TAWIRI project proposal

Habitat Use in Issa Chimpanzees: Does perceived risk influence behaviour?

Introduction

The way animals use space is a fundamental aspect of animal spatial ecology. Gaining insight into animal spatial utilisation facilitates a deeper understanding of their social structure and ranging patterns (Willems and Hill, 2009) and has important implications for species interactions and conservation efforts (Pearce et al., 2013). Factors such as resource distribution, predation risk and the potential for encountering hostile neighbours (Willems and Hill, 2009) contribute to the creation of a "landscape of fear" (LoF), resulting in variations in spatial distribution and behavioural patterns. In primates, peripheral areas within their home range that are likely to present encounters with neighbouring groups are generally underutilised, suggesting individuals perceive these areas to be risky (Wrangham, 2007). The ability to assess environmental risks is crucial for primates in determining the safest and most suitable locations for survival (Willems and Hill, 2009). In chimpanzees (*Pan troglodytes schweinfurthii*), where the likelihood of lethal and aggressive intergroup encounters is significant, the risks associated with these peripheral regions of the home range are heightened (Wilson et al., 2007) and have vital effects on behaviour and ecology. Yet, despite more than 400 combined years of study, there has only been a single study of LoF in chimpanzees and any other ape for that matter.

Literature review

Studies investigating how animals use space have primarily focused on how predation risk influences spatial range use. This has contributed to the development of a LoF framework, which posits that animals learn about spatiotemporal variation in risk through predator presence. Their learned fear shaped behavioural decisions about when and where to engage in specific activites (e.g., resting, aggregations, etc.) with individuals modifying behaviours in response to perceived predation risk (Laundré et al., 2010). Primates are an optimal study taxon for examining these dynamics, as most live in multi-predator environments and have evolved distinct behavioural responses to various predators (Cheney et al., 1987). For example, vervet monkeys (*Chlorocebus pygerythrus*) avoid certain areas where they perceived threats from baboons and leopards (Willems and Hill, 2009). Similarly, spatial variation in predation risk from eagles was a key driver of range use in samango monkeys (*Cercopithecus mitis albogularis*), with individuals selecting higher trees and greater understory visibility (Coleman and Hill, 2014).

Although the LoF framework is well established in predator-primate studies, it has rarely been applied to intergroup encounters, despite their potential to create spatial heterogeneity in risk landscapes (Willems & Hill, 2009). Additionally, most research has focused on a limited number of species, with only one study on apes (see Wilson et al., 2007). Existing research on intergroup encounters primarily examines face-to-face contests and responses to immediate, brief signalling behaviours, leaving a gap in our understanding of how competition from conspecific neighbours influences space use—particularly in primate groups with permanent home ranges (Abrahms et al., 2017). Nearly all primate species exhibit intergroup encounters, and thus, they are not predicted to use home ranges uniformly or randomly, but rather, will adjust their space use to avoid encountering neighbouring groups and conflict (Benadi et al., 2008). Mechanistic home range analysis provides strong evidence for the role of intergroup

interactions in shaping spatial behaviour, demonstrating that indirect interactions significantly influence the use of home range boundaries (Moorcroft et al., 2006). The ability of interaction-based models to accurately represent individual home range configurations underscores the significance of interactions in governing spatial patterns (Ellison et al., 2020).

Individuals face a trade-off between maximising energy intake and minimising the risks of harm, a concept central to optimal foraging theory. This theory suggests that animals should leave feeding sites earlier when the danger of predation or injury increases (Brown 1988; Gilliam and Fraser, 1987). Additionally, foraging is expected to decrease when the energy obtained no longer offsets the associated risks (Brown, 1988). The quitting harvest rate, therefore, serves as an indicator of perceived environmental danger (Brown, 1999). While substantial research has focused on how prey species alter their foraging in response to risk (Lima 1998; Lima and Dill, 1990), the ways in which perceived threats like intergroup conflict shape foraging behaviours remain unexplored (Emerson et al., 2011).

In primates, the periphery of the home range is underused, for example in spider monkeys (*Atelidae ateles*) (Chapman, 1990), red-tailed monkeys (*Cercopithecus ascanius*) (Lambert, 1990) and chimpanzees (Herbinger et al., 2001). In Phayre's leaf monkeys (*Trachypithecus phayrei*), forest edges and the presence of neighbouring groups significantly affect border use, with individuals spending more time in core areas (Gibson and Koenig, 2011). In contrast, white-faced capuchins (*Cebus imitator*) vocalised more at the periphery, potentially to signal their presence to other groups, but their foraging behaviour in these risky zones remained unchanged, suggesting that resource availability in these areas might outweigh the costs of intergroup encounters (Torrez-Herrera et al., 2020).

The Risk Hypothesis posits that in primate species with a high risk of lethal intergroup encounters, peripheral areas are more likely to be underutilised, as individuals perceive these zones as high risk (Wrangham, 2007). A study of Verreaux's sifaka (*Propithecus verreaux*), a species with moderate to low levels of intergroup threat, showed that the likelihood of encountering neighbours did not significantly influence spatial range use, and activity patterns in core and peripheral areas were similar (Benadi et al., 2008). In chimpanzees, lethal intergroup encounters are common. Intergroup relations among chimpanzees have been extensively studied, with evidence from Ngogo and Kanyawara communities (Kibale, Uganda), revealing that relations between neighbouring chimpanzee communities are antagonistic, with aggression and hostility toward outsiders being part of the evolved behavioural repertoire of chimpanzees (Watts et al., 2006). Chimpanzees have been reported to employ two strategies to reduce the risk of being attacked at border zones. First, they may travel in parties with more males when visiting the periphery (Bauer, 1980). Second, they may refrain from producing loud vocalisations in the periphery to avoid the risk of being detected by hostile, larger-grouped neighbours (Mitani and Watts, 2005). For example, Wilson et al. (2007) found that Kanyawara chimpanzee parties near the periphery consisted of more males, reflecting the need for greater protection in risky areas. However, these parties were not necessarily more silent at the periphery, possibly reflecting the competing demands of avoiding detection by neighbours while signalling territorial ownership (Wilson et al., 2007).

Statement of problem and justification

The influence of intergroup threat on spatial range use in primates has rarely been studied empirically (Benadi et al., 2008) and never in chimpanzees. Most research on chimpanzees focuses on forest-dwelling populations, leaving a significant gap in our understanding of

chimpanzees across the ecological spectrum, including in savannah-woodland environments that characterise their distribution at the periphery (Senegal and western Tanzania) of their distribution. The Issa Valley, one of the driest, most open, and most seasonal habitats inhabited by chimpanzees (Drummond-Clarke et al., 2022) provides a unique opportunity to study ranging behaviour in response to spatial variation in risk. Savanna-mosaic environments like Issa are characterised by lower forest cover and higher ecological heterogeneity compared to forests (van Leeuwen et al., 2020). Issa is home to several large terrestrial predator species with observed encounters with chimpanzees. This, along with the habitat and the presence of neighbouring communities, makes it an ideal location for studying home range dynamics. Chimpanzees living in these landscapes have shown that they show variation in sociality as a result of the 'extreme' environment compared to their forest-dwelling counterparts (Moore, 1996). Understanding how chimpanzees navigate such risks is essential for uncovering behavioural adaptations that may differ from those observed in forested environments (Kalan et al., 2020), increasing our understanding of home range use in territorial species in highly heterogeneous habitats. Furthermore, savanna-mosaic habitats are thought to resemble early hominin environments, offering insights into the pressures that shaped hominin space use behaviour. By examining how chimpanzees at Issa respond to spatial variations in risk, this study aims to enhance our understanding of the species' behavioural diversity and offers insight into adaptations that may have been critical during human evolution.

Objectives

The aim of this study is to investigate whether spatial variation in perceived risk within a savannah-mosaic habitat influences chimpanzee behaviour.

If chimpanzees perceive peripheral areas of the home range to be risky, I hypothesise that:

1. Chimpanzees will spend less time resting (lying/sitting with minimal active engagement) and grooming (mutual or self-grooming) and more time engaging in vigilance behaviours (upright posture, scanning, fixed gaze, head movements) at the periphery of their home range compared to the core.

2. Chimpanzees will exploit food resources less in high-risk peripheral areas than in safer core areas, with shorter feeding durations and lower fruit consumption.

Methodology

Study site

The Issa Valley, located 100 km east of Lake Tanganyika in western Tanzania, is comprised of numerous valleys separated by steep mountains and plateaus, ranging from 900 to 1,800 m above sea level (Drummond-Clarke et al., 2022). Classified as a savannah-mosaic environment, it includes deciduous miombo woodland, swamp, seasonally inundated grasslands, and small riverine and closed forests, covering 7% of the study area (Piel et al., 2017). One of the driest and most seasonal chimpanzee habitats, the annual rain falls entirely over five months from Nov–Apr (van Leeuwen et al., 2020)

Data collection and analyses

This study will focus on a community of 29 wild, fully habituated chimpanzees. The sample will consist of 13 individuals (7 adult males and 6 adult females). The study will incorporate

desk-based analyses of long-term behavioural and GPS data previously collected between 2018-2022, totalling 114349 observations. This dataset includes information on the date, time, focal individual, GPS coordinates, activity budgets and foraged tree species.

Due to the scarcity of intergroup encounter observations (Drummond-Clarke, 2023), the territory periphery will be used as a proxy for increased risk of intergroup encounters. To define these spatial zones, GPS data from the long-term behavioural dataset will be analysed using utilisation distributions using Kernel Density Estimation (KDE) in QGIS (version 3.34.14), this statistical procedure provides a robust technique for range use analyses, estimating the probability of occurrence within the study area based on GPS measurements taken on the centre of mass of the group (Willems and Hill). KDE will be used to generate home range contours with appropriate bandwidth selection (using least-squares cross-validation if possible). Core areas will be defined as the 50% kernel density contour, representing areas of highest use. Peripheral areas will be defined as those falling outside the 50% but within the 95% kernel density contour, excluding rare excursions to avoid inflation of home range estimates. The existing dataset will be used to quantify activity patterns (grooming, resting, vigilance) and feeding behaviours across core and peripheral zones. Fieldwork will be conducted over a 10-week period between May and July 2025 to collect targeted behavioural observations that extend beyond the scope of the existing long-term dataset. The primary aim of this focused data collection period is to validate observed trends and capture seasonal variations and context-specific behaviours related to spatial risk perception among chimpanzees. Randomised focal-individual follows will be used to systematically observe and record chimpanzee behaviour. Focal individuals will be selected randomly each day to minimise sampling bias and ensure a comprehensive dataset. **Instantaneous scan sampling** will be conducted every 1 minute during each focal follow. At each interval, the following behavioural data will be recorded:

- **Resting:** Lying or sitting with minimal active engagement.
- **Grooming:** Mutual or self-grooming, including initiator and recipient information if applicable.
- **Vigilance:** Upright posture, scanning, fixed gaze, and head movements.
- **Feeding:** Duration of feeding events and the number of fruits consumed.

Each focal individual's location will be recorded using a **handheld GPS device** (Garmin). All information will be imported into QGIS.

All data and statistical analyses will be conducted using R Studio (Mac version 4.4.2).

Defining Hypotheses:
H1: Grooming and resting will decrease in the periphery compared to core areas.
H2: Vigilance will increase in the periphery compared to core areas.
H3: Feeding duration will be shorter and less frequent in the periphery compared to core areas

Generalised Linear Mixed Effects Models (GLMMs) will be used to test these hypotheses with core vs. periphery included as a fixed effect and focal individual ID included as a random effect. Moran's I will be included to test for spatial autocorrelation to ensure independence of observations.

Expected outcomes

This study aims to provide novel insights into how intergroup threat influences chimpanzee ranging behaviour, addressing a significant gap in primate socioecology. By applying the landscape of fear (LoF) framework to intergroup interactions, this research will enhance our understanding of how primates navigate social and spatial risks beyond predation. Furthermore, by examining a savanna- woodland population, this research will contribute to the understanding of ecological flexibility in chimpanzees, a species typically studied in forested environments. The data collected and analysed will contribute directly to my master's dissertation at UCL. All findings will be shared with the local government and the Tanzania Wildlife Research Institute (TAWIRI) and Tanzania Commission for Science and Technology (COSTECH). The research project will hopefully lead to the publishing of an academic paper and the presentation of findings at the Primate Society of Great Britain's conference. Furthermore, my time in the field will enable me to develop essential skills in field primatology, including behavioural observation techniques, data collection and analysis.

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