ALTERED HABITATS ALTER HABITS: BEHAVIOUR AND SPACE USE OF ASIAN ELEPHANTS IN THE VALPARAI PLATEAU

by

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Enrolment no: 50BB24A73022

Dissertation Thesis

Submitted to Academy of Scientific and Innovative Research

For the partial fulfilment for the degree

Master of Science
in
Wildlife Science

Under the supervision of

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Ananda Kumar, Nature Conservation Foundation (Co–Supervisor)
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भारतीय वन्यजीव संस्थान
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AcSIR

17th July 2026

DECLARATION

I hereby declare that the work conducted under the thesis entitled **"ALTERED HABITATS ALTER HABITS: BEHAVIOUR AND SPACE USE OF ASIAN ELEPHANTS IN THE VALPARAI PLATEAU"**, is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master's in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of **Dr. Parag Nigam, Scientist-G** (Supervisor) of Wildlife Institute of India, Dehradun and co-supervision of **Dr. Ananda Kumar, Senior Scientist** of Nature Conservation Foundation and **Dr. Anukul Nath** of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

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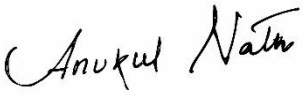

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CERTIFICATE

This is to certify that the thesis by **JOSHIKA KOMARLA** entitled **"ALTERED HABITATS ALTER HABITS: BEHAVIOUR AND SPACE USE OF ASIAN ELEPHANTS IN THE VALPARAI PLATEAU"** is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master's in Wildlife Science**.

Joshika Komarla has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

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Acknowledgements

No other section of this thesis has been procrastinated over as much as this one. However, writing it now – I feel this may have been for the best, as whatever I write now will suffer very few edits, making it the sincerest part of the thesis.

I extend my gratitude to the Director, Dean, and Registrar of the Wildlife Institute of India for providing me with the opportunity to enrol in this course. It has been the opportunity of a lifetime, and I am endlessly grateful for it. I also thank the Tamil Nadu Forest Department for facilitating my study in the beautiful landscape that is the Valparai Plateau.

The Wildlife Institute of India is an ensemble production comprising incredible faculty and support staff, all of whom have directly contributed to my growth and development over the past two years. I thank them all. In this, I single out my course directors, Dr Sutirtha Dutta & Dr Amit Kumar, both of whom left no stone unturned in ensuring that our coursework was as extensive as possible.

Particularly, I am indebted to Dr Sutirtha Dutta (a man with infinite patience) for humouring me always and guiding me through two term papers as well as any crises endured in a thesis that was not his to supervise. I also extend my gratitude to Dr Vishnupriya Kolipakam, who has sat through many of my random musings and directed rants (at deserving individuals). I would also like to thank Dr Bivash Pandav for teaching me to read and respect the forest. In all three, I have observed qualities that I would very much like to emulate someday.

Conceptualising a thesis can be a very daunting task when done alone, and it was a fate I was spared from thanks to my incredible supervisors, Dr Parag Nigam, Dr Ananda Kumar, and Dr Anukul Nath.

I thank Dr Parag Nigam for believing in my abilities to carry out this study and for doting out encouragement and motivation whenever required. From providing me with logistics on the field to giving me a proper water bottle when he saw me drinking from a tattered plastic one on campus, he was instrumental in every part of this thesis.

Were it not for Dr Ananda's critique of my first term paper as well as his prompt reply to my email in the third semester, this thesis may well have been based on ungulate behaviour. Not only did his deep natural history observations on the elephants of Valparai provide the underpinnings for the questions answered by this thesis, but he also accompanied me in my initial field days and guided me on how to interpret elephant behaviour. I cannot thank him enough for always explaining concepts again unprompted when he would see any signs of apparent confusion on my face.

Finally, I thank Dr Anukul Nath, my go-to for brainstorming as well as all things statistical and logistical, who has accompanied me as this thesis journeyed from the dry deciduous forests of Bandhavgarh to the evergreen backdrop of the Anamalais.

I would be remiss if I did not mention the support of the Nature Conservation Foundation team in Valparai. I thank Divya, Sridhar, and Srini for making my stay pleasant and facilitating my logistics. I thank Ganesh for always being one call away to discuss anything from elephants to the ginger tea at Parry's. Finally, I thank Aditya, a constant presence in my ecological coming-of-age, who has seen me grow from an unsure and shaky volunteer to a master's student pursuing a thesis.

I thank my field assistants as well as the elephant tracking team, Vignesh, Gopi, Pradeep, and Prakash. I will always cherish those moments when we ran both towards and away from elephants.

To Niranjana, Ahir, Nandu, Pranjali, Sujay, Akshay, Stella Akka and Sneha, I thank you all for being the best field mates a girl could ask for. I take a moment to remember Pappu, the cute basecamp pup who may now reside as digested metabolic matter in the belly of a leopard.

The last two years passed by as a blurry ball of fun and fear. These emotions I have shared with my friends Srinjan, Mencho, Bryan, Tanya, Himani, and Srajal. From endless nights spent discussing everything and nothing, scribbling equations on walls, watching IPL matches, eating our hearts out in Clement Town, to sharing looks of exhaustion in the field – we have done it all together.

To Shreyas – my favourite field partner, I did not know colours, butterflies, or line transects could ever be so fun. I thank you especially for never letting me give up and believing in me more than I ever have.

The foundation of it all - my family. I thank them for encouraging me to pursue my passion, even when I myself resisted. I thank my mother for yelling at any teachers who suggested her child may not be fit for science. I thank my father for buying me kites that we would trek up hills with and fly together. I thank my sister for being my harshest critic and my fiercest supporter. I thank my grandmother for being my ever-present lunch partner. To Nala, my best friend – the upturn in my life that I carry wherever I go.

Grand and grey - I observed them night and day,

Dusting, feeding and sometimes fuming,

Watching giants in fields of tea,

It is unending - as far as the eye can see,

A cow walks in tandem with her calf,

It all feels so simple; I can't help but laugh.

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Abstract

As habitat loss and fragmentation continue to increase, mega-herbivores such as Asian elephants (*Elephas maximus)* increasingly traverse mixed-use landscapes where human-elephant encounters are frequent. Such encounters may influence elephant behaviour by altering activity patterns over time, modifying the relative frequencies of behavioural events, and shaping the behavioural repertoire exhibited. In this context, I examined the effect of human presence and associated activities on elephant behaviour on the Valparai Plateau, a rainforest-plantation mosaic in the Anamalai Hills of the Southern Western Ghats.

Behavioural observations were conducted over a 104-day field season using 370 instantaneous group scans and 499 focal observations of identified individuals. My findings suggest that human presence did not have a measurable impact on the behavioural composition of time activity patterns; however, encounter characteristics – particularly crowd size and human identity – did account for variations in these patterns. Increasing crowd size was associated with a 10 % reduction in predicted time allocated to foraging. Behavioural events such as vigilance, avoidance, and agitation were more sensitive to anthropogenic influence, with effects evident in both coarse- and fine-scale analyses. The odds of stress-induced behaviours were sevenfold in the presence of humans; however, beyond a threshold distance of approximately 70 meters (69.9 meters), the likelihood of such responses declined substantially. Proximity to elephants and human identity were important predictors for this response. Additionally, different human groups elicited different stress-induced responses, with Forest Department personnel eliciting more avoidance and agitation responses than expected; however, this pattern requires further quantitative assessment. Herd cohesion was not affected by human presence and was weakly affected by encounter characteristics, with biological parameters like age and sex explaining the pattern better.

Habitat selection analysis using Manly's Selection Ratio suggests that natural habitats such as forest fragments, riparian sections, as well as *Eucalyptus* stands were preferentially selected for, and used disproportionately to their availability, whereas dominant landscape features like tea and coffee plantations , were used less than expected relative to their availability, during daylight hours.

These findings suggest that elephants inhabiting mixed-use landscapes with a long history of both human use and elephant activity may tolerate human presence at a broad level, but certain encounters may still be perceived as risky.

Introduction

The Asian elephant population worldwide has nearly halved over the past 75 years (Williams et al., 2020). Approximately 50,000 individuals remain in the wild, of which an estimated 44 percent range within India (Qureshi et al., 2025). As a result, the future persistence of the species is closely linked to conservation outcomes within the nation. However, the trend of global decline is mirrored within India as well (Qureshi et al., 2025).

Habitat loss, fragmentation, and human-induced pressures are among the primary drivers of this decline (Leimgruber et al., 2003). Habitat loss and fragmentation pose challenges for elephants due to their ecological requirements. Elephants assimilate only half of the nutrients they consume to meet daily energy demands and thus require near-constant feeding and large-scale ranging (Campos-Arceiz & Blake, 2011). Habitat loss and fragmentation disrupt established foraging patterns by altering resource availability. As a result, elephants have begun expanding into human-use landscapes such as agricultural and plantation mosaics as natural habitats become increasingly scarce. In such landscapes, humans act as drivers of habitat modification as well as active and dynamic stimuli that elephants must contend with (Tuomainen & Candolin, 2012; Wong & Candolin, 2014).

Space use and behaviour represent two linked mechanisms that enable elephants to persist within such landscapes. Behaviour can be considered as the immediate mechanism through which individuals respond to changes in their environment (Sih et al., 2004), whereas space use describes the patterns in which individuals distribute themselves through space and time (Manly et al., 2002).

At a fine scale, individuals respond behaviourally to perceived risks in their immediate environment (Frid and Dill, 2002). These decisions accumulate over time to influence broader patterns of space use (Manly et al., 2002). Conversely, space use may influence the frequency and nature of human-elephant interactions.

Together, these two mechanisms shape how elephants perceive and navigate human-use landscapes. Alterations in either of the two mechanisms enable elephants to persist within human-modified landscapes. (Graham et al., 2009; Srinivasiah et al., 2012).

The long-term persistence of elephants in human-use landscapes may depend partly on their ability to adapt behaviourally and spatially to altered environmental conditions (Tigas et al., 2002). Thus, understanding both behavioural responses and space use patterns is essential for evaluating how elephants navigate shared landscapes. Such behavioural adaptations have been documented in Africa, where African savannah elephants have been observed moving rapidly through areas associated with human activity while spending longer periods in lower-risk habitats, demonstrating the role of risk assessment decisions in shaping patterns of space use (Graham et al., 2009).

Ecological research on Asian Elephants in human-use landscapes in India has been limited compared to studies conducted in large, continuous forest tracts. (Anoop et al., 2023; Baskaran et al., 1993; Baskaran et al., 2010; Desai & Baskaran, 1996; Sukumar, 1989). Such research has generated substantial knowledge regarding distribution, density, movement patterns, diet, behaviour, and habitat use (Jathanna et al., 2015; Gubbi et al., 2014; Nandini et al., 2017; Puri et al., 2025; Revathe et al., 2020; Sharma et al., 2020); however, it remains skewed towards Protected Areas (PAs).

This contrast is striking when one considers that most elephants within the country navigate a mosaic of multi-use forest-agricultural interfaces where interactions with people are frequent and inevitable (Pandey et al., 2024; Madhusudan et al., 2015). As a result, understanding how elephants respond behaviourally and spatially to human activities has become important for informing effective strategies for coexistence in shared landscapes.

Behavioural studies in human-use landscapes are important for two reasons. First, they help identify the ecological and anthropogenic factors that influence elephant behaviour within habitat mosaics. Second, repeated interactions between elephants and people may alter behavioural repertoires through processes such

as habituation, risk avoidance, or behavioural plasticity (Pokharel & Sharma, 2026). Understanding these behavioural responses has significant conservation implications, as changes in behaviour can affect both the persistence of elephant populations and the frequency of human-elephant interactions. Thus, behavioural studies provide invaluable insights for the development of effective conflict mitigation strategies (Whitehouse & Kerley, 2002).

Landscapes with a history of land-use conversion and long-term elephant activity may be particularly valuable model systems for examining these questions, as elephants have had the opportunity to adjust to sustained human presence over multiple generations. Such systems allow us to investigate whether elephant responses are driven primarily by human presence or, over time, by context and the nature of human activities (Kumar et al., 2010b; Vijayakrishnan et al., 2018).

One landscape that offers an opportunity to address this gap is the Valparai Plateau, a 220 km² rainforest-plantation mosaic located in the Anamalai Hills of the Southern Western Ghats. Historically, this landscape was part of a contiguous forest habitat that supported the largest elephant population in India. Over time, this population has fragmented into two due to habitat loss and fragmentation through plantation expansion, human settlements, infrastructure development, and other forms of landscape modification (Qureshi et al., 2025).

Unlike many human-dominated landscapes where elephants have recently ranged into human-use areas, elephants in Valparai continue to occupy a landscape that has supported human presence for over a century. An early account of the region, written by C.R.T. Congreve (Congreve, 1942), is attached below:

> "*It is very difficult, if not impossible, for people at the present time to visualise what this district was like when we first came to it in 1897. There were miles and miles of evergreen forest, with a few main paths running through it made by the huge herds of elephants which roamed there in the dry weather between November and April."*

The present-day seasonal activity of elephants remains broadly consistent with this historical account. The plateau supports approximately 120 elephants annually alongside a human population of 70,000, with a density of approximately 320 people/km².

Kumar et al. (2010a) found that elephants within this landscape used rainforest fragments and riparian habitats disproportionately relative to their availability, whereas tea plantations were avoided during the day and used frequently at night. Similarly, Vijayakrishnan et al. (2024) showed that elephants make extensive use of the plantation–forest mosaic, exhibiting strong selection for riparian habitats and rainforest fragments. Comparable patterns have also been documented elsewhere in southern India, where elephants preferentially used forest fragments and monoculture refuges during periods of high human activity and shifted habitat use in response to landscape modification (Krishnan et al., 2019). Together, these studies indicate that elephant space use in human-use landscapes is non-random and reflects a balance between resource access and risk avoidance.

Similarly, behavioural studies conducted within the plateau further suggest that elephant behaviour is influenced by human presence and activities (Kumar & Singh, 2010b; Vijayakrishnan et al., 2018). Kumar & Singh (2010b) found that feeding, vigilance, agitation, and herd cohesion changed across different habitat types. In addition, closer human proximity and larger numbers of people reduced feeding and increased agitation in elephants.

Vijayakrishnan et al. (2018) investigated the physiological aspects of behavioural responses by comparing herds in Valparai with those of forest elephants in the nearby Vazhachal Reserved Forest. Their research revealed that elephants on the plateau did not exhibit elevated baseline faecal glucocorticoid metabolite (FGM) concentrations or stress levels compared with individuals in adjacent forest habitats. Rather, physiological stress responses were heightened following direct negative interactions, such as elephant drives.

These studies collectively indicate that elephant responses are shaped less by human presence itself and more by the context, intensity, and nature of human-elephant interactions, which are more significant than human presence alone.

Together, these studies provide a foundation for understanding elephant ecology within a human-use landscape such as Valparai. However, such landscapes are dynamic systems characterised by both changing ecological conditions and patterns of human activity. Long-term monitoring or systematic and periodic studies are required to assess whether previously documented behavioural and spatial patterns remain consistent over time and to contribute to the broader understanding of elephant persistence in shared landscapes. Building on previous research, this thesis aims to add to the body of work and assess the following aspects of elephant ecology within the Valparai Plateau:

1. Assessing elephant behavioural responses across a gradient of human stimuli.
2. Examining the influence of habitat classes on elephants' space use.

Answering such questions can inform conservation planning by identifying conditions that facilitate coexistence. In this context, the thesis directly contributes to the growing need for ecological and behavioural insights of wide-ranging megaherbivores from shared landscapes, where coexistence is a lived reality.

Aim, Objectives & Research Questions

This study aims to address knowledge gaps regarding Asian elephant space use and behaviour in response to anthropogenic stimuli in an altered landscape.

Objectives

1. To understand how human presence & associated disturbances affect the behaviour of elephants in a human-modified landscape.
2. To understand how habitat characteristics influence Asian elephants' space use within a human-modified landscape.

Table 1. Research Questions, Hypotheses, & Predictions

Research Question	***Hypothesis***	***Prediction***
Do human presence and associated activity influence elephant time-activity budgets?	Human presence and associated activity will affect the time-activity budget of elephants by altering the proportion of time spent in different behavioural states.	Human presence is expected to be a perceived risk, which may reduce the proportion of time spent on foraging and increase the proportion of time spent in locomotion. Furthermore, the local context explained by the degree of human activity, the number of humans present, their proximity to the elephants, and who they are will better explain variation in time-activity budgets than human presence alone. (Frid & Dill, 2002; Kumar et al., 2010b; Srinivasaiah et al., 2012; Vijayakrishnan et al., 2018).
Does human presence and associated activity influence the occurrence and composition of stress-induced behavioural responses*, such as vigilance, avoidance, and agitation?	Stress-induced events represent immediate responses to perceived risk and will vary according to human presence and associated activity.	Stress-induced events may serve as indicators of perceived risk and may occur more frequently in the presence of humans. The occurrence of such events may be influenced by the degree of human activity, who the human is, the number of humans present, and their distance from the elephants. Furthermore, the local context created by these variables is expected to influence the nature of the behavioural response, with higher levels of human disturbance, a larger number of people, and closer human proximity shifting responses from low-intensity vigilance towards avoidance and agitation. (Kumar et al., 2010b; Friswold et al., 2026; Srinivasiah et al., 2012; Vijayakrishnan et al., 2018)
Does human presence and associated activity influence elephant group cohesion?	Elephant groups will increase group cohesion when exposed to the perceived risk of human	Nearest-neighbour distance (NND) will decrease in the presence of humans. The local

Research Question	*Hypothesis*	*Prediction*
	presence and associated activity.	human context will further influence this relation. (Kumar et al., 2010b; Srinivasiah et al., 2012)
How do elephants use habitats within a human-modified landscape?	Space use is non-random and influenced by habitat characteristics.	Habitats that provide cover and reduced human activity will be used more frequently than highly disturbed habitats. (Kumar et al. 2010a; Vijayakrishnan et al., 2024)

** The definition for stress-induced behavioural responses has been elucidated in the further section Field Methods.*

Study Area

The Western Ghats comprise a biodiversity hotspot (Myers et al., 2000) and are characterised by a high diversity of flora and fauna (Pascal, 1988). The Palakad Gap in Kerala, one of two major gaps in the otherwise continuous mountain range, divides the Western Ghats into the Northern and the Southern Western Ghats. The Southern Western Ghats are characterised by a higher degree of endemicity and species richness than the rest of the range (Davidar et al. 2007; Gimaret-Carpentier et al. 2003; Pascal et al. 2004). Within this region lie the Anamalai Hills, or "Elephant Hills", which support the second-largest contiguous population of Asian elephants in India (Baskaran 2013; Kumar et al. 2004)

Nestled within these hills is the Valparai Plateau, a ~220 km² rainforest–plantation mosaic embedded within a larger network of PAs, including the Anamalai Tiger Reserve, Eravikulam National Park, and the Vazhachal Reserve Forest. The landscape is dominated by tea, coffee, and cardamom plantations owned by six major companies as well as eucalyptus plantations, interspersed with rainforest fragments (0.3–100+ ha),

riparian habitats, grasslands, and swamps (Raman & Mudappa, 2007). These remnant habitats support several endemic and threatened species. The natural vegetation corresponds to mid-elevation tropical wet evergreen forest (Ramachandra & Bharath, 2019) of the *Cullenia–Mesua–Palaquium* type, and the plateau receives ~3500 mm of rainfall annually, with elevations ranging from 1000 –1450 m. The region supports a dense human population (~320 people per km^2), many of whom are employed as plantation workers.

The plateau has historically been and continues to be used by elephants (Congreve 1942; Kumar et al 2002). Elephants navigate a mosaic, of which tea is the overarching matrix, to move between surrounding PAs. Approximately 120–140 elephants use the plateau annually, moving between plantations, settlements, natural habitats and adjoining protected forests (Raman & Mudappa, 2007; Kumar et al., 2010a; Vijayakrishnan et al., 2024). Although some male elephants reside year-round, their activity increases between October and March, aligning with the sampling timeframe. The region's unobstructed visibility facilitates direct behavioural observations, thereby providing an opportunity to conduct elephant behavioural observations in altered environments, which remain understudied compared with natural habitats or PAs (Jabili et al., 2025; Revathe et al., 2020).

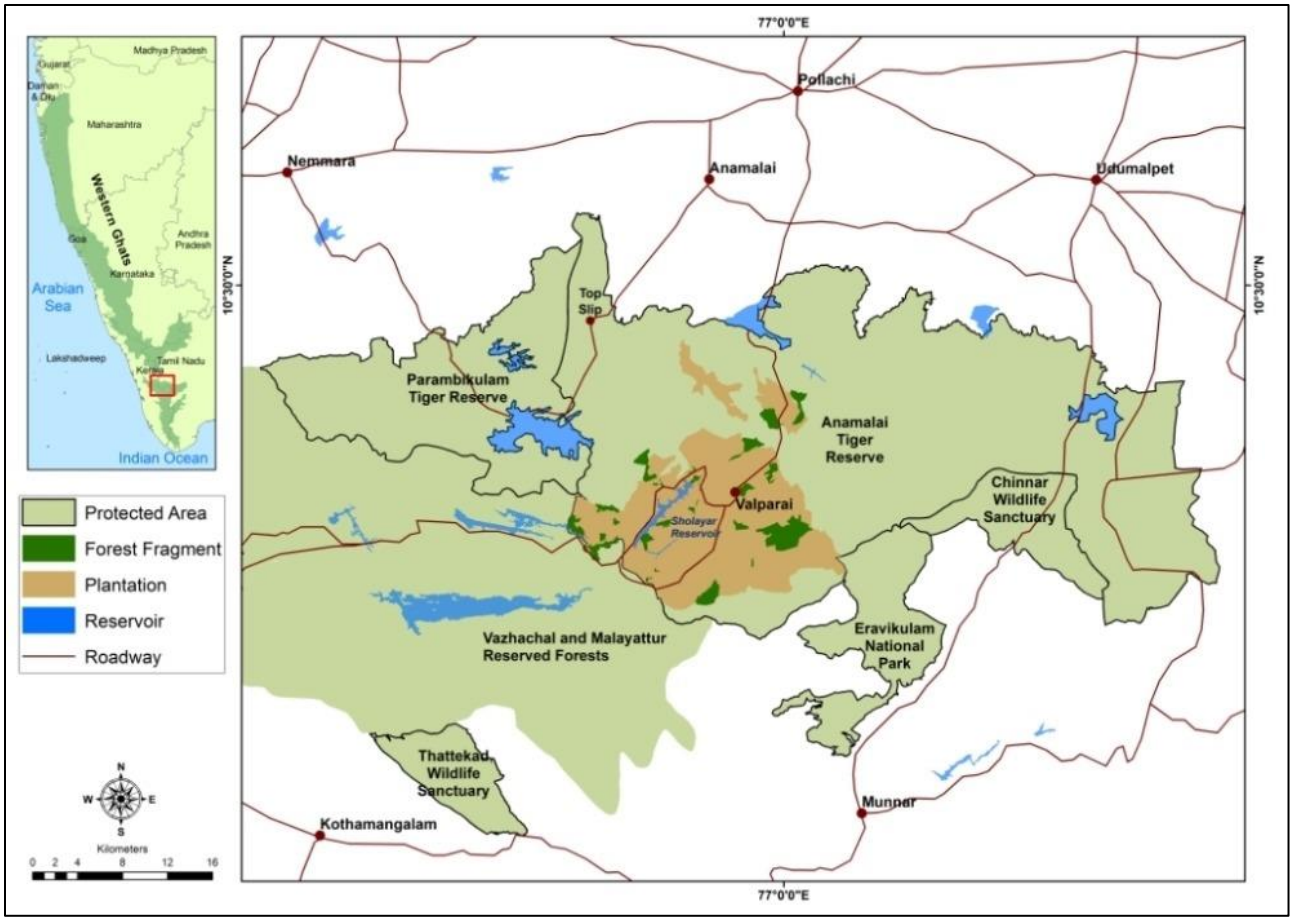

Figure 1. A map of the Valparai Plateau (orange) with rainforest fragments (dark green) surrounded by Protected Areas (light green) in the Anamalai hills.

Chapter: Risky Business - Behavioural & Spatial Responses of Asian Elephants to Human Presence and Activity in a Human-Use Landscape

Introduction

Behaviour concerns how organisms allocate their finite currency of time among competing physiological and ecological demands (Caraco, 1979; Krebs & Davies, 2012). At a broad scale, this allocation is reflected by behavioural states such as foraging, locomotion, and resting, which together comprise an individual's time-activity budget.

Among free-ranging elephants, foraging, locomotion, and rest typically comprise the dominant components of an elephant's time activity budget. Foraging occupies the largest proportion of the activity budget and reflects the substantial energetic requirements of a large-bodied herbivore (Sukumar, 2003; Campos-Arceiz & Blake, 2011). Locomotion facilitates movement between habitat patches, while resting encompasses inactive behavioural states, including sleeping and prolonged inactivity.

Elephants also exhibit a range of behavioural events, including vigilance, avoidance, agitation, social interactions, vocalisations, and self-directed behaviours. Vigilance enables individuals to assess potential risks and monitor their surroundings; avoidance and agitation enable them to respond to perceived disturbances or threats in the immediate vicinity, and social interactions maintain group cohesion and individual relationships. Therefore, variations in the frequency of these events may reflect behavioural adaptations to environmental changes. In landscapes altered by human activity, such variations may serve as responses to anthropogenic influences.

Time as a finite resource underpins the economy of behavioural investment across states and events. Increased investment in one behavioural state or event necessarily reduces the time available for others. As

such, behavioural responses to disturbance stimuli may be mediated through trade-offs among competing behaviours. For instance, locomotion may occur at the cost of foraging under conditions of disturbance. Thus, examining trade-offs among behaviours and measuring changes in the frequencies of behavioural events may help assess how elephants respond to human presence and disturbance (Pokharel & Sharma, 2026).

Within the context of human-use landscapes, this chapter examines how human presence and associated activity influence elephant behaviour. The three questions initially outlined in the *Research Questions, Hypotheses, & Predictions* section were further broken down into a series of analytical questions. This is because all questions are analysed at two levels. First, human presence is treated as a coarse predictor representing whether humans were present or absent during observations.

Second, human activity is treated as a fine-scale predictor that captures all dimensions of perceived human risk based on the local context of human encounters, including human activity, the number of humans present and their proximity to elephants, and who the humans present were (Forest Department personnel, residents, or tourists).

Similarly, behavioural events were assessed both in terms of their occurrence and their composition. This framework allowed me to assess human effect on elephant behaviour at two complementary levels.

Table 2 Research questions, datasets, response variables, and analytical approaches used in the study.

S.N	Research Question	Dataset	Response Variable	Analytical Methods
1a	Does human presence influence elephant time-activity budgets?	Focal observations	Proportion of time spent foraging, moving, and resting within a focal observation (henceforth referred to as the behavioural composition of states)	Dirichlet Regression (Douma & Weedon, 2019; Pike et al., 2024)
1b	How does human activity influence elephant time-activity budgets?	Focal observations	Behavioural composition of states	Dirichlet Regression (Douma & Weedon, 2019; Pike et al., 2024)
2a	Do human presence and associated activity influence the composition of stress-induced behavioural responses such as vigilance, avoidance, and agitation?	Focal observations	Behavioural response category	Chi-Square Test of Independence
2b	Do human presence and associated activity influence the occurrence of stress-induced behavioural responses such as vigilance, avoidance, and agitation?	Focal observations	Behavioural event occurrence (present/absent)	Generalised Linear Mixed Models
3	Do human presence and associated activity influence elephant group cohesion?	Instantaneous group scans	Nearest-neighbour distance class	Wilcoxon Rank-Sum and Kruskal-Wallis Tests
4	How do elephants use habitats within a human-modified landscape?	GPS locations		First Order Manly's Selection Ratio

Methods & Materials

Field Methods

Elephants were tracked on a daily basis within plantations. Observations were made on my identified individuals using a combination of external morphological features, including ear shape, earlobe pattern, ear-tear patterns, pigmentation, notches and nicks, tail-hair shape, tusk size & wear, body size, and other noticeable features (Vidya et al., 2014). However, owing to the presence of a long-term elephant informant network (EIN) operating in the landscape, several individuals were known before the study commenced. Thus, individual IDs had to be generated for the few unknown or lesser-observed individuals in the landscape. Whenever elephants were sighted, the herd or solitary male ID, as well as the habitat type, surrounding habitat, and age-sex composition of the herd/individual, was recorded.

For each individual, age-sex class was recorded as adult male, adult female, sub-adult male, sub-adult female, juvenile male, juvenile female, and calf. I have attempted to assign these classes using the comparative size scale recommended by Fernando et al. (2022); however, due to the sloped terrain, it was difficult to distinguish adult females from sub-adult females. For example, sub-adult females positioned on the upper end of a slope would appear larger than nearby adult females, making comparisons unreliable. Additionally, relatively few sub-adult males were encountered during the study. As a result, age-sex classes were clubbed into adult females, adult males, young ones (including both juvenile and sub-adult individuals), and calves, which were less than a year old.

Table 3.Herd composition recorded for observed herds (age-sex taken in field retained)

Herd	Adult Females	Juvenile Females	Juvenile Males	Subadult Females	Subadult Males	Calves	Total
MGH	5	2	4	1	1	1	**14**
MPH	6	1	2	0	0	2	**11**
PTH*	4	4	1	0	0	2	**11**
STP	2	0	2	1	0	0	**5**
VGH	3	2	0	0	0	1	**6**
VTH	2	1	1	0	1	0	**5**
Total	**22**	**10**	**10**	**2**	**2**	**6**	**52**

Table 3 presents details of the age-sex composition of elephant herds that were behaviourally sampled during the study period. A total of 61 uniquely identified individuals were sampled across the study duration (52 individuals from herds and 9 adult males).

Adult males either ranged solitarily or formed fluid all-male groups (AMGs). The composition of these AMGs was not fixed, and males were often observed interacting with various conspecifics over time. On three separate occasions, two males (Spook and Sirius) have been observed interacting with herds (MGH & PTH and VTH, respectively). It is important to note that the sampled individuals represent a subset of the total individuals on the plateau for that season. It should also be noted that PTH would often fission into two herd groups. Whenever fission groups were encountered, the group with individual *af_pth_4* would be marked as PDH.

Non-invasive behavioural sampling was conducted using an ethogram. This ethogram was developed to facilitate non-invasive behavioural observations. Behaviours were compiled from previous studies on Asian and African elephants (Kumar & Singh, 2010b; Poole & Granli, 2009; Vijayakrishnan et al., 2018), and a pilot test was conducted in the field. Any new behaviours observed in the field were cross-referenced with established ethograms and validated before being added.

To facilitate observations, behaviours were broadly classified as states and events. Behavioural states included any behaviours that persisted for measurable durations. These included foraging, locomotion, and rest. Events comprised instantaneous behaviours or discrete events that could be quantified as counts or frequency of occurrence. These included vigilance, agitation, avoidance, self-directed behaviours and social interactions. Additionally, any audible vocalisations were also recorded.

For analytical purposes, low-frequency behaviours were grouped into broader categories based on ecological context. As a result, avoidance and agitation behaviours were grouped as escalation events, as they occurred as a signal of distress in response to a persistent stimulus. Along the same lines, Friswold et al. (2026) grouped a series of behaviours they found indicative of anthropogenically induced distress as stress-induced behaviours. Following a similar protocol, behaviours associated with vigilance, avoidance, and agitation that indicate perceived risk have been grouped as stress-induced behavioural responses. A complete ethogram is attached in Appendix A, and a subset of states is presented below in Table 4.

Table 4. A subset of the ethogram attached in Appendix A.

Category	Code	Behaviour	Description
Locomotion	*mo*	Ambling	Movement with seemingly no direction. Distinguishable from *exp* as the individual is not searching for vegetation or actively ingesting vegetation matter.
	pw	Purposeful walk	Distinguishable from *mo*, an individual displays directed movemen towards a particular patch or destination. Often accompanied by a hurried pace.
	pr	Procession	Elephants are observed walking in a single file from one patch to another. Typically observed when elephants are walking along tea-estate trails to cross into swamps or fragments.
Foraging	*fe*	Feeding	Active ingestion of vegetation using the trunk and mouth.
	exp	Explore	Movement within a foraging patch while searching or selecting vegetation. Feeding may occur intermittently.
	dr	Drinking	Water is sucked up using the trunk and transferred into the mouth.
	cl	Cleaning	Manipulation, or the cleaning of food items before ingestion. An individual may thrash, shake or strip vegetation using their trunk and limbs.
Rest	*st*	Standing	Standing inactive with eyes closed for a prolonged period of time.

Category	Code	Behaviour	Description
	sl	Sleeping	Lying down and resting.

Behaviour sampling methods were selected in line with the research questions posed in the Research Questions, Hypotheses, & Predictions section of the Introduction chapter. Herds or solitary individuals were located and observed from a minimum distance of 50 m (Evans & Harris, 2008). A 10-minute acclimatisation period was implemented at the start of the observational period in the field to mitigate potential observer bias in recording elephant behaviour. During this period, no behavioural data were collected. Observations were discontinued if the elephants displayed responses attributable to the observer, such as freezing, flight responses, or aggressive approaches toward the observer.

Instantaneous group scan observations were carried out at 15-minute intervals on all visible individuals within a herd (Altmann, 1974; Lehner, 1996). This method enables simultaneous data collection from multiple individuals within a group and is the most effective method for collecting data on group activity in elephants (Ruckstuhl, 1998; Michelena et al., 2004). A 10-minute interval between two sampling units for large herbivores is a suitable minimum interval for obtaining independent samples of behavioural observations (Shannon et al., 2008). Consequently, I chose to retain a 15-minute interval to ensure independence between consecutive samples. All observations of elephants were conducted during the daytime and divided into morning (0700 hr to 1300 hr) and afternoon/evening (1400 hr to 1900 hr) sessions. Variables collected included individual identity, age-sex class, nearest neighbour distance & identity, presence of humans, and, if present, number of people present, who the people are, their proximity to the elephants, and their activity ranked on a disturbance scale (described in the *Analytical Methods* below).

Focal animal sampling was used to quantify time activity budgets and counts of behavioural events. Focal observations are particularly well-suited for estimating trade-offs in the proportion of time allocated among competing behavioural states (Altmann, 1974). Thus, focal observations were used to quantify time

activity budgets of focal individuals (Lukacs et al., 2016). Behavioural states were recorded using a pinpoint sampling approach (Brereton et al., 2022). Each focal individual was observed continuously for five minutes. These five minutes were divided into fifteen consecutive 20-second intervals or bouts, within which the dominant behavioural state observed during each interval was recorded. Similar to instantaneous group scans, any human presence and associated stimuli were recorded.

Concurrently, behavioural events were sampled using continuous all-occurrence sampling (Altmann, 1974). During each interval, the counts of behavioural events were recorded, and the total count of events per focal observation was obtained by adding counts across intervals. This method was particularly helpful for enabling the simultaneous observation of states and events. Additionally, such an approach helped document short-duration and low-frequency behaviours that may not have been adequately represented using instantaneous scan sampling.

Opportunistic sequence sampling was employed when focal sampling could not be continued due to human-elephant interactions or sudden disturbances. Such instances included coordinated group movements into anthropogenic landscape features, such as roads and tea plantation trails, as well as human approaches to elephants (e.g., people attempting to take photographs or forest department personnel driving elephants away). During such events, sequential observations of all observable behaviours were conducted at 20-second intervals, similar to focal observations, for all visible group members. This approach allowed documentation of the sequence of behavioural responses exhibited by individuals and groups. Sampling continued until the interaction ended or behaviour returned to an apparent baseline state (such as foraging), or the elephants were no longer visible. (Altmann, 1974; Lehner, 1992).

Analytical Methods

1. Do human presence and associated activity influence elephant time-activity budgets?

All statistical analyses were performed in the R statistical environment (version 4.5.0) (R Core Team, 2025). Initially, generalised linear mixed models (GLMMs) were fitted to understand the effects of human presence and associated activity on individual behavioural states (foraging, resting, and locomotion). However, this approach fell short because behavioural states are mutually exclusive. An increase in the time allocated to one behaviour (say, foraging) will decrease the time available to others. Consequently, modelling each behavioural state separately fails to account for the compositional nature of the data and may not capture trade-offs among behaviours.

Thus, time-activity budgets were analysed employing Dirichlet regression using the package *DirichletRegression* (Maier, 2025). For each focal observation, the proportion of time allocated to foraging, locomotion, and resting was computed. Together, these proportions form a behavioural composition whose individual components are bound between 0 and 1 and collectively sum to 1. Using this approach, one can analyse behavioural states of mutually exclusive components as a behavioural composition. Model coefficients should be interpreted as relative changes in the allocation of time among competing behavioural states. Positive coefficients indicate that a predictor (say, human presence) is associated with an increase in the proportion of time allocated to a behavioural state, whereas a negative coefficient indicates the opposite (Maier, 2014; Douma & Weedon, 2019).

Human influence on elephant time-activity budgets was examined at two levels. First, human presence was treated as a binary predictor (present or absent). Using this approach, it was possible to determine whether the presence of people alone was sufficient to affect elephant time-activity budgets. A second set of analyses focused exclusively on observations involving human presence. These analyses examined the impact of variables such as the number of people, their distance from elephants, the nature of

their activities, and who the people were to determine which aspects of human activity most significantly affected the time-activity budget of elephants.

Table 5. Anthropogenic variables collected when humans were present

Variable	***Reasoning***
Human identity	*Who (**Forest Department personnel, residents, or tourists**) initiated or characterised the encounter*
Number of people	***Count** or the number of people or crowd size*
Distance from elephants	***Proximity** of people with reference to the herd or individual (measured in metres)*
Disturbance	***Intensity** of human activity as measured by the cumulative disturbance score*

Human activity was quantified using a score derived from stimuli recorded in the field. These stimuli included talking, shouting, vehicle idling or engine noise, honking, and direct approaches towards elephants (Friswold et al., 2026; Vidya et al., 2010; Vijayakrishnan et al., 2014). Each type of stimulus was assigned a score based on its perceived severity, and these scores were summed to generate a cumulative disturbance score for each observation.

Talking and vehicle idling often reflected routine plantation activities, such as workers conversing among themselves or vehicles moving through estates. These activities were generally not directed towards elephants and may therefore represent a lower level of perceived risk. In contrast, shouting and honking were more frequently associated with situations in which people actively responded to the presence of elephants, either because they had been startled or because they were attempting to drive elephants away from areas

with high human activity. Such behaviours were therefore considered more intrusive than routine background activities. As a result, talking and vehicle idling appeared less intrusive than shouting and honking, while direct approaches consistently represented the most intrusive form of disturbance and were, therefore, assigned the highest score. The cumulative score was intended to capture the overall environment experienced by elephants when people were present.

Direct approaches were always intentional and involved people moving towards elephants. Because these encounters represented the greatest degree of direct human intrusion and were consistently associated with behavioural responses from elephants during field observations, they were assigned the highest disturbance score.

$$Cumulative\ Disturbance\ Score = T + S + I + H + A$$

Table 6. Stimuli Score Assignment

Disturbance	**Score**
Talking (T)	1
Engine Idling (I)	1
Shouting (S)	2
Honking (H)	2
Approaching (A)	3

Human identity was recorded as a categorical variable indicating the group associated with the observed stimuli (Forest Department personnel, residents, or tourists). In situations where multiple groups were present simultaneously, groups were determined by which group initiated interactions or generated observed stimuli toward elephants, rather than by the overall composition of the crowd. This enabled us to

more accurately represent the context of the encounter. Crowd size – the overall number of people in the immediate vicinity – accounted for the total number of people, independent of human identity. Biological and environmental covariates were recorded during behavioural observations. These included age-sex class, Herd size, time of day, and habitat type. Age and sex were broadly categorised as adult males, adult females, juveniles, and calves.

The distances from elephants and the number of people were positively skewed and log-transformed prior to analysis. Subsequently, both were standardised using z-score transformation (mean = 0, SD = 1) to enable comparison among predictors measured on different scales (Schielzeth, 2010). The disturbance score was also standardised.

An information-theoretic approach (Anderson & Burnham, 2004) was used to answer the research questions outlined in the Introduction chapter. A set of candidate models was compiled in line with a series of biologically plausible hypotheses. The best-fit model was judged using Akaike's Information Criterion (AIC), which ranks models based on goodness-of-fit and model complexity.

Differences in AIC (ΔAIC) between each candidate model and the top-ranked model were used to assess relative support, where models with $\Delta AIC < 2$ were retained for interpretation (Anderson & Burnham, 2004).

2. Do human presence and associated activity influence the occurrence and composition of stress-induced behavioural responses, such as vigilance, avoidance, and agitation?*

Focal observations were used to assess the impact of human presence and associated activity on behavioural events such as vigilance, avoidance and agitation behaviours. Definitions for these behaviours were adapted from previous ethogram-based studies on Asian and African elephants (Kumar & Singh, 2010b; Poole & Granli, 2009; Vijayakrishnan et al., 2018). Vigilance behaviours comprise a set of low-energy scanning or alert behaviours, whereas avoidance and agitation behaviours may signal stronger arousal

responses to human presence and activity based on escalation of perceived risk. Following Friswold et al. (2026), I grouped behaviours associated with or indicators of anthropogenic disturbance as referred to as stress-induced behavioural responses. This classification represents an ocular estimate of a behavioural response and does not imply physiological stress as measured by Vijayakrishnan et al. (2018).

Behavioural responses were classified according to their respective behavioural codes and broader behavioural context (olfactory monitoring, postural vigilance, avoidance, and agitation). To evaluate the composition of behavioural responses varied in relation to human presence and the associated disturbance characteristics, contingency tables were constructed and analysed using a chi-squared test of independence (Martin & Bateson, 2007).

In addition to analysing behavioural response composition, the occurrence of stress-induced behaviours was coded as present (1) or absent (0) for each focal observation. Generalised Linear Mixed Models (GLMMs) (using package lme4) with a binomial family were fitted to assess whether human presence and associated activity influenced the occurrence of stress-induced responses. Candidate models were constructed and ranked using Akaike's Information Criterion (AIC), yielding a best-fit model retained for interpretation. The individual identity of each individual was used as a random effect to account for repeated observations of the same individuals.

3. Do human presence and associated activity influence elephant group cohesion?

Nearest-neighbour (NN) distance recorded during instantaneous group scans was used as a measure of group cohesion. Because NN distances were non-normally distributed and recorded in discrete distance classes (<3 m, 3-6 m, >6 m), non-parametric tests were used throughout. Human presence and time of day were examined using Wilcoxon rank-sum tests. Differences among age-sex classes were assessed using the Kruskal–Wallis tests followed by pairwise Wilcoxon rank-sum tests with Bonferroni correction. Associations between NN distance and continuous predictors, including herd size, cumulative disturbance score, distance to people, and number of people, were assessed using Spearman's rank correlation coefficient. Analyses were

conducted at two levels. First, NN distances recorded in the presence and absence of humans were compared to determine the effect of human presence. Second, analyses were restricted to observations with human presence, and the effects of human activity on NN distances were examined.

4. How do elephants use habitats within a human-modified landscape?

95 % Minimum Convex Polygons (MCP) were generated using the package *adehabitatHR* (Calenge et al., 2010) for the GPS locations of each herd and solitary males with more than 30 sightings across the study period. Temporal independence was enforced by only considering one location per day per herd/individual. The ranging pattern, approximated by computing 95% Minimum Convex Polygons (MCP), of herds and bulls with more than 30 sightings is described in Figures 11 and 12 in the Results section of this chapter. These MCPs were used to provide spatial context and visualise the spatial extent of herds and solitary males ranging across the plateau.

Additionally, population-level first-order habitat selection was computed using Manly's Selection Ratio (w_i) (Manly et al., 2002). To reduce temporal autocorrelation from repeated observations of the same individuals, locations of all tracked herds and solitary males were subject to a randomisation procedure to extract one randomly selected location per herd/ solitary male per day. Night-time locations were excluded from analyses due to insufficient observations. These randomised locations were subsequently pooled to assess habitat use versus availability across the Valparai Plateau.

Habitats were stratified into five classes, namely, Natural Vegetation, Tea, Coffee, Eucalyptus, and Others (settlements, roads, etc.). Kumar et al. (2010a) additionally assessed Riverine Vegetation as a separate class; however, considering that this study spanned one field season relative to their multi-year dataset, I chose to integrate riverine vegetation as part of Natural Vegetation to ensure sufficient sample sizes within habitat class. Output interpretation is based on w_i values. A w_i value greater than one indicates positive selection, or use, of habitat, whereas a w_i less than one indicates avoidance. Values equalling one indicate that the habitat in question has been used proportional to its availability.

Results

Fieldwork was conducted between 1 December 2025 and 15 March 2026, coinciding with the peak seasonal elephant activity in the study area. The study spanned 104 field days and comprised 370 instantaneous group scans conducted at 15-minute intervals and 499 focal observations of five minutes each. Instantaneous scan sampling represented 92.5 h of observation effort and 446.25 elephant-hours, with a mean (± SE) observation effort of 2.15 (± 0.20 hr). Focal observations amounted to 41.58 h of behavioural data, with a median of 5 focal bouts per individual (mean 10.12 ± 13.69). Such sampling effort is typical for behavioural observations conducted on free-ranging elephant populations based on repeated sampling across a set of individually identified individuals; with such datasets, the aim is to maximise encounters across a wide range of individuals to not lose observations within a highly seasonal pattern of occupancy or ranging (Altmann, 1974; O'Connell-Rodwell et al., 2024; Srinivasaiah et al., 2012).

Across the 370 instantaneous scans, 179 were recorded in the presence of humans and 191 in their absence. Similarly, of the 483 focal observations retained for analysis, 206 were recorded in the presence of humans and 277 in their absence. Overall, the ratio of scans across conditions was fairly balanced.

1a. Do human presence influence elephant time-activity budgets?

A candidate set of models was compiled to test the effects of human presence on the behavioural composition (Table 7). The best-fit model (**m_bio**) contained only biological parameters. Models with human presence did not improve model fit (ΔAIC > 2 for all; Table 7). Thus, this indicates that human presence did not have any measurable effect on the behavioural composition of observed individuals.

Table 7. Candidate Dirichlet models examining the effects of human presence on the time-activity budgets of observed individuals

S. No.	Model name	Parameters	df	ΔAIC
1	m_bio	Age-sex class + Herd size	15	
2	m_bio_env	Age-sex class + Herd size + Time of day + Habitat	21	1.38
3	m_bio_human	Human presence + Age-sex class + Herd size	18	2.55
4	m_global	Human presence + Age-sex class + Herd size + Time of day + Habitat	24	4.01
5	m_env	Time of day + Habitat	9	72.26
6	m_env_human	Human presence + Time of day + Habitat	12	73.43
7	m_null	Intercept only	3	103.64
8	m_human	Human presence	6	106.26

1b. Which characteristics of human disturbance influence elephant time-activity budgets?

Before modelling, variables were tested for collinearity. Correlations among the continuous variables (number of people, disturbance score, and distance from elephants) were weak (all $|r| < 0.30$), indicating limited collinearity. Kruskal-Wallis tests further indicated that the number of people, disturbance score, and distance from elephants differed significantly among human identity groups (all $p < 0.001$). This suggests that different groups of people (forest department personnel, locals, and tourists) were associated with different disturbance conditions. As a result, all disturbance variables were retained for modelling.

Table 8. Candidate Dirichlet models examining the effects of disturbance on the time-activity budgets of observed individuals

S.No.	Model	Parameters	df	ΔAIC
1	m_identity_people	Human identity + Number of people	12	
2	m_identity_disturbance	Human identity + Disturbance score	12	5.63
3	m_identity_bio	Human identity + Age-sex class + Herd size	21	13.15
4	m_bio	Age-sex class + Herd size	15	15.10
5	m_identity_risk	Human identity + Number of people + Distance + Disturbance score	18	17.31
6	m_identity_risk_bio	Human identity + Number of people + Distance + Disturbance score + Age-sex class + Herd size	30	26.53
7	m_identity	Human identity	9	30.51
8	m_env	Time of day + Habitat	9	32.19
9	m_identity_env	Human identity + Time of day + Habitat	15	32.59
10	m_global	Human identity + Number of people + Distance + Disturbance score + Age-sex class + Herd size + Time of day + Habitat	36	37.04
11	m_id_null	Intercept only	3	38.82
12	m_id_identity_distance	Human identity + Distance	12	42.86

The best-fit model (**m_identity_people**) included human identity and the number of people as parameters (Table 8). Interactions were tested using the best-fit additive model as a base, but did not

outperform the additive model, indicating that behavioural composition was best explained by additive effects of human identity and the number of people.

Table 9. Parameter estimates from the best-fit Dirichlet regression model examining the effects of human activity on behavioural composition

Predictor	**Estimate**	**SE**	**z-score**
β coefficients for proportion of time in foraging			
Intercept	0.54	0.20	2.70
Residents	-0.64	0.25	-2.56
Tourists	-0.27	0.32	-0.85
Number of people	-0.77	0.12	-6.60
β coefficients for proportion of time in locomotion			
Intercept	-1.26	0.15	-8.40
Residents	-0.20	0.22	-0.92
Tourists	0.40	0.29	1.42
Number of people	-0.30	0.10	-2.83
β coefficients for proportion of time in rest			
Intercept	-1.70	0.16	-11.46
Residents	0.17	0.22	0.77
Tourists	-0.11	0.27	-0.40
Number of people	-0.10	0.10	-0.94

Note: *Reference human identity = Forest Department personnel.*

On a small note on model output, negative coefficients for locomotion and rest with increasing crowd size may be misleading at face value, as all three behaviours appear to decline simultaneously. This is impossible in a composition without reallocation elsewhere. These coefficients decline with respect to the

intercept, not relative to each other. Thus, when all coefficients are negative, the component with the strongest negative coefficient is the only one that declines, and the rest absorb a share of proportionality from it. Thus, predicted compositions should be used for ecological interpretations. The predicted behavioural compositions per group at mean crowd size, as well as the predicted behavioural composition in response to increasing Herd size, are shown in Figure 2 and Figure 3, respectively. Both crowd size and human identity were associated with changes in behavioural composition. Primarily, this shift manifested as a relative decrease in the proportion of time allocated to foraging.

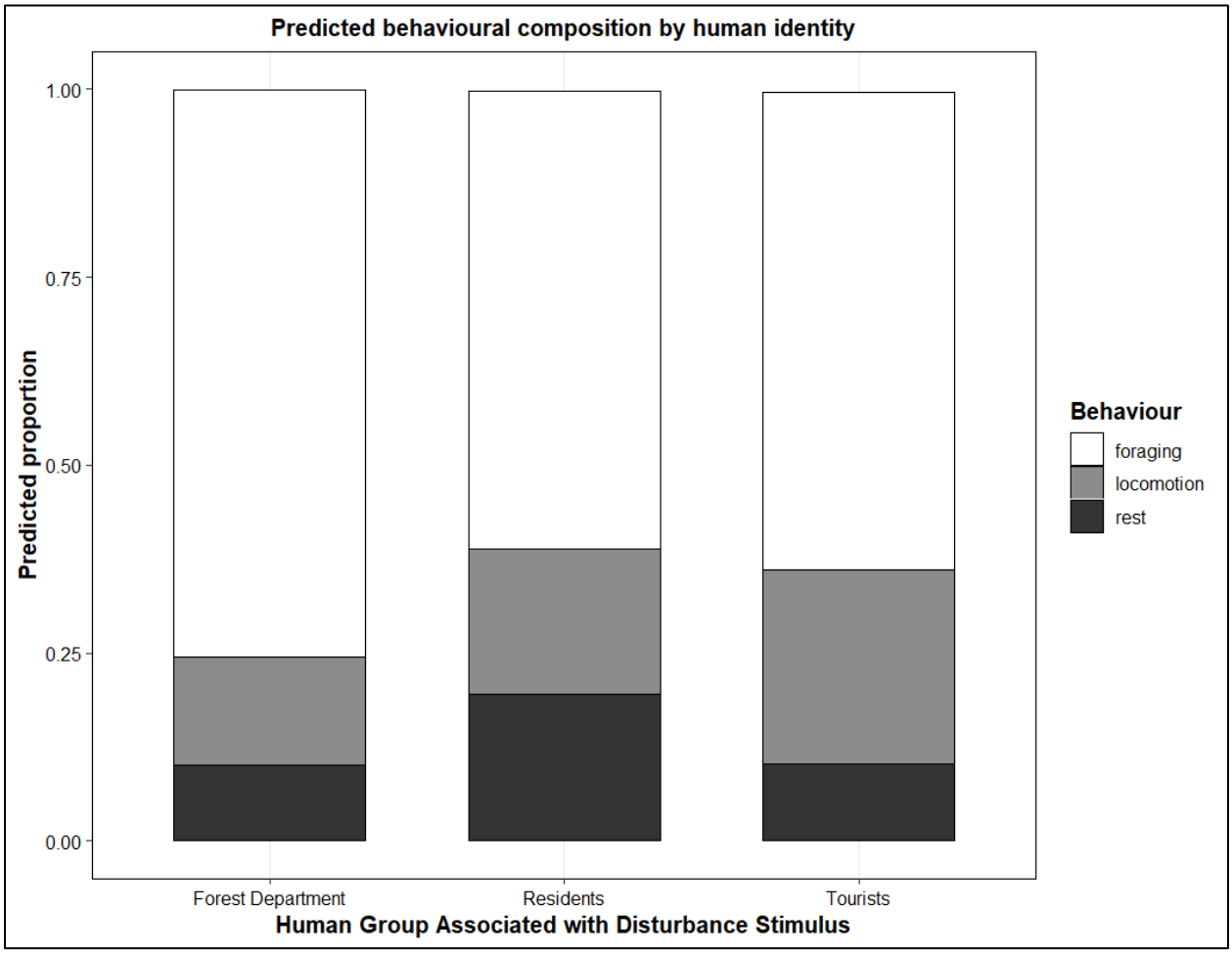

Figure 2. Predicted probability of behavioural composition by human identity.

Relative to Forest Department personnel, residents were associated with a strong reduction in foraging ($\beta = -0.64 \pm 0.25$, $z = -2.56$), with predicted foraging declining from 79% under Forest Department presence to 66.1% under resident presence. This reduction in foraging was accompanied by an increase in predicted time allocated to resting (8.3% to 16.3%) and a weak increase in locomotion (12.7% to 17.6%). Likewise, tourists were found to have a weak effect associated with a decline in foraging ($\beta = -0.27 \pm 0.32$, $z = -0.85$).

Although no strong effects were detected for human identity groups with respect to locomotion or rest, predicted rest increased substantially when residents were present, from 8.3% to 16.3% ($\beta = -0.20 \pm 0.22$, $z = -0.91$). The same was not true for tourist presence, for which the allocation remained nearly the same as for Forest Department personnel (8.3% to 8.8%). This indicates that the primary trade-offs in behavioural composition – rather than direct effects on any one particular behavioural state – may be between foraging and rest for residents and between foraging and locomotion for tourists.

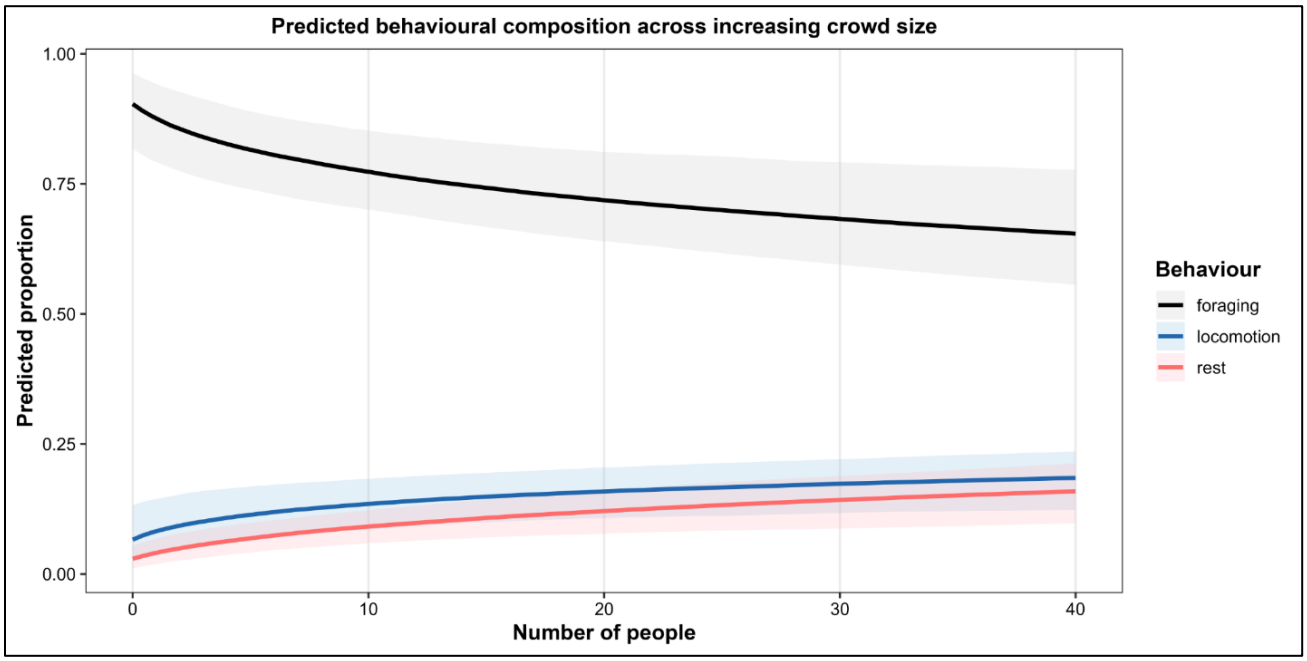

Figure 3. Predicted behavioural composition across increasing crowd size.

The number of people present was associated with the strongest and most consistent effect on behavioural composition across all human identity groups. At mean crowd size, elephants allocated 79.0% of their time to foraging, 12.7% to locomotion, and 8.3% to resting ($\beta = -0.77 \pm 0.12$, $z = -6.60$). At one standard deviation above mean crowd size, predicted foraging declined to 69.0%, while locomotion increased to 17.2% and resting increased to 13.8%. The sum of predicted proportions remained 1.0 across conditions, confirming that the observed increase in locomotion and rest represents genuine compositional reallocation rather than independent increases in these behaviours. This pattern reveals that increasing crowd size shifts the behavioural composition of the time activity budget almost entirely at the expense of foraging.

2a. Do human presence and associated activity influence the composition of stress-induced behavioural responses?

The counts of stress-induced behavioural responses differed between observations recorded in the presence and absence of humans (Figure 4). Across both conditions, ears spread (*es*) was the most frequently recorded response, followed by sniff the air (*sd*), freeze (*f*), and sniff the ground (*sm*). In contrast, certain responses, including orient away (*oa*), retreat (*rt*), move away (*ma*), run away (*ra*), and stare at stimulus (*sr*), occurred almost exclusively when humans were present. Tail erect and stiff (*tss*) was also more frequently observed in the presence of humans.

Since elephants in this landscape were mostly observed in tea plantations, where human presence is common, elephants were also frequently observed assessing the landscape in response to any auditory stimulus (e.g., excavators clearing tea bushes on the far side of the plantation) using *es*, *f* responses. Similarly, *sm*, *sd*, *es*, and *f* were commonly observed when elephants moved across tea estate trails in procession. Thus, low-order vigilance behaviours were also used to continuously assess human presence, thereby explaining their relative counts in observations without human presence.

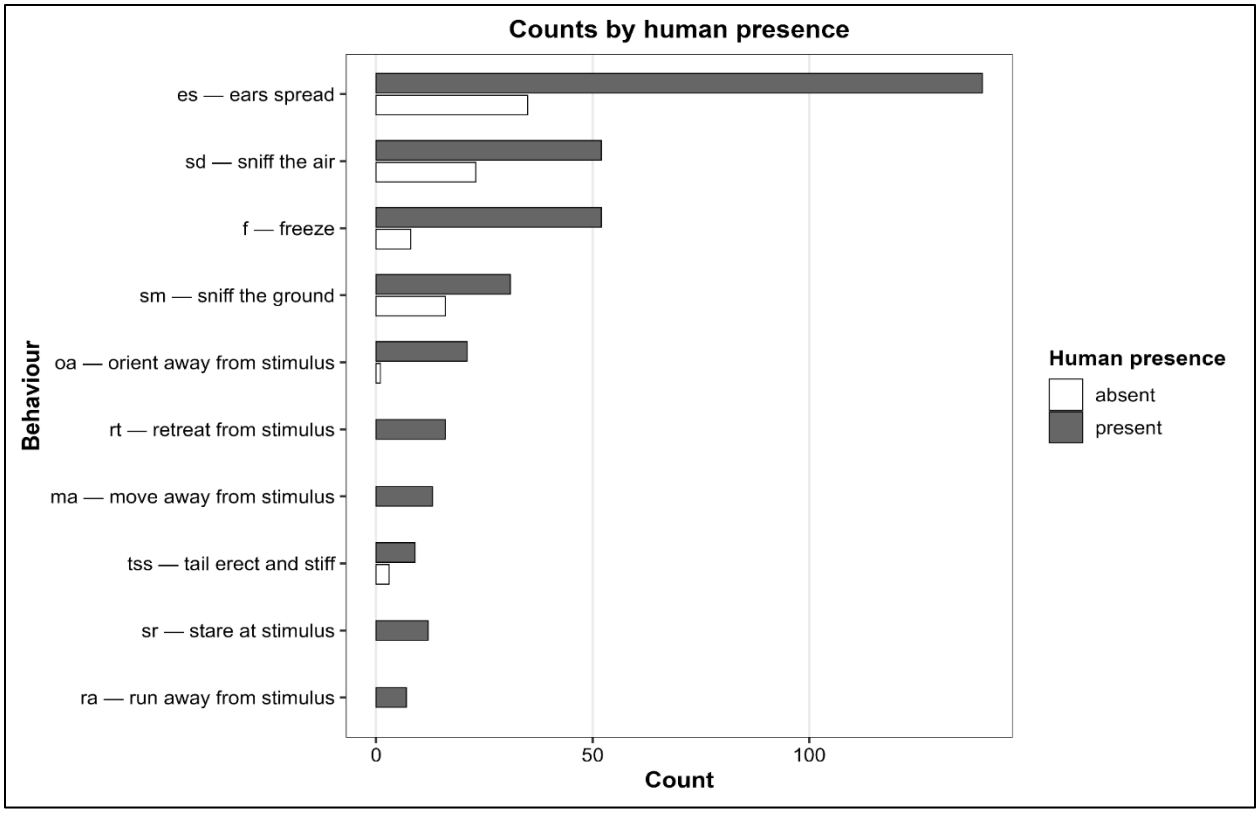

Figure 4. Relative counts of stress-induced behaviours across human-present versus human-absent observations,

To examine broader patterns in behavioural response composition, individual stress-induced responses were further classified into behavioural contexts based on the ElephantVoices Ethogram (Poole & Granli, 2020). These contexts group related behavioural responses according to their ecological function and include olfactory monitoring, postural vigilance, avoidance, and agitation (Table 10). For subsequent analyses, avoidance and agitation behaviours were combined into a single category representing escalated responses because agitation behaviours were rare and occurred primarily alongside avoidance responses.

Table 10. Classification of stress-induced responses into behavioural contexts adapted from the ElephantVoices Ethogram (Poole & Granli, 2020).

Behavioural Context	**Behaviour Code**	**Description**
Olfactory Monitoring	*sd*	Sniff the air
	sm	Sniff the ground
Postural Vigilance	*es*	Ears spread
	f	Freeze
	sr	Stare at the stimulus
	hr	Head raised
Avoidance	*oa*	Orient away from the stimulus
	rt	Retreat from the stimulus
	ra	Run away from the stimulus
	ma	Move away from the stimulus
Agitation	*tss*	Tail erect and stiff

Chi-square tests of independence were used to assess whether the composition of vigilance and other behavioural responses differed among human identity and age-sex classes.

The composition of stress-induced behavioural responses differed significantly among human identity groups (Pearson's $\chi^2 = 18.01$, df = 4, p = 0.001). Forest Department encounters were characterised by a greater proportion of escalated responses (25.6%) and olfactory monitoring responses (34.9%) than expected, while postural vigilance responses occurred less frequently than expected. In contrast, tourist encounters were dominated by postural vigilance responses (73.3%), which occurred more frequently than expected. No response category occurred more or less frequently than expected with residents.

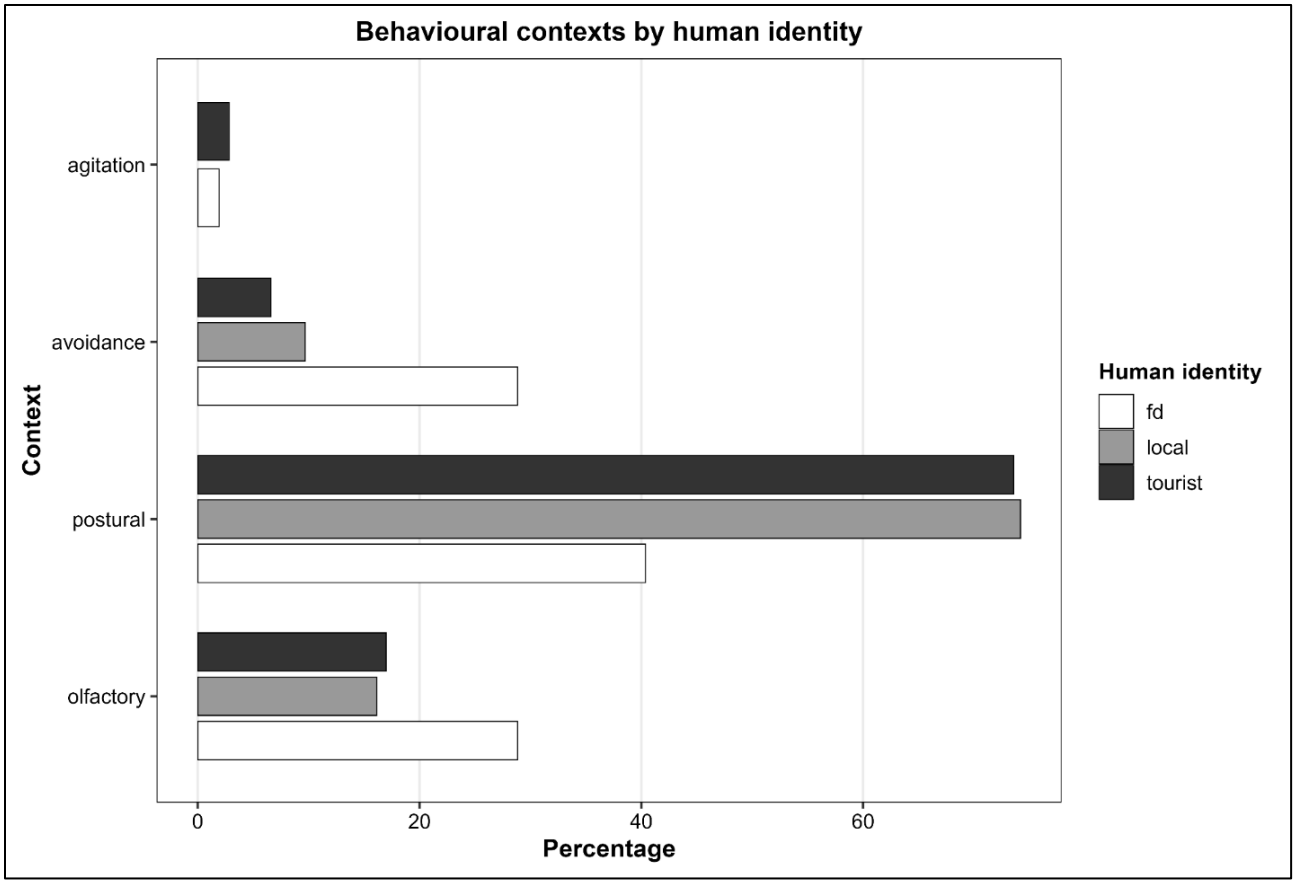

Figure 5. Behavioural contexts by human identity groups.

Behavioural response compositions varied significantly among different age-sex classes (Pearson's $\chi^2 = 30.80$, df = 6, $p < 0.001$). Adult males exhibited a lower-than-expected frequency of agitation and avoidance responses (4.7%), with the majority of their responses comprising postural vigilance (62.8%) and olfactory monitoring (32.6%). In contrast, juveniles displayed a higher proportion of agitation and avoidance responses (24.7%) and a lower incidence of postural vigilance than expected. Calves revealed the highest rates of agitation and avoidance responses (37.5%) and the lowest rates of postural vigilance (18.8%). However, given that the sample size was low with only 16 behavioural responses recorded for calves, these findings should be interpreted with caution. Adult females predominantly exhibited postural vigilance responses (61.2%), with lower proportions of olfactory monitoring (25.3%) and agitation and avoidance responses (13.5%). Collectively, these results indicate that younger elephants respond to perceived

disturbances or threats with more pronounced behavioural responses, whereas adult males primarily rely on postural and olfactory vigilance

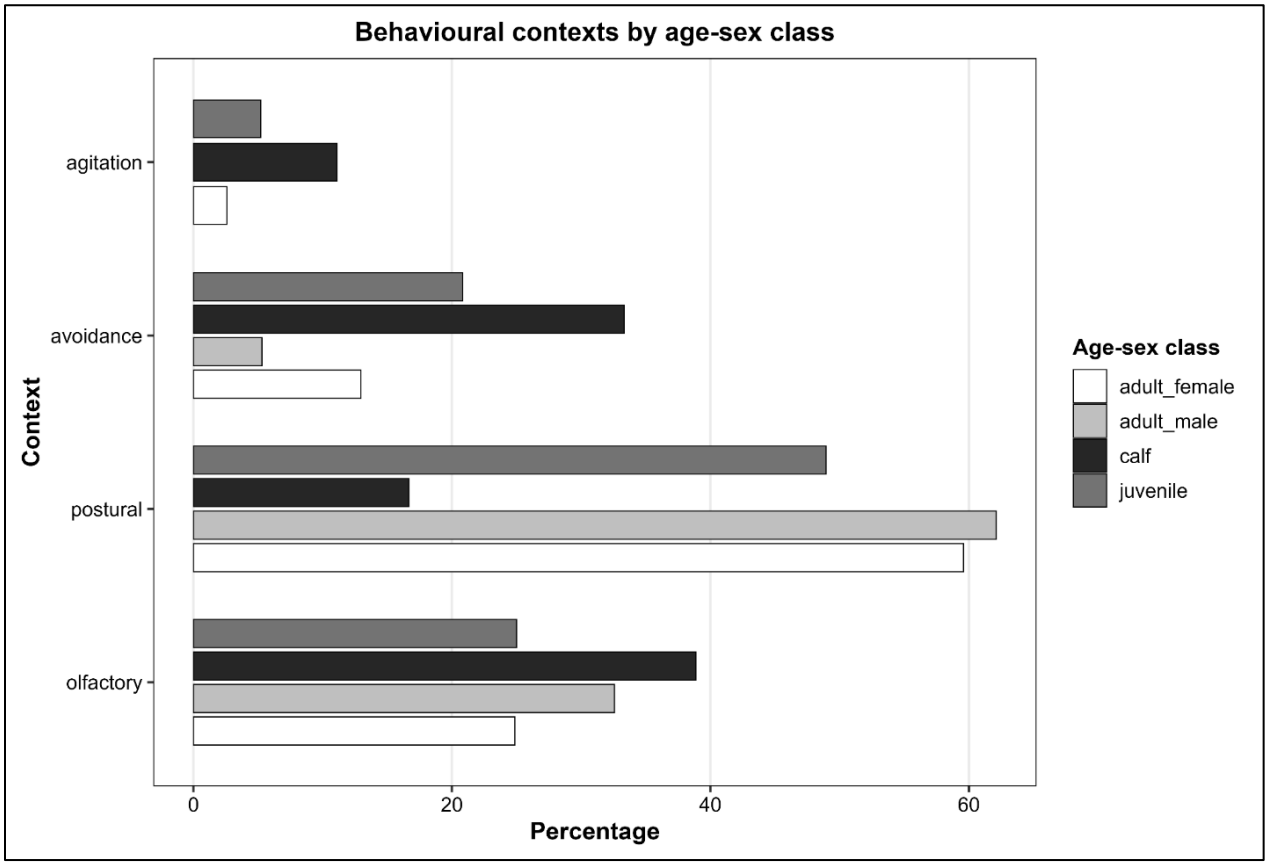

Figure 6. Behavioural contexts by age-sex class.

2b. Does human presence and associated activity influence the composition of stress-induced behavioural responses?

A candidate set of models was compiled to test the effects of human presence on the occurrence of vigilance and other behavioural responses (Table 11). The best-fit model (**m_vig_group_human**) contained only human presence and herd size as parameters.

Table 11. Candidate GLMMs examining the occurrence of vigilance and other behavioural responses to human presence.

Model	**Parameters**	**df**	**ΔAIC**
m_vig_group_human	Human presence + Herd size	4	
m_vig_presence_bio_human	Human presence + Age-sex class + Herd size	7	3.76
m_vig_presence_human	Human presence	3	4.51
m_vig_presence_global	Human presence + Age-sex class + Herd size + Habitat + Time of day	9	7.48
m_vig_presence_age_human	Human presence + Age-sex class	6	7.55
m_vig_presence_env_human	Human presence + Habitat + Time of day	5	8.34
m_vig_presence_bio	Age-sex class + Herd size	2	41.34
m_vig_presence_env	Habitat + Time of day	6	42.67
m_vig_presence_null	Intercept only	4	45.32

Note: *Elephant ID was included as a random intercept in all models.*

Interactions were tested using the best-fit additive model as the base, but they did not improve model fit and were not retained.

Table 12. Parameter estimates from the best-fit GLMM examining vigilance and other behavioural responses to human presence.

Predictor	**Estimate (β)**	**OR**	**SE**	**Z value**
Intercept	-2.62	0.073	0.29	-8.98
Human presence (present)	1.93	6.93	0.34	5.72
Herd Size	-0.48	0.62	0.19	-2.40

Human presence increased the odds of stress-induced behavioural responses approximately seven-fold (OR = 6.93, β = 1.93 ± 0.34, z = -8.98). Herd size had a strong negative effect on the occurrence of stress-induced behavioural responses, with a 1-SD increase in herd size associated with a 38% reduction in the odds of stress-induced behavioural responses (OR = 0.62, β = -0.48 ± 0.19, z = -2.40).

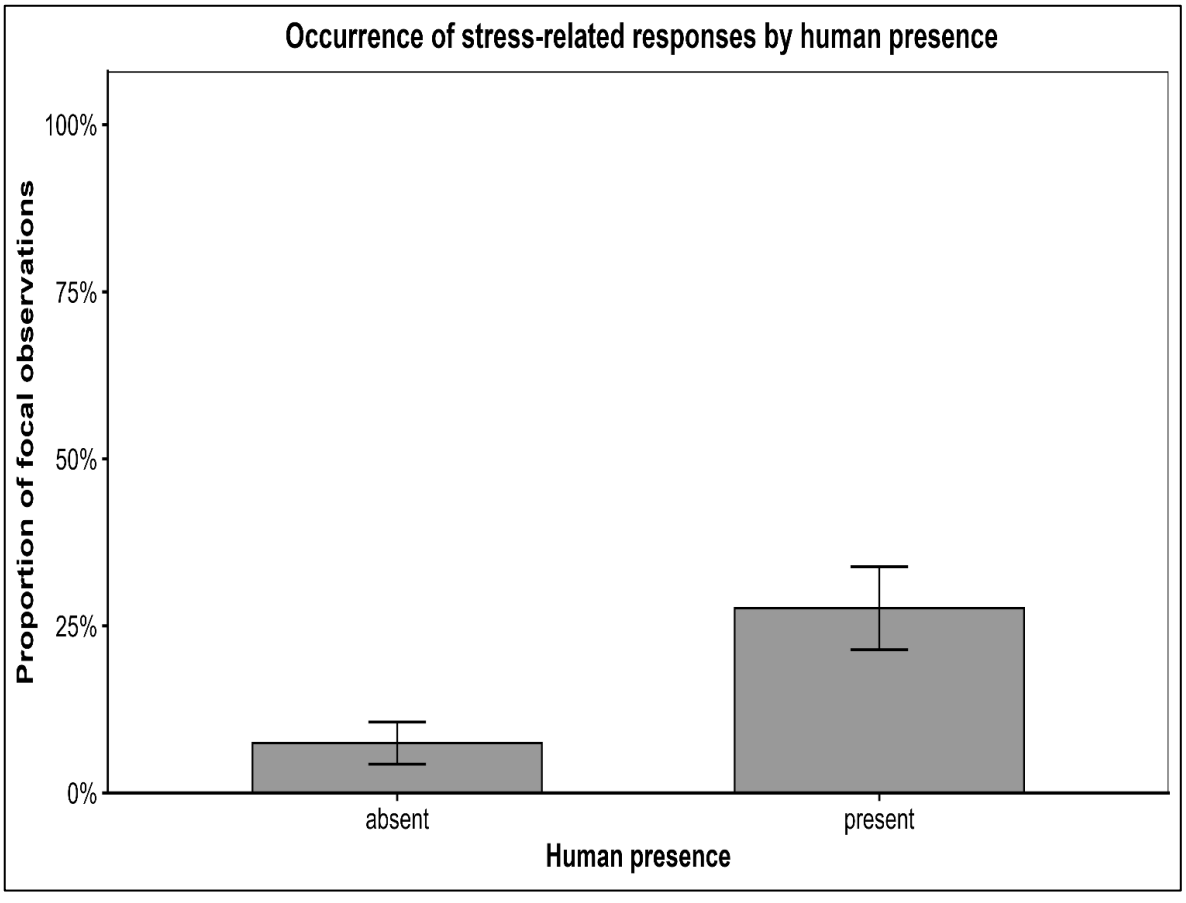

Figure 7. Occurrence of vigilance and other stress-related behaviours across observations.

I also assessed whether characteristics of human disturbance influenced the occurrence of stress-induced behavioural responses. As these behaviours had already been shown to increase in the presence of humans, analyses were restricted to focal observations conducted under those conditions. The occurrence of responses during each focal observation was used as the response variable. A candidate set of Generalised Linear Mixed Models (GLMMs) with a binomial family was used to examine the effects of the number of people & their proximity to elephants, disturbance, and human identity on the occurrence of behavioural responses.

Table 13. Candidate GLMMs examining the occurrence of stress-induced behavioural responses to disturbance.

Model	**Parameters**	**df**	**ΔAIC**
m_vig_identity_distance	Human identity + Distance	5	
m_vig_identity	Human identity	4	1.97
m_vig_null	Intercept only	2	2.30
m_vig_distance	Distance	3	3.18
m_vig_identity_people	Human identity + Number of people	5	3.19
m_vig_people	Number of people	3	3.51
m_vig_identity_disturbance	Human identity + Disturbance score	5	4.17
m_vig_bio	Age-sex class + Herd size	6	4.34
m_vig_disturbance	Disturbance score	3	4.39
m_vig_risk	Human identity + Number of people + Distance + Disturbance score	7	4.50

A candidate set of models was compiled to test the effects of human presence on the occurrence of stress-induced behavioural responses (Table 2.6). The best-fit model (**m_vig_identity_distance**) contained human identity and distance from elephants as parameters. Interactions were tested using the best-fit additive model as the base, but they did not improve model fit and were not retained.

Table 14. Model results from the best-fit GLMM examining stress-induced behavioural responses to disturbance.

Predictor	**β**	**OR**	**SE**	**z**
Intercept	-2.43	0.09	0.56	-4.30
Resident (vs FD)	1.52	4.56	0.79	1.93
Tourist (vs FD)	1.99	7.32	0.74	2.69
Distance from elephants	-0.69	0.50	0.35	-1.94

Relative to interactions with Forest Department personnel, the odds of stress-induced behavioural responses of elephants were approximately 4.6 times greater in the presence of residents (OR = 4.56, $\beta = 1.52 \pm 0.79$, $z = 1.93$) and 7.3 times greater in the presence of tourists (OR = 7.32, $\beta = 1.99 \pm 0.74$, $z = 2.69$). Distance from elephants had a moderate negative effect on behavioural responses, with a one-unit increase in log-transformed distance associated with an approximately 50% reduction in the odds of stress-induced behavioural responses (OR = 0.50, $\beta = -0.69 \pm 0.35$, $z = -1.94$).

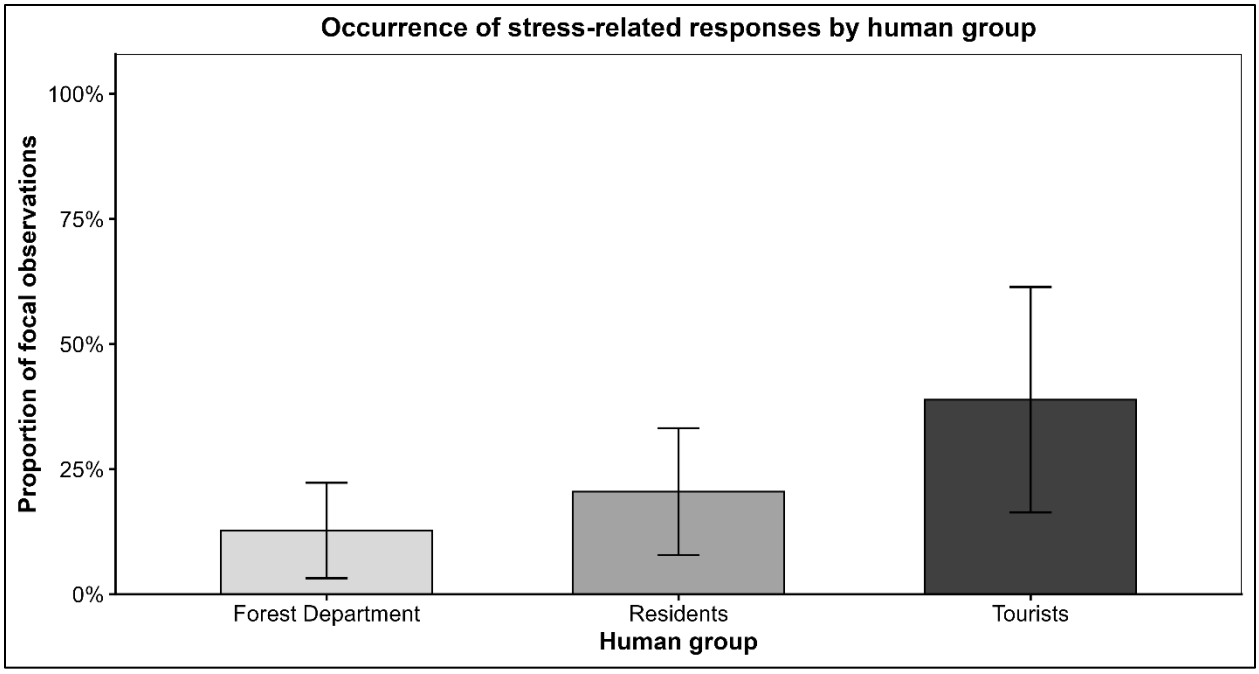

Figure 8. Occurrence of stress-induced behaviours by human identity group.

Model-derived predictions indicated a gradual decline of stress-related responses with increasing distance from humans. As this relationship was continuous rather than exhibiting a distinct threshold, the distance at which responses became uncommon depends on the predicted probability selected. For example, a predicted probability of 20% corresponds to a distance of approximately 20 m, whereas a predicted probability of 5% is reached beyond 200 m. Thus, I used the distance at which the predicted probability declined to 10% as a reference point, as this represents fewer than one response for every ten observations. However, it should be noted that this is not a discrete threshold but rather an indication that beyond approximately 70 m, it is less likely to see a response. Notably, this estimate is broadly in line with the >50 m distance reported by Kumar et al. (2010b).

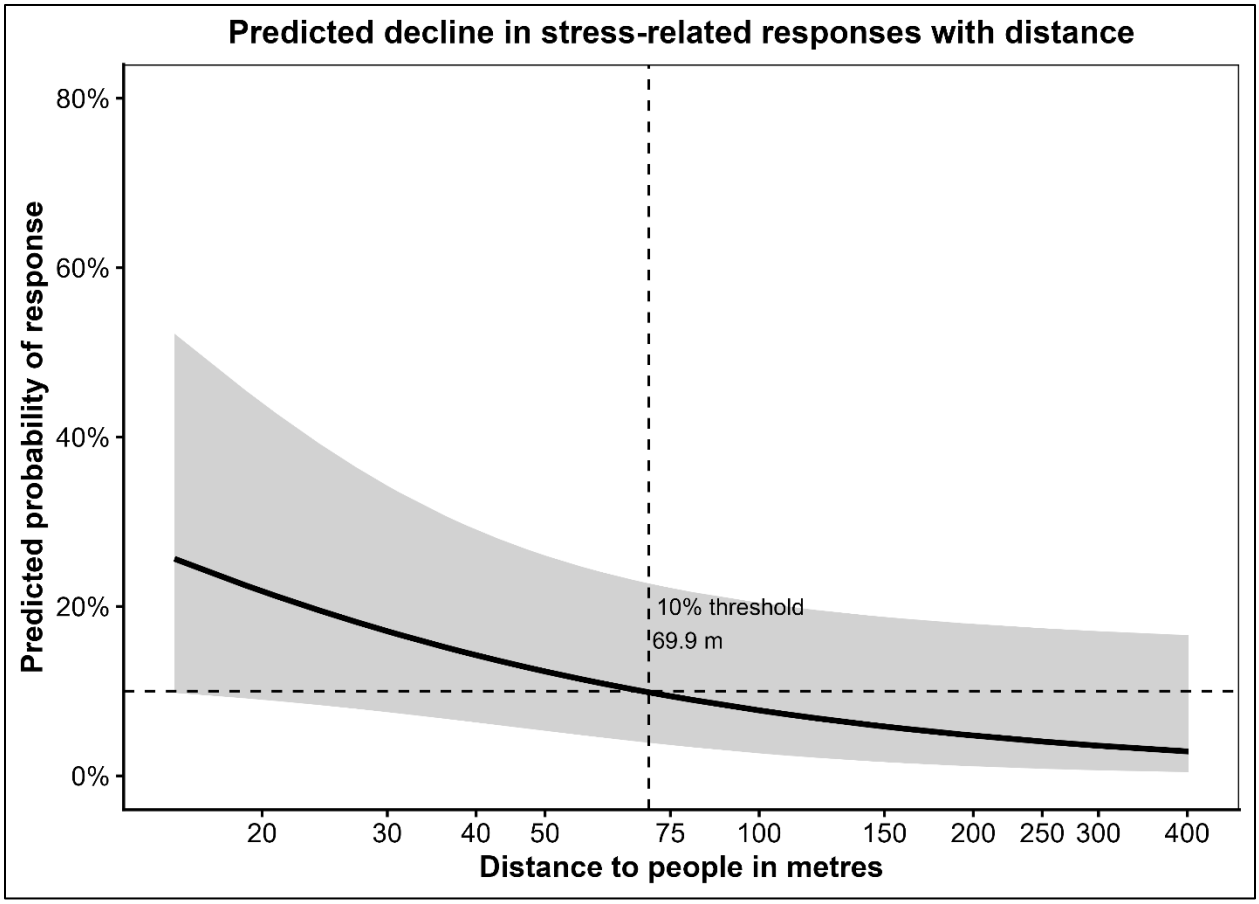

Figure 9. Predicted decline in stress-related behaviours as distance to people increases.

3a. Do elephant groups become more cohesive in response to human presence and disturbance?

NND was recorded in discrete distance classes (<3 m, 3-6 m, and >6 m). NND differed significantly among age-sex classes (Kruskal–Wallis $\chi^2 = 97.50$, df = 2, $p < 0.001$). Pairwise Wilcoxon tests with Bonferroni correction indicated significant differences among all age-sex classes (all adjusted $p < 0.001$).

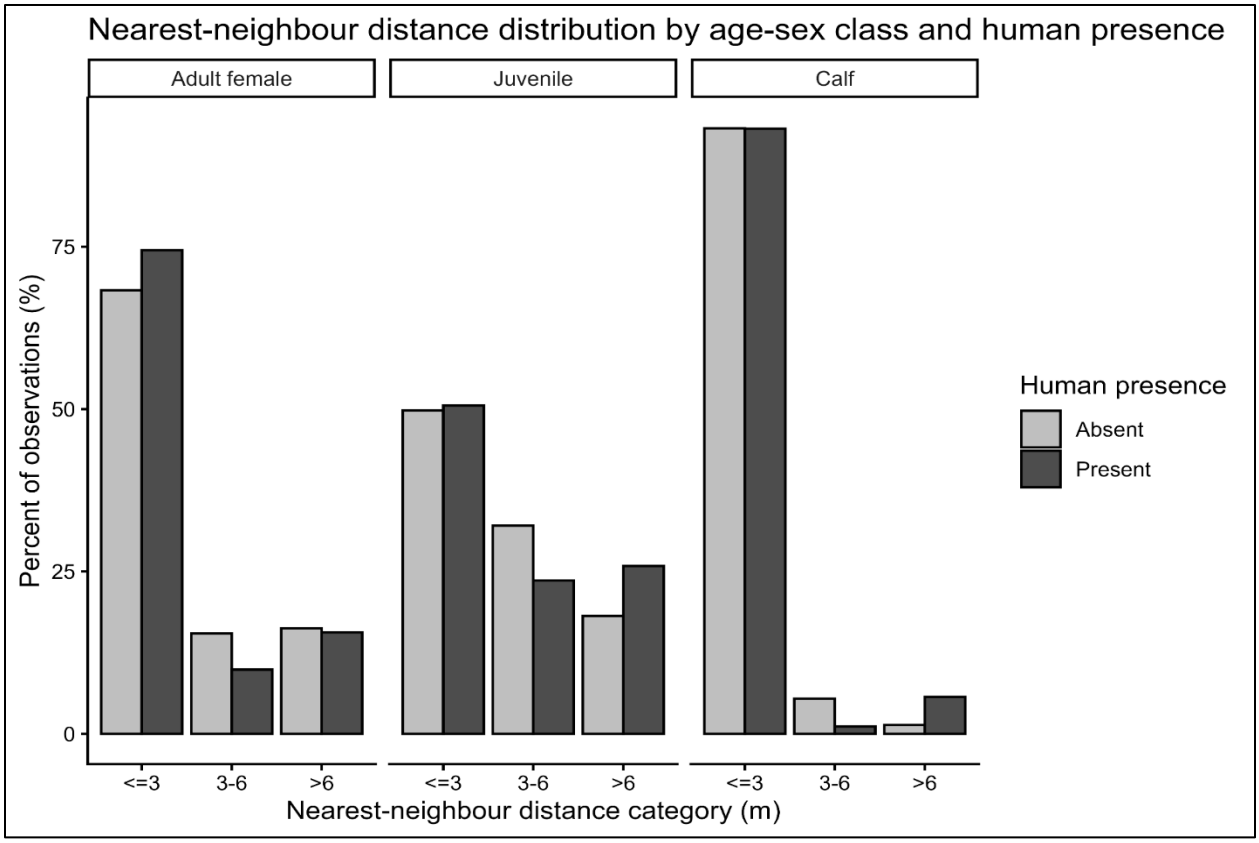

Figure 10. Nearest Neighbour Distance (NND) by age-sex classes and human presence.

However, Wilcoxon rank-sum tests indicated that NND did not differ between observations recorded in the presence and absence of humans (W = 127,535, p = 0.997). Considering juveniles were generally the most dispersed from the group, they were used to assess whether human presence influenced the age-sex class most likely to show changes in group cohesion; juvenile NND was analysed separately but did not differ between juvenile observations recorded in the presence and absence of humans (W = 20,205, p = 0.432, r = 0.039). Together, these results indicate that human presence alone did not influence group cohesion.

3b. Do elephant groups become more cohesive in response to human activities?

NND continued to vary among age-sex classes (Kruskal–Wallis $\chi^2 = 48.00$, df = 2, $p < 0.001$) in which humans were present. All pairwise comparisons remained significant even after Bonferroni correction (all adjusted $p \leq 0.001$).

NND showed a negative correlation with disturbance score (Spearman's $\rho = -0.138$, $p = 0.003$) and distance from elephants ($\rho = -0.119$, $p = 0.011$), showing that elephants tended to be more closely spaced during encounters when humans were in close proximity or creating disturbance. No significant relationship was found between NND and the number of people present ($\rho = -0.077$, $p = 0.100$). Additionally, elephant herd size was negatively correlated with NND ($\rho = -0.242$, $p < 0.001$), indicating that individuals in larger groups tended to be more closely spaced.

4. Do habitat characteristics influence elephant space use?

Table 15. Estimated ranging areas (95% MCP) of focal elephant herds and solitary males

Herd/Male ID	Area (in sq.km)	Number of locations
Spook	25.99	60
IG	22.47	62
PTH	59.97	134
MGH	25.34	49
VTH	17.65	76

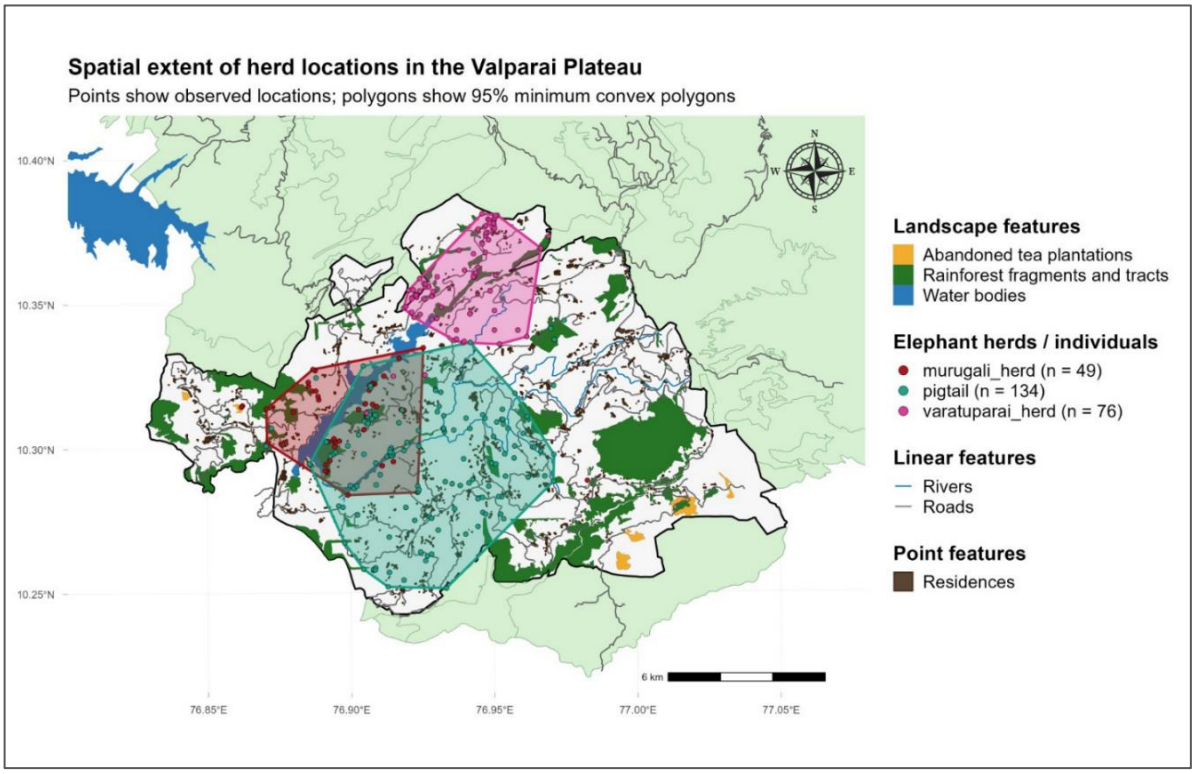

Figure 11. 95% MCPs were generated for selected herds across the Valparai Plateau.

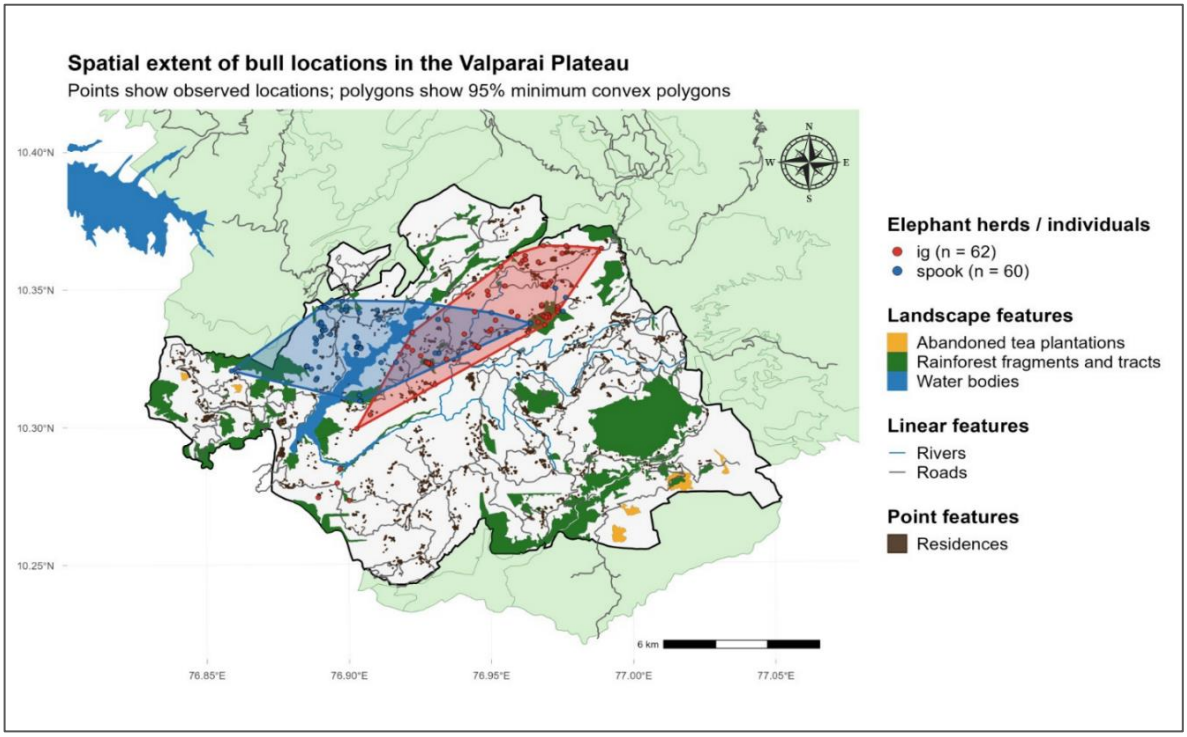

Figure 12. 95% MCPs generated for selected solitary males across the Valparai Plateau.

Estimated ranging areas varied considerably among selected herds and solitary males (Table 15, Figures 11 – 12). Among selected herds, PTH (Pigtail) had the largest estimated ranging area (59.97 km²). VTH (Varatuparai) exhibited the smallest ranging area, including both herds and solitary males. However, the spatial spread or distribution of locations may be more revealing than spatial area, as herds and solitary males utilised distinct regions of the plateau.

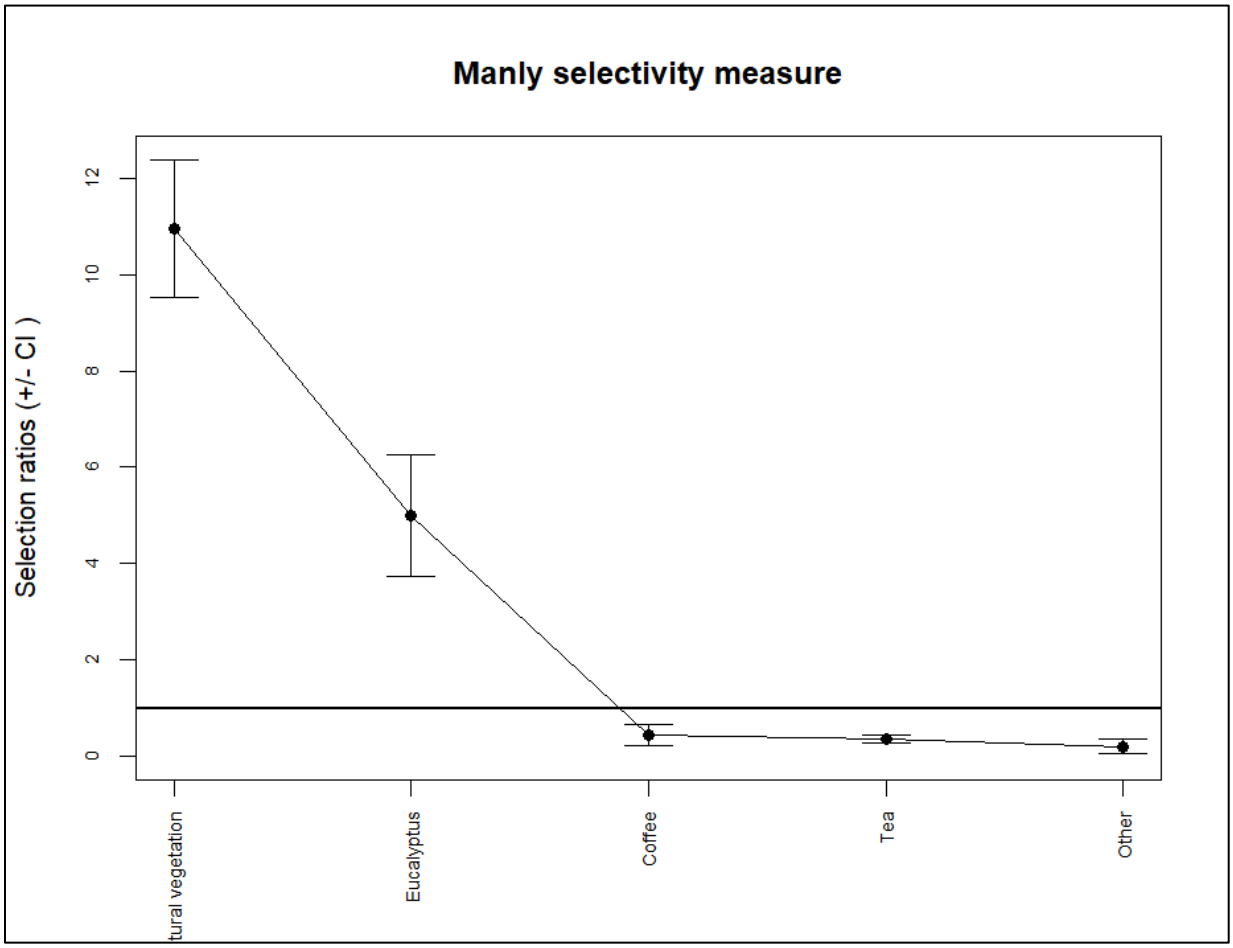

Figure 13. Comparison of observed use versus availability of habitat classes by elephants in Valparai

Population-level habitat selection differed significantly from expected results ($\chi^2 = 779.85$, df = 4, $p < 0.001$). Of all habitats, Natural Vegetation was most positively selected, or used more in proportion to its availability ($w_i = 10.95$). Similarly, Eucalyptus was also positively selected relative to availability ($w_i = 5.00$). Tea, Coffee

and Others as habitats were negatively selected in proportion to their availability (w_i = 0,36; w_i = 0.44; w_i = 0.20). Further, the selection of Natural Vegetation and Eucalyptus was also strengthened by the Standardised selection index (B_i), from which one can infer a hierarchy of habitat selection, indicating Natural Vegetation (Bi = 0.759) as the most positively selected habitat.

Discussion

As fragmentation and habitat loss continue to reduce the extent of continuous natural habitats, wide-ranging herbivores such as elephants are increasingly navigating human-use landscapes to access high-quality forage patches in forest-agricultural mosaics (de la Torre et al., 2022). These forays expose them to the risk of encountering people. Consequently, understanding how elephants respond to people within shared landscapes is important for developing strategies of coexistence. Previous studies that explore human-elephant interactions in human-use landscapes have demonstrated that anthropogenic impact can influence elephant behaviour at varying scales.

Figure 14. MGH herd in a defensive flank while Forest Department personnel, as well as a few residents attempt to repeatedly drive them away from worker housing in a tea plantation.

Kumar et al. (2010b) observed that feeding, agitation, and herd cohesion varied across habitats on the Valparai Plateau, while closer human proximity and larger numbers of people reduced feeding and increased agitation. Vijayakrishnan et al. (2018) found that the overall FGM concentration profiles of plateau elephants and the adjacent populations of forest elephants in the Vazachal Reserve Forest did not significantly differ. This similarly suggests that human–elephant encounters may be more informative indicators of physiological stress responses. Elsewhere in southern India, Sriniviasiah et al. (2012) reported reduced feeding among elephants observed in areas with high human disturbance. A concomitant increase in vigilance behaviours was also noted. Together, these studies suggest that anthropogenic impact can influence elephant behaviour across multiple scales. Following this line of reasoning, I tested this relation by evaluating human presence as a coarse indicator and encounter-specific characteristics as fine-scale predictors of behavioural responses.

Dirichlet regression results indicated that human presence alone did not detectably alter the time allocated among foraging, locomotion, and resting. This finding is consistent with the pattern of comparable FMG concentrations reported for plateau elephants relative to elephants in the adjoining Valparai and Vazhachal Reserve Forests (Vijayakrishnan et al., 2018). Together, these findings suggest that human presence alone may be too coarse a variable to capture the full spectrum of human–elephant interactions occurring within this landscape. However, elephants are highly social and cognitively complex; responses to people are likely influenced by individual experiences and idiosyncrasies (Srinivasiah et al., 2012).

A significant portion of the residents—approximately 50,000 individuals—on the Valparai Plateau are engaged in activities such as harvesting tea leaves, plucking coffee, applying pesticides, or operating vehicles. Their families often reside within estates in housing structures locally referred to as “lines” or “workers’ quarters”. Additionally, there are daily-wage labourers, small-scale businesspeople, and students who routinely traverse plantation areas. Given the inevitability of both people and elephants using these spaces, the odds of direct interactions are relatively high.

Residents, Forest Department personnel, and tourists represent the three most common categories of people encountered by elephants on the plateau. Each category encounters elephants under very different

circumstances. Residents often co-occur with elephants while carrying out routine daily activities whereas the Forest Department personnel are associated with monitoring and conflict-management operations, and tourists typically encounter elephants opportunistically. Depending on circumstances, Forest Department personnel may also drive or chase elephants away from settlements. Additionally, tourists frequently visit the plateau and are often aware of the high probability of sighting elephants (personal observation).

To explore whether these local contexts had differential effects, I concentrated exclusively on observations where humans were present and measured the effect of the number of humans present, who they were, their proximity to elephants, and their specific activities. My results suggest that elephant behaviour is significantly influenced by the context of human-elephant encounters. Human identity and crowd size explained behavioural variation better than human presence alone, indicating that elephants may assess not only whether people are present but also how many people are present and how they behave.

The proportion of time allocated to foraging decreased in the presence of residents. However, this reduction is spurious when taken in isolation. Residents and elephants frequently co-occur in contexts where elephants are already resting, particularly within tea estates and swamps during daylight hours. Thus, reduced foraging may reflect spatial cooccurrence as opposed to active disturbance.

Considering that elephants occupied this landscape for generations, we may speculate that elephants are habituated to the routine activity of residents working in plantations and may not perceive them as a significant threat. This suggests that elephants on the Valparai Plateau do not perceive all encounters with people as equally risky.

On the contrary, tourists were associated with a weaker decline in foraging as well as a corresponding increase in time allocated to locomotion. This may reflect that tourists elicit flight responses due to the disturbances that they are associated with. Tourists' encounters frequently resulted in crowding as multiple groups stop to observe elephants. Although these crowds often contained a mix of residents, tourists, and the Forest Department personnel, a majority of the disturbance stimuli were generated by tourists. Tourists were

observed shouting, hooting, and approaching elephants (personal observation). Consequently, Forest Department personnel intervened to drive elephants away as opposed to disperse or manage the crowd gathered. Additionally, elephants are most frequently encountered by tourists during road crossings. Often, these road crossings facilitated access to important habitat patches like riverine habitats, rainforest fragments, or swamps. In these situations, groups and solitary individuals have been observed either waiting for extended periods of time or foregoing foraging while repeatedly attempting to navigate the road during minimal human activity. In these situations, the effect of each disturbance stimulus may be effectively amplified by the increasing crowd size.

Figure 15. A resident attempts to stop vehicles to enable a solitary adult male to cross the road.

In contrast to the behavioural composition of time activity budgets, stress-induced behaviours were affected by anthropogenic influence at both coarse and fine scales. These behaviours are often immediate responses to changes in the local vicinity and may provide insight into how elephants are actively assessing and responding to proximate cues around them. Model-derived predictions indicate that stress-induced

behaviours reduce in frequency beyond approximately 70 m away from a herd or individual. This estimate is broadly supported by Kumar et al. 2010b who determined a threshold greater than 50 m.

Although stress-induced behaviours increased in the presence of all human groups, the composition of these responses differed across human groups. Forest Department were associated with a greater proportion of escalated responses more than expected, while tourists were associated with more postural vigilance responses than expected. This likely reflects differences in encounter contexts: Forest Department personnel may be involved in more intrusive interactions, such as chases and drives, whereas tourists may trigger frequent alertness.

Nearest-neighbour distances (NND) did not differ between observations recorded in the presence and absence of humans. However, within observations where humans were present, NND decreased with disturbance score and proximity to people, although these effects were weak. Age-sex class was a strong determinant of spacing within herds, with calf-cow units appearing to be highly associated, regardless of human presence, whereas juveniles tended to be more exploratory and dispersed. This result supports the findings of Srinivasaiah et al. (2012), who found that in Bannerghatta National Park, inter-individual distance lowered as human disturbance levels increased.

Together, these findings suggest that elephant responses within the Valparai Plateau are context-dependent and occur at various behavioural scales. Broad time activity budgets remained stable when human presence is taken as the sole indicator of anthropogenic impact. However, anthropogenic impact could be teased apart when encounter-specific characteristics were considered. Stress-induced behaviours were affected by anthropogenic impact at both broad and fine scales. These patterns suggest that although elephants may show some degree of tolerance toward human presence in the landscape, they still respond to specific stimuli perceived as highly intrusive or high risk.

The behavioural patterns in this study can also be interpreted in tandem with the broader spatial context of how elephants use the Valparai Plateau. The landscape is a mosaic whose dominant matrix

comprises tea. Although elephants were often encountered in tea plantations, habitat selection analyses revealed that elephants used both tea and coffee plantations less than expected based on their availability. Instead, they preferred the cover of Natural Vegetation, such as forest fragments and riparian habitats, as well as Eucalyptus stands during daylight hours. These findings broadly mirror the findings of Kumar et al. 2010(b), who also documented similar patterns. These findings illustrate that although elephants may be habituated to human presence within the plantation matrix, they still preferentially seek out a small proportion of the landscape in the form of Natural Vegetation and Eucalyptus.

Thus, future co-existence strategies should be formulated based on how human-elephant interactions unfold and how to manage them, as opposed to focusing solely on where they occur.

Limitations

There are a few limitations to be noted when interpreting the biological implications of this work.

Repeated observations of identified individuals were not explicitly accounted for in the Dirichlet regressions, as the *DirichletReg* package does not support mixed-effects modelling. Given that elephants are highly cognisant and social animals and have idiosyncratic responses (Srinivasiah et al., 2012), future efforts could employ Bayesian approaches implemented in *Stan* or *brms* packages. However, for this study, it was deemed that the present approach may be useful for examining trade-offs between behaviours at a population level.

Similarly, behavioural observations were not equally distributed among individuals, herds, human identity groups, and encounter context. Although this is a known limitation and common for field-based observational studies, it must be noted that such sampling may bias the relative strength of detectable patterns.

The chi-square tests for composition of stress-induced events were primarily exploratory. They proved valuable for identifying overarching ecological patterns in the responses exhibited by elephants. Additionally, a quantitative examination followed Vidya et al. (2010), where both stimuli and responses were

ranked using an ordinal scale to examine composition through ordinal multinomial models, which can be used as a framework to adopt inferential analysis in the future.

A disturbance score used in this study was developed based on field observations. While this allowed multiple stimuli to be ranked together, it is still a simplified approximation of how elephants may perceive human disturbance or risk. Different elephants may respond disproportionately to different stimuli based on past experiences, group composition, local context, and landscape elements.

Although opportunistic sequence data were collected every time elephants crossed anthropogenic structures or during drives and chases, this data could not be effectively analysed within the time available. Thus, all results presented indicate moderate disturbance contexts, as many chases or drives or road crossings that can be considered as highly intrusive disturbances that lasted for a considerable amount of time (often lasting over an hour) were not presented in the study or thesis.

It should be noted that this study was conducted in one field season in a landscape where both humans and elephants have shared space for generations. The responses of elephants within this landscape may therefore reflect local histories of exposure and reflect patterns of habituation, learning, and cultural transmission within this population. Long-term studies across multiple seasons and across multiple shared landscapes, each with its own local context and history, are needed to assess whether these patterns are consistent over time across different socio-ecological contexts.

Although exploratory spatial mapping was pursued using Minimum Convex Polygons due to a lack of time, these analyses did not compute spatial overlap among herds and solitary males. Additionally, MCPs are sensitive to sample size and may overestimate the actual area used (Börger et al., 2006; Laver & Kelly, 2008; Nilsen et al., 2008). Although Manly's selectivity ratio provides insights into how habitat classes are preferentially used, it cannot tell us which particular patches of natural habitat are preferred. Thus, future work can incorporate the use of Resource Selection Functions (RSFs). These analyses may help shed light on habitat characteristics and configuration affect elephants' space use.

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Appendix

Behaviour is generally described as a combination of states and events (Altman, 1974). States are behaviours that occur over extended periods of time and are generally mutually exclusive (e.g., foraging, locomotion, and resting). They can be measured as a proportion of an individual's time budget. Events are behaviours that are measured as frequencies and may co-occur within or between states. Together, these provide insight into how elephants proportion time and energy among competing physiological and ecological demands. This ethogram was adapted primarily from the ElephantVoices Elephant Ethogram (Poole & Granli, 2009) as well as several other studies on Asian elephants (Kumar et al., 2010b; Vijayakrishnan et ., 2018).

Category	Code	Behaviour	Description
Locomotion	*mo*	Ambling	Movement with seemingly no direction. Distinguishable from *exp* as the individual is not searching for vegetation or actively ingesting vegetation matter.
	pw	Purposeful walk	Distinguishable from *mo*, an individual displays directed movement towards a particular patch or destination. Often accompanied by a hurried pace.
	pr	Procession	Elephants are observed walking in a single file from one patch to another. Typically observed when elephants are walking along tea-estate trails to cross into swamps or natural vegetation.
Foraging	*Fe*	Feeding	Active ingestion of vegetation using the trunk and mouth.
	exp	Explore	Movement within a foraging patch while searching or selecting vegetation. Feeding may occur intermittently.
	dr	Drinking	Water is sucked up using the trunk and transferred into the mouth.
	cl	Cleaning	Manipulation, or the cleaning of food items before ingestion. An individual may thrash, shake or strip vegetation using their trunk and limbs.
Rest	*st*	Standing	Standing inactive with eyes closed for a prolonged period of time.
	sl	Sleeping	Lying down and resting.
Vigilance	*sd*	Sniff the air	Olfactory assessment of the surroundings. The individual raises the trunk into the air and sniffs.
	sm	Smell	Investigatory sniffing of the ground. Often observed in locomotion.
	f	Freeze	Sudden immobility in response to a stimulus (either noise, human presence, or both).
	sr	Stare response	Directed sustained visual orientation towards a stimulus. Individual may not blink or flap its ears. Similar to *f*, however, the individual directs its attention to a stimulus head-on.
	hr	Head raise	Head held high above the normal resting position while monitoring the surroundings.
	es	Ears spread	Ears spread and stiff while monitoring surroundings.
Agitation	*tss*	Tail stiff / tail spread	Tail held erect and stiffened, often forming a *J* or *S* shape, signifying agitation.

Category	Code	Behaviour	Description
Avoidance	*oa*	Orient away	Orientation away from a stimulus. An individual redirects its posture away from the stimulus.
	rt	Retreat	Movement away from a stimulus. A herd or individual leaves the patch in response to stimulus.
	ra	Run away	Rapid flight from a stimulus. Distinguishable from *rt* by hastened pace.
	ma	Move away	Movement away from a stimulus. However, individuals do not leave the patch they are in, unlike *rt*.
	baw	Back away	Backward movement away from a stimulus.
Aggressive Behaviours	*mc*	Mock charge	Move towards humans slowly or sometimes steadily with head held high, and trunk rolled up.
	a	Attack	Intentional physical attack on people.
Self-directed Behaviours	*ts*	Tail swing	Repeated winging of the tail.
	ef	Ear flap	Repeated flapping or movement of the ears.
	sp	Self-play	Play behaviour directed towards the self.
	boa	Body adornment	Placement of mud, dust, or vegetation on the body.
	tb	Trunk bite	Biting one's own trunk.
	eom	External object manipulation	Manipulation of non-food objects using trunk, feet or tusks.
	fc	Foot cross	Crossing of feet while stationary.
	fs	Foot swing	Repetitive swinging of a foot while stationary.
	ba	Bathing/Swimming	Bathing, wallowing, or swimming.
Vocalisations	*v*	Vocalisation	Audible vocal signal.
Social Behaviours	*tc*	Trunk contact	Using one's trunk to touch another individual.
	bat	Back towards	Turning the posterior towards another individual while moving backwards into proximity or contact.
	te	Trunk entangle	Intertwining trunks with another individual.
	x	Body contact	Direct physical contact between individuals.

Category	Code	Behaviour	Description
	pu	Push	Directed pushing of another individual using the trunk, head or body.
	px	Proximity	Maintaining proximity (within one body length) to another individual without physical contact.
	hu	Huddle	Unstructured close grouping of individuals with reduced inter-individual spacing.
	fl	Flank	Positioning alongside or around another individual, often maintaining proximity.
	fo	Follow	Directed movement following another individual.
	app	Approach	Non-aggressive movement towards another individual.
	tmc	Trunk-mouth contact	Placement of the trunk into another individual's mouth.
	pi	Play initiation	Behaviour that initiates a play interaction between individuals.
	cp	Contact play	Play involving physical contact.
	ncp	Non-contact play	Play without physical contact.
	nmcp	Nonmutual contac play initiation	Unreciprocated initiation of contact play.
	trn	Trunk nudge	Gentle nudge using the trunk.