity on or near the ground when humans are present (*Cercopithecus mitis erythrarcus*: Nowak et al., 2014). These examples highlight why observer-effects—on unhabituated through to well-habituated animals—must be understood, quantified, and incorporated into analyses of naturalistic behavior.

Quantitative monitoring of habituation also sheds light on adaptations to risk more generally. This is because predators evoke responses, trade-offs, and changes to substrate-use in primates, similar to those described above (Campbell et al., 2005; Cowlishaw, 1997b; Lima, 1998; Mourthé et al., 2007; Souza-Alves et al., 2019). The term "landscape of fear" (Laundré et al., 2001) has been widely adopted in the study of predator–prey dynamics but its definition has remained ambiguous, largely due to conflation of patterns of actual risk, perceived risk, and behavioral responses to perceived risk. This ambiguity results in the use of unsuitable proxies and circular inferences about risk and response, and inhibits nuanced exploration of the mechanisms linking the two (Gaynor et al., 2019). Landscapes of fear have been defined variously as (1) the mapped physical environment, (2) spatial variation in actual predation risk, or (3) spatial patterns in antipredator behaviors. Gaynor et al. (2019) propose a framework in which these are three distinct, measurable landscapes, related in nonlinear ways and linked by the true landscape of fear: a fourth distinct layer representing *spatial variation in risk perception*.

These are important distinctions for exploring how ecological factors mediate predator–prey dynamics. For instance, habitat structure is reported to affect risk-invoked behaviors in many prey species (Atuo & O'Connell, 2017; Gorini et al., 2011), including primates (Coleman & Hill, 2014; Enstam & Isbell, 2002, 2004; Hill & Weingrill, 2007). However, habitat could influence the cognitive experience of risk perception in several different ways. First, due to predators' habitat preferences or hunting techniques (ambush or cursorial), encounters between predators and prey are more likely in certain habitats and at certain times. Thus, prey might perceive greater risk in these areas and times, based on past experience. Second, habitat features such as low visibility reduce the probability of detecting predators, perhaps heightening perceived risk in certain habitats *regardless* of actual predator presence. And third, habitat features such as tree density might either aid or prevent primates escaping from predators, with these opportunities for risk mitigation altering the level of perceived risk that they experience (Hill & Weingrill, 2007).

For example, baboons' reported avoidance of areas with denser vegetation (Cowlishaw, 1997b; Hill & Weingrill, 2007; Rasmussen, 1983) might demonstrate a straightforward relationship between actual predation risk and prey response if predators are more prevalent or likely to attack in such habitats. However, even if predators are not actually present or concentrated in tall grass or wooded vegetation, it is argued that primates display heightened antipredator behaviors in such areas because reduced visibility increases the perception of risk in denser habitats (Altmann & Altmann, 1970; Cowlishaw, 1997b; Hill & Weingrill, 2007; Rasmussen, 1983). On the other hand, trees can provide refuge from predation and vantage points from which to detect terrestrial predators. Patas monkeys (*Erythrocebus patas*) were found to use taller-than-average trees to scan their surroundings and, despite predators being present across the landscape, made most successful predator detections from within these "tall habitats" (Enstam & Isbell, 2004).

Furthermore, the same risk stimulus—a mammalian predator alarm call—has been shown to evoke different antipredator responses depending on the habitat structure in which it is heard during playback experiments. Vervet monkeys (*Chlorocebus pygerythrus*) switched between arboreal and terrestrial escape strategies when they heard

the same call in different environments (Enstam & Isbell, 2002). This behavioral flexibility is also demonstrated in a study where vervet monkeys reduced their levels of vigilance in areas that became more open after a fire (Jaffe & Isbell, 2009). These examples highlight the varied and nonlinear effects that vegetation might have on risk perception, and demonstrate that primates employ a range of flexible and compensatory behaviors to minimize their exposure to risk in the environment.

Measuring variation in actual predation risk across an environment is difficult, due to the elusiveness of carnivores, and the fact that their distribution and density across the landscape changes with time of day, season, and availability of prey and water. This makes it hard to untangle the contributing roles of actual risk and external ecological factors to prey animals' perception of risk. Habituation provides a quasi-experimental setting in which focal animals are repeatedly exposed to the same risk stimulus (the presence of human observers) across time and habitat types. This provides an opportunity to elucidate the proximate effects of risk on behavior, as well as mediating effects of temporal and ecological factors on this relationship (Cowlishaw, 1997a; Frid & Dill, 2002; van Schaik et al., 1983).

Based on the assumption that perceived risk of humans declines with habituation, our study measures changes in (a) vocalization rates and (b) observer-directed vigilance during primate habituation, and tests how each of these response variables is affected by ecological and temporal factors. We also test whether prevalence of these antipredator behaviors predicts levels of terrestrial behavior in baboons.

2 | METHODS

2.1 | Study site and species

Gorongosa National Park (−18.96°, 34.36°), Mozambique, lies at the southern end of the East African Rift System (EARS). It is composed of approximately 4000 km^2 of heterogeneous habitats (Bouley et al., 2018; Stalmans & Beilfuss, 2008; Tinley, 1977) and is inhabited by over 200 troops of chacma baboons (Stalmans et al., 2018). Two focal troops were followed during this study: the Woodland Troop (WT) and the Floodplain Troop (FT), composed of 88 and 37 individuals respectively, based on counts at the end of the study period. As the names suggest, WT ranges predominantly in an *Acacia-Combretum* savannah woodland, while FT ranges predominantly in floodplain grasslands, although they return to riverine sleep sites with more tree coverage. The baboons forage on a range of fruits, seeds, and foliage, as well as grass, rhizomes, and insects. Occasionally, individuals in both troops were also observed hunting and eating small vertebrates such as young antelope, warthogs, and ducklings.

Civil war in Mozambique between 1977 and 1992 decimated wildlife in the park; populations of large herbivorous mammals declined by >90%, and apex predators were almost completely lost from the landscape (Daskin et al., 2016). Before the war, leopard (*Panthera pardus*) and lion (*Panthera leo*) were abundant in the park, and wild dog (*Lycaon pictus*) and spotted hyena (*Crocuta crocuta*) were present in smaller numbers (Tinley, 1977). A small and slowly growing lion population survived the war (Bouley et al., 2018) but the other three carnivore species were not seen in the park until a single leopard sighting in April 2018, and the reintroduction of a pack of wild dogs to the park in June 2018 (Atkins et al., 2019).

Reduced predation pressure since the war has facilitated rapid growth of several mammal populations, including baboons (Atkins et al., 2019), and the troops in this study have had limited exposure to large mammalian carnivores. As this study marks the first primatological research in the park, the troops had also experienced minimal exposure to humans—especially humans on foot and off-road—prior to the start of our data collection.

2.2 | Data collection

We collected data during day follows in which each focal troop was followed by one researcher and one park ranger between the hours of 06:00 and 18:00 (although logistical constraints often limited this period to between 07:00 and 17:00, especially for FT). These follows began in April 2018 for WT and May 2018 for FT, and ended in November 2018 for both troops due to park closure in the wet season. Throughout follows, we attempted to remain as close to the troops as possible without eliciting obvious fleeing behavior. We used handheld GPS devices (Garmin Oregon 700 and Garmin Map64) to record tracks of the daily follow routes, and customized applications on Apple iPads to collect time-stamped activity and habitat data.

The Animal Behavior Pro application (University of Kent, 2012) was used to conduct all-occurrence vocalization sampling for 5 min every 30 min throughout the day. We logged every vocalization heard during the sample as a "Bark," "Grunt," "Copulation Call," or "Contact Call." As the clearest indicators of external risk (Fischer et al., 2001), only barks are included in the analyses below. There is a risk that some contact calls might have been included in the "bark" category, as they are not always easy to distinguish from one another, and acoustic analyses suggest there is a graded variation of vocalizations between tonal contact calls and harsher alarm barks (Fischer et al., 2001). While we expect human presence to have an effect on alarm barks over time (declining with habituation), we would not expect it to influence the frequency of contact calls between baboons. However, potential impacts of both habitat and time of day on contact calls will be addressed in the discussion. To account for troop size, vocalization data from WT and FT were divided by 80 and 30, respectively, producing troop-adjusted vocalization rates.

The Animal Observer application (Dian Fossey Gorilla Fund International, 2012) was used to conduct activity scan samples every 30 min during follows until the September 14, 2018 and every 15 min after that date. As our analyses examine the probability of a behavior occurring per scan, this change in frequency should not affect our results. Scans were always conducted from left to right to minimize the chances of bias toward attention-catching behaviors, and were

conducted within a 5-min limit. During scans, we logged the activity, vigilance-state, and position (on or above the ground) of every monkey in view of the observer. Defining vigilance has proved problematic in primatology (Allan & Hill, 2018). To reduce ambiguity, vigilance was coded at the individual level as "looking directly at the observer during scan", or "not looking directly at the observer during scan". Individuals for whom vigilance-state was unknown were excluded from the analyses below. Terrestriality was coded according to the position of each individual baboon during scans; those on the ground were coded as "terrestrial," and those positioned on raised objects (such as rocks or fallen logs) or in trees were coded as "not terrestrial."

Habitat type and average height of ground cover were also recorded at the start of each scan, using the same application. For the analyses below, habitat type is coded as "More than 10% tree coverage," "Less than 10% tree coverage," or "Water." The 10% tree coverage threshold was chosen to distinguish habitats in which the lack of trees is likely to dictate terrestriality. "Water" includes large pans or riverbanks and was included as a separate habitat type due to increased vulnerability of baboons whilst drinking and the potential risks of encountering other animals at major water sources. Estimations of the height of ground cover were coded as "Low" (under 0.5 m tall) or "High" (over 0.5 m tall), based on the approximate shoulder height of a female chacma baboon, to account for potential effects of ground cover on visibility. Examples of habitat type combinations are shown in Figure 1. Time-stamped data were coded categorically as "AM" (06:00–09:59), "MID" (10:00–13:59), or "PM" (14:00–17:59).

2.3 | Statistical analyses

We began by running generalized linear models (GLMs) to determine whether (a) vocalization rates and (b) the probability of observer-directed vigilance changed over cumulative habituation time, measured in full follow days (>6 h data collection). We then tested whether these antipredator behaviors were significantly related to substrate-use by baboons. All models were fitted in R v4.0.2 and we used likelihood ratio tests (LRTs) and the drop1 function from the "stats" package to select models (R Core Team, 2020). Maps and graphs were produced using the "sf" (Pebesma, 2018), "ggmap" (Kahle & Wickham, 2013), and "ggplot2" (Wickham, 2009) packages in R.

2.4 | Vocalizations and vigilance models

2.4.1 | Vocalizations

Due to zero-inflation in the vocalization data we used a hurdle model to explore changes in vocalization rates over habituation time. First, we fitted a GLM with a binomial error distribution and a logit link function to model binary data, classified as "at least one bark" (1) or "no barks" (0) during a scan. Then we fitted a GLM with a gamma distribution and a log link function to all non-zero data to model bark rate as a continuous response. Predictions from each model were multiplied together to fit the final model.

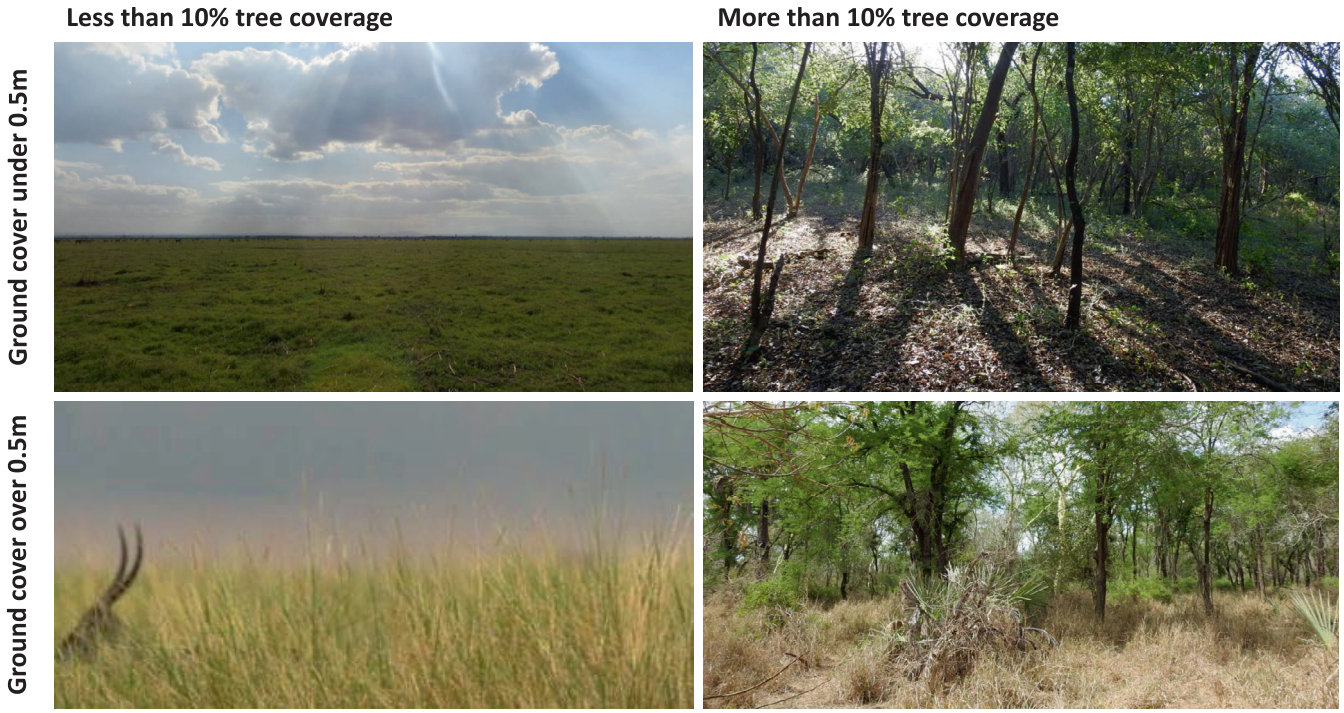


FIGURE 1 Examples of different habitat type combinations within the home ranges of the focal baboon troops

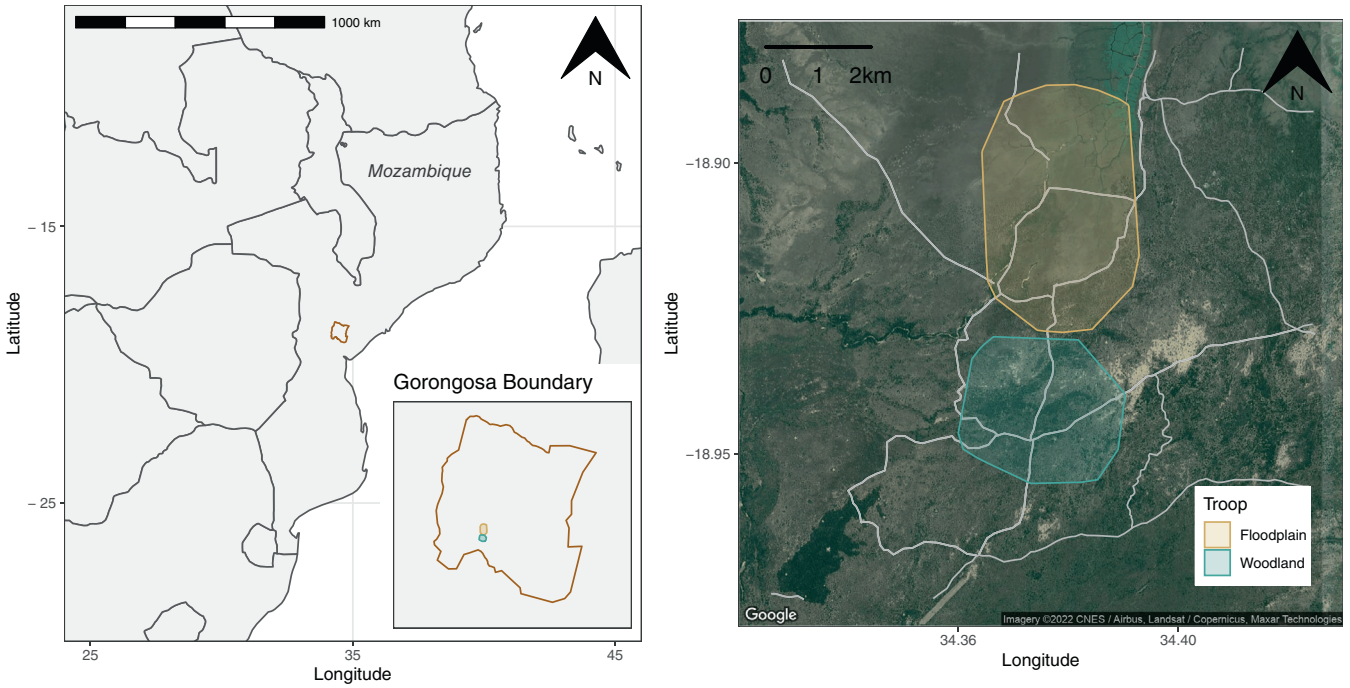


FIGURE 2 Map showing the location of Gorongosa National Park in Mozambique (left) with home ranges of the two focal troops highlighted within the park (inset) and shown as 95% minimum convex polygons overlaid upon roads (gray lines) and satellite imagery of vegetation within the park (right)

TABLE 1 Results of likelihood ratio tests for GLMs modeling (A) vocalization (i) probability and (ii) rates, and (B) observer-directed vigilance probability over habituation time, and across troops, habitat types, and times of day.

	(A) Vocalization models				(B) Vigilance model	
	(i) Binomial		(ii) Gamma		Binomial	
	LRT	*p*	AIC scaled dev.	*p*	LRT	*p*
Day Number	65.97	< 0.001***	128.13	< 0.001***	680.70	< 0.001***
Troop	412.30	< 0.001***	7.34	0.01**	540.12	< 0.001***
Diel	21.18	< 0.001***	9.93	0.01**	27.30	< 0.001***
Habitat*Cover	8.31	0.02*	1.14	0.57	52.51	< 0.001***

Note: Asterisks indicate statistical significance of *p*-values (* = < 0.05, ** = < 0.01, *** = < 0.001).

2.4.2 | Observer-directed vigilance

We used a binomial GLM with a logit link function to model the occurrence of observer-directed vigilance over habituation time. As described above, this was coded as a binary variable, with individuals classified as "looking directly at the observer during scan" (1), or "not looking directly at the observer during scan" (0).

2.4.3 | Terrestriality models

Using the response variables from the models described above, we ran binomial GLMs with logit link functions to model the effects of (a) vocalization rates and (b) the likelihood of observer-directed vigilance, on occurrence of terrestrial behavior. Terrestriality was coded as a binary variable at the individual level; "terrestrial" (1) or "not terrestrial" (0).

2.4.4 | Fixed effects

To account for potential intertroop differences, we included "Troop" as a fixed variable in all models described above. We also included time of day ("Diel"), habitat type ("Habitat"), and height of ground cover ("Cover") as fixed explanatory variables, with an interaction between Habitat and Cover as both are vegetation features. All were chosen for their ecological significance in mediating anti-predator responses.

2.5 | Ethical note

This work was carried out with ethical clearance from Oxford University (APA/1/5/ACER/23Jan2018) and from the Ministry of Tourism and the Gorongosa Restoration Project in Mozambique (permit numbers PNG/DSCi/C114/2018 and PNG/DSCi/C93/2018). All data

TABLE 2 Results from GLMs showing the effects of habituation time and fixed variables on (A) (i) Probability of vocalizations, (ii) rates of vocalizations, and (B) probability of observer-directed vigilance by baboons

GLM	Estimate	Std. error	*p*
(A-i) Vocalizations: Binomial			
(Intercept)	1.81	0.17	< 0.001***
Day Number	−0.01	0.00	< 0.001***
Troop: Floodplain	−2.62	0.14	< 0.001***
Diel: MID	−0.18	0.12	0.13
Diel: PM	0.30	0.13	0.02*
Habitat: Open	−0.75	0.15	< 0.001***
Habitat: Water	−0.18	0.14	0.19
Cover: High	0.41	0.14	< 0.003**
Habitat: Open*Cover: High	0.73	0.25	< 0.004**
Habitat: Water*Cover: High	0.15	0.39	0.70
(A-ii) Vocalizations: Gamma			
(Intercept)	1.12	0.11	< 0.001***
Day Number	−0.01	0.00	< 0.001***
Troop: Floodplain	−0.34	0.12	< 0.001***
Diel: MID	−0.15	0.09	0.09
Diel: PM	0.08	0.09	0.37
Habitat: Open	0.00	0.12	0.98
Habitat: Water	0.18	0.10	0.07
Cover: High	0.06	0.09	0.53
Habitat: Open*Cover: High	0.17	0.21	0.42
Habitat: Water*Cover: High	−0.23	0.38	0.54
(B) Vigilance			
(Intercept)	0.01	0.09	0.93
Day Number	−0.03	0.00	< 0.001***
Troop: Floodplain	−1.82	0.08	< 0.001***
Diel: MID	−0.06	0.07	0.35
Diel: PM	0.24	0.07	< 0.001***
Habitat: Open	−0.76	0.09	< 0.001***
Habitat: Water	−0.64	0.07	< 0.001***
Cover: High	0.23	0.08	0.004**
Habitat: Open*Cover: High	−0.56	0.21	0.01**
Habitat: Water*Cover: High	1.46	0.21	< 0.001***

Note: Asterisks indicate statistical significance of *p*-values (* = < 0.05, ** = < 0.01, *** = < 0.001).

collection was observational in the troops' natural habitats and researchers did not come into contact with any of the animals.

3 | RESULTS

Between April and November 2018, WT was followed for a total of 921 h, distributed over 106 full follow days (average length: 8.64 h) and 14 partial follow days (<6 h). FT was followed for a total of 576.5 h, distributed over 63 full follow days (average length: 7.98 h) and 22 partial follow days. The mean break between follows was 2.47 days for WT (range: 1–19 days) and 3.26 days for FT (range: 1–29 days). WT ranged within a total area of 8.7 km^2, predominantly in areas habitats with high tree coverage (72% of scans were conducted in habitats with more than 10% tree coverage, 9% in areas with less than 10% tree coverage, and 19% at major water sources). FT ranged within a total of 15.6 km^2, predominantly within open habitats (67% of scans were conducted in habitats with less than 10% tree coverage, 24% in habitats with more than 10% tree coverage, and 9% at major water sources). It should be noted that FT significantly shifted their ranging patterns halfway through the field season, accounting for the greater overall size of their range. The reasons for this shift are currently under investigation. The troops' home ranges are shown in Figure 2.

3.1 | Vocalizations and vigilance models

Likelihood Ratio Tests provide very strong evidence that Habituation time (Day Number) was a significant predictor of both the probability and rate of vocalizations, and of the probability of observer-directed vigilance during this study. Of the fixed variables, there is strong evidence that Troop and Diel affected response variables across all three models, and that an interaction between the vegetation variables Habitat and Cover affected the probability of vocalizations and vigilance, but not the rate of vocalizations. These results are summarized in Table 1.

3.1.1 | Results from vocalization hurdle model

The results from the vocalization hurdle model, listed in Table 2, provide very strong evidence that both the probability and rate of vocalizations during scans decreased over habituation time, and were significantly lower in FT than WT. The binomial model results (Table 2A-i demonstrate that vocalizations were more likely to occur later in the afternoon (PM) than at any other time of day and were less likely in habitats with less than 10% tree coverage than the other two habitat types. High ground cover increased the likelihood of vocalizations occurring, particularly in habitats with less than 10% tree coverage. The gamma model results (Table 2A-ii show that vocalization rates decreased significantly over habituation time and were consistently lower in FT, but there is no evidence that any of the other fixed effects influenced vocalization rates. Vocalization data and results from the hurdle model are plotted in Figure 3.

3.1.2 | Results from observer-directed vigilance model

The vigilance model results, also listed in Table 2 (model B), demonstrate very strong evidence that the probability of observer-directed

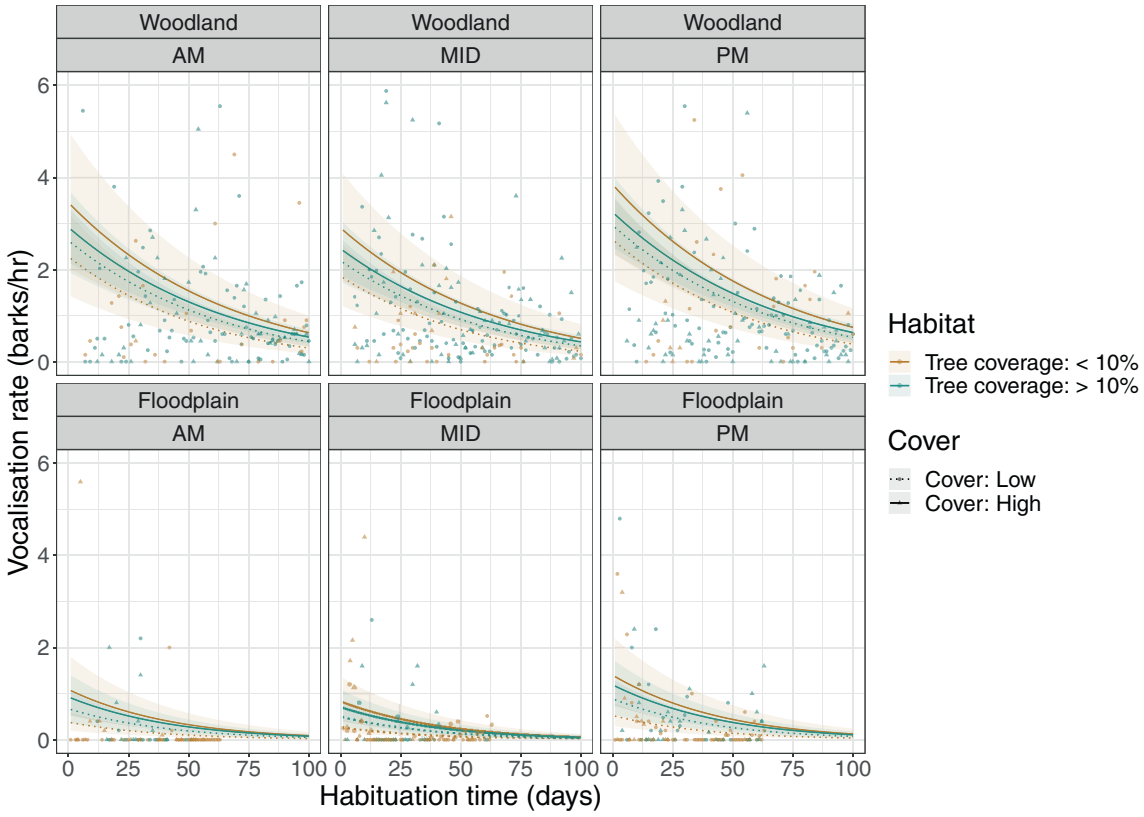


FIGURE 3 Changes in baboon vocalization rates over habituation time (measured in number of full day follows) for the woodland troop (top row) and floodplain troop (bottom row), grouped by time of day. Habitat types are differentiated by color, and ground cover by differently shaped data points and line types.

vigilance occurring during a scan decreased over habituation time and, as with vocalizations, was lower in FT than WT. The results provide strong evidence that observer-directed vigilance was more likely to occur in the late afternoon and in habitats with more than 10% tree coverage than the other two habitat types. High ground cover increased the likelihood of observer-directed vigilance. An interaction effect between habitat variables suggests that vigilance was most likely at water sources with high ground cover, and least likely in habitats with less than 10% tree coverage but high ground cover, compared to other habitat combinations. Vigilance data and results from this model are plotted in Figure 4.

3.2 | Terrestriality models

Table 3 summarizes the results from two GLMs, run with (A) vocalization rate and (B) likelihood of observer-directed vigilance as predictors of terrestriality. Both higher vocalization rates and levels of observer-directed vigilance predict a lower likelihood of baboons being on the ground during a scan. Inclusion of fixed variables in the models highlights that FT was more terrestrial than WT, that terrestriality was highest in late afternoon, and that baboons were more terrestrial in habitats with less than 10% tree coverage and at water sources than in habitats with more than 10% tree coverage. High ground cover significantly reduced terrestriality, particularly at water sources and areas with less than 10% tree coverage.

4 | DISCUSSION

We modeled the change in vocalization rates and levels of observer-directed vigilance over several months of habituation of two troops of chacma baboons, demonstrating that both measures declined with cumulative exposure to observers. Both measures also varied predictably by troop, time of day, the openness of the environment and ground cover. Both vocalization rates and observer-directed vigilance had a negative relationship with the likelihood of ground-use by the baboons.

Such models can be used to explore whether, or when, habituation achieves its purpose of allowing focal animals to treat observers as neutral stimuli in their environment. For example, based on daily means from our study, the likelihood of observer-directed vigilance dropped below 5% after 95 days in WT and after 44 days in FT. Although this threshold is somewhat arbitrary, recording and reporting such measures provides a standardized method for accounting for observer presence. By measuring the extent to which observers might be interfering with focal animals' normal activity patterns these indicators can be incorporated into analyses of behavioral data collected from different stages of habituation and from different study troops or sites. Such measurements could also serve as a reminder that observers might never be neutral features in study animals' environments. The growing use of remote sensing tools such as camera traps and activity loggers will shed light on the extent to which animals considered habituated to human observers are exhibiting "natural" behaviors.

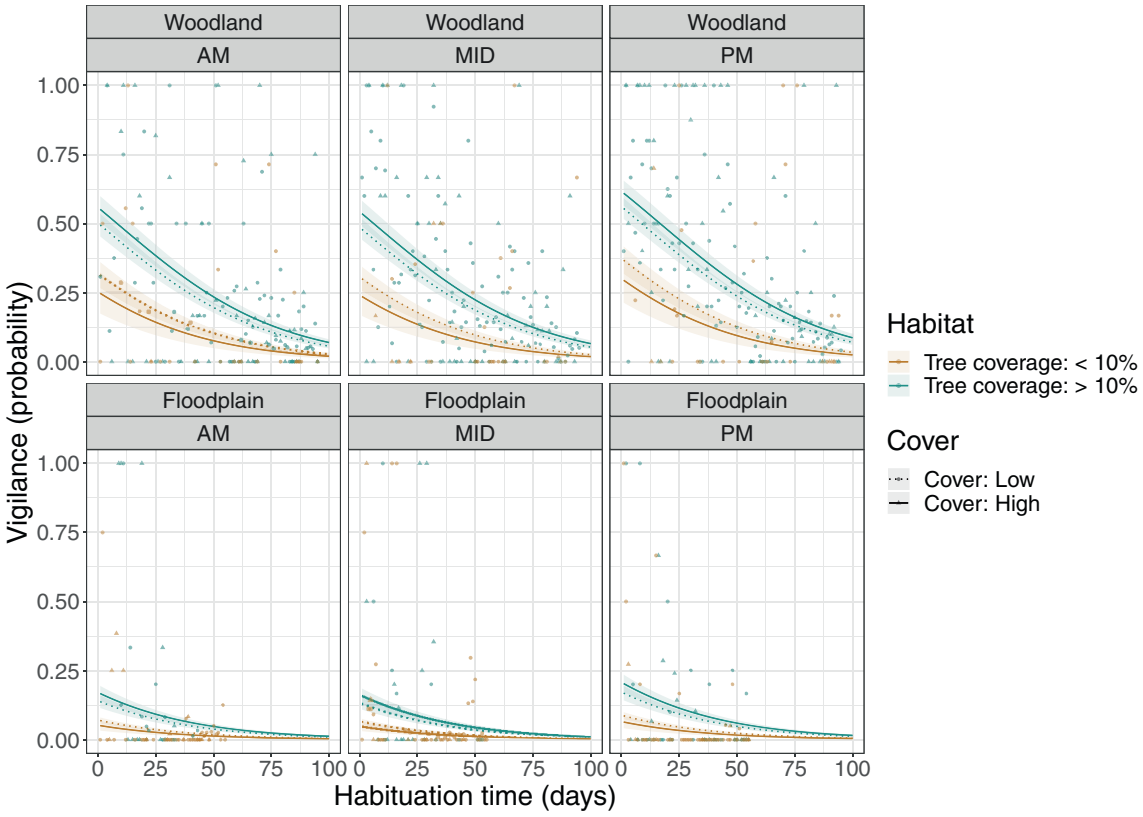


FIGURE 4 Changes in the probability of observer-directed vigilance over habituation time (measured in number of full day follows) for the woodland troop (top row) and floodplain troop (bottom row), grouped by time of day. Habitat types are differentiated by color, and ground cover by differently shaped data points and line types.

Our results also highlight that, even between the two troops in this study, habituation appears to have occurred at quite different rates; both vocalization rates and observer-directed vigilance were consistently lower in FT than WT throughout the study. There are several factors that might be at play here. WT is double the size of FT and it might have taken longer for all individuals in the bigger troop to be exposed to the observers. Furthermore, this study does not account for individual differences in tolerance to humans or risk, which could account for different rates of habituation both within and between troops (Allan et al., 2020). Alternatively, or additionally, difference in vocalizations and vigilance across the troops might reflect how habitat features in their respective home ranges influence their perceived risk of observers. Our results suggest that lower visibility in the predominantly closed habitats of WT increased antipredator behaviors in response to humans amongst these woodland-dwelling baboons compared to those ranging on the floodplain.

This pattern is also reflected within the home range of each troop, with both vocalizations and vigilance more likely to occur in areas where vegetation structure—greater tree density or taller ground cover—reduces visibility. Compared with other vegetation combinations, areas with tree density less than 10% but high ground cover predicted a greater likelihood of vocalizations but lower levels of vigilance, perhaps highlighting how vegetation structure determines the most appropriate responses to perceived risk. When available, trees might serve as lookout points from which to detect and be vigilant of risk, but when they are unavailable, vocalizations might be used to alert others to risk or to prevent separation of the troop in areas of high ground cover (Byrne, 1981).

Our results show that temporal as well as spatial factors mediate risk responses. Across habitat types, baboon vocalizations and vigilance were more likely in the late afternoon than earlier in the day, suggesting that the perceived risk of observers was heightened at this time of day. This might signal an adaptation to avoiding risk from predominantly nocturnal predators. The extant carnivore guild (with the exception of cheetahs) hunt most successfully at night and in crepuscular hours (Treves & Palmqvist, 2007), and many baboon predation events occur at their sleeping sites, to which they would be traveling in the late afternoon (Cowlishaw, 1994; Isbell et al., 2018). The reduction of visibility in twilight hours might also contribute to increases in vocalizations and vigilance towards the end of the day.

It should also be noted that some of the vocalizations recorded in our "bark" sample might in fact have been contact calls rather than alarm barks, as these two types of vocalization are not always clearly distinguishable (Fischer et al., 2001). Whilst we attribute the clear decline in bark rates over habituation time to a reduction in baboons' perceived risk of researcher presence, it is possible that the influence of both habitat type and time of day on vocalization rates might be capturing some effects of those variables on contact calls. For

TABLE 3 Results from GLMs using (A) vocalization rate, and (B) the likelihood of observer-directed vigilance as predictors for the occurrence of terrestrial behavior in baboons during habituation

GLM	Estimate	Std. error	*p* Value
(A) Vocalization rate as predictor			
(Intercept)	0.68	0.06	<0.001***
Vocalization rate	−0.17	0.05	<0.001***
Troop: Floodplain	0.66	0.07	<0.001***
Diel: MID	−0.01	0.05	0.88
Diel: PM	0.43	0.06	<0.001***
Habitat: Open	2.21	0.09	<0.001***
Habitat: Water	2.00	0.06	<0.001***
Cover: High	−0.85	0.06	<0.001***
Habitat: Open*Cover: High	−0.72	0.13	<0.001***
Habitat: Water*Cover: High	−2.13	0.17	<0.001***
(B) Vigilance as predictor			
(Intercept)	0.60	0.06	<0.001***
Vigilance	−0.51	0.24	0.03*
Troop: Floodplain	0.72	0.06	<0.001***
Diel: MID	0.01	0.05	0.82
Diel: PM	0.41	0.06	<0.001***
Habitat: Open	2.21	0.09	<0.001***
Habitat: Water	1.96	0.07	<0.001***
Cover: High	−0.87	0.06	<0.001***
Habitat: Open*Cover: High	−0.77	0.13	<0.001***
Habitat: Water*Cover: High	−2.04	0.18	<0.001***

Note: Asterisks indicate statistical significance of *p*-values (* = < 0.05, ** = < 0.01, *** = < 0.001).

example, baboons may need to make contact calls more frequently in closed environments or towards the evening as they congregate at their sleep sites, and this increase in vocalizations might have been recorded in our counts of barks. However, the fact that observer-directed vigilance is similarly influenced by these variables provides an independent source of evidence for the effects of habitat and diel periods on anti-predator behaviors.

Finally, we consider the relationship between antipredator behaviors and terrestriality. Baboons are a highly terrestrial species but—like most primates—rely on trees for refuge, for example by seeking out trees and cliffs as sleeping sites. Threat from large mammalian carnivores (or perceived threat from human observers) might therefore reduce baboons' time spent on the ground. Terrestriality is of course inextricably linked to habitat structure, and this is clear in the results from our analyses. The Floodplain Troop were found to be significantly more terrestrial than the Woodland Troop, and within each troop's home range the baboons were more likely to be on the ground in areas with minimal tree coverage and lower ground cover. They were also found to be more terrestrial in the late afternoon. This might be explained by baboons' tendency to forage for depletable resources, such as arboreal fruits, in the morning before feeding on less desirable but more abundant foods, such as seeds and grasses, later in the day (Noser & Byrne, 2007).

Beyond these predictable effects of habitat structure and possible consequences of daily routine, our analyses demonstrate that higher levels of antipredator behaviors—vocalizations and vigilance—predict lower occurrence of terrestriality in baboons. These results have implications for the study of both extant and extinct primate species. First, they imply that researchers may perceive a study group to be more arboreal than they really are before the effects of observer-induced fear wear off. And at the other extreme, when primates are well-habituated and observer presence keeps carnivores at bay, this shift in the landscape of fear might inflate the time focal primates spend on the ground. This again questions whether researchers can ever be considered neutral stimuli in their study animals' environments and emphasizes the need for incorporating quantified effects of observer-presence into behavioral studies.

The second set of implications of these results concerns the evolution of terrestriality in certain primate species, including baboons and humans. Although it is common for primates to occasionally come to the ground, particularly during travel, very few non-human species are considered terrestrial or even semiterrestrial (Galán-Acedo et al., 2019). Modern humans are unique among primates in both their obligate terrestriality and bipedalism. There has been more focus on the evolution of bipedality than terrestriality in our lineage, but their origins are not necessarily linked (Harcourt-Smith, 2010; Richmond et al., 2001).

Broad shifts in habitat structure from closed to more open environments have often been postulated as the primary driver of increasingly terrestrial adaptations in hominins and other African terrestrial primates (Dart, 1925, 1949; Harcourt-Smith, 2010; Jablonski, 2005; Senut et al., 2018). In the case of hominins, this "Savannah Hypothesis" has become more nuanced as evidence has emerged that the earliest hominins inhabited areas with relatively high tree coverage (Bobe et al., 2020; White et al., 2009) and that adaptations to arboreality are retained in species of the *Australopithecus*, *Paranthropus*, and *Homo* lineages (Dunmore et al., 2020; Feuerriegel et al., 2017; Richmond et al., 2020; Ruff, 2009; Stern & Susman, 1983; Ward, 2002). Some researchers have suggested that modern human locomotion emerged in a series of distinct shifts from "occasional" to "facultative," and then to "obligate" terrestrial bipedalism, each occurring in different ecological contexts and therefore influenced by separate selective forces (Harcourt-Smith, 2010; Jablonski, 2005). Our study indicates that the landscape of fear should be considered amongst such forces. Alongside changing habitat structure, turnovers in the African carnivore guild would have altered the amount and distribution of risk across certain habitats, particularly as the abundance and diversity of carnivores declined from the Pliocene to the modern day (Treves & Palmqvist, 2007). Our results indicate that reduced risk from terrestrial predators and a consequent rise in time spent on the ground might have helped drive terrestrial traits to fixation in African terrestrial primates, including hominins.

5 | CONCLUSION

In this study, we recorded chacma baboons' vocalizations and observer-directed vigilance over several months to monitor changes in the frequency of their anti-predator responses to humans during habituation, and possible effects on their terrestriality. Our results suggest that vegetation structures which reduce visibility increase perceived risk, and that baboons experience heightened perception of risk later in the day, which might be an adaptive response to avoiding predominantly nocturnal predators. Our results also indicate that, across habitats and times of day, higher levels of antipredator behaviors predict lower chances of baboons spending time on the ground, suggesting that perceived risk reduces terrestriality in baboons. A better understanding of the extent to which substrate-use is determined by risk perception will be significant for incorporating the effects of human presence into studies of primate behavior, and for understanding the origins and evolution of terrestriality – a rare trait amongst primates.

AUTHOR CONTRIBUTIONS

Philippa Hammond: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (equal); methodology (equal); project administration (equal); visualization (lead); writing – original draft (lead). **Lynn Lewis-Bevan:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); software (equal); writing – review and editing (supporting). **Dora Biro:** Conceptualization (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); supervision (equal); writing – review and editing (supporting). **Susana Carvalho:** Conceptualization (supporting); formal analysis (supporting); investigation (supporting); methodology (supporting); project administration (equal); resources (equal); supervision (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data collected and analyzed for this study are available from the corresponding author upon reasonable request.

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REFERENCES

Allan, A., Bailey, A., & Hill, R. (2020). Habituation is not neutral or equal: Individual differences in tolerance suggest an overlooked personality trait. *Science. Advances*, *6*(28), eaaz0870. https://doi.org/10.1126/sciadv.aaz0870

Allan, A., & Hill, R. (2018). What have we been looking at? A call for consistency in studies of primate vigilance. *American Journal of Physical Anthropology*, *165*, 4–22. https://doi.org/10.1002/ajpa.23381

Altmann, S., & Altmann, J. (1970). *Baboon ecology: African field research*. University of Chicago Press. https://scholar.google.com/scholar?hl=

en&as_sdt=0%2C5&q=altmann+and+altmann+1970+baboon+ecology&btnG=#d=gs_cit&p=&u=%2Fscholar%3Fq%3Dinfo%3AANY_WMFx32EJ%3Ascholar.google.com%2F%26output%3Dcite%26scirp%3D0%26hl%3Den

Atkins, J., Long, R., Pansu, J., Daskin, J., Potter, A., Stalmans, M. E., Tarnita, C. E., & Pringle, R. (2019). Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science*, *364*, 173–177. https://doi.org/10.1126/science.1205106

Atuo, F. A., & O'Connell, T. J. (2017). The landscape of fear as an emergent property of heterogeneity: Contrasting patterns of predation risk in grassland ecosystems. *Ecology and Evolution*, *7*(13), 4782–4793. https://doi.org/10.1002/ece3.3021

Barton, R. A., & Whiten, A. (1993). Feeding competition among female olive baboons. *Papio anubis*. *Animal Behaviour*, *46*(4), 777–789. https://doi.org/10.1006/anbe.1993.1255

Bobe, R., Manthi, F. K., Ward, C. V., Plavcan, J. M., & Carvalho, S. (2020). The ecology of Australopithecus anamensis in the early Pliocene of Kanapoi. *Kenya*. *Journal of Human Evolution*, *140*, 102717. https://doi.org/10.1016/j.jhevol.2019.102717

Bouley, P., Poulos, M., Branco, R., & Carter, N. H. (2018). Post-war recovery of the African lion in response to large-scale ecosystem restoration. *Biological Conservation*, *227*, 233–242. https://doi.org/10.1016/J.BIOCON.2018.08.024

Byrne, R. (1981). Distance vocalisations of Guinea baboons (Papio papio) in Senegal: An analysis of function. *Behaviour*, *78*(3–4), 283–312. https://brill.com/view/journals/beh/78/3-4/article-p283_7.xml

Campbell, C. J., Aureli, F., Chapman, C. A., Peninsula, R.-F. P., de Yucatan, G., Matthews, K., & Behavior, T. (2005). Terrestrial Behavior of Ateles spp. *International Journal of Primatology*, *26*(5), 1039–1051. https://doi.org/10.1007/s10764-005-6457-1

Coleman, B. T., & Hill, R. A. (2014). Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour*, *88*, 165–173. https://doi.org/10.1016/j.anbehav.2013.11.027

Cowlishaw, G. (1994). Vulnerability to predation in baboon populations. *Behaviour*, *131*(3), 293–304. https://doi.org/10.1163/156853994X00488

Cowlishaw, G. (1997a). Alarm calling and implications for risk perception in a desert baboon population. *Ethology*, *103*(5), 384–394. https://doi.org/10.1111/j.1439-0310.1997.tb00154.x

Cowlishaw, G. (1997b). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, *53*(4), 667–686. https://www.sciencedirect.com/science/article/pii/S0003347296902985

Dart, R. (1925). Australopithecus africanus the man-ape of South Africa. *Nature*, *115*(2884), 195–199. https://doi.org/10.1038/115195a0

Dart, R. (1949). The predatory implemental technique of Australopithecus. *American Journal of Physical Anthropology*, *7*(1), 1–38. https://doi.org/10.1002/AJPA.1330070103

Daskin, J. H., Stalmans, M., & Pringle, R. M. (2016). Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *Journal of Ecology*, *104*(1), 79–89. https://doi.org/10.1111/1365-2745.12483

Dunmore, C. J., Skinner, M. M., Bardo, A., Berger, L. R., Hublin, J.-J., Pahr, D. H., Rosas, A., Stephens, N. B., & Kivell, T. L. (2020). The position of Australopithecus sediba within fossil hominin hand use diversity. *Nature Ecology & Evolution*, *1–8*, 911–918. https://doi.org/10.1038/s41559-020-1207-5

Enstam, K., & Isbell, L. (2002). Comparison of responses to alarm calls by patas (Erythrocebus patas) and vervet (Cercopithecus aethiops) monkeys in relation to habitat structure. *American Journal of Physical Anthropology*, *119*(1), 3–14. https://doi.org/10.1002/ajpa.10104

Enstam, K., & Isbell, L. (2004). Microhabitat preference and vertical use of space by Patas monkeys (Erythrocebus patas) in relation to predation risk and habitat structure. *Folia Primatologica*, *75*, 70–84. https://doi.org/10.1159/000076265

Feuerriegel, E. M., Green, D. J., Walker, C. S., Schmid, P., Hawks, J., Berger, L. R., & Churchill, S. E. (2017). The upper limb of homo Naledi. *Journal of Human Evolution*, *104*, 155–173. https://doi.org/10.1016/J.JHEVOL.2016.09.013

Fischer, J., Hammerschmidt, K., Cheney, D. L., & Seyfarth, R. M. (2001). Acoustic features of female Chacma baboon barks. *Ethology*, *107*, 33–54. https://www.eva.mpg.de/documents/Wiley-Blackwell/Fischer_Acoustic_Ethology_2001_1556033.pdf

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1), 1–16. https://www.jstor.org/stable/26271862

Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E., & Arasa-Gisbert, R. (2019). Ecological traits of the world's primates. *Scientific Data*, *6*(1), 55. https://doi.org/10.1038/s41597-019-0059-9

Gaynor, K., Brown, J., Middleton, A., Power, M., & Brashares, J. (2019). Landscapes of fear: Spatial patterns of risk perception and response. *Trends in Ecology and Evolution*, *34*, 355–368. https://www.sciencedirect.com/science/article/pii/S0169534719300199

Gorini, L., Linnell, J. D. C., May, R., Panzacchi, M., Boitani, L., Odden, M., & Nilsen, Erlend. B. (2011). Habitat heterogeneity and mammalian predator-prey interactions. *Mammal Review*, *42*(1), 55–77. https://doi.org/10.1111/j.1365-2907.2011.00189.x

Harcourt-Smith, W. (2010). The first hominins and the origins of bipedalism. *Evolution: Education and Outreach*, *3*(3), 333–340. https://doi.org/10.1007/s12052-010-0257-6

Hill, R. A., & Weingrill, T. (2007). Predation risk and habitat use in Chacma baboons (Papio hamadryas ursinus). In *Primate anti-predator strategies* (pp. 339–354). Springer. https://doi.org/10.1007/978-0-387-34810-0_16

Isbell, L., Bidner, L., Van Cleave, E., Matsumoto-Oda, A., & Crofoot, M. (2018). GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. *Journal of Human Evolution*, *118*, 1–13. https://www.sciencedirect.com/science/article/pii/S0047248417304657

Isbell, L., & Young, T. (1993). Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Animal Behaviour*, *45*, 1233–1235. https://psycnet.apa.org/record/1993-44299-001

Jablonski, N. (2005). *The Rise and Fall of a Primate Genus*. Cambridge University Press.

Jack, K. M., Lenz, B. B., Healan, E., Rudman, S., Schoof, V. A. M., & Fedigan, L. (2008). The effects of observer presence on the behavior ofCebus capucinus in Costa Rica. *American Journal of Primatology*, *70*(5), 490–494. https://doi.org/10.1002/ajp.20512

Jaffe, K. E., & Isbell, L. (2009). After the fire: Benefits of reduced ground cover for Vervet monkeys (Cercopithecus aethiops). *American Journal of Primatology*, *71*, 252–260. https://doi.org/10.1002/ajp.20644

Johns, B. G. (1996). Responses of chimpanzees to habituation and tourism in the Kibale Forest. *Uganda*. *Biological Conservation*, *78*(3), 257–262. https://doi.org/10.1016/S0006-3207(96)00044-4

Kahle, D., & Wickham, H. (2013). Ggmap: Spatial visualization with ggplot2. *The R Journal*., *5(1)*, *144*.

Kummer, H. (Hans). (1997). *In quest of the sacred baboon: A scientist's journey*. Princeton University Press. https://books.google.co.uk/books?hl=en&lr=&id=A6w69c2y1MIC&oi=fnd&pg=PR11&dq=Kummer,+H.+(1995).+In+Quest+of+the+Sacred+Baboon.+Princeton,+NJ:+Princeton+University+Press.&ots=jpCbIMh_Y0&sig=MOyDaitI3QcW0L33nSqy2dl51qw&redir_esc=y#v=onepage&q&f=false

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, *79*(8), 1401–1409. https://doi.org/10.1139/z01-094

Lima, S. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, *48*(1), 25–34. https://www.jstor.org/stable/1313225

McLennan, M. R., & Hill, C. M. (2010). Chimpanzee responses to researchers in a disturbed forest-farm mosaic at Bulindi, western

Uganda. *American Journal of Primatology*, *72*(10), 907–918. https://doi.org/10.1002/ajp.20839

Mourthé, Í. M. C., Guedes, D., Fidelis, J., Boubli, J. P., Mendes, S. L., & Strier, K. B. (2007). Ground use by northern muriquis (Brachyteles hypoxanthus). *American Journal of Primatology*, *69*(6), 706–712. https://doi.org/10.1002/ajp.20405

Noser, R., & Byrne, R. W. (2007). Travel routes and planning of visits to out-of-sight resources in wild chacma baboons. *Papio ursinus*. *Animal Behaviour*, *73*(2), 257–266. https://doi.org/10.1016/J.ANBEHAV.2006.04.012

Nowak, K., le Roux, A., Richards, S. A., Scheijen, C. P. J., & Hill, R. A. (2014). Human observers impact habituated samango monkeys' perceived landscape of fear. *Behavioral Ecology*, *25*(5), 1199–1204. https://doi.org/10.1093/beheco/aru110

Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *R Journal*, *10*(1), 439–446. https://doi.org/10.32614/RJ-2018-009

R Core Team. (2020). *R: A language and environment for statistical computing*. Foundation for Statistical Computing. https://www.r-project.org/

Rasmussen, D. R. (1983). Correlates of patterns of range use of a troop of yellow baboons (Papio cynocephalus). II. Spatial structure, cover density, food gathering, and individual behaviour patterns. *Animal Behaviour*, *31*(3), 834–856. https://doi.org/10.1016/S0003-3472(83)80240-1

Richmond, B., Begun, D., & Strait, D. (2001). Origin of human bipedalism: The knuckle-walking hypothesis revisited. *American Journal of Physical Anthropology*, *116*(S33), 70–105. https://doi.org/10.1002/ajpa.10019

Richmond, B., Green, D., Lague, M., Chirchir, H., Behrensmeyer, A., Bobe, R., Bamford, M. K., Griffin, N. L., Gunz, P., Mbua, E., Merritt, S. R., Pobiner, B., Kiura, P., Kibunjia, M., Harris, J. W. K., & Braun, D. R. (2020). The upper limb of Paranthropus boisei from Ileret, Kenya. *Journal of Human Evolution*, *141*, 102727. https://doi.org/10.1016/j.jhevol.2019.102727

Ruff, C. (2009). Relative limb strength and locomotion in Homo habilis. *American Journal of Physical Anthropology*, *138*(1), 90–100. https://doi.org/10.1002/AJPA.20907

Samuni, L., Mundry, R., Terkel, J., Zuberbühler, K., & Hobaiter, C. (2014). Socially learned habituation to human observers in wild chimpanzees. *Animal Cognition*, *17*(4), 997–1005. https://doi.org/10.1007/s10071-014-0731-6

Schaller, G. (1962). *The ecology and Behavior of the mountain gorilla*. University of Wisconsin.

Senut, B., Pickford, M., Gommery, D., & Ségalen, L. (2018). Palaeoenvironments and the origin of hominid bipedalism. *Historical Biology*, *30*(2), 284–296. https://doi.org/10.1080/08912963.2017.1286337

Souza-Alves, J. P., Mourthe, I., Hilário, R. R., Bicca-Marques, J. C., Rehg, J., Gestich, C. C., Acero-Murcia, A. C., Adret, P., Aquino, R., Berthet, M., Bowler, M., Calouro, A. M., Canale, G. R., Cardoso, N. d. A., Caselli, C. B., Cäsar, C., Chagas, R. R. D., Clyvia, A., Corsini, C. F., … Barnett, A. A. (2019). Terrestrial Behavior in Titi monkeys (Callicebus, Cheracebus, and Plecturocebus): Potential correlates, patterns, and differences between genera. *International Journal of Primatology*, *40*(4–5), 553–572. https://doi.org/10.1007/s10764-019-00105-x

Stalmans, M., & Beilfuss, R. (2008). *Landscapes of the Gorongosa National Park*. Report prepared for Gorongosa Research Centre, Gorongosa National Park.

Stalmans, M., Peel, M., & Gonçalves, D. (2018). *2018*. Aerial wildlife count of the Parque Nacional da Gorongosa. https://gorongosa.org/wp-content/uploads/2020/08/gorongosaaerialwildlifecount2018_report_december2018.pdf

Stern, J. T., & Susman, R. L. (1983). The locomotor anatomy of Australopithecus afarensis. *American Journal of Physical Anthropology*, *60*(3), 279–317. https://doi.org/10.1002/AJPA.1330600302

Tinley, K. L. (1977). *Framework of the Gorongosa ecosystem*. DSc thesis, University of Pretoria, Pretoria. http://hdl.handle.net/2263/24526.

Treves, A., & Palmqvist, P. (2007). Reconstructing hominin interactions with mammalian carnivores (6.0–1.8 ma). In *Primate Anti-Predator Strategies* (pp. 355–381). Springer US. https://doi.org/10.1007/978-0-387-34810-0_17

Tutin, C. E. G., & Fernandez, M. (1991). Responses of wild chimpanzees and gorillas to the arrival of primatologists: Behaviour observed during habituation. In *Primate responses to environmental change* (pp. 187–197). Springer Netherlands. https://doi.org/10.1007/978-94-011-3110-0_10

van Schaik, C. P., van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in sumatran forest primates. *Primates*, *24*(2), 211–221. https://doi.org/10.1007/BF02381083

Ward, C. (2002). Interpreting the posture and locomotion of Australopithecus afarensis: Where do we stand? *American Journal of Physical Anthropology*, *119*(S35), 185–215. https://doi.org/10.1002/AJPA.10185

White, T., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C., Suwa, G., & WoldeGabriel, G. (2009). Ardipithecus ramidus and the paleobiology of early hominids. *Science*, *326*(5496), 64–86. http://science.sciencemag.org/content/326/5949/64.short

Wickham, H. (2009). *ggplot2*. Springer. https://doi.org/10.1007/978-0-387-98141-3

Williamson, E., & Feistner, A. (2003). *Habituating primates: Processes, techniques, variables and ethics. Field and laboratory methods in primatology: A practical guide*. Cambridge University Press (pp. 23–59). https://books.google.com/books?hl=en&lr=&id=9VsYBdd8KCYC&oi=fnd&pg=PA25&dq=Habituating+primates:+processes,+techniques,+variables+and+ethics+ELIZABETH+A.+WILLIAMSON1+AND+ANNA+T.+C.+FEISTNER+2&ots=5KCzsbFDek&sig=BKTF9CtbZBOVuYTMVYiFMUqzT3o

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