How individuals in a group move: Understanding coordination between individual chimpanzees in a savannah-woodland mosaic habitat

Introduction:

This project aims to understand how individuals move in coordination with each other in a fission fusion society as seen from the chimpanzees of the Issa Valley, Tanzania. This would entail understanding how multiple individuals can move in relation to one another from a distance. In fission fusion societies individuals form subgroups whose compositions are spatiotemporally dependent. The study of this coordination requires investigating the factors affecting communication and the consequent decision making the individuals make on movement and possible leadership. To overcome the logistical challenge of monitoring communication between individuals across long distances, machine learning algorithms will be used to analyse media from remote sensing technology recording simultaneously from multiple locations to identify callers and responders. whilst inter-party communication has been established as a mode for coordination, call producer and responder behaviour, requires further investigation. Specifically how social relationships affect which individuals communicate with who. Relatedly, I will address questions that integrate vocal behaviour with leadership, and what role these two key elements play in social (spatial) coordination. This project will uncover information on how fission fusion societies coordinate movement, long-distance communication between individuals, the movement of an endangered primate: the common chimpanzee. Furthermore, the chimpanzees of the Issa valley inhabit an environment that closely resembles the paleoenvironment of several early hominin species. Therefore they may provide a landscape analogous to how these hominins may have coordinated in these woodland savannah mosaic habitats. Understanding the mechanisms by which individuals and sub-groups coordinate between each other - in both auditory and visual domains - can provide us insights into how individuals optimise the benefits of group living while minimising the costs. We can then see how this coordination impacts their movement as a community.

Background

This project aims to understand how chimpanzees (*Pan troglodytes*) use vocalisations to coordinate their movements. This is especially important when we reconstruct the way that hominids responded when they transitioned from closed-canopy forest into woodland-dominated environments during the Pliocene (Negash et al., 2024). It is predicted that this transition caused lower population densities and larger home ranges, straining social organisation (Moore, 1996). Whilst we cannot directly test hominid sociality from the fossil record, investigating great apes that live in analogous habitats can inform these hypotheses. The chimpanzees of the Issa Valley, Tanzania, inhabit an environment that closely resembles the paleoenvironment of several early hominin species (Drummond-Clarke et al., 2022). Early hominin social dynamics likely featured flexible organization (Foley & Gamble, 2009; Malone et al., 2012; Potts, 2013) in response to seasonal environments (Sueur et al., 2011). By analysing chimpanzee communication and movement, we aim to shed light on how fission-fusion species, including human ancestors, adapted to woodland-grassland mosaics.

Literature Review

Role of vocal communication in coordinating movement

Individually encoding calls has been found in multiple species. In meerkats (*Suricata suricatta*), where groups are highly cohesive, contact calls update the presence and identify of neighbours, and maintain group cohesion, preventing individuals from being separated (Demartsev et al., 2024). How individuals respond to contact calls has not been as well as studied. One study that has attempted to look at response behaviour using audio playback on spider monkeys (*Ateles geoffroyi*), which exhibit fission fusion grouping dynamics, found that close associates only marginally responded more strongly than other conspecifics (Ramos-Fernandez, 2005).

Amongst chimpanzees, investigations into the role of acoustic communication in coordinating fission fusion dynamics have been limited to production, not response behaviour (Eleuteri et al., 2022; Fedurek et al., 2021; Mitani & Nishida, 1993). Indeed, pant-hoot vocalisations performed with buttress drumming are used while travelling, and may be used for the coordination of parties (Eleuteri et al., 2022; Fedurek et al., 2016; Mitani and Nishida, 1993). Shorter versions of pant-hoots and buttress drumming are used during dominance displays, however these are less individually unique as shorter vocalisations have reduced opportunity for variation. These vocalisations are also often masked with other sounds which are incorporated into the display, such as branch shaking, making them even less individually encoding (Eleuteri et al., 2022; Fedurek et al., 2016; Grampp et al., 2023). Whilst pant-hoot call hourly rate is positively associated with rank and the proximity of close affiliates (Mitani and Nishida, 1993), buttress drumming rates were not affected by either audience composition or rank of the individual (Eleuteri et al., 2022). The function of pant-hoots and buttress drumming to coordinate movement is further supported by findings that males stay within auditory range of these modalities of communication (Eckhardt et al., 2015).

Previous investigation into Issa chimpanzee vocalisations reveal seasonal (Crunchant et al., 2020), sexual (Crunchant et al., 2021) and diel (Piel, 2018) variation. Issa chimpanzees were less vocal than a forest-dwelling population (Crunchant et al. 2021). Whilst this implies that chimpanzees generally vocalise more often in denser habitats, the chimpanzees of Issa used loud calling vocalisations more often in the more open woodland than in the riparian forest habitats, in the latter habitat more short-distance vocalisations were used (Crunchant et al., 2021). This vegetation signature could be explained by increased party size, but could also be individuals exploiting a more optimum environment for sound transmission (Waser & Brown, 1986). Group size in Issa has been found to be positively correlated with loud calling behaviour, as larger groups are more likely to have more instances of aggression which result in more of these loud vocalisations such as screams and barks (Crunchant et al., 2021). However, a study outside of Issa, found that loud calls used during travelling were inversely related to sub-group size (Eleuteri et al., 2022). Therefore loud-calls used for coordination in the Issa Valley may not be positively correlated with group size. In the Issa Valley, loud calls serve different functions based on the time of calling; dusk calls may be used to coordinate sleeping clusters while nighttime calls may be used to communicate between parties (Piel, 2018). The current study will not only test these hypotheses, but with individuality included in the analyses, expand our understanding on the roles that sex, age, rank, and especially relationship quality have on counter-calls and subsequent reunion behaviours

Leadership in fission-fusion societies

In fission and fusion societies, both when to depart and how to reunite require coordination. Behaviours used to coordinate can be both acoustic and visual, with the former used in long distance communication (Zwamborn et al., 2023) and the latter when individuals are within sight of each other. Therefore, we can expect inter-party communication to be acoustic (Zwamborn et al., 2023) whilst intra-party more reliant on visual communication (Badihi et al., 2024). Therefore, fission events are more likely to contain visual communication, whilst fusion events are more likely to use acoustic communication, more specifically, loud calling behaviours. Inter-party communication in the context of party fusion is further exacerbated due to the social uncertainty of having multiple individuals meet after a period of time (Demartsev et al., 2023; Grampp et al., 2023).Therefore, more dynamic fission-fusion societies may be in higher need of communication to coordinate these departures and reunions.

We know almost nothing about what factors predict the production of signals indicating fission events in chimpanzees, or which individuals produce them or why. There are multiple factors that may predict the initiators of both departing and reuniting, including rank, age and energetic needs. Amongst multiple mammalian taxa, rank is a good predictor of who leads the group in despotic societies, whilst the individual with the highest energetic needs is most likely to lead the group in more egalitarian societies (King & Sueur, 2011; Zwamborn et al., 2023), regardless of fission fusion dynamics. Studies of collective decision making in egalitarian societies of vulturine guineafowl (*Acryllium vulturinum*) (Papageorgiou et al., 2024) and despotic societies of olive baboons (*Papio anubis*) (Strandburg-Peshkin et al., 2015), neither of which practice fission-fusion, both show that a group's geographic position relative to any one individual and the size of the group are likely to affect the likelihood of an individual joining a group. One study in a fission fusion society found that a group of bottle-nosed dolphins (*Tursiops truncatus*) had consistent leadership from certain individuals based on number of successful direction changes and holding a lead position in the group during travelling (Lewis et al., 2011); the authors postulated that the highly heterogenous landscape inhabited meant that only certain individuals with knowledge of the landscape were followed. However, factors from their life histories, social connectedness and rank were not well known, and so could not be tested. In a less socially dependent, more egalitarian fission-fusion society like bison (*Bison bison bison*) leadership emerged regardless of the informational state of others, where if an individual has meaningful information they are more likely to discount the social influence from others (Merkle et al., 2015). Individuals were seen to follow others depending on the familiarity of the area and the group (Merkle et al., 2015). In two species of primates, tonkean (*Macaca tonkeana*) and rhesus (*Macaca mulatta*) macaques, which exhibit low levels of fission and fusion dynamics, social affiliation was shown to be a strong predictor of which individual follows which during fission events (Sueur et al., 2010).

Knowledge gap:

Who communicates with who

Communication, and especially coordination, is a key element for reunions between members of fission-fusion societies, where individuals are spatially and temporally separated for variable time periods. While there is historic interest in the function of chimpanzee loud calls (Fedurek et al., 2016, 2021; Mitani & Nishida, 1993), and how social factors specifically affect the likelihood of producing these vocalisations used for coordination (Mitani and Nishida, 1993), there has been little investigation into the response behaviour of these loud calls. Response behaviour of communication for group coordination has been limited to close-distance soft "hoo" type vocalisations (Bouchard & Zuberbühler, 2022; Crockford et al., 2017) but this study will be the first to examine the response behaviour of loud calling vocalisations, providing insight into the spatial coordination of these fission and fusion dynamics at a much larger scale. Communication via loud calls such as pant-hoots, and buttress drumming, produced during travelling, is individually encoded and thus likely to be critical to decisions individuals make to join or avoid conspecifics (Desai et al., 2022; Eleuteri et al., 2022; Fedurek et al., 2021). However, due to the logistical challenge of simultaneously observing multiple parties across a large area, studies addressing caller-responder dynamics in large groups of large-bodied animals are limited. By identifying these responders (and non-responders) we can examine how vocalisations are used to recruit allies and selectively share information on caller identity and activity to other parties. Information can be selectively shared by masking parts of their vocalisations with noise using branches or shortening the duration of their call (Grampp et al., 2023). Using artificial intelligence and remote monitoring, this study will be the first to assess how relationship quality impacts communication and movement across a mosaic landscape.

Similar to the chimpanzees of the Issa Valley, early hominins are hypothesised to have had fission fusion social dynamics (Grove et al., 2012) in male-based philopatric societies (Copeland et al., 2011; Milich, 2024), which would have required coordination (Negash et al., 2024). Therefore, by understanding how the Issa chimpanzees coordinate their movement we may gain insight into how other male philopatric fission-fusion societies (e.g. australopithecines (Copeland et al., 2011)) may have navigated comparable open landscapes. I predict that the social correlates of response behaviour will reflect those of the initial callers as described by Mitani and Nishida (1993), where responders to callers are most likely to be individuals most closely associated to the caller and communication is most likely to occur between high ranking and/or older males. This aligns well with the mission of the Leakey foundation to better understand human origins through investigating aspects of hominin social behaviour using extant models.

Leadership as a driver of fission fusion dynamics

The results of this study will have impacts beyond primatology and our understanding of fission fusion dynamics. To understand these dynamics, the decision making process between group members and the consequent leadership that arises during travelling need to be investigated. Whilst resource distribution and sexual reproductive opportunities drive individual decision making in chimpanzees (Matthews et al., 2021), we know very little how leadership drives fission and fusion dynamics in this species. In other fission-fusion systems different factors have been shown to affect how individuals choose to follow who during fission events such as age (McComb et al., 2011), who has the most meaningful knowledge of the area (Lewis et al., 2011; Merkle et al., 2015), and social connectedness (Merkle et al., 2015; Sueur et al., 2010). However, we do not know how leadership in fission fusion systems affect fusion events. To investigate this we need to identify the individuals communicating to each other preceding reunion events between parties (Sueur et al., 2011). I predict that in Issa's chimpanzees, social connectedness as well as age and kin will be primary drivers of which individual communicates and with whom, and how those decisions influence movement and ultimately, community cohesion. In this way, my work will make key contributions to the field of leadership and coordinated movement in fission-fusion systems.

Monitoring chimpanzee movements

Finally, besides an intellectual contribution to key questions about movement coordination, my work will also advance the field of primate communication by incorporating traditional (focal follow behavioural observations) with innovative technological (motion-triggered cameras and acoustic sensors) methods and neural network algorithms to investigate fission fusion dynamics. Excitingly, this project will also be the first study to employ artificial intelligence and individual level speech recognition from landscape recordings to situate spatiotemporal patterns of individuals. Whilst past audio classification of non-human animals has been limited to convolutional neural networks (Gupta et al., 2021), we will be using recurrent neural networks as used in human speech recognition algorithms (Deng & Li, 2013; but see Leroux et al., 2021). This project will showcase how to use transfer learning to circumnavigate the lack of large datasets typically needed to train neural networks. We propose using algorithms pre-trained on human and/or bird and marine mammal data to then be further trained and fine-tuned to identify individual primates smaller datasets (Ghani et al., 2023; Yu et al., 2020). Given that 65% of primates are threatened with extinction and 75% have declining populations (Estrada et al., 2020; IUCN Red List, 2019), they both are in the most need of monitoring whilst simultaneously lacking data needed to monitor them.

Aims and objectives:

1. How communication affects movement
2. How identity of callers affect communication
3. How different parties within a community coordinate

Hypotheses and Predictions:

I hypothesise that pant-hoots are most likely to be responded to by individuals based on social factors to both the caller and the audience present. I predict that individuals most closely associated to the caller are most likely to respond and an inverse relationship with the likelihood of responding to the size and social association to the individual.

External factors such as time of day and behavioural sate are likely to affect the likelihood of response. I expect early morning and late evenings are likely to be the time most likely for individuals to responds to pant-hoots and pant-hoots are most likely to respond to calls when they are travelling.

Methodology:

Who communicates to who

Passive acoustic monitoring:

In the first field season, I will deploy 11 acoustic sensors each stationed in proximity to a motion triggered camera trap. These acoustic sensors will be arranged in a triangular array 1km apart from each other as to best localise the calls (Crunchant et al., 2022) in five areas. Each of these eleven acoustic sensors will be configured to run twice a day for four hours, once during dawn and once during dusk as they are the periods in which chimpanzees are most vocal (Crunchant et al., 2021; Piel, 2018). In the south-west artery of the valley, I will deploy five sensors in a bi-triangular array based on the heavy use of this area during this period by Crunchant et al. (2020).

Recording chimpanzee vocalisations from focal follows:

In the first field season, I will record chimpanzee vocalisations opportunistically using a recording apparatus with two microphones affixed to each other using a PVC clip which will be designed and 3D printed by VM. One microphone is the Sennheiser MKH 70 Long-gun Condenser Microphone, which will be used to capture high quality recordings of individuals; the second microphone is the MEM microphone used in the acoustic sensors known as CARACAL (Wijers et al., 2021). Both microphones will be connected to a h4n zoom recorder to temporarily store these recordings in the field. These microphones will then be covered by a protective microphone blimp to prevent damage. With each vocal event, I will also note the name of the individual(s) calling and the activity of the individual(s) (feeding, travelling, sitting, displaying, greeting, approaching food patch, etc.). I will also note the time and place of when fission and fusion events occur to test if vocalisations preceding these events were captured from the acoustic sensors.

<u>Individual classification using machine learning:</u>
A multilabel hybrid Long Short-Term Memory recurrent (LSTM)/convolutional neural network (CNN) algorithm will be trained on the audio collected from the focal follows of both the hand-held shotgun condenser microphone and the CARACAL microphone. We anticipate the audio from the hand-held shotgun condenser microphone will enable the algorithm to start distinguishing individuals and the audio from the CARACAL microphone will allow the algorithm to be applied to stationary CARACAL. These data will also be augmented by clipping the original recordings to different sizes to replicate natural variation in duration of calls and overlaying the audio with different types of background noise such as different environmental conditions and vocalisations from other non-chimpanzee animals found in the Issa valley. This algorithm will be using a pretrained acoustic feature extractor model, either VGGish (Yu et al., 2020) or Perch (Ghani et al., 2023) to produce simpler acoustic embeddings from the audio recordings to use as inputs to feed into the large multilabel LSTM CNN audio classifier. Using a multilabel classifier will allow the classification of multiple individuals within a recording; this will be especially useful in identifying individuals participating in choruses. This algorithm will then be used to identify individuals from the passive acoustic methods from the stationary CARACAL. Camera footage captured within an hour before and after the call from cameras within 1 km from the acoustic sensor will be used to collect data on how audience composition and behavioural states affect the likelihood of individuals calling and responding. Individuals from this footage will be passed through the "following things around" chimpanzee face detection algorithm (Bain et al., 2019; Schofield et al., 2019), set to a high threshold of probability for the algorithm to isolate the face. Once these faces are isolated, they will be identified using a face recognition model. Once these individuals have been identified it can further confirm which individuals responded to calls and which did not. This face recognition algorithm is a vgg16 image classification algorithm pretrained on the ImageNet model (Russakovsky et al., 2015), with the last layer trained to identify individual chimpanzees using transfer learning. This last layer was trained on images of individual chimpanzees from the Issa Valley, see more information in Section 6.

<u>Statistical modelling</u>
Using a generalised linear mixed model with a binomial distribution I will investigate whether an individual responds to calls from conspecifics (following Schel et al., 2013):

a) Strength of social bond calculated by social network analysis;
b) behavioural state of responder (if recorded in camera traps), specifically reunions;
c) individuals in the audience determined by the composition of the sub-group;
d) how time of day affects whether they are responding to a member within outside of their sub-group.

Leadership
In the second season I will follow chimpanzees, collecting behavioural data on questions surrounding leadership. Here, termite mounds will be targeted as termites are a preferred seasonal food source (Phillips et al., 2023) where we can reliably expect to capture incidences of departure in a group context after feeding bouts. These will then be monitored with a

camera on a wide lens to capture the social context and series of both visual and acoustic communications that precede a party fission or party fusion. From field observations we will identify who are initiators from three criteria:

a) The first individual in a party to signal moving via a short distance vocalisation such as a "travel hoo" (Crockford et al., 2018) or hand gestures such as the "travel with me" chest-scratch performed by Issa chimpanzees (Hobaiter and Byrne, 2014; personal communication Alex Piel) resulting in the rest of the group to transition their behavioural states to moving (King and Sueur, 2011);
b) The first individual to transition their behavioural state to moving before the rest of the party starts to move (King and Sueur, 2011);
c) The individual that is at the front of the party when all individuals in the party are moving (Lewis et al., 2011).

I will then test how often these three criteria are performed by the same individual, how consistently individuals are leaders in their parties, and how well rank and social connectedness explains leadership in chimpanzees. Here I will use a logistic regression model to test how party size, rank relative to the party and group composition (between all male, all female, and mixed sex parties) influence the probability of an individual being an initiator.

Expected output

Findings from this project will be used to inform my PhD thesis and be written in at least one academic papers. These findings will then also be presented at multiple conferences including the TAWIRI conference, international primatological society (IPS) conference and the association of for the study of animal behaviour (ASAB) conference. Whilst in the field I will also be mentoring masters students on focused on conservation, where I will help advise and assist on census studies using remote sensing technology and machine learning methods.

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