RESOURCE AVAILABILITY, WITHIN-CLAN AND BETWEEN-CLAN AGONISTIC INTERACTIONS, AND DOMINANCE RELATIONSHIPS AMONGST FEMALE ASIAN ELEPHANTS IN NAGARAHOLE NATIONAL PARK, SOUTHERN INDIA

A thesis submitted for the degree of

Doctor of Philosophy

by

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CERTIFICATE

This is to certify that the work presented in this thesis titled "**Resource Availability, Within-Clan and Between-Clan Agonistic Interactions, and Dominance Relationships amongst Female Asian Elephants in Nagarahole National Park, Southern India**" has been carried out by Mr. Hansraj Gautam under my supervision at the Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru, India, and that the results in this thesis have not previously formed the basis for the award of any other degree, diploma, or fellowship.

Date: Prof. T.N.C. Vidya

DECLARATION

I declare that the matter presented in my thesis titled "**Resource Availability, Within-Clan and Between-Clan Agonistic Interactions, and Dominance Relationships amongst Female Asian Elephants in Nagarahole National Park, Southern India**" is the result of studies carried out by me at the Evolutionary and Organismal Biology Unit of the Jawaharlal Nehru Centre for Advanced Scientific Research, Bangalore, India, under the supervision of Prof. T.N.C. Vidya, and that this work has not been submitted elsewhere for any other degree.

In keeping with the general practice of reporting scientific observations, due acknowledgement has been made wherever the work described has been based on the findings of other investigators. Any omission, which might have occurred by oversight, is regretted.

Place: Bengaluru Hansraj Gautam

Date:

To my parents and Neha

ACKNOWLEDGEMENTS

To the means which held my wings and pushed the ends further away.

अरी, यों भागती कबतक चलेगी ?
मुझे ओ वंचिके ! कब तक छलेगी ?
चुराओगी कहाँ तक दाँव मेरा ?
रखेगी रोक कबतक पाँव मेरा ?

अभी भी सत्त्व है उद्दाम तुमसे,
हृदय की भावना निष्काम तुमसे,
चले संघर्ष आठों याम तुमसे,
करूँगा अन्त तक संग्राम तुमसे ।

कहाँ तक शक्ति से वंचित करेगी ?
कहाँ तक सिद्धियां मेरी हरेगी ?
तुम्हारा छद्म सारा शेष होगा,
न संचय कर्ण का नि:शेष होगा ।

कवच-कुण्डल गया; पर, प्राण तो हैं,
भुजा में शक्ति, धनु पर बाण तो हैं,
गई एकघ्नि तो सब कुछ गया क्या ?
बचा मुझमें नहीं कुछ भी नया क्या ?

-from Rashmirathi by Ramdhari Singh ‘Dinkar’

I read this to myself during my weakest moments. I should tell myself that it must mean that I had life in me even in those moments.

I dedicate my thesis and my achievements to my parents, who have done more than they could to make it possible for me to reach here. Their belief in me is dear to me and I can never forget the sacrifices they have made in extremely hard situations to ensure that I keep progressing. On days when I felt that I have lost it all, their presence over phone made all the difference and kept me going. My father has been the world for me, especially during my school days. He could almost always convince me that I was capable of doing every possible thing. Life was so comfortable and full of happiness when I was around him rather than away. I remember the time when he used to drop me to my school on his cycle and I wish life had always been as smooth as those moments when I could just watch the world without having to worry about anything, for he was there to take care of everything. Bigger sacrifices have come from my mother who had to spend most of her life in scarcity in our village, while my father and I lived a more comfortable urban life. There were times when I used to visit my home, half of which was without any wall, and felt like wanting myself to run away from the sight, for the contrast with my comfort at JNC hostel was too painful to acknowledge even to myself. Or maybe I did not have the courage to face for even a week what my mother was living everyday. I wish I will get to spend more time with my mother and my father in future.

Of all the people, I am extremely lucky to have the company of Neha, my truest friend and the best person I know. To that statement though, I must also add that we two together are the best two people I know. We have been partners in many a small crimes, partners in watching many a big dreams, and we have also been partners in dreading that many of those dreams may shatter. Life in JNC wouldn't have been the same without her constant presence, and with her around, I have never felt away from home.

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During my PhD, I have had full freedom to take the research questions in the direction that I wanted to. It has greatly helped that I had her full interest when I discussed my work with her and her suggestions and constructive criticism have helped in vastly improving my thesis. She has patiently tried to understand whatever I said and I know that it has taken extra effort since I am very poor in articulating myself. She has also been very patient in dealing with my many careless mistakes both in my work and my conduct in the lab. One of the many positive parts of my time in this lab has been that I got full freedom and liberty to have my own work schedule, for which I am thankful to her and I believe that I have not misused this liberty. I must also admit here that I have certainly not been the most responsible of the lab members when it came to taking care of the lab.

I am especially grateful to her for being a very caring person and for being around when I faced some difficult situations in my personal life.

I must also add to acknowledgements the collective entity that is our lab, in which people have maintained a healthy working environment. The credit must go to every past and present member of the lab and I wish it maintains a welcoming nature for everyone. When I look back and remember the time when I joined this lab, I was a pretty blank slate in both professional and academic terms, and it is in this lab that I have learnt and grown as an individual as well as an academic.

I am thankful to my senior colleagues, Nandini and Keerthi, for the great time I had with them both in the field and the lab. My first year in the field was when Nandini was around and she was very helpful to me while learning about the field, especially with regard to learning Kannada. With her and Evangeline around, I had a nice time as we enjoyed many small things that we did. Also, as a senior colleague in the field, she was caring and ensured that as newcomers to the field, we did not face many problems. I had a fun time with Keerthi and we explored many new things and places in the field. It was also nice to have her humour and made the field time cheerful with her wit. She has also always been ready to help when I wanted some help with analyses as well as with other stuff about elephants. I also want to thank Revathe, who was my colleague during my last two field years. I have troubled her on many occasions when my field jeep would give up either in the field or in field station in the morning itself. She was helpful enough to have come with the new jeep to pull and start my jeep.

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I have spent around 4 and a half years in the field, and the time spent in field was wonderful because of the many gentle people in the field. I am extremely thankful to Ranganna, Krishna, Shankar, and Suresh, Althaf, Salim Anna, and Pramod for keeping us safe. Ranganna was great in the field and he literally held my hand and walked out of dangerous situations when elephants were around. His presence in the field used to give confidence while doing the transect work which involved risks from wild animals. Krishna and Shankar were fun company and they are very helpful with spotting the elephants and in helping us understand many things about the forest. They also patiently taught me and corrected my Kannada, although it remains broken till today. It was lovely being with them for breakfast and lunch, and all the photo sessions I had with them. Althaf, Salim Anna and Pramod were also a great company.

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Contents

THESIS ABSTRACT

Socioecological theory is a broad framework that attempts to explain the variation in sociality amongst animals in terms of responses to resource-risk distributions (for example, Crook and Gartlan 1966, Alexander 1974, Wrangham 1980, Terborgh and Janson 1986). The ecological model of female social relationships (EMFSR, Koenig *et al.* 2013), which is part of socioecological theory, posits that predation and food characteristics shape female social organisation by making dispersal risky and determining the strength of scramble and contest competition within and between groups (Wrangham 1980, van Schaik 1989, Isbell 1991, Wrangham *et al.* 1993, Isbell and van Vuren 1996, Isbell and Young 2002, Sterck *et al.* 1997). Assessments of the abundance and distribution of resources, feeding competition, and social relationships between individuals are required in order to test predictions from the ecological model of female social relationships. A vast majority of the studies on socioecology have been carried out on primates (for example, Chapman *et al.* 1995, Koenig and Borries 2006, Snaith and Chapman 2007, Chancellor and Isbell 2009, Grueter *et al.* 2016, Teichroeb and Sicotte 2018, apart from the references mentioned above) and studies of the EMFSR on other taxa are required (Clutton-Brock and Janson 2012). In this context, I examined the relationship between food resources and within- and between-group contests in a non-primate species, the Asian elephant (*Elephas maximus*), feeding primarily on grass, traditionally thought of as a low-quality resource, in Nagarahole National Park and Tiger Reserve, southern India.

This thesis is divided into two parts: 1) assessment of methods to estimate forage abundance for Asian elephants, and 2) investigation of the influence of ecological variation on contest competition within and between groups of female Asian elephants, and the social and foraging consequences of dominance interactions. Since it is important to measure resource abundance when examining the EMFSR but resource abundance is also difficult to directly measure for elephants and has rarely been done before, the first two data chapters deal with issues related to such measurements.

After an introduction to socioecological theory and the study system in ***Chapter 1***, I examined whether grass biomass measured from the clip-harvest method could be explained

well by visually estimated grass cover and measurement of height in ***Chapter 2***, ***The utility of visual estimation of cover for rapid assessment of graminoid abundance in forest and grassland habitats in studies of animal foraging***. Harvesting and measuring biomass is time-consuming and demands intensive field effort, especially when food plants have to be separated from non-food plants, and when resource abundance has to be estimated for wide-ranging species such as elephants. I found that visually-estimated cover was a good predictor of total graminoid biomass and species-wise graminoid biomass in both forest and grassland habitat. The addition of height data did not result in substantial improvement in estimation of graminoid biomass in the forest habitat but substantially improved the prediction of total graminoid biomass in the grassland. My results show that visually-estimated graminoid cover is a very useful measure and can be adopted in rapid surveys of estimating graminoid food abundance for elephants and other herbivores.

In ***Chapter 3***, ***NDVI is not reliable as a surrogate of forage abundance for a large herbivore in tropical forest habitat***, I examined whether the abundance of elephant food plants in forest habitats could be reliably mapped by using Normalised Difference Vegetation Index (NDVI), a widely used remotely-sensed measure of primary productivity and proxy of forage availability for herbivores. Although remotely sensed indices are effective in open habitats, they may not effectively reflect herbivore food abundance in tropical forests because of the presence of multiple vegetation strata and closed canopy, and because food species may form a small proportion of all the species available in a diverse forest. Based on field sampling 85 tree plots, 170 shrub/herb sub-plots, and 340 graminoid quadrats from 17 one-km line transects during the wet season of 2011, and 110 tree plots, 220 shrub/herb sub-plots, and 440 graminoid quadrats during the dry season of 2012, and analysis of NDVI data, I found a low correlation between NDVI and elephant food plant abundance in the grass, herb, shrub, and tree layers, due to different reasons. While NDVI was not related to herbaceous food plant abundance due to the proportional abundance of food herb species being very low relative to all herb species, NDVI performed badly for the tree category despite the moderately high proportional abundance of food tree species relative to all tree abundance, perhaps because the variables measured on ground (tree count and girth) did not relate to primary productivity. Interestingly, for the grass category, while the proportional abundance of food species was high, NDVI had a negative correlation with food grass abundance, because of a negative relationship between canopy cover and other vegetation (that contributed to NDVI) with grass abundance, possibly through shading and other negative effects. I found a spatial interpolation method (kriging) to perform better than NDVI at predicting grass abundance, but the variation explained was not high using kriging either. Thus, simple remote-sensing measures cannot be used as a proxy for forage abundance in such multi-storeyed forest habitats.

Due to the logistical constraints in subsequently sampling resource distribution in the forests manually as well as simultaneously sampling dominance relationships between individually identified elephants to test predictions of EMFSR, the second part of the thesis, on testing predictions from the ecological model of female social relationships, was carried out in an open grassland habitat around the Kabini reservoir in Nagarahole National Park. This part of the thesis includes two data chapters.

In ***Chapter 4***, ***A test of the socioecological model in female Asian elephants: the effects of food abundance, food distribution, and competitor density on within-clan and between-clan contests***, I present the first quantitative study of the rates of within-clan and between-clan agonistic interactions among female Asian elephants and their relationships with ecological factors such as food distribution and the number of competitors. The clan is the most inclusive unit of female social organisation (Nandini *et al.* 2018) and this work was carried out on individually-identified females from known clans. According to the EMFSR, when food resources are distributed in the form of large patches that can be usurped by groups, but not by individual females within groups, high between-group contest and low within-group contest are expected (Wrangham 1980, Isbell 1991), whereas when food is clumped in patches small enough to be usurpable by individuals within groups, strong within-group contest is expected (van Schaik 1989, Sterck *et al.* 1997). Food resource distributions that give rise to potentially strong between- as well as within-group contest may lead to dominant individuals tolerating the subordinates and reducing within-group contest if larger group size is advantageous in between-group contest (Sterck *et al.* 1997).

I quantified the distribution of grass within the grassland habitat in Kabini, in different plot-clusters within grassland stretches, called focal zones. In the same focal zones, I also quantified the rates of within-clan and between-clan agonistic interactions between individual females, the number of clans present, and the rate of between-clan agonistic encounters at the clan level. I collected these field data on food abundance and agonistic interactions amongst females during the dry seasons of 2015 and 2016. I found high rates of between-clan agonism both at the individual level and the clan-level, which were consistent with the grassland habitat being a food-rich small habitat patch surrounded by forests that have less grass in the dry season. These patterns conform to the EMFSR's prediction of strong between-group contest for large, high quality patches. However, in partial contradiction to prediction from the EMFSR, the rate of within-clan agonism could not be explained by the local dispersion of grass, although it was positively related to group size. The rate of individual-level agonism between clans was much higher than that within clans. The rate of clan-level agonistic between-clan encounters was strongly explained by the positive effect of the number of clans within the zone, and the duration of between-clan agonistic encounters was positively explained by grass biomass at the site of contest, thus supporting the role of food abundance in shaping between-clan contests. The high rates of within-clan and between-clan agonism have implications for social organisation and structure in female Asian elephants, and have been discussed in the context of the EMFSR.

Lastly, in ***Chapter 5***, ***Dominance relationships are not well-resolved and do not ensure access to better feeding sites in female Asian elephant groups in a grass-rich habitat***, I studied the dominance structure among adult females within eight focal clans, the relationship between rates of agonism and expression of dominance in clans, and the feeding consequences of dominance rank relationships. The EMFSR predicts a positive relationship between rates of agonism, expression of dominance hierarchies, and rank-related feeding benefits to dominant females (Janson and van Schaik 1988, van Schaik 1989, Sterck *et al.* 1997, see also Koenig and Borries 2009). In the Kabini population, I found that older females generally won agonistic interactions, although the oldest female was not necessarily the most dominant female. Although linear dominance hierarchies were not found, perhaps due to many unknown dyadic relationships, there was significant unidirectionality in the outcomes of dominance. The directional consistency index of dominance was positively related to clan-specific rates of agonism, as expected according to the EMFSR within this population, but the tests were not significant due to the small number of clans sampled. Feeding sites/areas selected by individual females/groups had slightly greater grass abundance than control sites/areas. However, dominance ranks of individuals were not significantly related to food abundance at feeding sites. The lack of rank-related skew in feeding success is consistent with weak dominance hierarchy.

Although the rates of agonism in Kabini were higher than those reported previously in African savannah elephants, our findings of lower directional consistency index contradict the EMFSR at the species/population level. Weak expression of dominance could be explained by intense feeding competition and high reversals arising due to the peculiar resource distribution, since Kabini is a resource-rich habitat in the lean season, which is reflected in the high elephant densities observed. I argue that this conforms to the Red Queen effect type of feeding competition (see Koenig and Borries 2009), according to which, weak expression of dominance accompanied by low rank-related skew is possible in a regime with high rates of agonism under certain narrow conditions of feeding competition. I discuss my findings in the context of what is known from other populations of Asian and African elephants, in the context of EMFSR and other explanations.

The thesis concludes with a short discussion (***Chapter 6***). This thesis is the first to explicitly test predictions of the EMFSR in elephants. While I find some support for some of the predictions, it would be desirable to have further studies testing some of these predictions in other habitats and testing other predictions in order to better understand the variations in the social organisation of different populations and species in the order Proboscidea.

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CHAPTER 1

General Introduction

Introduction

Group-living is associated with costs such as increased detection by predators (Alexander 1974, van Schaik 1989), resource competition (Crook and Gartlan 1966, Alexander 1974, Caraco and Wolf 1975, van Schaik *et al.* 1983, Janson 1985, 1988, Janson and van Schaik 1988, Wrangham *et al.* 1993), and disease spread (Alexander *et al.* 1974, Altizer *et al.* 2003). However, group-living may also confer benefits such as better cooperative defense and dilution effect against predators, cooperative defense of resources from competing conspecifics, cooperative offpring care, and social support during stressful conditions (see Terborgh and Janson 1986, Wrangham 1980, Silk 2007). Thus, the variation in sociality amongst animals has been postulated to be shaped by the distributions of resources and risks, in a broad framework called socioecological theory (Crook and Gartlan 1966, Alexander 1974, Wrangham 1980, Terborgh and Janson 1986, Clutton-Brock 1989, Emlen 1995, Silk *et al.* 2003). This framework was developed from studies on a range of social traits such as group size, group composition in terms of male-female numbers and kinship, dispersal patterns and transfer of individuals between groups, and agonistic and affiliative relationships within groups (reviewed in Clutton-Brock and Janson 2012, Koenig *et al.* 2013). The socioecological framework can be classified as dealing with two broad aspects of sociality. One part deals with the variations in social organisation with respect to mating systems and, hence, concerns competition with respect to mating (for example, Clutton-Brock 1989, Emlen 1995, referred to as ecological model of social organisation and mating systems in Koenig *et al.* 2013). The other branch of this framework specifically deals with variations in social organisation with respect to female group size and social relationships, and is referred to as the ecological model of female social relationships (Wrangham 1980, van Schaik 1989, Sterck *et al.* 1997, see Koenig *et al.* 2013). My thesis concerns the latter and henceforth, references to the “socioecological model” concern the ecological model of female social relationships.

The socioecological model posits predation and food characteristics as the primary variables that shape social organisation and structure. Conceptualised as a verbal model by Wrangham (1980) and developed further by others (Janson and van Schaik 1988, van Schaik 1989, Isbell 1991, Wrangham *et al.* 1993, Isbell and van Vuren 1996, Sterck *et al.* 1997), this model proposes that while predation makes dispersal risky and results in the formation of groups due to advantages of cooperative defense and dilution effect, the abundance and distribution of resources determine the regimes of two types of feeding competition (scramble and contest, Nicholson 1954) within and between groups (see Isbell and Young 2002). When food is limiting and is not monopolisable by individuals within a group, feeding competition is of scramble type (also called exploitative competition), in which food gains of all the individuals are diminished by the addition of another individual to the environment due to faster depletion of food. When food is present in monopolisable clumps, feeding competition is of contest type (also called interference competition), in which an individual with better resource holding potential can exclude an individual with poor resource holding potential, resulting in a skew in feeding gains between the individuals. The skew in resource gains can be proximally effected by the dominants directing agonism towards subordinates and excluding them from feeding sites, as well as by priority of access to resource sites based on dominance relationships between group members (see Janson and van Schaik 1988). Consequently, depending on the distribution of limiting food resources, feeding competition shapes female-bondedness, group size, and social relationships (elaborated upon in the section on *The ecological model of female social relationships* below).

Therefore, in order to test predictions from the ecological model of female social relationships, one needs to be able to assess the abundance and distribution of resources, feeding competition in the form of the extent of scramble and contest competition, and social relationships between individuals. A vast majority of the studies on socioecology have been carried out on primates (for example, Whitten 1983, van Schaik *et al.* 1983, Janson 1985, van Noordwijk and van Schaik 1987, Borries 1993, Koenig *et al.* 1998, Pruetz and Isbell 2000, Korstjens *et al.* 2002, Vogel 2005, Wright *et al.* 2014, Markham *et al.* 2015, Grueter *et al.* 2016, see Isbell and Young 2002 and Koenig 2002 for review), although studies that have actually measured resource availability are fewer in number (for example, Whitten 1983, Chapman *et al.* 1995, Koenig *et al.* 1998, Pruetz and Isbell 2000, Korstjens *et al.* 2002, Vogel and Janson 2009). There have been calls to examine socioecological predictions in non-primate species to understand the sources of variations in social organisation and structure in animals (Silk 2007, Clutton-Brock and Janson 2012). Therefore, in this thesis, I tried to address some predictions of the ecological model of female social relationships using the Asian elephant (*Elephas maximus*) as the study species.

This thesis is divided into two parts. I first assess methods to estimate forage abundance for Asian elephants. I then investigate the influence of ecological variation on contest competition within and between groups of female Asian elephants, and the social and foraging consequences of dominance interactions. In the following sections, I give a brief introduction to the Asian elephant and give some background to the topics investigated in this thesis, followed by a brief description of the study site.

Study species: the Asian elephant

The Asian elephant is among the three surviving species of Proboscideans. Due to its shrinking and fragmenting habitat, it is an endangered species, restricted to about 41,400-52,300 individuals, in small, medium, and large populations across South and South-east Asia (Sukumar 2003, IUCN Red List, Chowdhury *et al.* 2008). India supports more than half of all the Asian elephants in the world. Asian elephants are protected as a Schedule 1 species under the Wildlife Protection Act of India, 1972. Male and female Asian elephants show differences in morphology, dispersal, and social behaviour (McKay 1973, see Sukumar 2003, Vidya and Sukumar 2005). Adult males are much larger than adult females. Males often have tusks although tuskless males are found in different proportions in various populations, while females are tuskless but may have small tushes. Females are philopatric, while males disperse from their natal groups when they are about 10 years old (Desai and Johnsingh 1995) and only temporarily associate with other males and with female groups subsequently (Sukumar 1989, Keerthipriya *et al.* 2018). Females can become reproductively active around the age of ten years (de Silva *et al.* 2013, see Nandini *et al.* 2018), and while males may become sexually active and start coming into musth when they are about 15 years old, they are usually able to secure matings only later (Sukumar 2003, see Keerthipriya *et al.* 2018). The mating system in Asian elephants is polygynous (Sukumar 2003). Details about female social organisation are given below (section on *Female sociality in Asian elephants*).

As large-bodied animals, Asian elephants have substantial daily food requirements, and feed on about 160 to 240 kg of vegetation per day (Sukumar 2003). They exhibit fast ingesta-passage rate and hind-gut fermentation, which allow them to feed on large quantities of low-quality diet (see Clauss *et al.* 2007). As a result, elephants need to feed continuously, which is reflected in foraging being the dominant activity (41 to 67% time in Asian elephants in southern India, Baskaran *et al.* 2010) in their time budget (Owen-Smith 1988).

Consequently, in agreement with the observed allometric relationship between body size and ranging (Ofstad *et al.* 2016), Asian elephants show long daily-movement and large home ranges of several hundred square kilometres (Baskaran and Desai 1996, Sukumar 2003 Fernando *et al.* 2008). Teeth morphology and digestive physiology suggest that Asian elephants have adapted to grass-rich diet in their evolutionarily history (see Clauss *et al.* 2007). Accordingly, many studies have reported grass as a major component of their diet (McKay 1973, Sivaganesan 1991, Baskaran *et al.* 2010), although the proportion of browse may be higher depending on the habitat (Sukumar 2003, Roy *et al.* 2006). Great flexibility in food plant selection and a wide dietary niche consisting of numerous food plant species have been observed, making Asian elephants dispersal agents for several plant species (McKay 1973, Sivaganesan 1991, Sukumar 2003, Baskaran *et al.* 2010, Campos-Arceiz and Blake 2011, Sekar *et al.* 2015). Due to their flexible and wide diet breadth, Asian elephants inhabit a diversity of habitats, ranging from dry thorn forest, savannah-woodland, and secondary deciduous forests to semi-evergreen and evergreen forests.

Estimating forage abundance for elephants

Studies on the ecology and behaviour of large mammals can be challenging due to their large home ranges, because field biologists need to distribute their sampling effort widely to cover a substantial area representative of such species' habitat. Sampling large areas requires extensive manpower, time, and sampling effort, which are almost always limited. The requirements of effort and logistics multiply when the objective is to assess detailed habitat characteristics, such as the abundance and distribution of food resources (see Baird 1980, Hermy 1988, Sivaganesan 1991, Harmoney *et al.* 1997, Pruetz and Isbell 2000, Saïd *et al.* 2005). In order to overcome such challenges, field biologists either follow rapid survey methods and measure indirect variables (see Noyce and Coy 1990, Hutto 1990, Harmoney *et al.* 1997, Saïd *et al.* 2005) or employ technological advances such as satellite- or airborne-system- assisted remote sensing to monitor habitat characteristics and radio- or satellite- telemetry to study the occupancy, movement, and ranging of animals (see Leyequien *et al.* 2007, Hebblewhite and Hayden 2010, Pettorelli *et al.* 2011, He *et al.* 2015). However, it is necessary to validate the transferability of rapid surveys or technology-assisted methods to new habitats, since differences in physical conditions between habitats could result in differences in the performance of such methods. One such case is transferring the use of rapid vegetation surveys and remote sensing methods, which perform well in grasslands and open canopy vegetation, to forest habitats with dense canopy and complex vegetation structure, in order to evaluate the abundance of herbivore forage.

As explained in the previous section, Asian elephants, which often inhabit closed-canopy forests, are wide-ranging (Desai and Baskaran 1996) and have a wide dietary niche consisting of numerous plant species (Sukumar 1990, Sivaganesan 1991, Baskaran *et al.* 2010). Therefore, sampling of resource availability for the species through traditional vegetation surveys (Sivaganesan 1991, Baskaran *et al.* 2010, se also Blake 2002 for African forest elephants) is challenging, to say the least. Moreover, since Asian elephants inhabit tropical forests with high plant diversity, measuring abundance of their food plants may not be straightforward, either by simple vegetation surveys of abundance of all plants, since it also includes non-food vegetation, or through remote-sensing methods, because exclusion of the abundant non-food vegetation would be required in such assessments. Therefore, in the first part (consisting of two chapters) of my thesis, I explored the performance of two methods of rapid assessment of forage abundance for elephants in forest as well as grassland habitat.

In the first chapter of this part, I focused on grasses, which form a major component of elephant diet in the study landscape in southern India (Easa 1999, Baskaran *et al.* 2010), and assessed whether harvested grass biomass could be predicted by rapidly measured surrogates such as visually-estimated grass cover and height. This was examined for individual species-level abundance as well as for total grass abundance. If biomass could be predicted reasonably by visually-estimated cover, the field effort required in intensive and time-consuming clip-harvesting, sorting the grass individuals into different species, and instant weighing of biomass could be avoided. The results from this chapter show that while visually estimated cover is a good predictor grass biomass in both forests and habitats, the additional utility of height in the forest habitat is limited.

In the second chapter of this part of the thesis, I assessed whether a widely used remotely-sensed measure of vegetation productivity, NDVI (normalised vegetation index, Rouse *et al.* 1974), could be used to reliably map the abundance of elephant food plants in the study area in southern India. Satellite-based remote sensing is being increasingly used by researchers to monitor different types of habitats in studies of ecology and conservation because of its advantage in providing data at multiple spatio-temporal extents and resolutions (Leyequien *et al.* 2007, He *et al.* 2015). Drawing from the ability of NDVI to map vegetation productivity in different types of habitats (Roy and Ravan 1996, Sannier *et al.* 2002, Sjöström*et al.* 2009), ecologists and conservationists have found NDVI to be of high utility to monitor a variety of habitats (Pettorelli *et al.* 2005, He *et al.* 2015). Thus, NDVI has been used by researchers working on animal-habitat relationships to develop species distribution models (Leyequien *et al.* 2007, He *et al.* 2015), as an indicator of suitability and productivity of animal habitats (Pettorelli *et al.* 2011), as an index of vegetation greenness (for example, Young *et al.* 2009, Marshal *et al.* 2010), and as a surrogate of resource abundance and quality (for example, Zinner *et al.* 2001, Ryan *et al.* 2012, Duffy and Pettorelli 2012, Borowik *et al.* 2013, Tsalyuk *et al.* 2019), for a variety of species. However, while remotely-sensed vegetation indices may reflect resource availability and productivity for generalist foragers in open habitats like grasslands and savannahs (for example, Kawamura *et al.* 2005, Ryan *et al.* 2012, Zengeya *et al.* 2013), its use as a measure of forage abundance and quality may be limited in forest habitats, which have complex vegetation structure that may comprise vegetation components that are irrelevant to wildlife (see Borowik *et al.* 2013), especially if non-food plant species represent a substantial part of the vegetation. In such cases, field-verification of reliability of such remotely-sensed indices should be a pre-requisite for ecologists (for example, Willems *et al.* 2009, Borowik *et al.* 2013), without which foraging-related inferences about its ecology- or conservation-related aspects from such studies cannot be relied upon. Although wildlife biologists in tropical forests have used such indirect indices of forage abundance and quality (for example, Zinner *et al.* 2001, Rood *et al.* 2010, Srinivasaiah *et al.* 2012, Youngentob *et al.* 2015, Pokharel *et al.* 2019), field-verification from forests are rare (Willems *et al.* 2009, Borowik *et al.* 2013), especially for tropical forests with abundant overstorey vegetation. Therefore, I conducted a field-based verification of NDVI's performance in mapping the abundance of elephant food plants in Nagarahole National Park, southern India. I found that NDVI was not very satisfactory in measuring abundance of elephant food plants in any of the vegetation strata and hence, cannot be used as a proxy for forage availability for elephants. Since elephants have a wide dietary niche compared to other sympatric herbivores in southern India (Ahrestani *et al.* 2012), this study has implications for the use of such indices in research on other animals also.

Among the two methods of rapid assessment of abundance of elephant food plants, while the visually estimated cover was a reliable proxy of grass abundance, remotely sensed NDVI did not result in good prediction of elephant food abundance. Thus, in order to assess resource abundance and distribution available for Asian elephants in forests, to study the predictions of socioecological theory, there did not seem to be a substitute for field-based, detailed manual surveys. Due to logistical constraints in subsequently sampling resource distribution in the forests as well as simultaneously sampling dominance relationships between individually identified elephants, the second part of the thesis, on testing predictions from the ecological model of female social relationships, was carried out in grassland habitat around the Kabini reservoir in Nagarahole National Park (described in a section below). This second part included sampling grass abundance and distribution at a small spatial scale, examining between- and within-group agonism rates, as well as examining dominance relationships between individual females within groups, and the consequences of those relationships while foraging. In the sections below, I describe the ecological model of female social relationships and describe female sociality in Asian elephants, providing a rationale for the work carried out in the second part.

The ecological model of female social relationships

As mentioned above, the ecological model of female social relationships proposes that food abundance and distribution give rise to different types and extents of feeding competition within and between female groups, which can, in turn, shape female social relationships (Wrangham 1980, Janson and van Schaik 1988, van Schaik 1989, Isbell 1991, Wrangham *et al.* 1993, Isbell and van Vuren 1996, Sterck *et al.* 1997, Isbell and Young 2002, Koenig *et al.* 2013). There may also be important roles of predation and infanticide in the formation of groups (Alexander 1974, van Schaik 1989, van Schaik 1996). When food resources are evenly dispersed and cannot be usurped by entire groups or by females within groups, there is little contest competition between- or within- groups (Janson and van Schaik 1988, Sterck *et al.* 1997). Low cost of dispersal in this predominantly scramble scenario can facilitate female transfer between groups, giving rise to Dispersal-Egalitarian societies, with no dominance hierarchy within groups (Sterck *et al.* 1997). When limited food resources are distributed in the form of large patches that can be usurped by groups, but not by individual females within groups, low within-group contest and high between-group contest competition are expected. The latter would make dispersal costly since larger groups are expected to have an advantage in between-group contests. Therefore, this scenario is expected to give rise to Resident-Egalitarian societies, with females remaining in their natal groups and no dominance hierarchy within groups (see Sterck *et al.* 1997).

In contrast, when limited food is clumped in such a way that high quality food patches are small enough to be usurpable by individuals within groups, strong within-group contest is expected to ensue. Repeated agonistic interactions are expected to lead to the establishment of consistent dominance relationships and a transitive social structure, through interaction of differential competitive ability among group members and extended winner-loser effects (van Schaik 1989, Hemelrijk 2000, Chase *et al.* 2002, Dugatkin and Earley 2004, Koenig *et al.* 2013). Strong within-group contest may facilitate nepotistic relationships since females are expected to ally with relatives to cooperatively defend high quality patches from other group members. Females are not expected to disperse because of the social costs of dispersal. Thus, this food distribution is expected to create Resident-Nepotistic societies (Sterck *et al.* 1997). If food resources were distributed such that there were large patches that are usurpable by groups, in addition to smaller patches within them that are usurpable by individuals within groups, the competition regime would involve strong between-group, as well as within-group contest. If there are advantages of larger group size in between-group contest, dominant individuals are expected to tolerate subordinates and reduce the within-group contest, resulting in Resident-Nepotistic-Tolerant societies (see Sterck *et al.* 1997). Further, due to stronger within-group scramble in larger groups that suffer greater foraging and energetic costs (van Schaik *et al.* 1983, Wrangham *et al.* 1993, Chapman *et al.* 1995), the relative strengths of within-group and between-group competition is also predicted to determine the optimal group size in the respective habitat (Sterck *et al.* 1997, Markham *et al.* 2015, Grueter *et al.* 2018).

Verbal predictions of the ecological model of female social relationships have been subjected to multiple empirical tests within and between various primate taxa (reviewed in Koenig 2002, Isbell and Young 2002, Clutton-Brock and Janson 2012, see also Wheeler *et al.* 2013, Koenig *et al.* 2013), although it was soon realised that there exists continuity along the resident-dispersal, individualistic-nepotistic, and intolerant-tolerant aspects of sociality, requiring quantitative measures to place study species along these axes (see Sterck *et al.* 1997, Isbell and Young 2002, Clutton-Brock and Janson 2012). The model was also found to be insufficient in explaining variations in sociality on several occasions (see Steenbeek and van Schaik 2001, Sussman *et al.* 2005, Koenig and Borries 2009, Lawler 2011, Clutton-Brock and Janson 2012), resulting in the addition of more variables such as infanticide by males, phylogeny, and habitat saturation (van Schaik 1996, Steenbeek and van Schaik 2001, di Fiore and Rendall 1994, see Sterck *et al.* 1997, Thierry 2013). This has invited criticism among primatologists since it has been opined that, by the addition of more variables, the model does not remain the same "socioecological model" (Thierry 2008, Lawler 2011, Clutton-Brock and Janson 2012, see also Sussman *et al.* 2005). Others, while acknowledging limitations of the model, have scrutinised the studies inconsistent with the model and found some of the inconsistencies to be the result of using indirect measures of resource distribution and contest competition (Koenig and Borries 2006, Koenig and Borries 2009, Wheeler *et al.* 2013, Koenig *et al.* 2013). Although sociality and different aspects of it are very complex traits to be explained by ecological determinism based primarily on competition, in the absence of any other model of social relationships (but see Whitehead 1991, Sussman *et al.* 2005, see also Koenig *et al.* 2006, Lawler 2011, for benefits of cooperation and affiliation as functions of sociality) with more explanatory power, the socioecological model, along with the use of additional variables, remains popular in studies of sociality and continues to generate research on social organisation and structure in primates (for example, Wheeler *et al.* 2013, Koenig *et al.* 2013, Markham *et al.* 2015, Grueter *et al.* 2018, Teichroeb and Sicotte 2018, see also Snaith and Chapman 2007, Clutton-Brock and Janson 2012), as well as on other mammals (for example, Smith *et al.* 2008, de Silva *et al.* 2017, Nandini *et al.* 2018).

In contrast to societies with stable groups, in which within-group competition is unavoidable, fission-fusion societies are believed to be a flexible solution to within-group competition since fissions minimise the costs of within-group competition while fusions may help retain benefits of sociality (Kummer 1971, see Aureli *et al.* 2008). The variable nature of group size in such societies presents a challenge to study within-group and between-group competition conceptualised in the socioecological model. The second part of my thesis attempts to quantify the consequences of resource distribution and contest competition in female Asian elephants, which are known to show fission-fusion social organisation (see section on *Female sociality in Asian elephants* below). Since issues have been raised with respect to the use of indirect variables such as diet type as a proxy for food distribution (see Snaith and Chapman 2007, Wheeler *et al.* 2013) and agonistic contests as an indicator of dominance-related skew in foraging success (Koenig 2002, Koenig and Borries 2009), I have conducted direct measurement of these variables with which I attempt to test some of the predictions of the socioecological model to understand the role of within-group and between-group competition in shaping sociality in female Asian elephants. Since field-based quantitative assessments of the model's predictions are rare for non-primate taxa and there have been calls to address this gap (Clutton-Brock and Janson 2012), this field study will contribute further to the assessment of socioecological theory and understanding of social organisation in mammals.

Therefore, in the second part of my thesis, I first quantify the relationship between resource distribution and the rate of agonistic contests within and between clans of female Asian elephants. In the subsequent chapter, I study the dominance structure resulting from such competition, following which, I explore if more dominant females occupy better quality feeding sites. The field data used in different chapters of this thesis are from multiple years and cover different habitats in Nagarahole National Park in southern India. I collected data during four years, in the period starting from August 2011 to June 2016, and a part of the data collection was carried out along with others. I describe female sociality in Asian elephants and the study area in the sections below.

Female sociality in Asian elephants

In contrast to the relatively well known social organisation and structure in African savannah elephants (Douglas-Hamilton 1972, Moss 1988, Wittemyer *et al.* 2005, Archie *et al.* 2006, Wittemyer and Getz 2007), the understanding of the social behaviour of Asian elephants was limited for a long time in the then-absence of long-term studies of individually identified elephants. As mentioned in an earlier section above, male and female Asian elephants were known to live in different societies, with females being philopatric and males dispersing from their natal herds (McKay 1973, Sukumar 1989, Desai and Johnsingh 1995, Fernando and Lande 2000, Vidya and Sukumar 2005). Among early studies of Asian elephants, McKay (1973) found, in Sri Lanka, that female elephants live in "herds" which divide into sub-units consisting of adult females and their offsprings, which join again to form larger groups. This was evidence of fission-fusion sociality. Sukumar (1989) observed aggregations of elephants in southern India and, in addition to family groups, proposed higher social organisations in form of "bond groups" and "clans", similar to the social organisation seen in African savannah elephants, whereas Fernando and Lande (2000) did not find groupings at social levels higher than "family groups" in Sri Lanka. These family groups were found to comprise adult females from single matrilines, based on mitochondrial DNA (Fernando and Lande 2001), and subsequent work using nuclear microsatellite DNA showed adult females of "family groups" to be closely related (Vidya and Sukumar 2005).

With the advent of long-term studies of individually identified females, quantification of association patterns, and social network analysis, de Silva *et al.* (2011) found long-term associates, larger social units (communities found through social network analysis) than those seen associating in the field, and these communities in the population connected to one another. Subsequent long-term study in the Nagarahole and Bandipur National Parks and Tiger Reserves (Kabini population) in southern India also showed extended social networks of females, with the most inclusive social unit being referred to as a clan (Nandini *et al.* 2018). Females within clans showed individual-based to flexibly-nested multilevel fission-fusion societies (Nandini *et al.* 2018). Although female Asian elephant societies in Uda Walawe and Kabini showed weaker associations and were less connected at the level of the population than those in African savannah populations (de Silva and Wittemyer 2012, Nandini *et al.* 2018), there was some similarity in hierarchical community detection of Uda Walawe, Kabini, and Samburu (African savannah elephant) populations, suggesting some basic social similarity. However, average group sizes were smaller in the Asian elephant populations than the Samburu population, which may have given rise to the observed differences in sociality (Nandini *et al.* 2018). It was also found within the Kabini population that the average group size was small (2.4 adult females, SD=1.837) and the average group size did not increase with increasing clan size, suggesting a constraint on group size (Nandini *et al.* 2017). Fission-fusion dynamics allowed for females to meet their clan-mates and maintain social connections (Nandini *et al.* 2017).

Dominance in female Asian elephants has only recently been examined. A comparative study by de Silva *et al.* (2017) found that dominance hierarchy in female Asian elephants in Uda Walawe was not resolved, showed high reversals against hierarchy, and showed low transitivity (see also Nandini 2016 discussed below), in contrast to African savannah elephants (Archie *et al.* 2006, Wittemyer and Getz 2007). A study by Nandini (2016) in Kabini found that female dominance is age-based and unidirectional. However, linear dominance hierarchies were not found, in contrast to the more despotic dominance seen in African elephants (Archie *et al.* 2006, Wittemyer and Getz 2007) and similar to the later findings of de Silva *et al.* (2017). However, between-group dominance was commonly observed in the Kabini population (Nandini 2016), in contrast to other studies on Asian elephants, in which between-group dominance has been seen rarely (Baskaran 1998, de Silva *et al.* 2017). It was also found that larger groups tended to win between-clan contests (Nandini 2016). However, how group-living and social relationships in Asian elephants are linked to feeding competition arising from ecological variations has not been examined before. Moreover, whether dominance confers any foraging or energetic benefit remains an unexplored central aspect of socioecology in all extant elephant species.

Study area: Nagarahole National Park and Kabini backwaters

The field studies presented in this thesis have been conducted in the forests and grassland habitat around the Kabini backwaters of Nagarahole National Park and Tiger Reserve. Nagarahole National Park and Tiger Reserve lies in the Nilgiris-Eastern Ghats landscape in southern India, which is a large contiguous habitat for a rich diversity of flora and fauna, including the largest connected population of Asian elephants in the world. Nagarahole National Park has forest types ranging from semi-evergreen and moist deciduous forests in the west to dry deciduous forests and dry scrub patches in the central and eastern stretches (Pascal 1986, 1988), although dry forests show composition and functionality that is characteristic of mesic savannahs (Ratnam *et al.* 2019). The west-to-east gradient in vegetation types is seen across the Western Ghats, due to the gradient in rainfall received (the western parts receive higher rainfall than the eastern parts, Pascal 1986). Apart from a number of waterholes that dry up in summer, some streams and rivers, such as Kabini and Nagarahole, and many artificial waterholes have water perennially and support the wildlife in this area. Nagarahole and Bandipur National Parks supports a moderate to high density of elephants (<2.0 elephants/km^2, Baskaran and Sukumar 2011), which range across the adjacent protected and reserved forests also (pers. obs.). Construction of the Beechanahalli Dam on the River Kabini has resulted in the formation of the Kabini reservoir between Nagarahole and Bandipur forests. A grassland habitat (~6-8 km^2) is formed around the reservoir during the dry season when the Kabini backwaters recede, and this area becomes the source of abundant water and grass for elephants and other herbivores in the otherwise water- and food-scarce area. The open grassland area also allows for good visibility for observing elephant behaviour and social interactions.

Outline of the thesis

This thesis has six chapters, including the Introduction and Conclusion. The four chapters following the Introduction are data chapters and are presented in manuscript format, two of which are already published. The second chapter is on the assessment of the utility of visually estimated cover and additional utility of height in predicting total biomass and species-level biomass of elephant food graminoid species, in the forest and grassland habitats of Nagarahole National Park. In the third chapter, I assess the reliability of remotely-sensed NDVI (normalised difference vegetation index) as a proxy of food abundance for elephants in the forest habitat, comparing vegetation-plot sampling of elephant forage abundance in the field with satellite data. Extra attention in this chapter has been given to abundance of graminoids, the major component of elephant diet, for which I explore reasons for the absence of a positive relationship between graminoid abundance and NDVI. I also assess the performance of spatial interpolation of field data in predicting the abundance of graminoids.

The fourth and fifth chapters are on tests of the socioecological model of female social relationships, in the grassland habitat in Kabini. In the fourth chapter, I look at the influence of food abundance, food distribution, and competitor density effects of group size and group density, on agonistic behaviour within and between female clans. This study explores possible ecological explanations for occurrence of within-group and between-clan dominance. The fifth chapter involves a study of the structure of dominance relationships within clans, the relationship between agonism and dominance structure within this population, and quantification of proximate foraging benefits of dominance rank relationships in terms of quality of feeding sites occupied by different group members. This chapter also attempts a preliminary synthesis of how the socioecological model performs in explaining the social structure of different Asian and African elephant populations with respect to their ecology, as observed by previous researchers. The sixth chapter summarises and briefly discusses the findings from the data chapters, and suggests future work to understand female sociality in elephants.

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CHAPTER 2

The Utility of Visual Estimation of Cover for Rapid Assessment of Graminoid Abundance in Forest and Grassland Habitats in Studies of Animal Foraging

Title: The utility of visual estimation of cover for rapid assessment of graminoid abundance in forest and grassland habitats in studies of animal foraging

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Abstract

Questions: To assess the feasibility of using visually-estimated vegetation cover in rapid assessment of herbivore food species abundance in the grass layer, we asked the following questions: 1) What is the relationship between total graminoid cover and biomass in forests, and does height improve the prediction of biomass from cover? 2) How does total cover relate to biomass in a grassland habitat? 3) How does elephant food species graminoid cover relate to individual species biomass? 4) How well does species diversity of forest understorey grass layer, calculated from cover data, mirror that calculated from biomass data? *Location*: Nagarahole National Park, India. *Methods*: We estimated the abundance of graminoids through visual estimation of cover and weighed harvested biomass in forest and grassland plots. In forests, two estimates of total graminoid abundance (total graminoid cover and sum of species covers) were used. In the grassland, only total graminoid abundance was measured. We examined the relationship between cover estimates and biomass, and the additional utility of height in predicting biomass, using multiple regressions and AIC-based model selection. We also assessed similarity in cover- and biomass-based Simpson's and Shannon-Wiener diversity indices using regressions. *Results:* Graminoid cover explained a large portion of variation in total graminoid biomass in forest and grassland habitats. The sum of species covers was better than total cover in estimating total graminoid biomass in the forests. The benefit of including height to estimate total biomass was moderate in forests but substantial in grasslands. Cover estimates were good proxies of food species biomass, and the addition of height did not yield better models for most species. Species diversity indices calculated from cover largely matched those based on biomass. *Conclusions:* Visual estimation of species cover is a good alternative to biomass harvesting for rapid assessment of abundance of graminoids consumed by generalist herbivores, like elephants.

Keywords

Elephant food species, forage distribution, graminoids, grasslands, rapid assessment methods, species diversity, vegetation abundance, visual estimation of cover, tropical forests.

Introduction

Ecologists estimate vegetation abundance in order to study various structural and functional attributes of plant communities (for example, Hermy 1988, Guo and Rundel 1997, Chiarucci *et al.* 1999, Henschel *et al.* 2005, Lavorel *et al.* 2008), the productivity of animals' habitats (for example, Hutto 1990, Säid *et al.* 2005, Pettorelli *et al.* 2011, Iversion *et al.* 2014) and its effect on foraging behaviour (for example, Wilmshurst *et al.* 1999), and the impact of animal activities on vegetation (for example, Pekin *et al.* 2015). While studies of plant community structure and function may require intensive measurements of species abundance or traits (for example, Chiarucci *et al.* 1999, Lavorel *et al.* 2008), assessment of resource availability for animals often necessitates sampling over large spatial scales (see Pettorelli *et al.* 2011), which would, therefore, benefit from rapid methods of estimating species abundance. The estimation of forage abundance is a pre-requisite in studies of ecological and behavioural aspects of foraging ecology (Hutto 1990, Säid *et al.* 2005), but the collection of detailed forage abundance data may be very demanding in terms of effort, time, and resources, which are limitations for most field biologists. Different methods of estimating vegetation abundance vary in their sensitivity to vegetation structure, accuracy, precision, practicality, time and manpower required, and destructive nature (see Harmoney *et al.* 1997, Wilson 2011), and no single method is clearly superior in all these respects. Given the apparent trade-off in methods between accuracy and speed, it has been suggested that the choice of method should be based on the objective of the study and after consideration of the advantages and limitations of each method (Elzinga *et al.* 1998, Lavorel *et al.* 2008, Wilson 2011, Redjadj *et al.* 2012).

The diet of the study animal and the vegetation structure in its habitat will together determine whether the measurement of forage abundance should be carried out on all components of the vegetation or only on a portion of the vegetation (such as specific plants or plant parts). For example, all the vegetation of a largely monocultural grassland may be considered for quantifying the food abundance of a grazing herbivore, whereas many components of vegetation (herbs, shrubs, and tree species) in a forest or woodland may not be part of the same animal's diet, and only the food component of the vegetation should be measured. Second, in studies of foraging, ecologists are also often interested in studying whether an animal shows selectivity at the species level during feeding (for example, Owen-Smith and Chafota 2012) and whether it maintains species diversity in its diet (for example, Marsh *et al.* 2006). It is, therefore, also important for the method of estimation of forage abundance to provide species-level detail. Given the considerations above, several methods of abundance estimation become impractical or too time-consuming to implement in diverse habitats, primarily because the vegetation layers that are not relevant to foraging may dominate the biomass in forests with rich biodiversity. Unlike other estimation methods, the biomass harvest method (for example, Drew 1944, Hermy 1988) and the visual estimation of cover (Kennedy and Addison 1987) can be applied even when a selected portion of vegetation is to be quantified. However, biomass-harvesting can be time-consuming if species have to be weighed separately, as this requires sorting of individuals into different species by hand (Harmony *et al.* 1997, Lavorel *et al.* 2008). In this regard, the use of visual estimation of cover may be advantageous, as it allows for rapid assessment of portions of vegetation and is also non-destructive.

We, therefore, tested the utility of the visual estimation method in predicting biomass in the context of forage availability for herbivores in general and for Asian elephants in a tropical forest in southern India in particular. Elephants are considered generalist herbivores, but primarily feed on grasses in the lower vegetation strata, in addition to stems and bark of woody species in the upper strata (Owen-Smith 1988, Sukumar 1990, Baskaran *et al.* 2010). Although their diet consists of numerous species, in species-rich tropical forests, this number may be a small proportion (Blake 2002, Gautam *et al.* 2019) of all the species present. The estimation of abundance of woody species is simple as it involves the counting of trees and measurements of tree-girth which can be done rapidly since the number per plot is usually low. However, elephant food species in understorey vegetation are represented by numerous individuals that are difficult to count within limited time. Moreover, most of the vegetation represented by herbs and shrubs is not consumed by elephants (in our study area, the abundance of food species as a percentage of all species in the respective vegetation strata during the wet and dry seasons, respectively, was about 23% and 10% for herbs, 18% and 16% for shrubs and 80% and 85% for graminoids, Gautam *et al.* 2019). Therefore, in such habitats, the focus should be on estimating the abundance of only food plant species in the lower strata of the forest. The dominance of grasses in Asian elephant diet (Baskaran *et al.* 2010) makes its quantification crucial, and we explored the utility of the visual estimation method in assessing graminoid biomass. Since other herbivores in similar deciduous forests are also primarily grazers (Ahrestani *et al.* 2012), our results would also have implications for the quantification of resource abundance for such herbivores, in case the visual method proves reliable for biomass estimation. Therefore, we assessed the utility of visually estimated cover in explaining elephant food graminoid biomass, as well as total graminoid biomass, which would establish the generality of the method for use in other species. We investigated the utility of this rapid method at the community level, as well as at the more detailed species level. We also examined the additional utility of height, another variable which can be rapidly measured, in modelling graminoid biomass in two types of habitats, forest and grassland. Such questions regarding biomass of graminoids have been rarely addressed in forest habitats (for example, Andariese and Covington 1986), especially in the context of forage availability for wildlife.

Previous studies have found strong correlations between visual estimates and biomass (Hermy 1988, Guo and Rundel 1997, Chiarucci *et al.* 1999, Henschel *et al.* 2005, Axmanová *et al.* 2012) but were not carried out in the context of sampling food availability for wildlife. On the other hand, studies on foraging ecology have sometimes used visual estimation for assessment of forage distribution (for example, Noyce and Coy 1990, Blake 2002, Rebollo *et al.* 2013, Iversion *et al.* 2014), but the relationship between visual estimates and biomass of relevant food species has seldom been tested rigorously in a complex habitat (but see Noyce & Coy 1990 for bear foods), which is important before making inferences about the relationship between resource distribution and forage selection.

The questions we addressed in this paper were the following:

1. What is the relationship between visually-estimated total graminoid cover and total graminoid biomass (measured through the standard biomass-harvest method) in forest habitats, and does the inclusion of height or using the visually-estimated sum of species covers improve the prediction of total graminoid biomass? This question would help find out if the visual estimation method can be used in general in a forest with multiple strata, in studies of foraging by grazing herbivores.
2. Does the relationship between visually-estimated total graminoid cover and total graminoid biomass (as seen from the results of question 1) also hold in a grassland habitat, and does the inclusion of height improve the prediction of total graminoid abundance?
3. How do visually-estimated species covers of individual graminoid food species of elephants relate to their respective species biomass measurements in forest habitats?

Since the proportion of food graminoid species represents only a small fraction of all species in the herbaceous stratum of the vegetation in the forest sampled (HG and TNCV, unpublished data), the visually estimated cover could be used to assess food species abundance and also estimate proportional abundance of different species, if there was a high correlation between visually-estimated species cover and species biomass.

4. How accurately do species diversity indices of the grass layer in forest habitat, measured by visual estimates, reflect the diversity indices obtained from biomass data? It would be desirable to obtain good diversity estimates in order to study selectivity of species and selection of different kinds of vegetation patches by herbivores.

Methods

Study area

The study was carried out in Nagarahole National Park (644 km^2, 11.85°–12.26° N, 76.00°–76.28° E), which is a part of the larger contiguous Nilgiris-Eastern Ghats landscape in southern India (Figure 1). The forest is tropical deciduous, comprising several strata, and is home to several herbivores, including Asian elephants, on which a long-term study based on individually identified elephants is currently ongoing (see Vidya *et al.* 2014). Along the southern boundary of the park flows the river Kabini, on which a dam was constructed during the 1970s to create a reservoir that extends along the southern boundary of the park. During the dry season, when the waters of the reservoir recede, the exposed area forms a grassland consisting mostly of just two short grass species (*Cynodon dactylon* and *Sporobolus* sp., which are also found in the forest, see Supplementary Material 1) and attracts a large number of elephants, deer, and gaur. The graminoids in the grassland are shorter (mean height 5.7 cm) and more continuously distributed compared to those in the forests (mean weighted average of species heights 24.6 cm), where they are more sparsely distributed. Both the grassland and the forest habitat are used by elephants, and data on graminoid abundance were collected from both types of habitats, as described below.

Data sampling and analysis

Forest data

Data collection in forests was done from November to December 2013. Based on a forest type classification map of the region developed by Pascal (1982), Nagarahole National Park was divided into the three major forest types: dry deciduous forest, moist deciduous forest, and teak plantations. We had previously divided the area into a 2 km × 2 km grid and placed 60 1-km line transects in randomly selected cells in order to map the distribution of elephant food resources. During the present study, 23 of these transects in the southern and central parts of the park and 17 additional transects, at least half a km away from each other and at least 100 m away from forest roads, were chosen for sampling. Care was taken to adequately represent all three forest types (based on their availability) in the sampling sites. Sampled locations are mapped in Figure 1.

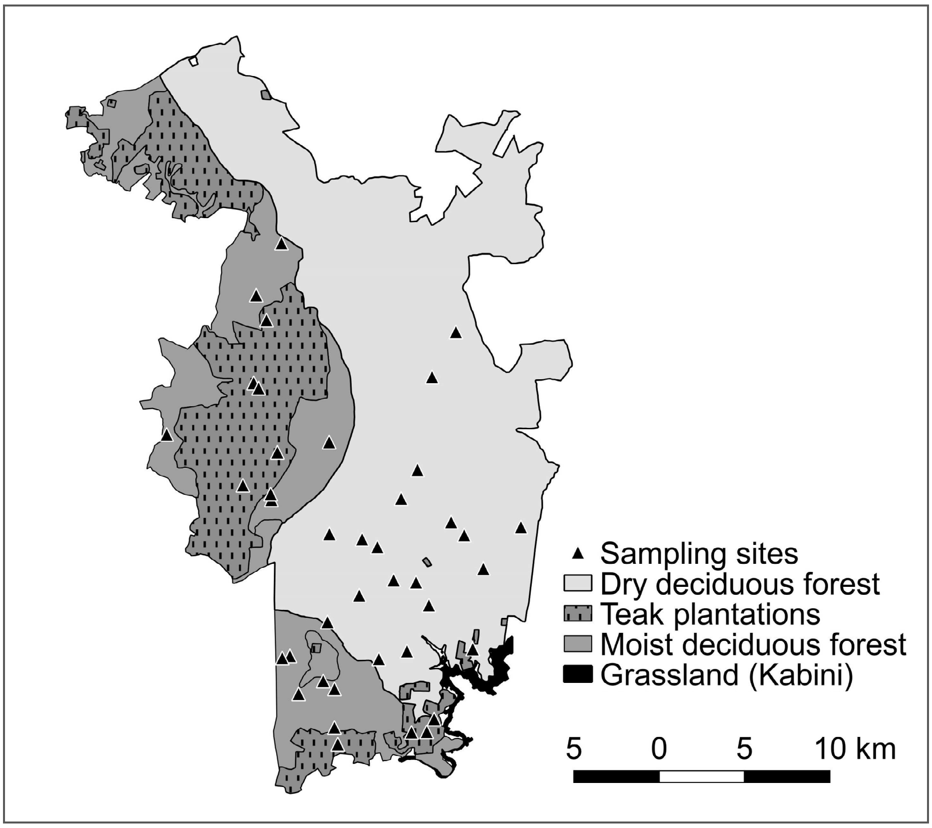


Figure 1. Locations of sampling sites in Nagarahole National Park. The forest type classification is based on Pascal (1982).

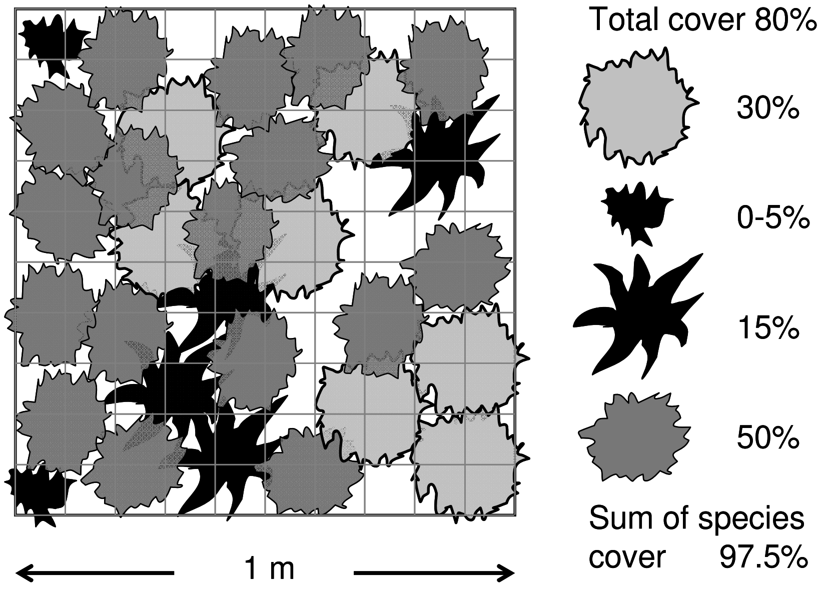


Figure 2. Scheme of the used 1 m × 1 m sampling quadrat, showing estimates of total cover, individual species covers of four species (shown as different combinations of shape and colour), and sum of species cover. The sum of species cover is higher than total cover primarily because of between-species overlaps.

Sampling was carried out in 20 m × 5 m plots at the start or end of each of the 40 1-km transects. In each of these 20 m × 5 m plots, three 1 m × 1 m quadrats were sampled, equidistant along a straight diagonal line (except one plot, in which only two quadrats could be sampled due to the presence of dense *Lantana* thickets). This resulted in 119 quadrats sampled. We sampled all graminoid plants, including *Poaceae* (grasses), *Juncaceae* and *Cyperaceae*. Graminoid abundance was measured at two levels: total graminoid abundance (all the graminoid species present) and species-level abundance. First, total graminoid cover was visually estimated by a single observer (HG) as the percentage of quadrat area covered by all graminoids (Figure 2). Second, species cover for each graminoid species was visually estimated, independent of the cover of other species. Cover was estimated to the closest 5% or in interval bin of 5% (for low values such as 0 to 5% cover), in which case, the middle value of the interval was chosen as the cover value. Values of less than 5% were applied in the case of rare species that were represented by only one or two individuals in the quadrat. Four individuals (except in the case of rare species, in which fewer than four individuals were available) of each species were arbitrarily selected, their natural standing heights (i.e.

without straightening the plant) were measured, and the average of these was used as the height for that species. The total graminoid (fresh) biomass was measured in the field using a digital weighing balance (with 1-gram precision) after harvesting all the graminoids from the ground level. Individuals were then hand-sorted into the respective species, and the biomass of each species was measured.

At the level of the graminoid community, two measures of visually-estimated overall graminoid abundance were used: total graminoid cover as described above, and the sum of species cover (the sum of individual graminoid species covers; the value might exceed 100% since each species was assessed independently; see Figure 2). Total graminoid biomass was normally distributed whereas individual species biomass data were non-normal and were, therefore, log-transformed for the analyses. However, the analyses were also performed on untransformed data to evaluate the robustness of the results. We first used homogeneity of regression slopes test (Zar 1974) to inspect the effect of forest type (dry deciduous, moist deciduous and teak forests) on the relationship between total graminoid biomass and overall graminoid cover. Similar relationships between total biomass and overall cover in different forest types would result in a homogeneity of slopes. We then performed multiple regressions of biomass on both estimates of overall graminoid cover to assess the utility of both measures in predicting total graminoid biomass. We also used the weighted average of graminoid species heights (weighted according to species cover) as an additional explanatory variable and performed multiple regressions to test the utility of height in improving total biomass estimates. Akaike information criterion with small sample correction (AICc, Hurvich and Tsai 1989) was used for selection from the regression models including and excluding height. Although a homogeneity of slopes was identified (see Results) and plots from all forest types thus could be combined for further analyses, we used forest type as a factor to account for the off-chance that pooling the data would affect the results. In order to include the information on forest type in multiple regressions, two dummy categorical variables were generated: deciduous (category 1) or not (category 0 representing teak plantation), and moist deciduous (1) or not (0 representing dry deciduous forest when the previous categorical variable had value 1). These two variables were included in all regression analyses of data from the forest habitats. At the level of individual species, multiple regressions (including the variables for forest type) of species cover on species biomass were carried out for 10 common species (the other species were present in fewer than 10 plots) all of which happened to be elephant food species. We also checked whether multiple regressions that included the individual species' height explained variation in individual species' biomass better compared to regressions lacking this information. Model selection from the two types of regression models was done on the basis of AICc. All the regressions described above were carried out on data from two spatial scales: a) 1 m × 1 m quadrat level on which the measurements were originally made, and b) 20 m × 5 m plot level, such that the plots were spatially independent. Values of different variables in 1 m × 1 m quadrats were averaged to obtain values for the 20 m × 5 m plots.

We also carried out multiple regressions to find out how closely species diversity calculated using visually assessed cover data matched that calculated using biomass data. We calculated two commonly used measures of species diversity, Simpson's diversity index and Shannon-Wiener index of diversity (see Southwood and Henderson 2000). We calculated diversity of a) all the graminoid species and b) only elephant food species. Diversity index values from the three quadrats of every plot were averaged, and analyses were carried out using the average index value for each plot. Forest type variables were used as described above in all multiple regressions.

Grassland data

Seven large stretches (called zones) across the length of the grassland were sampled. A zone would, therefore, be somewhat analogous to the 20 m × 5 m plots in the forest, within which quadrats were sampled, although zones were much larger and quadrats within zones were randomly placed. Within each zone, 20 independent quadrats (1 m × 1 m) were marked, each chosen by walking from the centre of the zone up to a randomly chosen distance and along a randomly chosen direction (distance and angle obtained from a random number generator). Visual estimation of total graminoid cover was carried out in these quadrats and graminoid heights were measured before harvesting the above-ground biomass. Species-level data were not sampled since the only two grass species present could not be differentiated in their non-flowering states. Both these grasses are fed upon by elephants. The data were collected during four 30-day periods between mid-February and mid-June 2015 with equal numbers of random quadrats sampled in each period. Biomass measurements for 10 quadrats could not be performed because of heavy rain, which might have affected the weight significantly.

General regression models were used to analyse data from grassland quadrats. Total graminoid biomass was used as a dependent variable, total graminoid cover as an independent variable, and month and zone as categorical predictors to control for the effect of variation due to time and location, respectively. The analysis was done both with and without graminoid height as a continuous predictor.

Analyses were performed using Statistica 8 (StatSoft 2007).

Results

Relationship between visually-estimated total graminoid cover and total graminoid biomass in forest habitat

Based on the analysis of data from the 40 plots sampled in the three forest types, the mean graminoid biomass was 0.204 kg/m^2 (95% CI: 0.165 to 0.241 kg/m^2). We found no effect of forest type on the relationship between total biomass and total cover, between total biomass and the sum of species covers, or between total biomass and weighted average of species heights (see Table 1). The statistics for regression tests of how well the graminoid biomass is explained by cover and height are shown in Table 2. We found that both total graminoid cover and the sum of graminoid species cover were able to explain a large amount of variation in total biomass, with the sum of species cover showing a slightly higher coefficient of determination than the total cover (scatter-plots shown in Figure 3). Inclusion of weighted average of species heights to the multiple regression increased the coefficient of determination slightly in the case of sum of species cover and total cover compared to the respective models without the inclusion of height (Table 2). The small difference in AICc in both cases suggested that the models including height were not significantly better.

Relationship between visually-estimated species covers of graminoid food species of elephants and their respective species biomass in forest habitat

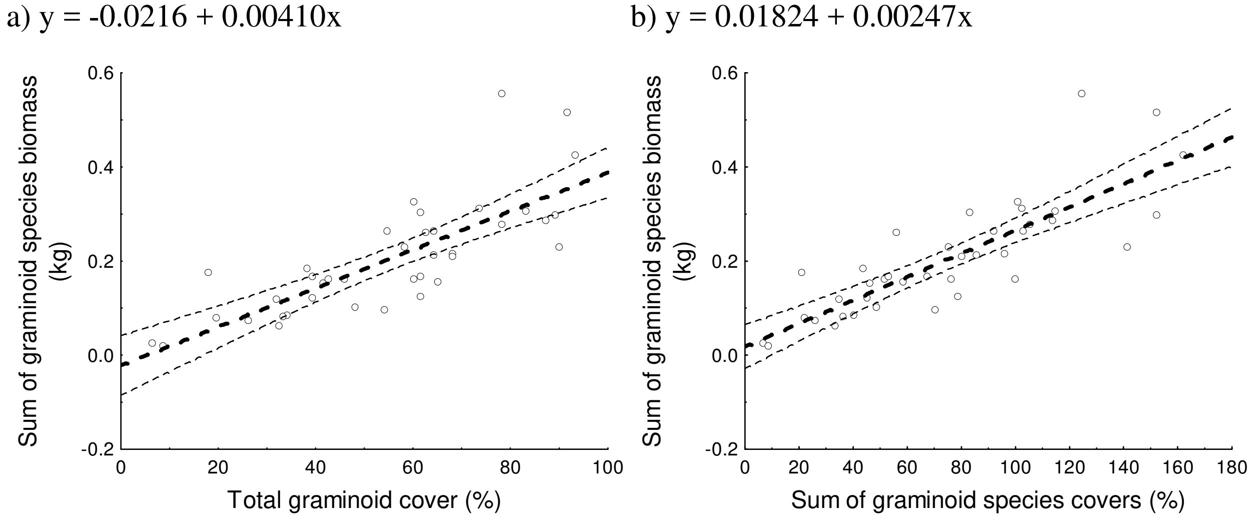
Analyses of species-wise abundance at the plot level showed strong relationships between biomass and visually-estimated species cover for all the common (present in 10 or more plots) graminoid species (R^2 values between 0.63 and 0.98; Table 3). Multiple regressions using species average height as an additional predictor variable also yielded high R^2 values (between 0.69 and 0.98; Table 3), although average height had a significant effect in the regression only in the case of *Oplismenus compositus* and *Digitaria* sp.2 at the plot level (Table 3). With the exception of *Oplismenus compositus*, the AICc values for all other species tested were lower when height was not included in the model. However, the differences in AICc values between the respective models were small, indicating that the models with and without heights largely performed equally well. Also at the quadrat level (Table 4) we obtained high regression coefficients from the models that used species cover (between 0.68 and 0.90) and the models that used both species cover and height (between 0.68 and 0.90), with height having a significant effect in the case of *Cyrtococcum accrescens*, *Cyrtococcum oxyphyllum*, *Cyrtococcum patens*, *Oplismenus compositus*, and *Oryza sativa*. The AICc values were lower in the models that included height in these species but none of the species showed large differences (>10) in AICc (Table 4).

Table 1. Results of homogeneity of slopes test to examine the effect of forest type on the regression slopes of graminoid biomass on three continuous predictors: sum of species covers, total cover, and weighted average of species heights.

Effect	Sum of species cover	Total cover	Weighted heights
Effect of forest type	$F[2, 33] = 0.35$ $P = 0.704$	$F[2, 33] = 0.43$ $P = 0.652$	$F[2, 33] = 1.13$ $P = 0.336$
Effect of continuous predictor	$F[1, 33] = 57.21$ $P < 0.001$	$F[1, 33] = 35.34$ $P < 0.001$	$F[1, 33] = 1.07$ $P = 0.308$

Table 2. Results of plot-level (20 m × 5 m) and quadrat level (1 m × 1 m) regressions to examine how visual estimates of cover explain total graminoid biomass in forest habitat, and the additional utility of weighted average of species heights in improving the total biomass estimates. $P < 0.05$ for all beta coefficient values. AICc can be used to compare the regressions with and without average species height. The difference between a model with the lowest AICc and other models are not considered significant if the difference in AICc is less than two. The model with the lowest AICc is moderately better than the other models if the difference in AICc is between 4 and 7, and model with the lowest AICc is considerably better than the other models if the difference in AICc is > 10.

Level of analysis	Continuous predictors	R, R^2	F test results	Effect size (η^2)	AICc
Plot level	Total cover	0.80, 0.63	$F[3,35] = 20.1$ $P < 0.001$	0.58	-198.2
	Total cover + Weighted height	0.82, 0.68	$F[4,34] = 17.8$, $P < 0.001$	0.59 0.05	-200.7
	Sum of species cover	0.84, 0.70	$F[3,35] = 27.4$, $P < 0.001$	0.66	-206.3
	Sum of species cover + Weighted height	0.86, 0.74	$F[4,34] = 24.0$, $P < 0.001$	0.67 0.04	-209.0
Quadrat level	Total cover	0.78, 0.61	$F[3,111] = 58.7$, $P < 0.001$	0.58	-535.6
	Total cover + Weighted height	0.80, 0.64	$F[4,110] = 48.6$, $P < 0.001$	0.56 0.03	-541.2
	Sum of species cover	0.85, 0.71	$F[3,111] = 92.8$, $P < 0.001$	0.69	-570.6
	Sum of species cover + Weighted height	0.86, 0.74	$F[4,110] = 79.0$, $P < 0.001$	0.68 0.03	-579.9



a) $y = -0.0216 + 0.00410x$

b) $y = 0.01824 + 0.00247x$

Figure 3. Scatter plots for the plot-level graminoid abundance data from the forest plots, showing the relation between a) visually-assessed total graminoid cover and total graminoid biomass and b) the sum of visually-assessed individual graminoid species cover and total graminoid biomass. Confidence-interval bands (95% C.I.) are shown as thin dashed lines around the fitted line shown as a thick dashed line.

Table 3. Results for plot-level regressions of graminoid species biomass on 1) visually-estimated species cover, and 2) visually-estimated species cover and measured average species height, in forest habitat. Details of the regressions are shown based on analysis of log-transformed data along with R^2 untransformed data (shown as R^2 (untr.)). P values for the regressions are not shown separately, except for *Digitaria* sp.2, because all the other P values (for transformed and untransformed data) were lower than 0.001. #Effect of habitat in multiple regression was significant. **Effect of height was significant. See Table 2 for interpretation of AICc differences.

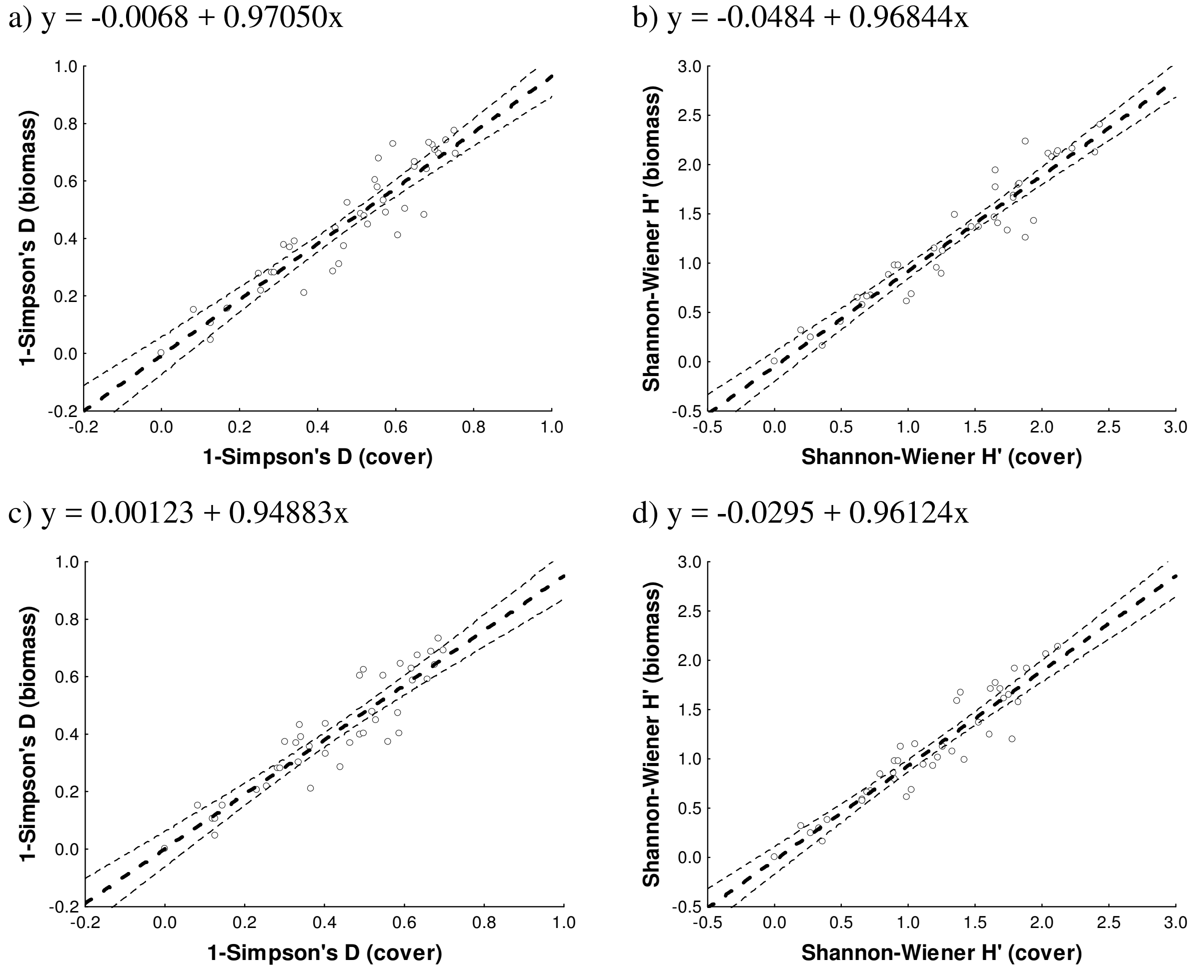
Species	Species cover						Species cover and avg. species height					
	F	df_1, df_2	R	R^2	AICc	R^2 (untr.)	F	df_1, df_2	R	R^2	AICc	R^2 (untr.)
Axonopus compressus	22.36	3,15	0.90	0.82 #	-57.69	0.71	15.77	4,14	0.90	0.82 #	-54.56	0.71
Chloris dolichostachya	73.62	3,14	0.97	0.94 #	-58.16	0.93 #	56.32	4,13	0.97	0.95 #	-56.40	0.94 #
Cynodon dactylon	58.58	3,10	0.97	0.95	-42.22	0.83	39.93	4,9	0.97	0.95	-38.30	0.85
Cyrtococcum accrescens	38.47	3,22	0.92	0.84	-65.74	0.67 #	29.80	4,21	0.92	0.85	-64.67	0.69
Cyrtococcum oxyphyllum	56.99	3,16	0.96	0.91	-58.39	0.87	41.34	4,15	0.96	0.92	-55.79	0.88
Cyrtococcum patens	113.81	3,8	0.99	0.98	-40.45	0.89	82.59	4,7	0.99	0.98	-36.97	0.89
Digitaria sp.2	4.03	3,7; P= 0.059	0.80	0.63	-23.69	0.74	3.33	4,6; P= 0.092	0.83	0.69	-20.29	0.90**
Kyllinga monocephala	82.01	3,15	0.97	0.94	-48.02	0.89	57.55	4,14	0.97	0.94	-44.81	0.89
Oplismenus compositus	74.09	3,33	0.93	0.87	-100.1	0.79	64.40	4,32	0.94	0.89**	-103.4	0.84**
Oryza sativa	21.02	3,10	0.93	0.86	-36.39	0.86	16.17	4,9	0.94	0.88	-33.94	0.87

Table 4. Results for quadrat-level regressions of graminoid species biomass on visually-estimated species cover, and of species biomass on visually-estimated species cover and measured average species height for forest habitat. Details of the regressions are shown based on analysis of log-transformed data along with R^2 untransformed data (shown as R^2 (untr.)). P<0.001 for multiple regressions. #Effect of habitat in multiple regression was significant. **Effect of height was significant. See Table 2 for interpretation of AICc differences.

Species	Species cover						Species cover and avg. species height					
	F	*df*$_1$, *df*$_2$	*R*	R^2	AICc	R^2 (untr.)	*F*	*df*$_1$, *df*$_2$	*R*	R^2	AICc	R^2 (untr.)
Axonopus compressus	25.84	3,26	0.87	0.75	-61.57	0.76	19.79	4,25	0.87	0.76	-60.24	0.76
Chloris dolichostachya	36.68	3,32	0.88	0.77	-83.80	0.88	27.18	4,31	0.88	0.78	-81.81	0.88
Cynodon dactylon	55.33	3,21	0.94	0.89	-67.24	0.83	45.49	4,20	0.95	0.90	-67.53	0.83
Cyrtococcum accrescens	50.27	3,41	0.89	0.79 #	-98.43	0.53	39.72	4,40	0.89	0.80	-98.76	0.61**
Cyrtococcum oxyphyllum	59.39	3,38	0.91	0.82	-100.9	0.70	52.63	4,37	0.92	0.85**	-105.3	0.72
Cyrtococcum patens	42.47	3,16	0.94	0.89	-55.75	0.74	31.50	4,15	0.95	0.89	-53.53	0.81**
Digitaria sp.2	10.69	3,15	0.83	0.68	-26.19	0.81	7.48	4,14	0.83	0.68	-22.94	0.81
Kyllinga monocephala	81.55	3,28	0.95	0.90	-78.76	0.81	63.29	4,27	0.95	0.90	-78.17	0.82
Oplismenus compositus	91.64	3,82	0.88	0.77	-170.5	0.73	73.76	4,81	0.89	0.78**	-173.8	0.74**
Oryza sativa	24.31	3,14	0.92	0.84	-43.74	0.85	27.39	4,13	0.94	0.89**	-47.90	0.89**

Relationship between diversity indices calculated from visually-estimated species covers and the respective species biomass in forest habitat

The average number of graminoid species per 1 m × 1 m quadrat was 4.7 (95% CI: 4.02–5.38) out of which the average number of food species per quadrat was 3.74 (95% CI: 3.24–4.24). Species diversity calculated using visually-estimated cover explained a large proportion of variance in the diversity calculated using biomass data, at both the plot level (20 m × 5 m) and quadrat level, and when diversity was measured by both the Simpson's diversity index and the Shannon-Wiener diversity index (Figure 4, Table 5). Regressions of biomass-based diversity on visual cover-based diversity using only elephant food graminoid species also showed strong relationships (Table 5).


a) y = -0.0068 + 0.97050x

b) y = -0.0484 + 0.96844x

c) y = 0.00123 + 0.94883x

d) y = -0.0295 + 0.96124x

Figure 4. Scatter plots for the plot-level graminoid abundance data from the forest plots, showing the relationships between Simpson's diversity indices (1-*D*) calculated from cover and biomass data (a, c) and Shannon-Wiener diversity indices (*H'*) calculated from cover

and biomass data (b, d). All graminoid species are included in a) and b), while only elephant food species are included in c) and d). Confidence-interval bands (95% C. I.) are shown as thin dashed lines around the fitted line, shown as a thick dashed line.

Relationship between visually-estimated total graminoid cover and total graminoid biomass in grassland habitat

Based on data from 550 quadrats, the mean graminoid biomass was calculated to be 0.684 kg/m^2 (95% CI: 0.655–0.712 kg/m^2). Visual estimation of total graminoid cover, along with month and zone as categorical predictors, explained total graminoid biomass to a large extent (Table 6). The effects of total graminoid cover and month were significant, whereas zone did not have a significant effect. The addition of average height improved the R^2 value, and showed significant effects of total graminoid cover, height, and month, but not zone, on biomass (Table 6).

Table 5. Results from multiple regressions to examine the relationship between diversity indices calculated using biomass data and cover data. $P < 0.001$ in all cases.

Scale	All graminoid species		Food graminoid species	
	Simpson's index (1-D)	Shannon-Wiener index (H')	Simpson's index (1-D)	Shannon-Wiener index (H')
Plot Level	$R = 0.93$, $R^2 = 0.87$, $F[3,36] = 79.92$	$R = 0.85$, $R^2 = 0.72$, $F[3,36] = 30.12$	$R = 0.92$, $R^2 = 0.85$, $F[3,36] = 67.42$	$R = 0.95$, $R^2 = 0.89$, $F[3,36] = 101.44$
Quadrat Level	$R = 0.89$, $R^2 = 0.80$, $F[3,115] = 150.47$	$R = 0.93$, $R^2 = 0.86$, $F[3,115] = 232.56$	$R = 0.88$, $R^2 = 0.78$, $F[3,115] = 132.86$	$R = 0.92$, $R^2 = 0.84$, $F[3,115] = 205.55$

Table 6. Results from general regression tests to check the utility of total cover and the additional utility of average height in predicting total graminoid biomass in the grassland habitat. Zone and month were the categorical predictors.

Continuous predictors	Regression results	Effect size (η^2)
Total cover	$R = 0.78$, $R^2 = 0.61$, $F[3, 545] = 281.6$, $P < 0.001$, AICc = -1687.5	0.28
Total cover and average height	$R = 0.83$, $R^2 = 0.69$, $F[4, 544] = 306.8$, $P < 0.001$, AICc = -1819.85	0.22 (total cover); 0.13 (average height)

Discussion

We found that visual assessment of cover, which allows for rapid sampling, performed very well in assessing forage availability in forest and grassland habitats. Using this method, we were able to obtain fairly accurate estimates of biomass of graminoids in general and food graminoids of Asian elephants in particular. Although biomass harvest method is an ideal measure of abundance of herbaceous vegetation, its implementation in forests has limitations with respect to time and effort, as mentioned in the Introduction. Biomass harvesting also has limitations with respect to permits in critical wildlife areas because of its destructive nature, unlike visual estimation of cover. We found that visually estimated cover, which does not suffer from these drawbacks, was a good proxy for biomass of individual food species, as well as total graminoid biomass, in complex forest habitats. Such estimation of individual species or portions of the vegetation (in our study area, since herbs are more abundant than graminoids, it is difficult to segregate and harvest graminoids) is not feasible with other non-destructive methods (discussed in Radloff and Mucina 2007, Redjadj *et al.* 2012, Walter *et al.* 2015).

An objection to the visual estimation of species covers had been that the “sum of species covers” as a measure of total cover would give “non-sense numbers” that exceeded 100% (Wilson 2011). The author further argued that there was no particular reason why between-species leaf overlaps would be helpful while within-species overlaps would not be important. However, empirically, the sum of species covers performed better at explaining total graminoid biomass in our study, and, perhaps, this is because it incorporates at least some overlap component (see Figure 2), unlike the total graminoid cover. The sum of graminoid species covers may perhaps perform better than total graminoid cover when the within-species leaf overlap is smaller than the between-species leaf overlap. We speculate that this might be true of forests with multiple strata, in which individuals in the lower strata avoid self-shading and individuals of the same species are not very close to one another in order to reduce competition. Since the sum of graminoid species cover better represents total biomass compared to total cover (as discussed above) and since species-level cover estimates are highly related to species biomass, one can obtain good estimates of the proportional abundance of foods by dividing the sum of food species covers by the sum of all species covers. This would be useful for studies of foraging ecology in tropical forests with high diversity where food species are a small fraction of the total number of species present.

The inclusion of height in regression models yielded mixed results. In the forests, total graminoid biomass and species biomass were explained adequately by cover and most models that included height were not substantially better than those that did not include height (small differences in AICc). The effect of height was not significant at the individual species-level also for most food species. On the other hand, the relationship between cover and total graminoid biomass was improved by the inclusion of average height in the grassland habitat. This pattern may result from higher variability in total cover (average total graminoid cover = 54.9%; CV total graminoid cover = 42.3%) than in height (CV weighted height = 32%) in forest habitat. As cover by graminoids saturates (total cover estimate has an upper limit of 100% whereas biomass and height are not limited) and relative variability in cover decreases vis-à-vis height, the explanatory power of height with respect to that of cover is expected to increase. In habitats with high graminoid cover, such as grasslands or swamps, measurement of height may be useful in prediction of biomass. In the grassland habitat in our study, where cover was closer to saturation and less variable (average total cover = 87.3%; CV for total graminoid cover = 19.2%; CV for height = 46.8%), the effect of height relative to that of graminoid cover was greater (Table 6) than that in the forest habitat (Table 2). We thus found that there was no overwhelming benefit to including height in forest habitat, while it might be worthwhile measuring height in grassland habitat.

The improvement in biomass estimation models after inclusion of height has also been reported in other grassland habitats like tussock-grasslands in alpine Andes (Oliveras *et al.* 2013) and rangelands in Argentina (Guevara *et al.* 2002). In forest habitats, such relationships have been rarely studied for graminoids, although in a study in pine forests of Arizona, height did not result in substantial improvement to predictive power of models that used only cover (Andariese and Covington 1986). In habitats where cover is near saturation value (100%), we suggest that measurement of height can substantially improve biomass estimates, as seen in grassland habitat in our study. The limited predictive power of cover in plots with high cover values (above 80%) has also been discussed in Axmanová *et al.* (2012) for wet meadows of temperate Central Europe. One caveat is that we do not know whether graminoid height itself affects selection of foraging sites by animals.

We also found that the species diversity of graminoids calculated from cover data explained large portions of variation in the diversity indices measured from biomass data when used along with forest type as a categorical variable. This similarity in community characteristics calculated using the two methods further support the utility of visual estimation as a rapid assessment method in foraging ecology since ecologists may also be interested in assessing the diversity of foraging sites in order to test whether an animal selects a few food items or feeds on a wide range of species (for example, Owen-Smith and Chafota 2012). Quantification of diversity may also be helpful while studying if the study animal avoids accumulation of specific secondary metabolites (see Codron *et al.* 2007) by feeding on a diverse range of plants (Marsh *et al.* 2006).

One possible limitation of this study is that we measured fresh rather than dry biomass. Fresh biomass has a component of leaf water content, which can change temporally based on environmental conditions. Therefore, the cover-biomass relationship that we recovered may not be the same as that based on dry biomass measurement. However, it is often of interest to measure fresh biomass in studies of foraging because that is the weight of food that an animal would consume. We addressed the issue of observer bias associated with the visual method (Tonteri 1990) to some extent by having a single observer (HG) carrying out the cover estimation from all sites. As observer-related errors can cumulatively become large if many observers are involved in data collection (Tonteri 1990, Klimeš 2003), it would be otherwise necessary to consider the error across observers before the final estimation.

In summary, we found that the visual estimation method performs very well in assessing forage availability in a tropical forest and a grassland habitat, and can, therefore, be used in studies of elephant habitat and forage selection. This will save time and allow for sampling a larger number of sites. Our study was carried out in tropical deciduous forests, which constitute more than 65% of the total forest area in India (Reddy *et al.* 2015) and about one-sixth of the forest cover in south-east Asia (Wohlfart *et al.* 2014). It is likely that the positive relationship between cover and biomass will hold in similar forests, although the strength of the relationship may vary geographically. We do not imply that the relationships we found are completely transferable to other locations and suggest independent assessments in order to develop site-specific cover-to-biomass models. However, since we show that visual estimates of cover can be very useful in studies of foraging, this opens up the method for use by various researchers, who may have otherwise been deterred from using this based on a few previous studies. Moreover, since other sympatric ungulates like *Axis axis* and *Bos gaurus* are also primarily grazers (Ahrestani *et al.* 2012), the visual estimation method should also work well for quantifying the resource distribution for these generalist ungulates in our study site and similar deciduous forests.

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Supplementary Material

Supplementary Material 1. List of graminoid species.

The list of graminoid species found in forest quadrats is given below in Table 1. Food species have been classified based on observations in another study, in which sampling was done over a larger extent and over two seasons (HG and TNCV unpublished data). The grassland sampled has two short grass species, *Cynodon dactylon* and *Sporobolus* sp.1.

Supplementary Material 1, Table 1. A list of graminoid species found in the forest quadrats. Species consumed by elephants are marked with asterisks. Some species could not be identified and thus their local names or IDs have not been italicised.

Graminoid species	**Graminoid species (contd.)**	**Graminoid species (contd.)**
Alloteropsis cimicina	*Echinochloa colonum*	*Sporobolus* sp.2 *
Apluda mutica *	*Fimbristylis* sp.	*Thelepogon elegans*
Axonopus compressus *	*Heteropogon contortus* *	*Themeda* sp.2 *
Brachiaria semiundulata	*Ischaemum timorense* *	*Themeda triandria* *
Carex sp.	*Kyllinga monocephala* *	*Urochloa reptans*
Chloris dolichostachya *	*Lepturus radicans*	Unidentified Grass 3
Cynodon dactylon *	*Oplismenus compositus* *	Unidentified Grass 11
Cyperus iria	*Oryza sativa* *	Unidentified Grass 17 *
Cyperus sp.2	*Panicum montanum*	Unidentified Grass 22
Cyrtococcum accrescens *	*Paspalidium flavidum*	Unidentified Grass 29
Cyrtococcum oxyphyllum *	*Paspalum conjugatum*	Unidentified Grass 55
Cyrtococcum patens *	*Paspalum scrobiculatum*	Unidentified Grass 56
Dendrocalamus sp.	*Pseudanthistiria umbellata*	Unidentified Grass 58
Dichanthium insculptum	*Scleria lithosperma*	Unidentified Grass 7
Dichanthium sp.2	*Setaria pumila*	Unidentified Grass 9
Digitaria adscendens *	*Sporobolus coromandelianum*	Unidentified Tall Grass
Digitaria sp.2 *	*Sporobolus marginatus*	Unidentified Grass (Magge)

CHAPTER 3

NDVI is not Reliable as a Surrogate of Forage Abundance for a Large Herbivore in Tropical Forest Habitat

Title: NDVI is not reliable as a surrogate of forage abundance for a large herbivore in tropical forest habitat

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Author contributions:

HG and TNCV designed the methodology. HG, EA, and MK collected field data; HG did the analyses with inputs from TNCV. HG and TNCV wrote the manuscript and all the authors read and approved the final draft.

Abstract

Remotely-sensed vegetation indices are increasingly being used in wildlife studies but field-based support for their utility as a measure of forage availability come largely from open-canopy habitats. We assessed whether normalised difference vegetation index (NDVI) represents forage availability for Asian elephants in a southern Indian tropical forest. We found that the number of food species was a small percentage of all plant species. NDVI was not a good measure of food abundance in any vegetation category partly because of (a) small to moderate proportional abundances of food species relative to the total abundance of all species in that category (herbs and shrubs), (b) abundant overstorey vegetation resulting in low correlations between NDVI and food abundance, despite a high proportional abundance of food species and a concordance between total abundance and food species abundance (graminoids), and (c) the relevant variables measured and important as food at the ground level (count and GBH) not being related to primary productivity (trees and recruits). NDVI had a negative relationship with the total abundance of graminoids, which represent a bulk of elephant and other herbivore diet, because of negative interaction with other vegetation and canopy cover that positively explained NDVI. Spatially interpolated total graminoid abundance modelled from field data outperformed NDVI in predicting total graminoid abundance, although interpolation models of food graminoid abundance were not satisfactory. Our results reject the utility of NDVI in mapping elephant forage abundance in tropical forests, a finding that has implications for studies of other herbivores also.

Keywords

Food plants, Asian elephant, southern India, forest habitats, multi-storey vegetation, normalised difference vegetation index, field methods, graminoids.

Introduction

The distribution and abundance of food resources are among the principal habitat descriptors affecting foraging, movement, habitat selection, and distribution of animals (Pyke *et al.* 1977 Johnson *et al.* 2001, van Beest *et al.* 2010). Food abundance is especially important in shaping the ecology of large herbivores because digestive efficiency declines and dietary requirement increases allometrically with increasing body size, with ramifications on foraging time and ranging (Hanley 1982, Owen-Smith 1988, Ofstad *et al.* 2016). Therefore, reliable quantification of food resources is crucial to studying the ecological relationships of large herbivores with their habitat, which would be a prerequisite for scientific conservation and management of wild populations and the ecosystems that they inhabit (Gordon *et al.* 2004). However, since large herbivores are usually wide-ranging (Ofstad *et al.* 2016), reliable assessment of forage distribution based on field inventory of food species can be demanding in terms of time, effort, and logistics (see Saïd *et al.* 2005). Therefore, ecologists have been increasingly using vegetation indices derived from satellite-based remote-sensing data, such as Normalised Difference Vegetation Index (NDVI, Rouse *et al.* 1974) as indirect measures of forage abundance and habitat quality for developing species distribution or habitat suitability models, and in studies of animal movement, ranging, and population ecology (reviewed in Pettorelli *et al.* 2005, 2011, Leyequien *et al.* 2007, He *et al.* 2015).

Animal-habitat relations have been analysed using NDVI in wide-ranging animals such as elephants (Marshal *et al.* 2010, Rood *et al.* 2010, Duffy and Pettorelli 2012), ungulates (Pettorelli *et al.* 2006, Ryan *et al.* 2012, Prokopenko *et al.* 2017), marsupials (Youngentob *et al.* 2015), and primates (Zinner *et al.* 2001, Willems *et al.* 2009). However, although NDVI has been found to be a good surrogate of total vegetation biomass/primary productivity in various habitats (examples: savannahs: Sjöström *et al.* 2009, Wu *et al.* 2013; savannah-steppe mixed landscapes: Sannier *et al.* 2002; shrublands: Wilson *et al.* 2011; tropical forests: Roy and Ravan 1996, Madugundu *et al.* 2008, Das and Singh 2016), tests of whether NDVI or other similar indices actually reflect the abundance or quality of vegetation relevant to the focal animal are unfortunately rare and largely restricted to open habitats such as grasslands and savannahs (for example, Kawamura *et al.* 2005, Ryan *et al.* 2012, Zengeya *et al.* 2013). We could find only one such study in temperate forest (Borowik *et al.* 2013) and one from a tropical forest habitat (Willems *et al.* 2009), despite the use of

NDVI in studies of animal ecology in those habitats (Zinner *et al.* 2001, Rood *et al.* 2010, Srinivasaiah *et al.* 2012, Marasinghe *et al.* 2014, Lakshminarayanan *et al.* 2015, Rahman *et al.* 2017, Pokharel *et al.* 2018). If remotely sensed indices do not reflect forage abundance, their use in studies of foraging and habitat use would lead to artefactual results.

The possible limitations of using remotely-sensed indices to assess herbivore forage in forest habitats stem from the following: (1) the complexity of multi-storey vegetation structure in forest habitats, and (2) the small proportion of all plant species in forests that the focal herbivore feeds upon. Because satellite-based vegetation indices assess greenness of the vegetation detected from above, more abundant productive strata (for example, tree canopy) contribute more to such indices than the understorey. Therefore, while NDVI may be correlated with vegetation accessible to herbivores in grasslands, savannahs, open woodlands, and other open habitats with sparse tree cover, NDVI in forest habitat may simply reflect the highly productive, closed top tree canopy layer that is inaccessible and irrelevant to foraging by large herbivores (see Borowik *et al.* 2013). The second limitation is dependent on the extent of forage selectivity by the herbivore and may be greater in forests than in open areas because of the diversity of species available. A high correlation of NDVI with all vegetation may be sufficient to map food resources of generalist herbivores (for example, moose, Belovsky 1978, and African savannah elephants, Owen-Smith 1988) that feed on most components of the accessible vegetation. However, quantification of food resources for selective foragers (for example, primarily frugivorous primates, see Wheeler *et al.* 2013; browsers like kudu, Owen-Smith and Novellie 1982, reindeer and musk-oxen, Kazmin *et al.* 2011; and grazers like rhinoceros and hippopotamus, Owen-Smith 1988) would be more complex if their food species represent only a fraction of the accessible vegetation in the habitat.

Elephants are mega-herbivores that feed on a wide variety of plants (McKay 1973, Owen-Smith 1988, Sukumar 1990, Baskaran *et al.* 2010) and have often been classified as generalist feeders (Owen-Smith 1988, Sukumar 1990, but see Owen-Smith and Chafota 2012). However, despite their wide dietary niche compared to those of other sympatric herbivores (Ahrestani *et al.* 2012), Asian elephants may exert considerable choice during feeding in any particular season/habitat, resulting in a small number of plant species forming a large proportion of their diet (Sukumar 1990, Easa 1999, Baskaran *et al.* 2010). The bulk of the diet of Asian elephants is represented by grasses (McKay 1973, Easa 1999, Baskaran *et al.* 2010) despite their lower availability (in terms of biomass) compared to browse (trees, shrubs and non-grass herbaceous plants) in forests. The rich plant diversity of the tropical forests that Asian elephants inhabit (see Myers 2000, Hedges *et al.* 2008) may further lower the proportion of elephant food species there compared to that in less diverse or grass-rich savannah habitats. Therefore, the notion of generalist/selective foraging does not directly map on to dietary niche breadth, and Asian elephants may be considered selective feeders in tropical forest habitats. The small proportion of food plants, along with access to only the lower strata of vegetation (bark and stems of trees and shrubs in addition to grass), may result in remotely-sensed indices that measure overall vegetation productivity not adequately capturing forage availability. Therefore, our objective was to assess whether NDVI can be used as a proxy for forage availability for Asian elephants in a tropical forest.

Based on the possible limitations of using remotely-sensed indices to assess herbivore forage in tropical forests mentioned above, we wanted to find out whether food species abundance matched the distribution of total species abundance in the study area. If the abundance of food plants in a vegetation category was not in tight synchrony with overall vegetation abundance in that category, NDVI would be unlikely to capture variations in food plant availability even if it reflected total abundance. We separately wanted to find out whether NDVI reflected fine-scale total species abundance so that it could be used to measure overall (within a vegetation category) plant abundance, especially in the graminoid category that is important for elephants and other large herbivores. We also wanted to find out whether NDVI reflected fine-scale actual food species abundance, given the presence of non-food vegetation, in addition to the inaccessibility of vegetation categories that NDVI might measure. Since mapping the spatial distribution of graminoids would be useful in understanding the ecology of various herbivores, we also wanted to find out if spatial interpolation from ground data would be as useful as or more useful than NDVI in carrying out such mapping. Since the Asian elephant has a wide dietary niche breadth, the correlation between NDVI and forage abundance is expected to be higher in this species than in other herbivores in tropical forests. Consequently, if NDVI is not a good surrogate of forage abundance in this species, it would likely be less useful in other, more selective feeders. Since NDVI is widely used by wildlife biologists (Pettorelli *et al.* 2011), this study would further our understanding on the applications of such indices in studying wildlife-habitat relations, the knowledge of which can be helpful as ongoing human-induced landscape changes demand scientific monitoring and conservation of wildlife habitats (Gordon *et al.* 2004, Sunderland *et al.* 2009).

Thus, the questions we addressed in this paper were the following:
(1) Does the seasonal and spatial variation in elephant food species abundance match the distribution of total species abundance in different vegetation categories (strata) in a tropical forest?
(2) To what extent does NDVI reflect the fine scale distribution of (a) total species abundance and (b) food species abundance in different vegetation categories, and, since graminoids have a large contribution to elephant diet but non-graminoid vegetation could affect the relationship between NDV and graminoid abundance, (c) how is relationship between graminoid abundance and NDVI linked to the abundance of non-graminoid vegetation?
(3) Can a spatial interpolation model be used as an alternative to NDVI as a reliable spatial model of graminoid abundance?

Methods

Vegetation Sampling

The study was carried out from September 2011 to May 2012 in Nagarahole National Park, which lies in the Nilgiris-Eastern Ghats landscape in southern India (Figure 1), and offers a large contiguous forest landscape with a variety of habitat types to the Asian elephant and other wild animals. We gridded Nagarahole National Park (area: 644 km^2, 11°51'10.944"-12°15'39.204" N, 76°0'2.7"-76°16'47.856" E) into 2 km x 2 km cells, chose randomly selected cells, and placed 1-km long line-transects according to a stratified sampling regime (Figure 1). Due to logistics and time constraints, the northern parts of the park were not sampled and we sampled 17 transects during the wet season (17 September 2011 – 13 December 2011) and 22 (of which 16 had been sampled in wet season) transects during the following dry season (29 February 2012 – 14 May 2012). Transects were selected in order to sample the three forest types proportionate to the areas they covered. Ground-truthing revealed a smaller area covered by teak plantations compared to that based on Pascal's (1982) map, resulting in reassigning three "teak plantation" transects as moist deciduous forest and one "dry deciduous" transect as teak plantation transect (shown by asterisks in

Figure 1). Therefore, 9, 6, and 2 transects were sampled in the dry deciduous forest, moist deciduous forest, and teak plantation, respectively, in the wet season, and 11, 9, and 2, respectively, in the dry season.

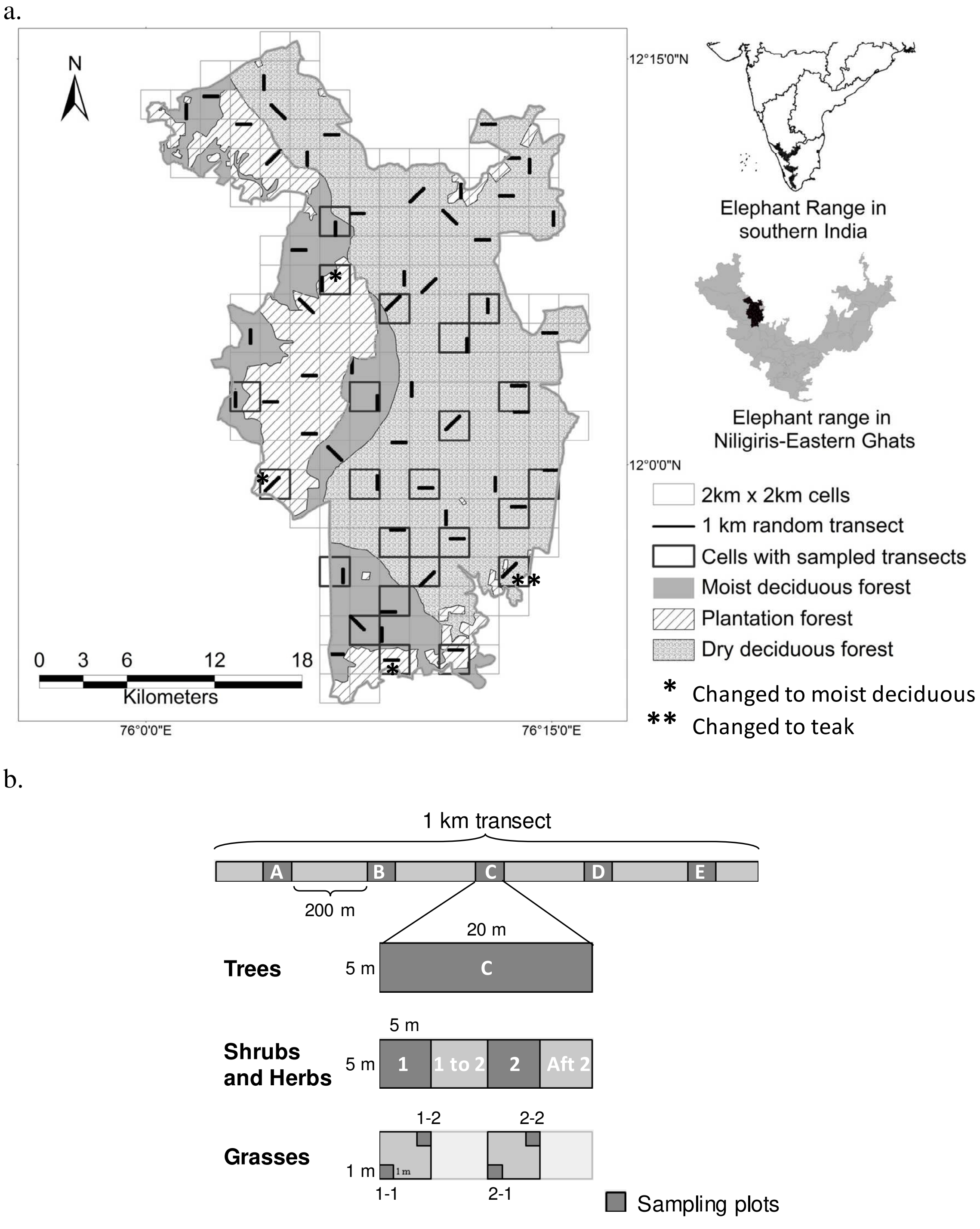

Figure 1. a) Map showing the study area and the location of 60 randomly placed 1-km transects within different forest types (based on Pascal 1982) in Nagarahole National Park.

Sampled transects are marked with dark (2 km x 2 km) cell boundaries. Transects in reassigned forest types are marked with asterisks. b) Schematic of the sampling regime showing a 1-km line transect and the vegetation plots within that were sampled for different plant categories.

Along each transect, we sampled five plots of 20 m x 5 m, spaced at 200 m intervals, and collected abundance data from different vegetation categories: trees, recruits, shrubs, herbs, and graminoids. Graminoids included mostly Poaceae members but also a few Cyperaceae and Juncaceae species, and herbs included non-graminoid herbaceous plants. Individuals of tree species with girth at breast height (GBH) of at least 10 cm were classified as trees, while individuals of these species with a girth of less than 10 cm were classified as recruits. We recorded the number of individuals and GBH of trees and the number of individuals of recruits within the 20 m x 5 m plots. Within each 20 m x 5 m plot, we sampled two 5 m x 5 m sub-plots for shrubs and herbs, and four 1 m x 1 m quadrats for graminoids (Figure 1). Shrub, herb, and graminoid abundance was assessed by visually estimating the percentage cover of each species within the sampling sub-plot / quadrat (Gautam *et al.* 2017; visual estimation has also been used successfully by Tsalyuk *et al.* 2017). We photographed the canopy (using a Canon SX120 IS digital camera - 10 megapixels) from a height of 1 m at each of the 1 m x 1 m quadrats in order to measure canopy cover. We sampled 85 tree plots, 170 shrub/herb sub-plots, and 340 graminoid quadrats from 17 one-km line transects during the wet season of 2011, and 110 tree plots, 220 shrub/herb sub-plots, and 440 graminoid quadrats during the dry season of 2012.

Data processing

We used the species wise abundances (recorded as counts or cover proportions) to calculate total species abundance for each vegetation category, as the sum of species abundance of all species in that category. Similarly, the sum of elephant food species abundance was calculated for each vegetation category. The list of elephant food species in the study area was compiled from (1) our visual observations (during 2012-2013) of feeding by elephants and debarking marks on trees in the study area, and (2) from three previous studies of elephant feeding ecology in neighbouring areas (details in Supplementary Material 1).

We obtained high resolution satellite images, chosen for least cloud cover over the study area, from the middle of the wet season (16 November 2011, LISS 3, 23.5 m resolution) and the dry season (03 March 2012, LISS 4, 5.8 m resolution) from National Remote Sensing Centre, Hyderabad, India, and processed according to standard image processing procedure (Lillesand *et al.* 2004). Radiometric correction by dark-pixel subtraction and resampling to a common (23.5 m) resolution (resampling was done for the LISS 4 image which was of 5.8 m resolution) was performed. NDVI was calculated from near infra red (NIR) and red (R) bands by the formula, NDVI=(NIR-R)/(NIR+R) (Rouse *et al.* 1974). Satellite image processing and NDVI calculation was carried out in Erdas Imagine 9.1 (Leica Geosystems 2005) and NDVI values for each plot were extracted using Spatial Analyst of ArcMap 10.1 (ESRI 2012).

Photographs taken of the canopy were processed in Black Spot Leaf Area Calculator (Varma and Osuri 2013) to obtain canopy cover by classifying the image into dark (regions that intercept light) and light areas. The canopy covers taken above four different places in each 20 m x 5 m plot were averaged and used as the representative value for that plot.

Data analysis

1) Seasonal and spatial variation in elephant food species abundance and total species abundance

We used nested ANOVAs (Doncaster and Davy 2007, pp. 214-216) to examine spatial and seasonal variation in elephant food species abundance and total species abundance. Nested repeated-measures ANOVAs were carried out on elephant food species or total species abundance, separately for each vegetation category except trees, with season as a within-subject effect, plot (20 m x 5 m, random subject) nested under transect (random effect), and transect nested under forest type (fixed effect). The nested design was used to account for variations arising from different spatial scales i.e., the forest type and transect scale. Since equal numbers of transects in each forest type were required across seasons to carry out nested ANOVAs, 6 transects each from the dry deciduous and moist deciduous forests that were sampled in both seasons were used, and the remaining transects were excluded (Supplementary Material 2). Since the count or girth of trees was not expected to change appreciably across a single season, nested ANOVAs, with plots nested under transects and transects nested under forest type, were carried out for elephant food tree species and all tree species separately. Nine transects each from dry and moist deciduous forests sampled during the dry season were used for these ANOVAs (Supplementary Material 2). We regressed elephant food species abundance on the total species abundance, separately for each vegetation category and season, to examine the extent to which elephant food species abundance was predicted by total species abundance. Forest type was used as a categorical predictor in all regressions. Data from all transects were used for these regressions.

2) Relationship of NDVI with total species abundance and elephant food species abundance

In order to understand the extent to which NDVI explains total species and elephant food species abundance, we carried out separate general linear regressions of the two on NDVI, using forest type as a categorical predictor. These regressions were carried out for each vegetation category and season. We found, based on the analysis above, that NDVI was significantly negatively correlated with total and elephant food graminoid abundance in the dry season and with total graminoid abundance in wet season (see Results). Since graminoids are important in elephant and ungulate diet, we examined whether their negative relationship with NDVI was linked to different non-graminoid vegetation variables, which might have inhibitory effects of shade on graminoid abundance. In order to do this, we looked at the vegetation variables that contributed most to NDVI by performing best-subsets regression of NDVI on continuous predictors that included the total abundance of each vegetation category and canopy cover, along with forest type as a categorical predictor. These analyses were performed separately for each season. We then performed best-subsets regression of total graminoid species abundance on other vegetation variables (total abundance of trees, recruits, shrubs, herbs) and canopy cover to find out whether non-graminoid vegetation variables were affecting graminoid abundance. Best subsets regression models were selected using Mallows' Cp statistic (Mallows 1973; best models have lowest Cp values closest to the number of parameters, p). Effect sizes of predictor variables were estimated using η^2 ($SS_{effect}/SS_{corrected\ total}$, see Fritz *et al.* 2012) which was calculated from tables of univariate tests of significance.

3) Comparing NDVI versus spatial interpolation in mapping graminoid abundance

The use of NDVI to model graminoid abundance was compared with the spatial interpolation method in which graminoid abundance data collected from the field were interpolated in Spatial Analyst of ArcMap 10 using ordinary kriging, a widely used interpolation method (see Li and Heap 2008). This weighted moving-average method estimates values of unknown locations based on autocorrelation information within the dataset. During estimation, weights are assigned to neighbouring data points based on the variogram (a plot of variances at different lag-distances) of the existing data, and the overall predicted error variance is kept minimal. Of the 110 plots sampled in the dry season, 55 randomly selected plots were used as the training dataset for preparing an interpolated spatial model, whereas 50 plots were used to test how well interpolation could predict the sum of graminoid abundance (5 plots were excluded because they had burnt undergrowth). Spatial interpolation was repeated 10 times in the manner above, selecting 55 random plots as the training dataset each time (however, in every training dataset, 4 plots with maximum northing, southing, easting and westing were not random, in order to retain the maximum spatial extent of sampling). This analysis was also done on data from the wet season with 45 plots in the training dataset and 40 in the verification dataset. Coefficients of determination (R^2) were obtained after regressing the observed graminoid abundance on the modelled graminoid abundance (from the 10 datasets). Using the same verification plots from the 10 datasets, the observed graminoid abundance was also regressed on NDVI to obtain R^2 for the NDVI model. Wilcoxon matched-pairs test was used to compare R^2values between the interpolation model and the NDVI model. Similarly, kriging and NDVI models were also compared using data on abundance of only the elephant food grass species. Whether increasing the sample size of the training dataset from 55 to 75 plots (30 verification plots) improved the prediction from interpolation was also examined using the dry season dataset (insufficient data from the wet season) on total grass abundance and 10 iterations.

Statistica 7 software (StatSoft 2004) was used to carry out all statistical tests.

Results

1) Seasonal and spatial variation in elephant food species abundance and total species abundance

We recorded 435 plant species, of which 60 (13.79%) were elephant food species (Supplementary Material 3). The mean proportional abundance of food species (elephant food species abundance divided by the total species abundance, and averaged across all plots) was high (~0.8) among graminoids, moderately high (>0.5) for trees and recruits, and low (<0.25) among herbs and shrubs (Supplementary Material 3).

There was a fair amount of spatial and seasonal variability in both elephant food species and total species abundance, with 75 percent (18 out of 24) of the effects (forest type, transect, season, and interactions) being concordant between food species and all species (ANOVA results in Table 1). However, graminoid elephant food species and total species abundance differed in 2 out of 5 effects. Forest type significantly affected total abundance in the graminoid and shrub categories, and in the tree category based on counts but not GBH. Graminoids and trees (count) were more abundant in the dry deciduous forest than in the moist deciduous forest, whereas shrubs were more abundant in the moist deciduous forest (see Supplementary Material 4). Total species abundance in all categories except tree GBH differed significantly across transects (Table 1, Supplementary Material 4). There was also a significant seasonal effect on total species abundance in all categories examined except for recruits (Table 1), with abundances being lower in the dry season compared to the wet season (Supplementary Material 4).

Unlike in the case of total abundance, there was no effect of forest type on elephant food species abundance, except for food recruits being more abundant in the dry deciduous forest than in the moist deciduous forest (Table 1, see also Supplementary Material 4). However, elephant food species abundance varied at the level of transects in all categories except for graminoids and tree GBH (Supplementary Material 4). Seasonal differences in elephant food species abundance were similar to those of total species abundance in the respective categories, with food graminoids, herbs, and shrubs, but not food recruit counts, being more abundant in the wet season than in the dry season (Table 1, Supplementary Material 4).

Table 1. ANOVA results for different vegetation categories showing spatial and seasonal variation in elephant food species abundance and total species abundance. Plot (subject) was nested under transect (random effect), transect nested under forest type (fixed effect) and season was the within-subject repeated measure. Season was not included for tree count and tree GBH. The cells filled with grey point to differences in effects on elephant food species abundance and total species abundance.

Vegetation categories	Dependent variable	Forest type	Season	Transect (Forest type)	Season x Forest type	Season x Transect (Forest type)
Graminoids	Total abundance	$F_{1,10}=8.882$, **$P=0.014$**	$F_{1,10}=21.014$, **$P=0.001$**	$F_{10,48}=2.568$, **$P=0.014$**	$F_{1,10}=2.724$, $P=0.130$	$F_{10,48}=4.701$, **$P<0.001$**
	Elephant food species abundance	$F_{1,10}=0.462$, $P=0.512$	$F_{1,10}=16.902$, **$P=0.002$**	$F_{10,48}=1.977$, $P=0.057$	$F_{1,10}=0.408$, $P=0.537$	$F_{10,48}=3.385$, **$P=0.002$**
Herbs	Total abundance	$F_{1,10}=0.178$, $P=0.682$	$F_{1,10}=48.554$, **$P<0.001$**	$F_{10,48}=3.489$, **$P=0.002$**	$F_{1,10}=0.674$, $P=0.431$	$F_{10,48}=4.327$, **$P<0.001$**
	Elephant food species abundance	$F_{1,10}=2.390$, $P=0.153$	$F_{1,10}=32.417$, **$P<0.001$**	$F_{10,48}=4.809$, **$P<0.001$**	$F_{1,10}=6.093$, **$P=0.033$**	$F_{10,48}=4.510$, **$P<0.001$**
Shrubs	Total abundance	$F_{1,10}=7.162$, **$P=0.023$**	$F_{1,10}=40.521$, **$P<0.001$**	$F_{10,48}=2.836$, **$P=0.007$**	$F_{1,10}=0.429$, $P=0.527$	$F_{10,48}=3.071$, **$P=0.004$**
	Elephant food species abundance	$F_{1,10}=0.092$, $P=0.768$	$F_{1,10}=7.217$, **$P=0.023$**	$F_{10,48}=4.502$, **$P<0.001$**	$F_{1,10}=0.441$, $P=0.521$	$F_{10,48}=3.186$, **$P=0.003$**

Vegetation categories	Dependent variable	Forest type	Season	Transect (Forest type)	Season x Forest type	Season x Transect (Forest type)
Recruits	Total abundance	$F_{1,10}$=4.756, P=0.054	$F_{1,10}$=0.069, P=0.798	$F_{10,48}$=3.902, **P<0.001**	$F_{1,10}$=0.006, P=0.941	$F_{10,48}$=8.405, **P<0.001**
	Elephant food species abundance	$F_{1,10}$=8.779, **P=0.014**	$F_{1,10}$=0.468, P=0.509	$F_{10,48}$=3.267, **P=0.003**	$F_{1,10}$=0.052, P=0.824	$F_{10,48}$=5.097, **P<0.001**
Trees (tree count)	Total abundance	$F_{1,16}$=5.039, **P=0.039**		$F_{16,72}$=3.230, **P<0.001**		
	Elephant food species abundance	$F_{1,16}$=2.751, P=0.117	N.A.	$F_{16,72}$=3.960, **P<0.001**	N.A.	N.A.
Trees (GBH)	Total abundance	$F_{1,16}$=0.410, P=0.531		$F_{16,72}$=0.894, P=0.578		
	Elephant food species abundance	$F_{1,16}$=0.122, P=0.732	N.A.	$F_{16,72}$=1.605, P=0.089	N.A.	N.A.

General regressions showed that total abundance, along with forest type, was significantly related to elephant food species abundance in different categories to varying extents (Table 2). In both the wet and dry seasons, the effect sizes (η^2) of total abundance were large (>0.5) for graminoids, recruits and trees, but low to moderate (less than or close to 0.25) for herbs and shrubs.

Table 2. Results of general regressions of elephant food species abundance (dependent variable) on total abundance (continuous predictor) and forest type (categorical predictor) for different vegetation categories. Effect sizes (η^2) in this and other tables were calculated based on univariate tests of significance.

Season	Vegetation category	*F* test results			Multiple R^2	η^2 (forest type)	η^2 (total abundance)
		df_1, df_2	*F*	*P*			
Wet season	Graminoids	2, 82	58.614	**<0.001**	0.588	**0.034**, ***P*=0.010**	**0.565**, ***P*<0.001**
	Herbs	2, 82	11.389	**<0.001**	0.217	0.035, *P*=0.057	**0.206**, ***P*<0.001**
	Shrubs	2, 82	3.835	**0.026**	0.086	0.000, *P*=0.954	**0.083**, ***P*=0.008**
	Recruits	2, 82	232.405	**<0.001**	0.850	**0.009**, ***P*=0.050**	**0.796**, ***P*<0.001**
	Tree count	NA			NA	NA	
	Tree girth	NA			NA	NA	
Dry season	Graminoids	2, 107,	141.998	**<0.001**	0.726	0.003, *P*=0.335	**0.661**, ***P*<0.001**
	Herbs	2, 107	19.811	**<0.001**	0.270	0.002, *P*=0.621	**0.269**, ***P*<0.001**
	Shrubs	2, 107	8.562	**<0.001**	0.138	0.010, *P*=0.273	**0.137**, ***P*<0.001**
	Recruits	2, 107	327.646	**<0.001**	0.860	0.004, *P*=0.096	**0.854**, ***P*<0.001**
	Tree count	2, 107	142.184	**<0.001**	0.727	0.001, *P*=0.481	**0.724**, ***P*<0.001**
	Tree girth	2, 107	121.896	**<0.001**	0.695	0.008, *P*=0.102	**0.686**, ***P*<0.001**

2) Relationship of NDVI with total species abundance and elephant food species abundance

a) NDVI and total abundance

General regressions of total abundance on NDVI and forest type for different vegetation categories yielded significant regression models in the case of graminoids and shrubs in the dry and wet seasons (Table 3). However, NDVI, by itself, showed a significant effect only on the total abundance of shrubs in the wet season and total abundance of graminoids in the dry season. The latter effect of NDVI on total graminoid abundance in the dry season was negative, with larger NDVI values indicating lower graminoid abundance.

b) NDVI and food species abundance

General regressions of elephant food species abundance in different vegetation categories on NDVI and forest type yielded different regression models in the dry and wet seasons (Table 4). In the wet season, the regressions of NDVI, along with forest type, on food species abundance of herbs and recruits were significant, whereas the regressions were not significant for other vegetation categories. In the dry season, the regressions of food species abundance of graminoids, and trees (tree count) on NDVI and forest type were significant. However, even when the regressions were significant, the effect sizes of NDVI were low (<0.10 in all cases, Table 4).

Table 3. Results of general regressions of total abundance (dependent variable) on NDVI (continuous predictor) and forest type (categorical predictor) for different vegetation categories.

Season	Vegetation category	*F* test results			Multiple R^2	η^2 (forest type)	η^2 (NDVI)
		df_1, df_2	*F*	*P*			
Wet season)	Graminoids	2, 82	8.552	**<0.001**	0.173	**0.116**, ***P*=0.001**	0.031, *P*=0.088
	Herbs	2, 82	0.308	0.736	0.007,	0.007, *P*=0.442	0.001, *P*=0.769
	Shrubs	2, 82	12.08	**<0.001**	0.228	**0.082**, ***P*=0.005**	**0.108**, ***P*=0.001**
	Recruits	2, 82	1.964	0.147	0.046	0.005, *P*=0.496	0.033, *P*=0.096
	Tree count	2, 82	0.739	0.481	0.018	0.008, *P*=0.398	0.012, *P*=0.311
	Tree girth	2, 82	0.222	0.801	0.005	0.005, *P*=0.511	0.000, *P*=0.965
Dry season	Graminoids	2, 107	23.09	**<0.001**	0.301	**0.041**, ***P*=0.025**	**0.111**, ***P*<0.001**
	Herbs	2, 107	0.080	0.923	0.001	0.000, *P*=0.891	0.000, *P*=828
	Shrubs	2, 107	5.555	**0.005**	0.094	0.027, *P*=0.084	0.013, *P*=0.228
	Recruits	2, 107	0.286	0.752	0.005	0.005, *P*=0.467	0.001, *P*=0.780
	Tree count	2, 107	0.895	0.412	0.016	0.001, *P*=0.812	0.013, *P*=0.235
	Tree girth	2, 107	0.267	0.766	0.005	0.003, *P*=0.578	0.005, *P*=0.478

Table 4. Results of general regressions of elephant food species abundance (dependent variable) on NDVI (continuous predictor) and forest type (categorical predictor) for different vegetation strata.

Season	Vegetation strata	*F* test results			Multiple R^2	η^2 (Forest type)	η^2 (NDVI)
		df_1, df_2	*F*	*P*			
Wet season)	Graminoids	2, 82	0.740	0.480	0.018	0.010, *P*=0.362	0.008, *P*=0.402
	Herbs	2, 82	4.374	**0.016**	0.096	0.004, *P*=0.567	**0.091**, ***P*=0.005**
	Shrubs	2, 82	1.564	0.215	0.037	0.002, *P*=0.708	0.034, *P*=0.091
	Recruits	2, 82	16.132	**<0.001**	0.282	**0.231**, ***P*<0.001**	**0.044**, ***P*=0.029**
	Tree count	2, 82	1.542	0.220	0.036	0.035, *P*=0.088	0.002, *P*=0.695
	Tree girth	2, 82	1.703	0.189	0.040	0.036, *P*=0.085	0.006, *P*=0.492
Dry season	Graminoids	2, 107	15.906	**<0.001**	0.229	**0.058**, ***P*=0.010**	**0.048**, ***P*=0.018**
	Herbs	2, 107	0.863	0.425	0.016	0.003, *P*=0.565	0.015, *P*=0.200
	Shrubs	2, 107	2.481	0.088	0.044	0.017, *P*=0.163	**0.043**, ***P*=0.028**
	Recruits	2, 107	1.266	0.286	0.023	0.002, *P*=0.642	0.008, *P*=0.354
	Tree count	2, 107	4.256	**0.017**	0.074	0.008, *P*=0.348	**0.066**, ***P*=0.007**
	Tree girth	2, 107	2.047	0.134	0.037	0.000, *P*=0.849	0.027, *P*=0.088

Table 5. Best-subset regression models of the dependence of NDVI on the abundance of different vegetation categories and canopy cover (all continuous predictors) and forest type (categorical predictor).

Response Variable	*F* test results			Multiple R^2	β-coefficient (1.96 S.E. of β)	η^2	Mallows' *Cp*
	df_1, df_2	*F*	*P*				
NDVI (wet season) Model 1	3, 80	6.966	**<0.001**	0.207	Shrubs: 0.370 (0.199) Recruits: -0.229 (0.223) Tree count: 0.218 (0.220)	Shrubs: **0.130**, **P<0.001** Recruits: **0.040**, **P=0.048** Tree count:0.037, P=0.055	3.7
NDVI (wet season) Model 2	2, 81	8.973	**<0.001**	0.181	Shrubs: 0.364 (0.120) Canopy cover: 0.168 (0.120)	Shrubs: **0.132**, **P<0.001** Canopy cover: 0.028, P=0.102	2.315
NDVI (wet season) Model 3	4, 79	5.491	**<0.001**	0.218	Shrubs: 0.353 (0.202) Recruits: -0.202 (0.229) Tree count: 0.183 (0.230) Canopy cover: 0.109 (0.208)	Shrubs: **0.121, P<0.001** Recruits: 0.031, P=0.089 Tree count: 0.025, P=0.123 Canopy cover: 0.011, P=0.308	2.764
NDVI (dry season) Model 1	3, 105	61.592	**<0.001**	0.638	Canopy: 0.607 (0.137) Forest type: -0.285 (0.136) Tree count: -0.191 (0.118)	Canopy cover: **0.364**, **P<0.001** Forest type: **0.081**, **P<0.001** Tree count: **0.049, P=0.002**	3.1

Response Variable	*F* test results			Multiple R^2	β-coefficient (1.96 S.E. of β)	η^2	Mallows' *Cp*
NDVI (dry season) Model 2	4, 104	46.701	**<0.001**	0.642	Canopy cover: 0.596 (0.138) Forest type: -0.289 (0.136) Tree count: -0.236 (0.139) Tree GBH: 0.083 (0.139)	Canopy cover: **0.350**, ***P*<0.001** Forest type: **0.084**, ***P*<0.001** Tree count: **0.054**, ***P*=0.001** Tree GBH: 0.007, *P*=0.244	2.171
NDVI (dry season) Model 3	4, 104	46.668	**<0.001**	0.642	Canopy cover: 0.573 (0.148) Forest type: -0.264 (0.140) Tree count: -0.183 (0.118) Grasses: -0.083 (0.141)	Canopy cover: **0.309**, ***P*<0.001** Forest type: **0.074**, ***P*<0.001** Tree count: **0.050**, ***P*=0.003** Grasses: 0.007, *P*=0.253	2.217

c) Relationship between graminoid abundance and NDVI with respect to non-graminoid vegetation abundance

An examination of the components of vegetation that contributed to NDVI showed that the best regression model of wet season data included the total abundance of shrubs, recruits, and tree count, and explained 20.7 percent of the variation in NDVI (Table 5). Based on dry season data, the best multiple regression model of NDVI included forest type, canopy cover, and tree count, and explained a much larger variation (63.8%) in NDVI. The top three models for each season are shown in Table 5.

The best subset regression model explaining the total abundance of graminoids in the wet season consisted of three variables – forest type, canopy cover, and shrub abundance – and explained 43.2 percent of the variation in the total abundance of graminoids. In the dry season, total graminoid abundance was best explained by a model which consisted of forest type, canopy cover, abundance of herbs, shrubs, recruits and tree count, and explained 38.2

percent variation in graminoid abundance. Canopy cover had a negative effect on total graminoid abundance in both the seasons, and its effect relative to those of other vegetation components was larger. The top three models for each season are shown in Table 6.

3) Comparing NDVI versus spatial interpolation in mapping graminoid abundance

Spatial interpolation of field data using kriging explained a greater amount of variation in graminoid abundance than NDVI, based on both the 50 dry season verification plots (kriging: mean R^2=0.491, SD=0.078, NDVI: mean R^2=0.331, SD=0.060, negative relationship between NDVI and graminoid abundance; Wilcoxon matched-pairs test: T=0.00, Z=2.803, N=10, P<0.05), and the 40 wet season verification plots (kriging: mean R^2=0.174, SD=0.113, NDVI: mean R^2=0.032, SD=0.022, no significant relationship between NDVI and graminoid abundance; Wilcoxon matched-pairs test: T=3.00, Z=2.497, N=10, P<0.05; Figure 2, see Figure 3). Similar analyses on the abundance of food graminoids showed that both NDVI (mean R^2=0.279, SD=0.067) and kriging (mean R^2=0.309, SD=0.089) explained significant variation in food graminoid abundance in the dry season but they were not significantly different from each other (Wilcoxon matched-pairs test: T=19.00, Z=0.866, N=10, P=0.386; see Figure 2). Neither NDVI (mean R^2=0.005, SD=0.005) nor kriging (mean R^2=0.030, SD=0.022) explained significant variation in food graminoid abundance in the wet season (Figure 2, see Supplementary Material 5). Increasing the number of training plots used in the kriging model (dry season) did not significantly improve the coefficient of determination either for total graminoid abundance (mean R^2=0.491, SD=0.078 for 55 plot sets, mean R^2=0.498, SD=0.074 for 75 plot sets) or for food graminoid abundance (mean R^2=0.309, SD=0.089 for 55 plot sets, mean R^2=0.314, SD=0.070 for 75 plot sets; Supplementary Material 5).

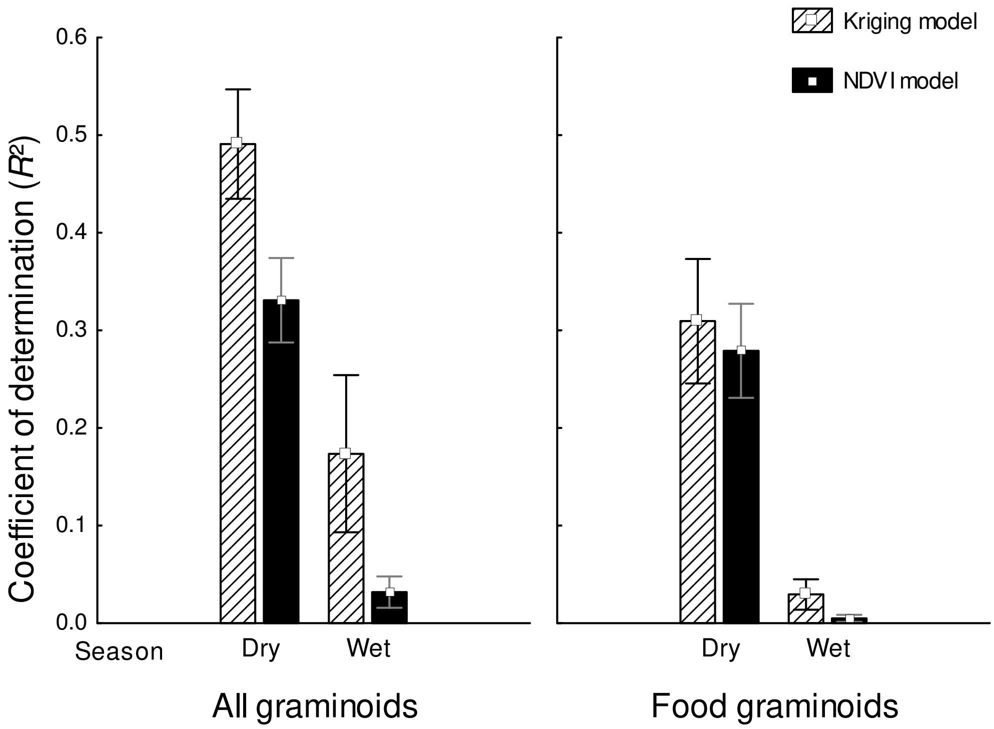

Figure 2. Mean and 1.96 S.E. of coefficient of determination (R^2) obtained from the two types of regression models of graminoid abundance, NDVI and kriging, in the dry and wet seasons. R^2 is shown for both total graminoid abundance as well as elephant food graminoid abundance.

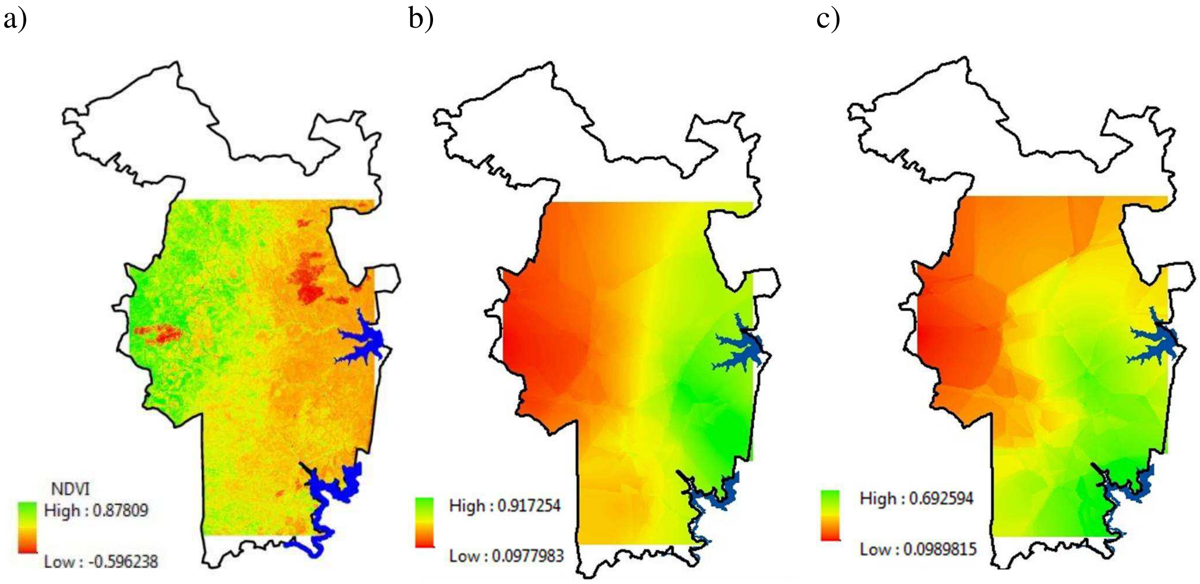

Figure 3. Maps showing a) NDVI, b) kriging (spatial interpolation) model of total graminoid

abundance, and c) kriging model of food graminoid abundance in dry season (see Supplementary Material 5 for wet season). Kriging estimates shown are from one random dataset each. The red patches in the NDVI map are areas affected by forest fire.

Table 6. Best subset regression models explaining the dependence of total graminoid abundance on other vegetation variables (continuous predictors) and forest type (categorical predictor).

Response Variable	*F* test results			Multiple R^2	*β*-coefficient	η^2	Mallows' *Cp*
	df_1, df_2	*F*	*P*				
Graminoids (wet season) Model 1	3, 80	20.280	**<0.001**	0.432	Canopy: -0.472 (0.171) Shrubs: -0.264 (0.177) Forest type: 0.168 (0.180)	Canopy cover: **0.242**, ***P*<0.001** Shrubs: **0.071**, ***P*=0.004** Forest type: 0.028, *P*=0.070	-1.0
Graminoids (wet season) Model 2	4, 79	15.399	**<0.001**	0.438	Canopy cover: -0.464 (0.172) Shrubs: -0.250 (0.180) Forest type: 0.167 (0.180) Recruits: 0.080 (0.170)	Canopy cover: **0.237**, ***P*<0.001** Shrubs: **0.062**, ***P*=0.008** Forest type: 0.028, *P*=0.073 Recruits: 0.007, *P*=0.356	2.179
Graminoids (wet season) Model 3	2, 81	27.919	**<0.001**	0.408	Canopy cover: -0.504 (0.170) Shrubs: -0.318 (0.170)	Canopy cover: **0.264**, ***P*<0.001** Shrubs: **0.105**, ***P*<0.001**	2.253

Response	F test results			Multiple	β-coefficient	η^2	Mallows’
Variable	df_1, df_2	F	P	R^2			Cp
Graminoids (dry season) Model 1	6, 102	10.507	**<0.001**	0.382	Canopy: -0.370 (0.184) Forest type: 0.225 (0.184) Herbs: 0.183 (0.167) Tree count: 0.160 (0.179) Shrubs: -0.147 (0.169) Recruits: -0.133 (0.170)	Canopy cover: **0.114**, **P<0.001** Forest type: **0.042**, **P=0.018** Herbs: **0.034**, **P=0.034** Tree count: 0.022, P=0.083 Shrubs: 0.021, P=0.091 Recruits: 0.017, P=0.129	5.0
Graminoids (dry season) Model 2	4, 104	14.424	**<0.001**	0.357	Canopy cover: -0.367 (0.181) Forest type: 0.229 (0.185) Shrubs: -0.145 (0.163) Herbs: 0.122 (0.156)	Canopy cover: **0.121**, **P<0.001** Forest type: **0.045**, **P=0.017** Shrubs: 0.023, P=0.084 Herbs: 0.018, P=0.130	7.633
Graminoids (dry season) Model 3	4, 104	14.364	**<0.001**	0.356	Canopy cover: -0.404 (0.183) Forest type: 0.243 (0.182) Herbs: 0.154 (0.165) Tree count: 0.145 (0.168)	Canopy cover: **0.137**, **P<0.001** Forest type: **0.050**, **P=0.010** Herbs: 0.024, P=0.071 Tree count: 0.021, P=0.093	7.792

Discussion

This is one of the first studies examining the use of NDVI as a proxy for food abundance of herbivores in tropical forest habitat. We found that NDVI was not a good predictor of elephant forage in any vegetation category in Nagarahole National Park. This resulted both from the small proportional abundance of food species relative to the abundance of all plants, as well as from the complexity of multi-storey vegetation structure resulting in NDVI poorly capturing total vegetation abundance. The proportion of food species was low overall (13.79%), although the proportional abundance of food species was high within the graminoid category (~80%). The relationship between total abundance and elephant food species abundance was also stronger amongst graminoids than amongst herbs or shrubs. However, despite the greater proportional abundance of food graminoid species and the ability of total abundance to predict food species abundance to some extent in the graminoid category, NDVI was not a good measure of food graminoid abundance because of the multi-storey vegetation giving rise to a negative relationship between NDVI and total graminoid abundance (see below). NDVI was also not a good measure of food species abundance in the recruit and tree categories despite a moderate proportional abundance (>50%) of food plants and a strong relationship between total abundance and food species abundance because there was no significant relationship between NDVI and total abundance in these strata. The non-significant relationship between NDVI and tree abundance may be the result of the variables that we measured at the ground level – total tree count and GBH – not representing the primary productivity of trees. Although canopy volume, rather than tree count or GBH, can be measured as the primary productivity of trees, tree canopy is largely not relevant to foraging by elephants and terrestrial ungulates. It was not surprising that NDVI was not a good predictor of food abundance in the herb and shrub strata, which had a low (<25%) proportional abundance of food species, as well as a low correlation between total abundance and food species abundance.

Previous assessments of NDVI as a measure of food abundance or quality for mammals have been carried out in relatively open-canopy habitats, with the exception of two studies. Willems *et al.* (2009), in a study of vervet monkey ranging in South Africa, found that while NDVI was strongly correlated with leaf abundance (Pearson's r= 0.923), the abundance of relevant food resources was not linearly correlated with NDVI, although a quadratic polynomial curve provided very good fit. Borowik *et al.* (2013) found the relationship between NDVI and ground vegetation biomass in a temperate forest to be positive in spring but negative in summer (when shrub and tree leaves were fully developed) and suggested that canopy closure in the productive season may dominate the signals received by satellite sensors and may also negatively affect ground vegetation. Their latter results are similar to the negative relationship between NDVI and graminoid abundance that we observed in both seasons in our study. Some previous studies in open habitats have also not found very high correlations between NDVI and forage abundance or quality. Zengeya *et al.* (2013) found NDVI obtained from multispectral data to explain low to moderate proportions (R^2=0.01 and 0.48) of forage quality (nitrogen concentration) for cattle and wild ungulates in a rangeland in Zimbabwe. Tsalyuk *et al.* (2017) also found only a moderate proportion of variation (R^2=0.30 to 0.43) in total abundance of different vegetation categories in mixed-savannah habitat in Etosha National Park to be explained by average annual NDVI, although much stronger relationships were found based on multi-year NDVIs. In contrast, in steppe grasslands of Inner Mongolia (China), Kawamura *et al.* (2005) found that NDVI explained large variation in total biomass (53-75%), live biomass (54-74%), and standing crude protein (48-68%).

In tropical forests, primary productivity is often concentrated in the canopy layers (see Thakur *et al.* 2017, Roy and Ravan 1996), which are beyond the reach of terrestrial animals. We found that canopy cover contributed significantly to NDVI in the dry season, whereas the effects of other vegetation variables, when significant, were small. The difference in the predictability of NDVI from canopy cover and vegetation between the dry and wet seasons (*Multiple* R^2 in the wet season: 0.21; dry season: 0.64) suggests a saturation of the relationship between NDVI and vegetation variables when the productivity is high, as highlighted previously also (see Pettorelli *et al.* 2011, Leyequien *et al.* 2013). Canopy cover, although positively related to NDVI, negatively affected the abundance of graminoids, the primary forage of elephants and ungulates (Baskaran *et al.* 2010, Ahrestani *et al.* 2012). Total graminoid abundance was also affected to a smaller extent by other vegetation categories in the upper layers (see Table 6), possibly through shading or allelopathic effects. Thus, the presence of multi-storey vegetation seems to result in the negative relationship between NDVI and graminoid abundance (Figure 4). This negative (and somewhat weak) relationship between NDVI and graminoid abundance is likely to be found across other tropical forests also because of a somewhat continuous canopy layer. Canopy tree density was negatively related to the abundance of elephant food plants in the understorey in the tropical rainforest of Congo also (Blake 2002, pp. 38-40).

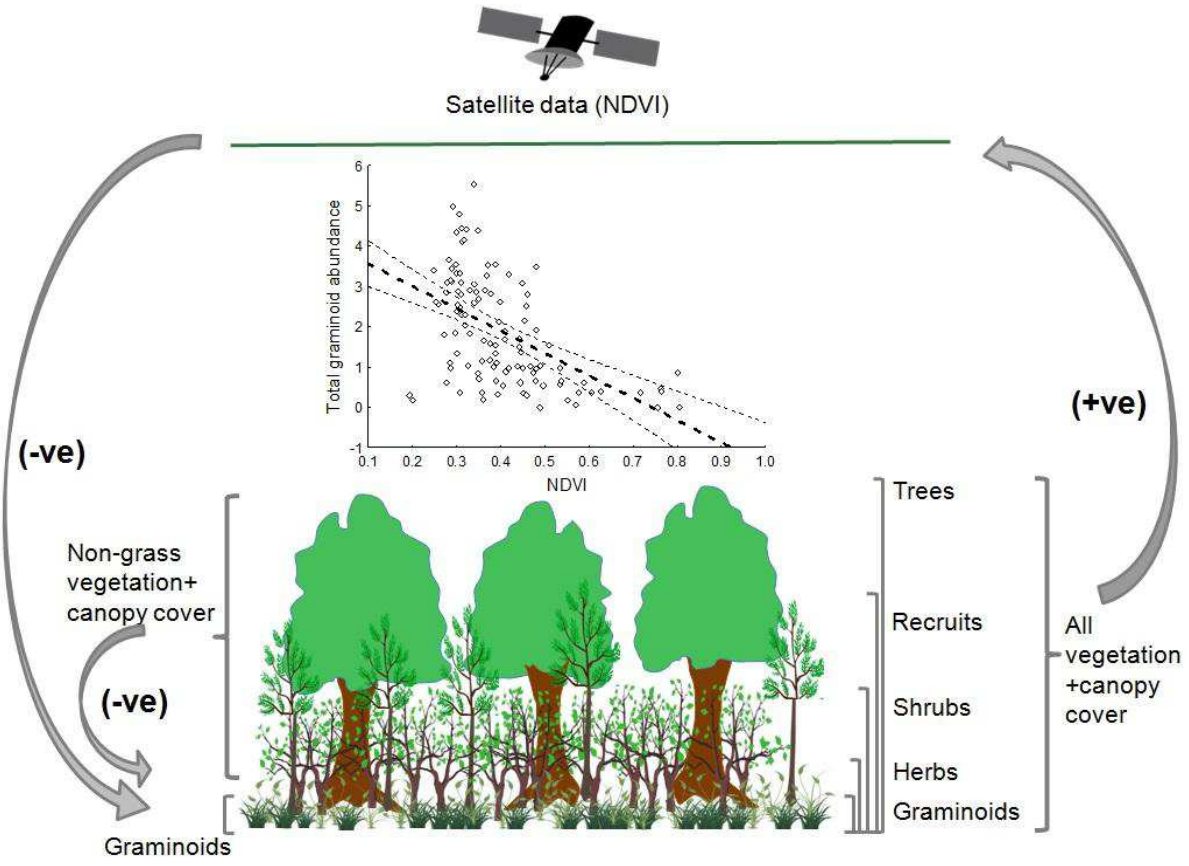

Figure 4. A schematic representation of the relationship between graminoid abundance, non-graminoid vegetation and satellite-derived NDVI productivity.

Based on our results, we caution against the use of NDVI and other remotely-sensed vegetation indices as a proxy for food abundance of large herbivores in tropical forests. The advantage of rapid mapping of vegetation abundance (Roy and Ravan 1996, Kawamura *et al*. 2005, Wilson *et al*. 2011) and landscape heterogeneity (for example, Murwira and Skidmore 2005) has made NDVI a popular habitat covariate in studies of animal ecology (see Pettorelli *et al*. 2005, 2011), but with little attempt to test its validity for specific habitats/species. For example, studies on Asian elephant habitat use (Rood *et al*. 2010, Srinivasaiah *et al*. 2012, Marasinghe *et al*. 2014, Lakshminarayanan *et al*. 2015) that have used NDVI as a proxy of forage abundance cite papers that either themselves (Pettorelli *et al*. 2011) caution against the use of NDVI in densely vegetated areas because the linear relation between NDVI and leaf area index does not hold, or are studies from structurally different vegetation (Hansen *et al.* 2009 based on tundra vegetation, Wittemyer *et al.* 2007, Young *et al.* 2009, based on African savannahs) that do not actually examine the relationship between NDVI and animal forage abundance. Moreover, associations between NDVI and animal habitat use may result from correlated responses to other environmental variables such as water availability, protection status/human disturbance, or shade rather than forage abundance. For example, in large, deforested landscapes, preference of areas with high NDVI could be interpreted either as a preference for greater or a specific type of forest cover or less human disturbance. Simultaneous use of multiple remotely-sensed indices that are known to be correlated in deciduous forests (see Madugundu *et al.* 2008) and arbitrary justification regarding what they represent (for example, leaf area index as a proxy of shade and NDVI as a proxy for food in Srinivasaiah *et al.* 2012) can also make it difficult to tease apart various effects such as food, human disturbance, and shade on habitat use. We found considerable spatial and seasonal heterogeneity in food abundance in our study area, which is expected to affect spatio-temporal patterns of movement, foraging, and habitat use, as seen in African elephants (for example, Blake 2002, Marshal *et al.* 2010). Total abundance or NDVI that do not reflect food species abundance patterns would, therefore, yield misleading results. NDVI has been used as a proxy for resource availability or habitat quality in tropical forest habitats in the case of other mammalian taxa such as primates (Zinner *et al.* 2001), ungulates (Rahman *et al.* 2017), and arboreal marsupials (Youngentob *et al.* 2015) also, and field-based sampling of relevant vegetation in these habitats are required to validate how useful NDVI is in mapping forage abundance.

While spatial interpolation (kriging) performed better than NDVI in explaining variation in total graminoid abundance, neither method was useful in estimating food graminoid abundance. We suggest that ecologists studying large mammal foraging in tropical forests, directly measure food abundance from field sampling rather than vegetation indices unless verification is carried out or alternative rapid methods are developed. However, our results relating to the lack of use of NDVI as a useful habitat covariate for wild herbivores should not be extended without testing to very different spatiotemporal scales than what was studied here. Our study area was spread over a few hundred sq. km. and our data were from fine-scale plots, relevant to the spatial scale at which elephants feed. Our results also held at the resolution of 1-km transects (Supplementary Material 5). At even coarser resolutions in large and diverse landscapes, NDVI may be a proxy of habitat suitability, because high

NDVI would then be associated with structural aspects of the landscape, for which the focal species may have a preference. It is also possible that NDVI may be temporally related to food abundance (for example, across months) and, hence, may be useful to map temporal trends rather than actual abundance estimates, although this has to be verified based on field data.

The inability of NDVI to map elephant food resources as shown in our paper poses a challenge for the development of alternate remote-sensing methods for estimation of herbivore food abundance that can overcome the substantial effort and logistics demanded by field sampling. It might be useful to explore the methods developed to model understorey vegetation (see Pisek 2018) and then incorporate additional tools, if required. Previously, Resasco *et al.* (2007) used satellite images from leaf-on and leaf-off phases of overstorey canopy to map the distribution of an invasive understorey shrub (*Lonicera maackii*) in deciduous forests, although the use of leaf-on and leaf-off images, if successful, would only help map the annual rather than seasonal distribution. Further, the presence of other understorey layers such as herbs (as seen in Resasco *et al.* 2007) and shrubs may also affect the success of this method. Lindermann *et al.* (2004) used Landsat spectral bands and artificial neural networks to model the distribution of understorey bamboo for giant panda (*Ailuropoda melanoleuca*) in forests that had midstorey and overstorey vegetation. However, the mapping of actual abundance rather than presence/absence, and that too of grasses that are more difficult to detect than bamboo, using these spectral bands remains to be tested. Wadey *et al.* (2018) have used tasseled cap transformed wetness component (obtained from multispectral data) that divides the habitat in continuous classes, and found that Asian elephants in Malaysia selected low wetness areas, which were suggested to correspond to open grass habitats. However, this method too needs to be verified with field data on grass abundance and does not address the problem of interference by tree canopy layers, especially in areas with high canopy cover. While modelling understorey biomass of a boreal forest, Muukkonen and Heiskanen (2005) obtained low success (R^2=0.15) by using two spectral bands of ASTER in a non-linear regression equation and moderate success (R^2=0.37) using a neural network model. In another study, hyperspectral remote sensing products were used by Skidmore *et al.* (2010) for mapping of the quality (nitrogen and polyphenol content) of grass and tree foliage of herbivores in savannahs and woodlands. The use of such high spectral-resolution datasets may be more informative than coarse bands in mapping grass abundance. Finally, it might also be worth exploring the additional use of three-dimensional mapping technologies like LiDAR that has helped develop forest understorey models with variable accuracy (reviewed in Pisek 2018).

To conclude, we find that the abundance of non-food vegetation undermines the utility of NDVI as an indicator of elephant food in a forest habitat. Since deciduous forests account for one-sixth of all forests in South-east Asia (Wohlfart *et al.* 2014), which harbour many endemic and threatened populations of grazing ungulates and other large mammals that largely feed on understorey vegetation and are likely to be more selective feeders than elephants, our results have wider implications for ecological studies in these habitats.

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Supplementary Material

Supplementary Material 1. Elephant food species in the vegetation plots.

The elephant food species found in the vegetation plots are shown in Table 1 below. Identification of some species as food species is based on earlier studies from Mudumalai Tiger Reserve (Sivaganesan 1991, Baskaran *et al.* 2010) and Wayanad Wildlife Sanctuary (Easa 1999), both in the Nilgiris-Eastern Ghats landscape, and close to Nagarahole National Park.

Supplementary Material 1, Table 1. List of elephant food species found in the vegetation plots. Plants that could not be identified are referred to by their local name in most cases.

1. *Acacia ferruginea*
2. *Adina cordifolia*
3. *Apluda mutica*
4. *Argyreia cuneata*
5. *Argyreia* sp.
6. *Asparagus racemosus*
7. *Axonopus compressus*
8. *Bambusa arundinacea*
9. *Bauhinia racemosa*
10. *Bridelia crenulata*
11. *Cassia occidentalis*
12. *Cassia tora*
13. *Chloris dolichostachya*
14. *Cynodon dactylon*
15. *Cyrtococcum accrescens*
16. *Cyrtococcum oxyphyllum*
17. *Cyrtococcum patens*
18. *Dalbergia latifolia*
19. *Dalbergia paniculata*
20. *Desmodium latifolium*
21. *Digitaria adscendens*
22. Doddimara
23. *Ficus mysorensis*
24. *Flemingia* sp.
25. Goddhamara
26. Grass Unidentified 17
27. *Grewia hirsuta*
28. *Grewia tiliifolia*
29. *Helicteres isora*
30. Hesaremara
31. *Heteropogon contortus*
32. *Ischaemum timorense*
33. *Kydia calycina*
34. *Kyllinga monocephala*
35. *Meyna laxiflora*
36. *Mimosa pudica*
37. *Mitragyna parvifolia*
38. *Naringi crenulata*
39. *Oplismenus compositus*
40. *Oryza sativa*
41. *Phyllanthus emblica*
42. *Premna latifolia*
43. *Pterocarpus marsupium*
44. *Randia dumetorum*
45. *Santalum album*
46. *Schleichera oleosa*
47. *Scutia myrtina*
48. *Shorea roxburghii*
49. *Sporobolus* sp.
50. Sulligida
51. Sulligida 2
52. *Tamarindus indica*
53. *Tectona grandis*
54. *Terminalia chebula*
55. *Terminalia tomentosa*
56. *Themeda* sp.
57. *Themeda triandra*
58. Wild turmeric (*Curcuma* sp.)
59. *Zizyphus oenoplia*
60. *Zizyphus rugosa*

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1. Baskaran N, Balasubramanian M, Swaminathan S and Desai AA (2010). Feeding ecology of the Asian elephant *Elephas maximus* Linnaeus in the Nilgiri Biosphere Reserve, southern India. *Journal of the Bombay Natural History Society* 107: 3–13.
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Supplementary Material 2. Line-transects sampled and used in ANOVAs on resource abundance.

Since equal numbers of transects in each forest type were required across seasons to carry out nested ANOVAs, we retained equal numbers of transects from the dry deciduous and moist deciduous forests that were sampled in both seasons, and excluded the remaining transects. The details are given in the table below.

Supplementary Material 2, Table 1. Number of 1 km line-transects sampled and used in ANOVAs on the abundance of elephant food species and all species. Each transect has five plots.

Analysis	Vegetation category	Dry deciduous Transects[1]		Moist deciduous transects[1]		Teak plantation transects	
		Sampled	Used	Sampled	Used	Sampled	Used
Nested, repeated measures ANOVA	Graminoids, herbs, shrubs, recruits (wet season)	9	6	6	6	2	NA
	Graminoids, herbs, shrubs, recruits (dry season)	11	6	9	6	2	NA
Nested ANOVA	Trees (count and GBH)	11	9	9	9	2	NA

[1] For moist deciduous forest, the same six transects that were sampled in the wet season were considered in the dry season for the analysis and the additional three transects sampled in the dry season were excluded. In case of dry deciduous forest, of the nine transects sampled in the wet season, we excluded a transect at the edge of the protected-area boundary, one that was at the transition between dry deciduous and teak plantation, and another one from two transects that were very close to each other in order to achieve a balanced design.

Supplementary Material 3. Number and mean proportional abundance of food species.

We calculated the proportional abundance of food species by dividing the elephant food species abundance by the total species abundance in each vegetation category in each plot. The proportional abundance of food species was averaged across the sampled plots (to give mean proportional food species abundance). These values and the numbers of species recorded are shown in the table below.

Supplementary Material 3, Table 1. Total number of species, number of elephant food species, and mean proportional abundance of food species in different vegetation categories.

Vegetation category	Total number of species	Number of food species	Mean (SD) proportional food species abundance in the wet season	Mean (SD) proportional food species abundance in the dry season
Graminoids	77	16 (20.78%)	0.80 (0.261)	0.85 (0.266)
Herbs	181	9 (4.97%)	0.23 (0.183)	0.09 (0.141)
Shrubs	48	6 (12.5%)	0.18 (0.142)	0.16 (0.136)
Recruits	120	28 (23.33%)	0.58 (0.241)	0.60 (0.265)
Trees	79	25 (31.65%)	NA	0.54 (0.317; count) 0.59 (0.315; GBH)

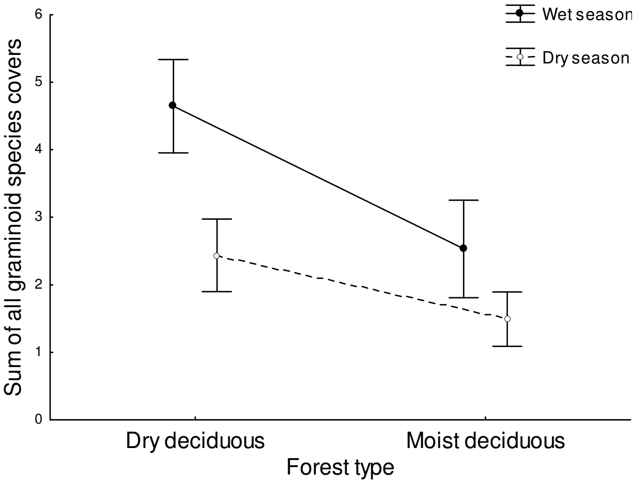
Supplementary Material 4. Total and food species abundance in various vegetation strata, seasons, forest types, and transects.

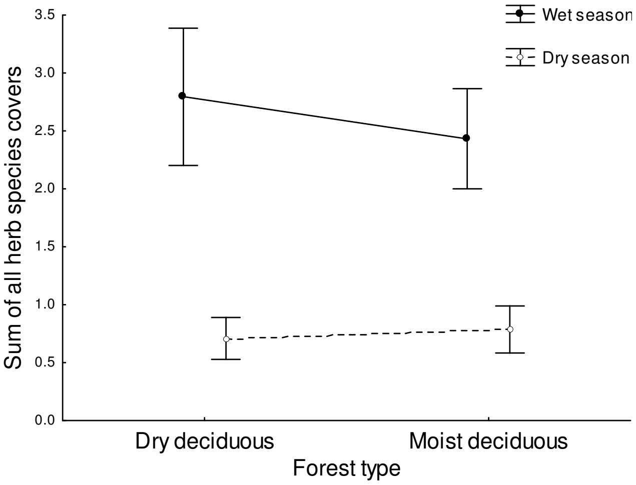
As explained in the main text, we found spatial and seasonal variation in elephant food species abundance and total species abundance in different vegetation categories (main text, Table 1). In the table and figures below, total and food species abundance in different vegetation strata in different seasons, forest types, and transects are shown.

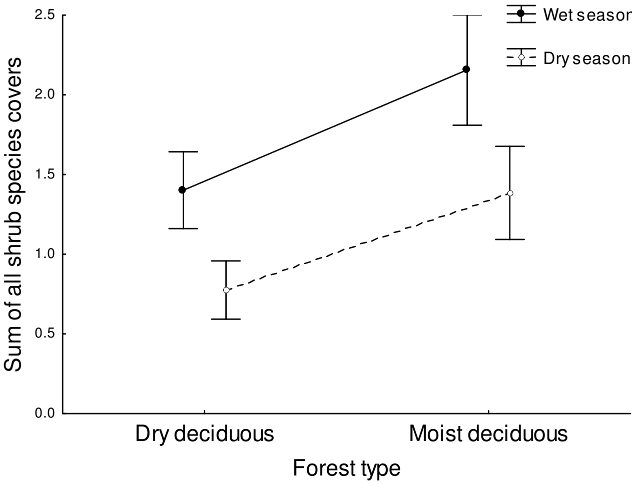
Supplementary Material 4, Table 1. Mean and 1.96 S.E. (within parentheses) total (sum of all species) abundance and food species (sum of food species) abundance (shown as sum of counts/proportions) in respective vegetation strata for the ANOVA tests shown in Table 1 (main text). Values are shown for different seasons and forest types, and their combinations.

	Graminoids		Herbs		Shrubs		Recruits		Trees	
Forest type / season	Total sp.	Food sp.	Total sp.	Food sp.	Total sp.	Food sp.	Total sp.	Food sp.	Total sp.	Food sp.
Overall	2.776	2.015	1.680	0.361	1.429	0.239	27.99	17.150	8.189	4.633
	(0.353)	(0.277)	(0.251)	(0.083)	(0.156)	(0.042)	(4.68)	(3.069)	(1.225)	(0.973)
Wet season	3.588	2.599	2.614	0.629	1.779	0.301	27.383	16.150	-	-
	(0.547)	(0.449)	(0.351)	(0.130)	(0.222)	(0.069)	(6.758)	(4.340)		
Dry season	1.964	1.431	0.747	0.093	1.080	0.176	28.600	18.150	-	-
	(0.342)	(0.252)	(0.129)	(0.041)	(0.181)	(0.043)	(6.540)	(4.362)		
DDF	3.541	2.158	1.752	0.266	1.088	0.226	38.217	25.233	10.200	5.911
	(0.503)	(0.407)	(0.397)	(0.084)	(0.164)	(0.043)	(7.775)	(5.136)	(1.767)	(1.453)
MDF	2.011	1.872	1.609	0.456	1.770	0.251	17.767	9.067	6.178	3.356
	(0.416)	(0.376)	(0.309)	(0.141)	(0.237)	(0.073)	(3.798)	(1.762)	(1.498)	(1.197)
DDF x Dry season	2.437	1.484	0.708	0.114	0.775	0.179	39.000	26.567	-	-
	(0.515)	(0.362)	(0.173)	(0.058)	(0.175)	(0.051)	(10.417)	(7.072)		
DDF x Wet season	4.646	2.833	2.795	0.418	1.402	0.273	37.433	23.900	-	-
	(0.664)	(0.650)	(0.568)	(0.139)	(0.230)	(0.066)	(11.718)	(7.539)		
MDF x Dry season	1.492	1.379	0.786	0.071	1.385	0.173	18.200	9.733	-	-
	(0.388)	(0.356)	(0.194)	(0.057)	(0.280)	(0.070)	(6.702)	(2.939)		
MDF x Wet season	2.531	2.365	2.432	0.840	2.156	0.330	17.333	8.400	-	-
	(0.694)	(0.620)	(0.413)	(0.195)	(0.332)	(0.123)	(4.667)	(1.970)		

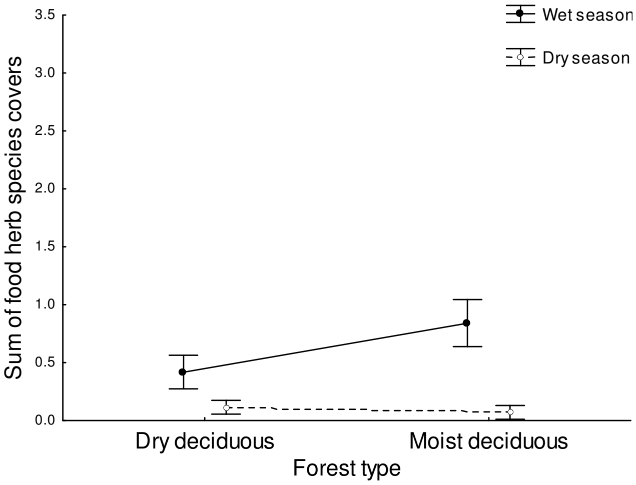
Sum of all species abundance

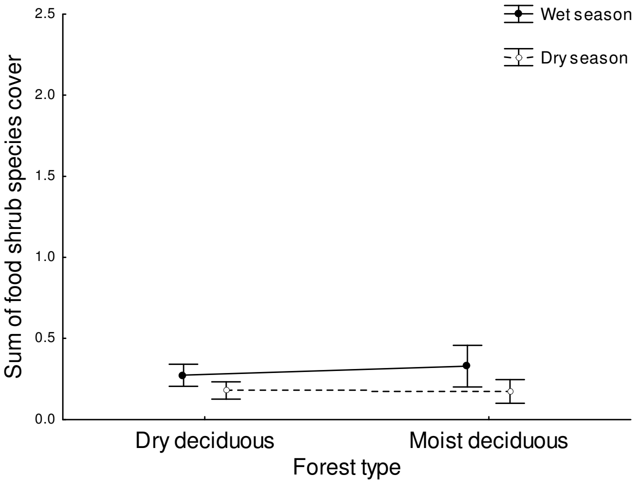


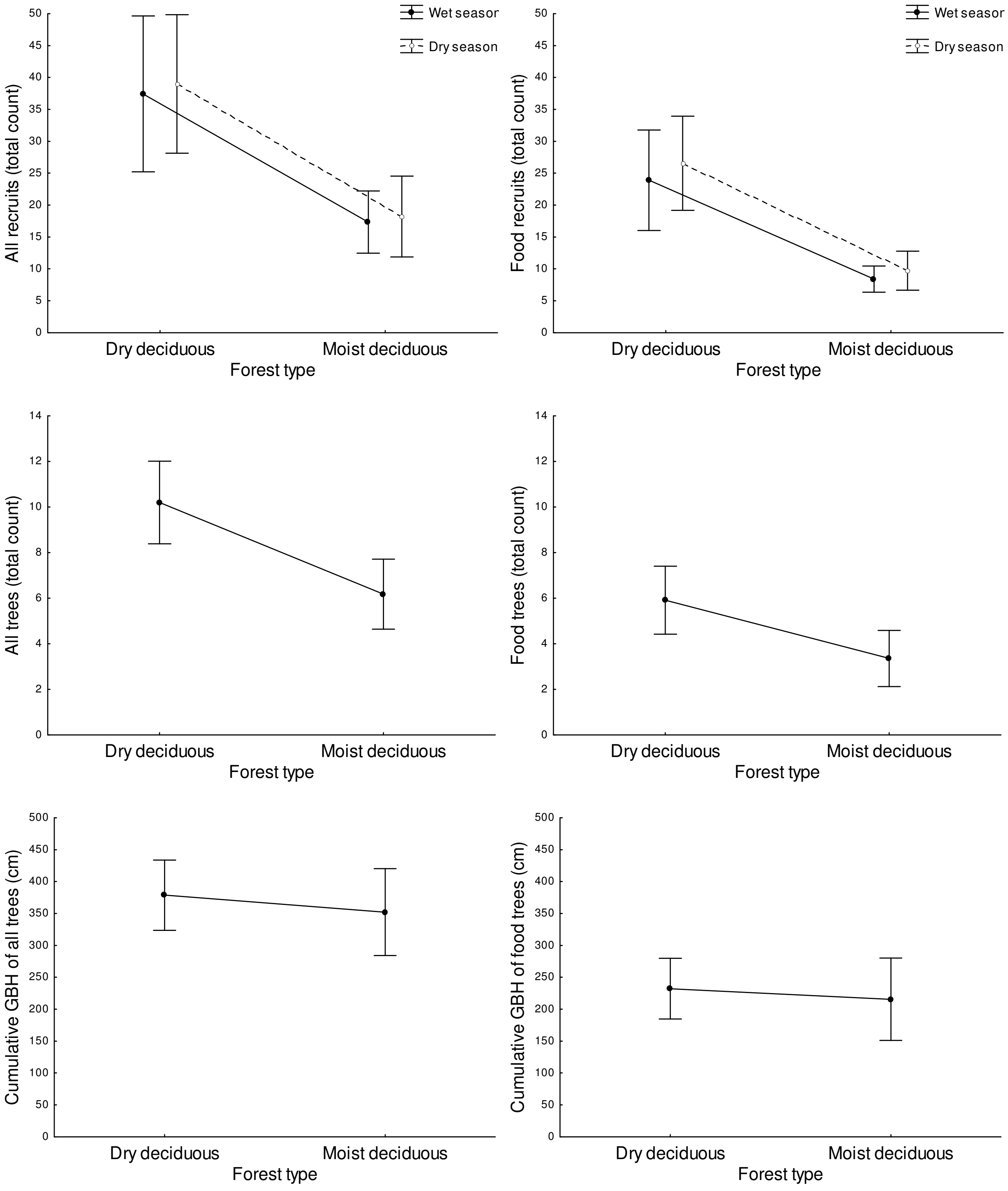




Sum of elephant food species abundance



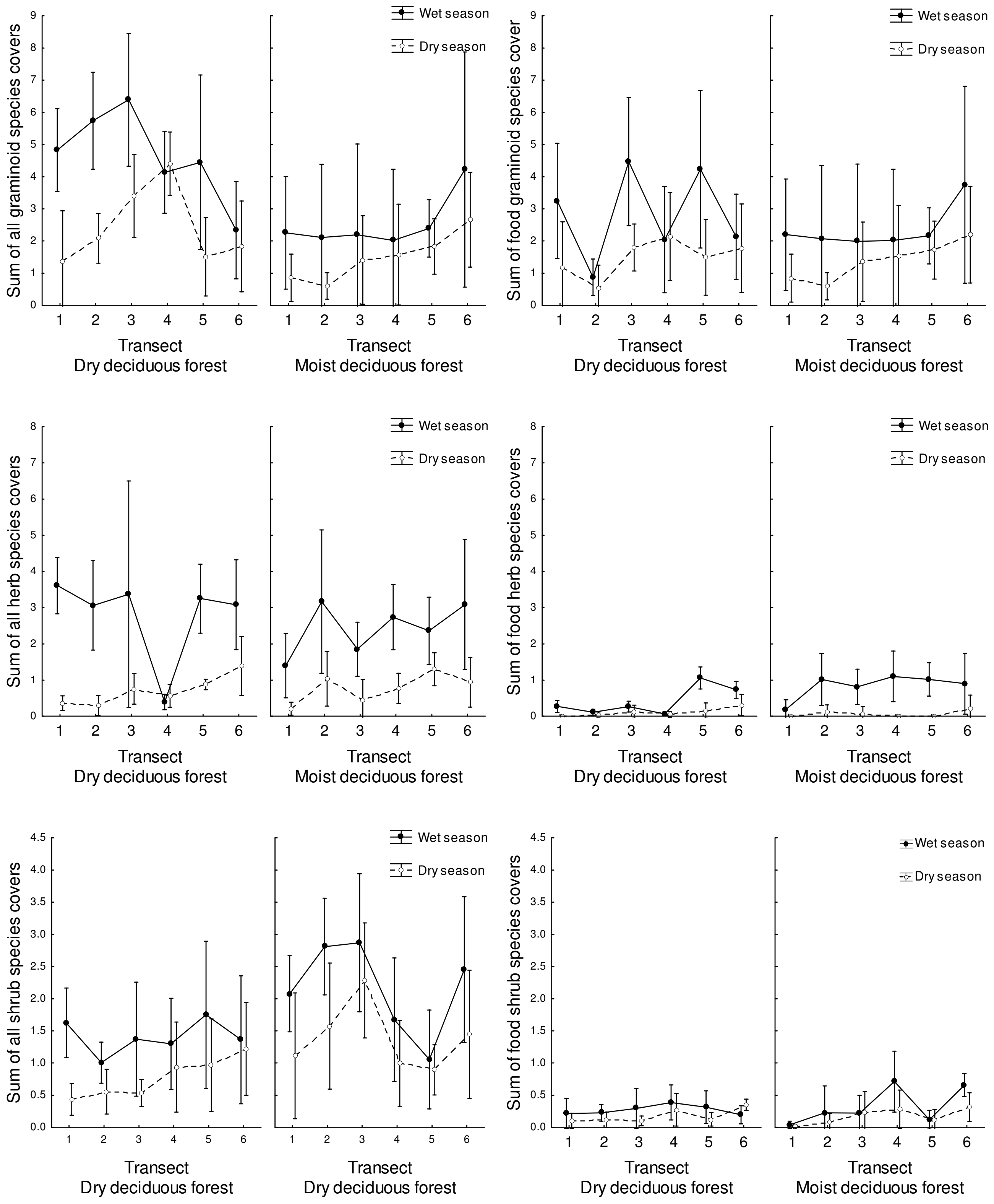


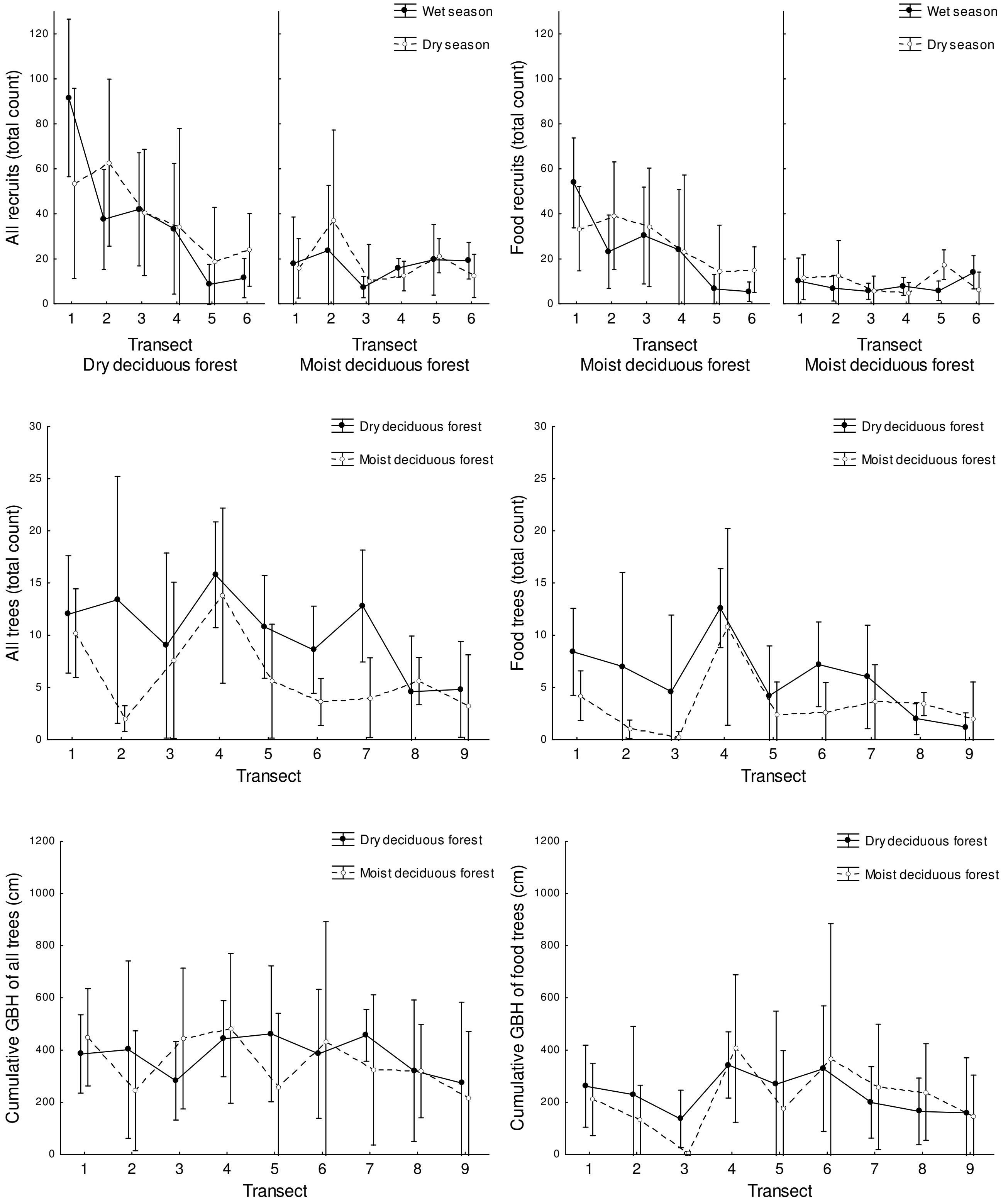


Supplementary Material 4, Figure 1. Graphs showing mean and 95% CI total and food species abundance (sum of proportions, not percentages for grasses, herbs, and shrubs and sum of counts for trees and recruits) in respective vegetation strata for the ANOVA tests shown in Table 1. Values are calculated for pooled data and for different seasons and forest types, and their combinations.

Sum of all species abundance

Sum of elephant food species abundance



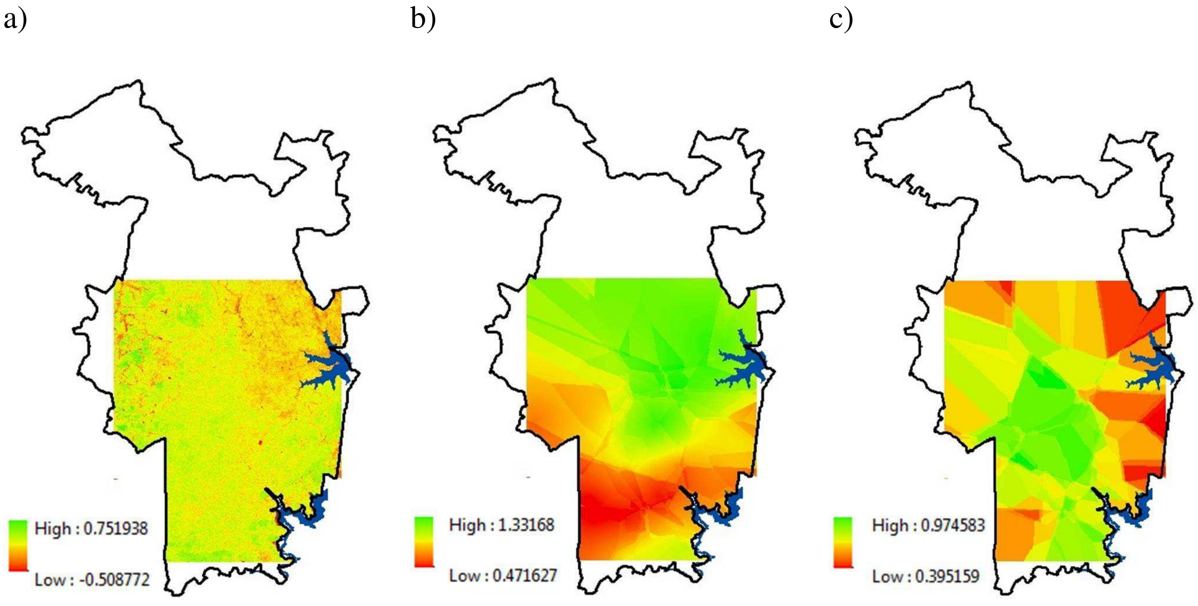


Supplementary Material 4, Figure 2. Plots of sum of food species abundance and sum of all species abundance (in terms of sum of proportions, not percentages for grasses, herbs, and shrubs and counts for trees and recruits) in different transects nested in dry and moist deciduous forests in the two seasons.

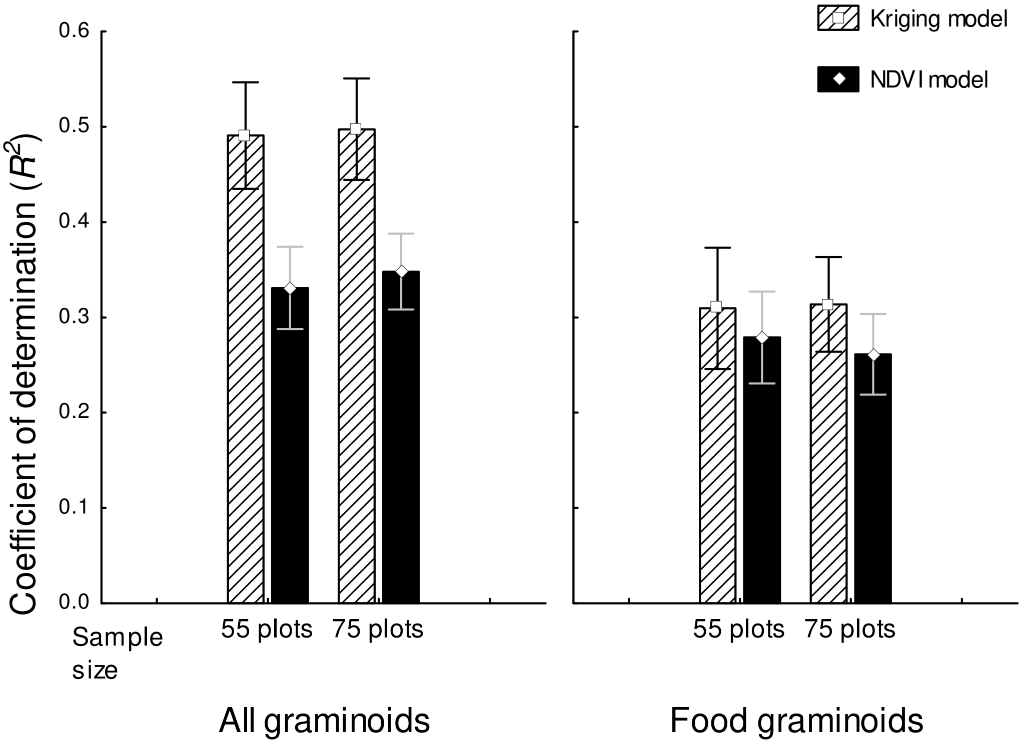
Supplementary Material 5. NDVI, kriging, and graminoid abundance.

As explained in the main text, we had found that NDVI and kriging explained significant variation in food graminoid abundance in the dry season but they were not significantly different from each other (Figure 2 of the main text). The maps showing NDVI and kriging in the wet season are in Figure 1 below. We found that neither NDVI (mean R^2=0.005, SD=0.005) nor kriging (mean R^2=0.030, SD=0.022) explained significant variation in food graminoid abundance in the wet season (Figure 2 below).

We also increased the number of training plots used in the kriging model for the dry season but it did not significantly improve the coefficient of determination either for total graminoid abundance (mean R^2=0.491, SD=0.078 for 55 plot sets, mean R^2=0.498, SD=0.074 for 75 plot sets) or for food graminoid abundance (mean R^2=0.309, SD=0.089 for 55 plot sets, mean R^2=0.314, SD=0.070 for 75 plot sets; Figure 2 below).



Supplementary Material 5, Figure 1. Maps showing a) NDVI, and kriging (spatial interpolation) models of b) total graminoid abundance and c) food graminoid abundance in the wet season.



Supplementary Material 5, Figure 2. Mean and 1.96 S.E. of coefficient of determination obtained from spatial interpolation (kriging) of total and elephant food graminoid abundance in the dry season using training datasets of 55 plots (50 verification plots) and 75 plots (30 verification plots). Values for NDVI models are also presented for comparison.

Effect of NDVI on graminoid abundance at the resolution of transects instead of plots

As explained in the Methods, we had used 20 m x 5 m plots as the unit of analyses. As our study area was spread over a few hundred square kilometres, these fine-scale plots were relevant to the spatial scale at which elephants feed. Using these plots, we had found that spatial interpolation (kriging) performed better than NDVI in explaining variation in total graminoid abundance, but that neither method was useful in estimating food graminoid abundance, especially in the wet season. In order to see if these results held at a coarser spatial scale, we also carried out general regression analyses at the resolution of 1-km transects (rather than 20 m x 5 m plots). We used the five plots from each transect to calculate the average NDVI, total graminoid species abundance and elephant food graminoid species abundance to take representative values for each transect. We performed separate general regressions of total graminoid abundance and elephant food graminoid abundance on NDVI to test if NDVI could predict these variables at the level of transects.

We found that there was a negative effect of NDVI on total graminoids abundance in the dry season ($F[2,19]=9.343$, *Multiple* $R^2=0.496$, $P=0.001$; $\beta_{NDVI}=-0.542$ (1.96 S.E. of $\beta=0.425$), $P=0.022$) and no significant effect in the wet season ($F[2,14]=1.514$, *Multiple* $R^2=0.178$, $P=0.254$; $\beta_{NDVI}=-0.384$ (1.96 S.E. of $\beta=0.476$), $P=0.136$). The effect of NDVI on food graminoid abundance was not significant in either dry season ($F[2,19]=7.654$, *Multiple* $R^2=0.446$, $P=0.004$; $\beta_{NDVI}=-0.401$ (1.96 S.E. of $\beta=0.446$), $P=0.094$) or in the wet season ($F[2,14]=0.371$, *Multiple* $R^2=0.050$, $P=0.697$; $\beta_{NDVI}=-0.156$ (1.96 S.E. of $\beta=0.511$), $P=0.560$). These results are similar to the trends seen in our analyses done at the level of plots (Table 3, Table 4) and show that NDVI is not a positive correlate of either total graminoid abundance or food graminoid abundance in our study area.

CHAPTER 4

A Test of the Socioecological Model in Female Asian Elephants: The Effects of Food Abundance, Food Distribution, and Competitor Density on Within-Clan and Between-Clan Contests

Title: A test of the socioecological model in female Asian elephants: the effects of food abundance, food distribution, and competitor density on within-clan and between-clan contests

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Author contributions:

HG and TNCV conceived this work. HG collected the field data and carried out data analyses. HG primarily and TNCV wrote the manuscript.

Abstract

Socioecological theory, which attributes variation in social organisation in female-bonded species to differences in within- and between-group feeding competition shaped by food distribution, remains largely unexplored in non-primate species. In the first such attempt on a non-primate mammal, we studied the patterns of agonistic contests within- and between-clans (the most inclusive social unit) of female Asian elephants with respect to food distribution, food abundance, and competitor density effects of group size and clan density. We directly quantified the distribution of grass biomass in different stretches of a grassland habitat around the Kabini backwaters, as well as the adjacent forest habitat, in Nagarahole National Park, southern India. We also quantified agonistic interactions among adult females in the grassland habitat to obtain rates of individual-level within-clan and between-clan agonism, and clan-level between-clan encounters. The occurrence of more frequent between-clan encounters in contrast to what was known from forest habitats, and stronger individual-level between-clan agonism than within-clan agonism was consistent with the grassland being a food-rich habitat patch as compared to the adjacent forest, as expected from socioecological theory. Within-clan agonism was not influenced by grass abundance or distribution within the grassland habitat, in contradiction to classic socioecological predictions, but interestingly increased with female group size until a group size of five, suggesting that the opposing forces of within-group and between-group competition may govern group size, as large group size is advantageous in this strong between-clan contest regime. The rate of (clan-level) between-clan agonistic encounters was positively explained by the number of clans. Although the rate of between-clan encounters was not related to grass biomass in focal zones, the duration of such encounters was positively related to grass biomass at the site of contest. We discuss contest competition in female elephant societies in the context of socioecological theory.

Keywords

Socioecological theory, group size, feeding competition, within-group and between-group contest, agonism, food abundance and distribution, competitor density, fission-fusion, Asian elephants, Kabini Elephant Project, Nagarahole National Park.

Introduction

Socioecological theory offers a framework to explain variation in animal societies based on resource-risk distributions (Crook and Gartlan 1966, Alexander 1974, Terborgh and Janson 1986, Clutton-Brock 1989, Emlen 1995). The ecological model of female social relationships (EMFSR), which is part of the larger socioecological framework, proposes that feeding competition is a pivotal variable that shapes social organisation and structure in female-bonded groups (Wrangham 1980, van Schaik 1989, Isbell 1991, Sterck *et al.* 1997). Food characteristics, such as distribution, abundance, and quality, are expected to shape feeding competition regime. Within groups, scramble or exploitative competition is expected to predominate when limited food is dispersed and cannot be usurped by individuals, whereas strong contest or interference competition is expected when high quality food is present in usurpable clumps or patches (Janson 1985, van Schaik 1989, Isbell 1991). Between groups, contest competition is expected when food patches are large and can be usurped by groups (Wrangham 1980, Isbell 1991). Potentially strong and simultaneous between-group and within-group contest are expected to result in within-group contest being ameliorated via greater tolerance shown by dominant members of the group towards subordinates, since larger group sizes are likely to be advantageous during between-group contests (see Sterck *et al.* 1997, Isbell and Young 2002).

The role of food characteristics in shaping competition regimes and social relationships has been studied and discussed many times (for example, Janson 1985, Chapman *et al.* 1995, Koenig *et al.* 1998, Pruetz and Isbell 2000, Korstjens *et al.* 2002, see also Koenig 2002, Snaith and Chapman 2007). Based on mixed empirical findings, it has sometimes been suggested that other factors such as predation (Alexander 1974, van Schaik 1989), infanticide (van Schaik 1996, Steenbeek and van Schaik 2001), or phylogenetic constraints (di Fiore and Rendall 1994, see Thierry 2013) may be as or more important than food characteristics in shaping female social organisation (see also Thierry 2008, Lawler 2011). Others (for example, Koenig and Borries 2009, Koenig *et al.* 2013) have defended the EMFSR, asserting that the model is based on solid reasoning. The interpretation of food abundance and distribution from indirect indicators such as diet type has been questioned instead (Snaith and Chapman 2007, Koenig *et al.* 2013, Wheeler *et al.* 2013), underlining the need for field-based quantification of food characteristics to test the ecological basis of contest competition. As contest competition may also be influenced by competitor density, group size and group spread may also be important to examine in the field (Wittig and Boesch 2003, Koenig and Borries 2006, Wheeler *et al.* 2013, see also van Schaik *et al.* 1983).

Despite the EMFSR not being conceptually restricted to specific taxa, it has been popular primarily among primatologists, and has rarely been examined in other mammals (but see, for example, Holekamp *et al.* 1996, Smith *et al.* 2008, Wittemyer *et al.* 2007, see also Caraco and Wolf 1975, Monaghan and Metcalfe 1985, Schmidt and Mech 1997). Thus, studies of the EMFSR on other taxa are desirable (Clutton-Brock and Janson 2012, see also Silk 2007). Even among primates, there has been a much larger body of work on the relationship between food distribution and within-group contest (for example, Janson 1985, Koenig *et al.* 1998, Pruetz and Isbell 2000, Korstjens *et al.* 2002, Koenig and Borries 2006, Chancellor and Isbell 2009, Hanya 2009) rather than on between-group contest (for example, Wilson *et al.* 2012, Brown 2013, Roth and Cords 2016, Pal *et al.* 2018). This is despite the fact that one of the principal disagreements between Wrangham's (1980) and van Schaik's (1989) early formulations of EMFSR was on the role of between-group contest in shaping female societies. Many studies of between-group contest have largely focused on territorial behaviour or factors affecting outcomes of the contests or their consequences for group members (for example, Cheney 1987, Markham *et al.* 2012, Willems and van Schaik 2015, Roth and Cords 2016, Majolo *et al.* 2016, Mirville *et al.* 2018) rather than the effect of food distribution on between-group contests. Moreover, studies of within- and between-group contests have been carried out more often on frugivores (for example, Janson 1985, Vogel and Janson 2009, Chancellor and Isbell 2009, Hanya 2009) than on folivores (for example, Koenig *et al.* 1998, Harris 2006, Grueter *et al.* 2016, Teichroeb and Sicotte 2018), which were initially thought to face reduced feeding competition because of their seemingly low quality or continuously distributed and abundant diet (Wrangham 1980, van Schaik 1989, Isbell 1991). In the context of the above, we wanted to examine the relationship between food resources and rates of within- and between-group contests in a non-primate species, the Asian elephant (*Elephas maximus*), feeding primarily on grass, traditionally thought of as a low quality resource, in Nagarahole National Park and Tiger Reserve (Kabini population), southern India.

Asian elephants exhibit female-bonded groups (Sukumar 1989, Fernando and Lande 2000, de Silva *et al.* 2011), with the most inclusive social unit being the clan (Nandini *et al.* 2018).

Females within clans show fission-fusion dynamics, in which clan-members are usually distributed across multiple groups, whose group compositions can change across hours (Nandini *et al.* 2017, 2018). A group is a “party” seen together in the field, with individuals usually within ~50 m of one another and showing coordinated movement. The home ranges of clans may overlap extensively (for example, Baskaran and Desai 1996, Fernando *et al.* 2008), a trait that is usually related to infrequent aggression during between-clan encounters since less exclusive ranges are associated with lower incentives of between-group aggression (see Cheney 1987, Willems and van Schaik 2015, see also Brown 2013, Pisor and Surbeck 2019). Male Asian elephants disperse away from their natal groups (Desai and Johnsingh 1995, Vidya and Sukumar 2005) and are largely solitary thereafter (Keerthipriya *et al.* 2018). Predation risk to adult female elephants in southern India is negligible, although calves may be occasionally taken by tigers. Female groups are not known to face any infanticide risks from males. Therefore, food characteristics, rather than predation or infanticide, are expected to shape group size and competition regimes in this species. Moreover, as female and male societies are largely separate, within- and between-group contest in this species do not typically involve the participation of adult males, unlike that found in some primates (for example, Cooper *et al.* 2004, Brown 2013, Pal *et al.* 2018). Thus, the Asian elephant is an excellent non-primate species in which to examine predictions of the EMFSR.

The Kabini elephant population, in which this study was carried out, has been monitored (Kabini Elephant Project) since 2009 and several hundred individuals identified and their clans known (see Methods). Contest competition is known to exist between adult females within clans as well as between clans in this population (Nandini 2016). Since elephants show fission-fusion societies, groups of females from the same or different clans can potentially interact with one another. However, we hardly ever found group-level agonistic interaction between groups from the same clan; therefore, between-group agonism in this paper refers to agonism between clans. The nature of dominance relationships has also been studied in another Asian elephant population (de Silva *et al.* 2017), but there has been no actual quantification of food resources or an attempt to relate them to contest competition in any elephant species. In this paper, we directly quantify food abundance and distribution in a small grassland habitat, and study their relationship with the frequency of agonistic interactions within and between clans. We also examine the effect of group size on such interactions. Proximal understanding of agonistic contest competition in Asian elephants can help in assessing the socioecological model in a species that falls towards the egalitarian side (Nandini 2016, de Silva *et al.* 2017) of the egalitarian-despotic continuum.

We addressed the following specific questions.

1) How does grass abundance in the Kabini grassland compare with that in the neighbouring forest habitat, and what is its distribution across and within different areas (focal zones) in the grassland?

Since between-group contests are more frequent in the Kabini grassland (Nandini 2016) compared to the nearby forests in the Nilgiri Biosphere Reserve (Baskaran 1998), we wanted to find out whether the former was richer in resources, possibly explaining the occurrence of between-group contests. We thus expected greater grass biomass in the Kabini grassland than in the forest, which also has grass understorey. We did not expect much spatial variation in grass abundance at a local level (within focal zones – see Methods) in the grassland because the grass layer appears to be continuous (see photos in Supplementary Material 1). However, we expected a few focal zones in the grassland to have greater grass biomass than others as grass height seemed to vary based on preliminary visual assessment.

2) How do the rates and intensities of individual-level agonism among females compare within and between clans?

As mentioned in the Introduction, strong between-group contest is expected according to the EMFSR when there are large patches with abundant food, whereas contest among females within groups is expected to be more frequent when feeding sites are clumped at the local level (Wrangham 1980, Sterck *et al.* 1997, see Koenig 2002, Snaith and Chapman 2007). Therefore, we expected that if the grassland habitat were a food-rich habitat and if there were significant differences in grass abundance across focal zones, agonism among individual females would be more frequent during between-clan encounters than within clans. This would not ensue merely because of the larger number of females present during between-clan encounters, but the rate of individual-level agonism (number of agonistic events per female per hour) during between-clan encounters would be greater than that within clans after controlling for the number of females. In this case, we also expected the intensity of agonistic interactions to be higher during between-clan than within-clan agonistic interactions. On the other hand, if there was little variation in grass abundance across zones and high local variability, we did not expect the rate of individual-level agonism to be different between and within clans (the presence of more than one clan in a feeding area would not increase the rate of individual-level agonism because females would not be expected to give up their feeding time to participate in between-clan agonistic interactions if the patches were not large enough to be usurped by clans).

3) Is the rate of within-clan agonism explained by variation in grass abundance, grass dispersion, and group size?

We wanted to examine whether the rate of (individual-level) within-clan agonistic interactions was explained by grass abundance and dispersion, and group size. From the classical prediction of EMFSR (for example, Koenig *et al.* 1998, Pruetz and Isbell 2000), we expected within-clan agonism to be more frequent when grass was more clumped at a small spatial scale. In accordance with simple models of feeding competition, we expected more frequent agonism where grass was scarce. We expected group size, which reflects local competitor density, to positively correlate to within-clan agonism (see Koenig and Borries 2006, Wheeler *et al.* 2013).

4) Is the rate of individual-level between-clan agonistic interactions explained by variation in grass abundance, grass dispersion, and group size?

Similar to the question above, we also wanted to examine whether the rate of individual-level between-clan agonistic interactions was explained by grass abundance and dispersion, and group size. We expected the rate of individual-level agonistic interactions between clans to be positively related to food abundance at the site of contest. Further, we expected the rate of individual-level agonistic interactions between clans to be higher when the competing clans were evenly matched in group size, a determinant of resource holding potential of groups (for example, Roth and Cords 2016), than when there were large differences in group sizes.

5) Are the rate of clan-level between-clan agonistic encounters and the duration of such encounters related to grass abundance/distribution and group size or the number of clans?

As with individual-level interactions, we wanted to examine how well the rate of between-clan agonism at the level of the entire groups participating (clan-level) could be explained by grass abundance and dispersion, and clan (group) density. Game theory explanations expect the nature of contests to depend on the resource value of the site contested and resource holding potential of the contestants (for example, Markham *et al.* 2012, *sensu*

Smith and Parker 1976). Applying this to clan-level contests, we expected more frequent clan-level between-clan agonistic encounters in focal zones with more abundant grass since between-group contest is thought to be linked to food abundance (Koenig 2002). Further, we expected more frequent clan-level between-clan agonistic encounters in zones within which grass was heterogeneously distributed than in zones with dispersed grass (see Methods). Following from van Schaik's (1989) prediction of stronger between-group contest at high density, we also expected more frequent between-clan agonistic encounters when a larger number of clans was present in the zone. We expected the duration of such clan-level agonistic encounters to be positively related to food abundance at the site of contest. We also expected that the duration would be higher when the competing clans were evenly matched in group size than when there were large differences in group sizes.

Methods

Study area

We carried out the study in Nagarahole National Park and Tiger Reserve (11.85304°-12.26089° N, 76.00075°-76.27996° E) in the Nilgiris-Eastern Ghats landscape, southern India. Nagarahole largely comprises deciduous forest with grass and other herbaceous and shrubby plants in the understorey, but an open grassland is formed by the receding backwaters of the Kabini reservoir (formed by the Beechanahalli Dam built on the River Kabini that flows between Nagarahole and Bandipur National Parks) during the dry season (Figure 1a). This grassland supports a high density of wild herbivores, including elephants. Hundreds of elephants that use the Kabini reservoir and its surrounding forests have been identified based on natural physical characteristics (see Vidya *et al.* 2014) and monitored since 2009 as part of the long-term Kabini Elephant Project in order to understand their ecology and behaviour. The grassland around the backwaters has a continuous layer of grass (see Supplementary Material 1), which is the primary food for elephants there. Bamboo clumps around the backwaters that were previously used by elephants died out after the mass-flowering in 2011. The home ranges of female clans in this population have not been studied so far, but those of two clans in the Mudumalai forest in the same landscape were found to be about 600 km^2 and to show a high degree of overlap (Baskaran and Desai 1996). Based on preliminary data from our project, we knew that multiple clans used the Kabini grassland at the same time and showed between-clan aggression. We did not find single clans excluding portions of the grassland from other clans. There was spatio-seasonal variation in the abundance of elephant food plants in the forests of Nagarahole (Gautam *et al*. 2019).

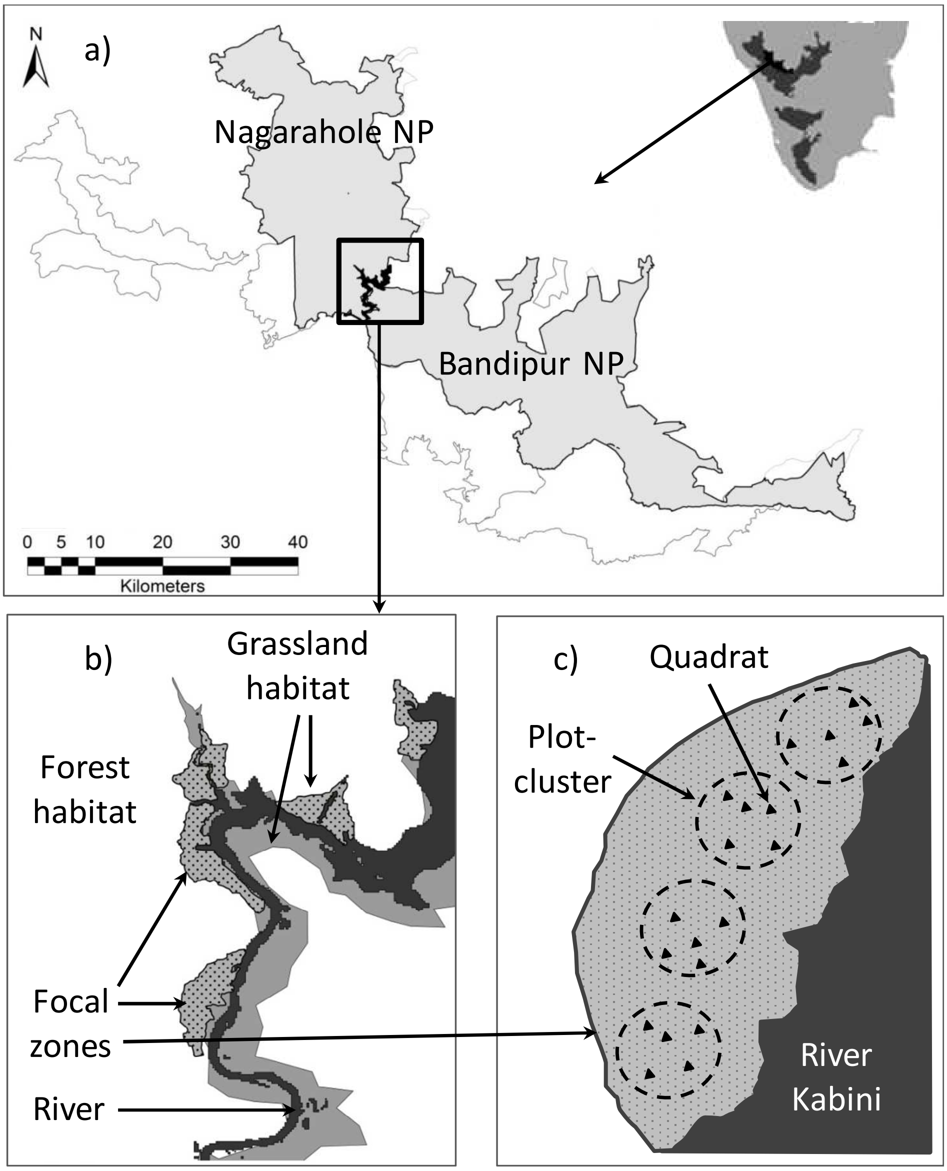

Figure 1. a) Maps showing the location of Nagarahole and Bandipur National Parks and the Kabini backwaters between them, in southern India. The rectangle placed in the centre highlights the backwaters area which is an open grassland during the dry season. b) Map of the Kabini backwaters area showing the outlines of the six focal zones (grey dot-filled polygons) sampled in the grassland habitat (in grey). c) An illustration of the sampling scheme used to sample grass abundance, showing five quadrats each in four plot-clusters in a focal zone.

Data collection

Sampling of grass abundance and distribution

Around the backwaters area, six grassland stretches along the river, henceforth called focal zones (Figure 1b), were selected for sampling. Each focal zone allowed for clear visibility of a considerably large grassland area from either end, and could be demarcated from adjacent zones by either the abrupt narrowing of grassland strips along the river or by physical breaks such as small streams. Because of water lever fluctuations in the reservoir, the areas of focal zones varied across different months (Supplementary Material 2). We sampled four periods of about 30 days (henceforth, referred to as months) during the dry seasons of 2015 and 2016. In each focal zone, we sampled 20 1 m x 1 m quadrats each month, almost always on a single day in the middle of each 30-day period. These 20 quadrats were distributed within each zone in 4 clusters (henceforth plot-clusters) of 5 quadrats each (see Figure 1c) in order to sample different areas within a zone and assess the variability of grass abundance at a local scale. While the centre of a plot-cluster was fixed across months, we laid the five constituent quadrats by walking random distances along a random direction (using randomly generated numbers between 1 to 100 for distance in metres and 0 to 360 for angle in degrees) each month. In case the random distance/angle led a quadrat out of the zone (towards forest, water, or to grassland areas outside the zone) due to the small size of the zones, we chose another combination of distance and angle. Such physical constraints usually kept the longest diameter of the plot-cluster less than 100 m. Random sampling was chosen because grass appeared to be continuously spread and it was not possible to visually detect either the centre or the extent of patches, unlike in studies on primates where patches may be more clearly delineated (tree trunk and canopy spread, for example, Vogel and Janson 2011). We visually estimated the percentage grass cover (see Gautam *et al.* 2017), measured grass height, and harvested fresh biomass from each quadrat (see Supplementary Material 1). We measured grass height in a quadrat as the average of the natural standing heights (i.e. without straightening the plant) of ten grass stems within that quadrat. We clipped all the grass above the ground level, separated them from herbs if they existed, and weighed the fresh harvested grass biomass in the field using a digital weighing balance.

For comparison of grass abundance between the grassland and the forest habitat, we used harvested grass biomass data from vegetation transects sampled previously (Gautam *et al.* 2017) from forests of Nagarahole National Park. The three major forest types (dry deciduous, moist deciduous and teak forests) were sampled proportionate to their land-cover. We collected data from the forests at the end of the wet season (November-December).

Sampling of focal zones to quantify within-clan and between-clan agonism

We carried out full-day observations on selected focal zones during the four sampling months each year to quantify elephant visits and agonistic interactions between elephants. We selected the focal zone to be sampled based on rotational sequence, and sampled each zone on three sampling days during each sampling month in 2015 and four such days in each sampling month in 2016. We additionally carried out opportunistic sampling on the remaining days when possible in order to maximise observations of agonistic behaviour. On each sampling day, the observer (HG) remained in the selected focal zone from approximately 6:30 AM to approximately 06:30 PM (based on permits) and recorded all elephant visits to the zone. We collected details on the time of arrival and departure of elephant groups, group size, group composition (counts of adults, sub-adults, juveniles, and calves, of each sex), and the identities of all the individuals based on natural physical characteristics (see Vidya *et al.* 2014), subsequently verified from photographs and videos. As mentioned above, a female group is a party or set of adult females (and other associated individuals) seen in the field that show coordinated movement and/or affiliative behaviour and are usually within ~50 m of one another (see Nandini *et al.* 2018). Female groups are usually subsets of clans, which are the most inclusive female social units, and within which associations are fluid, showing fission-fusion dynamics (Nandini *et al.* 2017, 2018). In cases multiple groups arrived and it was not possible to record them simultaneously, we focused our sampling on the group that was closer to the observer or that settled down to feeding or seemed more likely to settle down earlier based on its movement.

Since the open grassland had complete visibility, we used focal group sampling (see Altmann 1974) to record agonistic interactions between adult females, defined as females that were at least 10 years old (see Nandini *et al.* 2018) at the mid-point of the sampling period, i.e., 1 October 2015. Adult females are, henceforth, referred to simply as females in this paper. Such agonistic interactions could occur between females within groups, and therefore, belonging to the same clan, or between members of different groups belonging to different clans. As mentioned above, we hardly ever saw group-level agonistic interaction between different groups belonging to the same clan. Therefore, our interest was in comparing within-clan and between-clan agonistic interactions. We recorded focal observations using a Sony HDR-XR100E video camera and noted down GPS locations and the predominant activity of the group (feeding, using water/puddles, or other activity). We focussed videos in such a way as to attempt recording all the females within a group. However, if the females were spread over a large area and recording of all females was not possible, we took down field notes on the females outside the video frame. This rarely happened during within-clan agonism.

For all focal group observations, we also noted down the nearest plot-cluster so that the relationship between grass abundance/distribution and agonism could be examined. We did not assign any plot-cluster to a focal group observation if the focal group was more than 100 m away from the centres of all plot-clusters.

Video scoring

We used the video recordings to score (in VLC media player) agonistic interactions between females. Agonistic interactions included aggressive behaviours such as displacement, supplant, pushing, shoving, trunk wrestling, hitting, kicking, chasing, charging, placing trunk over opponent's head to dominate, and pulling tail, and submissive behaviours such as turning away and showing back/urinating/shaking head after advancing towards an opponent, submissively walking backwards towards the opponent, and avoidance. We also used supplemental field notes, but excluded any focal group observation from calculations of rates of agonism if we did not have a complete record of agonistic behaviours performed by all females. We also excluded focal videos if the elephants were disturbed and their activity disrupted.

We classified focal observations of individual-level agonistic interactions between females into two categories – within-clan and between-clan agonism. Between-clan interactions could be examined at the level of the individual females participating, as well as at the level of the entire groups present, which we refer to as clan-level interactions/encounters or outcomes. We recorded the time of individual interactions, and the identities of the initiator, recipient, winner, and loser in within-clan and between-clan agonistic interactions between females. In addition to these individual-level details, in the case of between-clan interactions, we also recorded the start and end time of clan-level between-clan encounters (see below), clan identities of the competing groups, and whether the group won or lost if there was a clear resolution at the level of the entire between-clan encounter. We noted a between-clan encounter as having begun if the individuals at the closest edges of two groups from different clans approached to within a distance equivalent to the spread of the larger of the two groups, or to within a distance of ~50 m (if their spread was smaller than ~50 m). We noted the encounter as having ended if one or both clans started walking away and the distance between them exceeded this threshold. We classified between-clan encounters as agonistic, if there was at least one agonistic interaction between females of the competing clans, or not. We scored the outcome of the entire between-clan agonistic encounter (clan-level outcome), which could comprise multiple individual-level agonistic interactions between the females of the participating clans, as having a clear resolution if one of the two interacting groups (the winning clan) dominated and completely displaced the other group (losing clan) from the place of encounter by more than the maximum group spread of the larger of the two groups (or by more than ~50 m if their spread was much smaller).

Data analysis

1. How does grass abundance in the Kabini grassland compare with that in the neighbouring forest habitat, and what is its distribution across and within different areas (focal zones) in the grassland?

In order to test for differences in grass abundance between the grassland and forest habitats, we compared the harvested biomass from the plot-clusters (average of five 1 m x 1 m quadrats each) in the grassland habitat (*N*=95 and 96 plot-clusters in 2015 and 2016, respectively) with that from plots in forest habitat (*N*=40 plots, averages of three 1 m x 1 m quadrats per plot). Since the forest data were collected only once and in a previous year (end of wet season of 2013), we compared it separately with the grassland data from 2015 and 2016. Data from the forest were collected at the end of the wet season and grass abundance in the forest is expected to become even lower as the forest becomes drier in the following dry season months (personal observations) when grassland habitat was sampled. Hence, any positive difference in the grass biomass between grassland and forest from the compared datasets would be smaller than if the forest data were from the dry season. We performed *t*-tests with unequal variances, since the two habitat types had unequal variances, in MS Excel. Along with these statistical tests, we also used previously published grass biomass from Bandipur National Park (Devidas 1995), to compare with our forest data and further establish the difference between grassland and forest. For this, we calculated the average grass biomass from the same months as in our sampling (February to June), and used

Welch's test (Welch 1938, see Fagerland and Sandvik 2009) to compare the averages.

In order to examine the distribution of grass abundance in the grassland habitat, we used three measures of grass abundance – biomass, cover, and average height. We averaged values of each grass abundance variable from the five 1 m x 1 m quadrats of each plot-cluster to obtain average abundances that we refer to as within-plot-cluster biomass/cover/height. We also calculated variability as the coefficient of variation (CV=standard deviation to mean ratio) based on the five quadrats of each plot-cluster to obtain within-plot-cluster CV in grass biomass, cover, and height. These values would indicate the local abundance and local variability within a plot-cluster, which would be relevant to within-clan feeding competition. For the four plot-clusters (out of 192), in which data from a quadrat each was missing either due to rain or other logistical problems in the field, we assigned the average abundance value of the other quadrats to the missing cell.

We averaged grass abundances from all the four plot-clusters within each zone to obtain within-zone grass biomass/cover/height, which was taken as representative of the zone's average grass abundance. We also calculated the within-zone CV in grass biomass/cover/height across the four plot-clusters within a zone, as estimates of the variability within each zone. Within-zone abundance and variability were expected to influence between-clan contest, the former being a measure of average food abundance for the entire zone and the latter providing information on heterogeneity across plot-clusters, which could presumably be perceived by clans to contest for foraging patches.

We then used a mixed-effects General Linear Model (GLM) to test the effects of year (random factor), month (fixed factor), zone (fixed factor), and their two-way and three-way interactions on the dependent variable, which was the within-plot-cluster grass abundance (a separate GLM was carried out for within-plot-cluster biomass, cover, and height). As mentioned above, the five constituent quadrats of each plot cluster were chosen randomly each month; therefore, month was not a repeated-measure. Month was treated as a fixed effect and not as a replicate like year because a change in months was expected to correlate with temporal changes in the habitat (both in forest and backwaters) as the dry season progressed from February to May. Data were missing for one data point (plot-cluster), and we used the mean of the other three plot-clusters for this point in order to obtain a balanced design.

2. How do the rates and intensities of individual-level agonism among females compare within and between clans?

Since we wanted to compare the rate of individual-level agonism within and between clans, we focused on the occurrence of agonistic contests and not their outcomes. We used the average rate of agonistic interactions between females (individual-level agonism), calculated from focal group observations, as a measure of contest competition (see Koenig *et al.* 2013). We only included focal observations in which the group's predominant activity was foraging, so that the rates of agonism primarily reflected interference during foraging, and consequently, loss of feeding time and opportunities (see Janson 1985). We considered an agonistic interaction between two females to be independent of another interaction between the same pair if the two interactions were at least 15 minutes apart. This was because we found that in more than 95% of the cases, the interval between an individual-level agonistic interaction and the subsequent interaction involving the same dyad was less than or up to 15 minutes, making this a meaningful cut-off for both within-clan and between-clan individual level agonism (Supplementary Material 3). We classified interactions that occurred within 15 minutes of each other involving the same dyad as non-independent interactions. We excluded focal group observation videos if they were shorter than 15 minutes. Additionally, if the same group (same female composition) was recorded again for within-clan agonism after an interval, we included the subsequent video for scoring only if there was a gap of at least 15 minutes.

In order to calculate the rate of individual-level agonism during between-clan interactions, we used focal group observations of all between-clan encounters, whether they were agonistic or not. We used a 2.5-hour cut-off to define independence of focal group observations on between-clan encounters. This was because more than 95% of between-clan encounters at the level of the clans, for which exact start and end times were known, occurred for less than or up to 2.5 hours (Supplementary Material 3). Subsequent encounters between the same two clans were considered non-independent at the clan-level and excluded from this analysis if they occurred within 2.5 hours of the first encounter.

We used only the independent individual-level interactions from each independent focal session (either within or between clans) to calculate the rates of individual-level agonism in two ways: rate of agonism per female per hour and dyadic rate of agonism (see Table 1 for formulae). While the rate of agonism per female per hour reflects contest or interference competition (see Wheeler *et al.* 2013, Koenig *et al.* 2013), the dyadic rate of agonism measures a female's interaction rate with every other competitor (Cowl and Shultz 2017). We additionally calculated the simple ratio of non-independent interactions to independent interactions (NI/I ratio) during each independent focal group observation with at least one individual-level agonistic event, as a measure of the intensity of individual-level agonism during within-clan and between-clan interactions.

We used linear mixed-effects models to investigate the effect of type of agonism (between-clan/within-clan, fixed effect) on rates of individual-level agonism. Since our agonism data were from multiple clans, we included clan identity as a random effect. However, there were not enough focal observations of both between-clan and within-clan agonism for many clans. Therefore, we used data from the five common clans (minimum of eight focal observations each of within- and between-clan agonism) for this analysis. In addition to this, we also plotted the rates of individual-level within-clan and between-clan agonism, including other clans as well. The mixed-effects model was used separately for the per female rate and dyadic rate of agonism. We also tested for the difference between within-clan and between-clan agonism in the intensity of agonism (NI/I ratio), but we used a fixed-effects model since clan did not explain any variation in NI/I ratio.

In order to examine if the rate of individual-level agonism within and between clans remained significant after controlling for the number of female competitors (group size for within-clan and sum of group sizes for between-clan encounters), we used a homogeneity-of-slopes test and regressed the rate of individual-level agonism on the number of female competitors, with type of encounter (within-clan and between-clan as two levels) as a categorical variable. Since clan identity did not explain much variance in the above analyses (see Results), and since many clan combinations had small sample sizes, clan identity was not included as a random effect.

Table 1. Formulae used to calculate a) the rate of agonism per female per hour (*sensu* Wheeler *et al.* 2013) and dyadic rate of agonism per hour (*sensu* Cowl and Shultz 2017) to compare individual-level agonism from each focal observation on within- or between-clan encounters, and b) the rate of clan-level between-clan agonistic encounters in each focal zone. In the case of individual-level agonism (within or between clans), I = number of independent individual-level agonistic interactions observed in a focal observation, t = duration of focal group observation, n=group size (for within-clan agonism), $n1$ and $n2$ = group sizes of the competing groups (for between-clan agonism). For the rate of clan-level agonism between-clans, I = number of agonistic between-clan encounters per 2.5-hour interval in a focal zone, N = number of clans in the focal zone during the corresponding interval.

	a) Individual-level agonistic interactions	
	Rate of agonism per female	Dyadic rate of agonism
Within-clan agonism	$\frac{2 \times I}{n \times t}$	$\frac{2 \times I}{n\,(n-1) \times t}$
Between-clan agonism	$\left[\frac{I}{n1 \times t} + \frac{I}{n2 \times t}\right]/2$	$\frac{I}{(n1 \times n2) \times t}$
	b) Clan-level between-clan agonism	
Clan-level between-clan agonism	$\frac{2 \times I}{N}$	

3. Is the rate of within-clan agonism explained by variation in grass abundance, grass dispersion, and group size?

In order to examine what explained within-clan agonism, we included only those independent focal group observations for which we also had data on grass abundance and variability, i.e., observations of groups that were within 100 m of the centre of one of the four plot-clusters that had been sampled for grass abundance. We used linear mixed-effects models (*lmer* function in *lme4* package in R, Bates *et al.* 2011, R Core Team 2018) to test how the within-clan rate of individual-level agonism (calculated for each focal group observation as described in the section above) was influenced by within-plot-cluster biomass, cover, and height, within-plot-cluster CV in biomass, cover, and height (from the nearest plot-cluster), female group size, month, and zone (all fixed effects), and clan identity and year (all random effects). We selected the best-subset model based on AICc (*dredge* function in *MuMIN* package, Barton and Barton 2012). In case the model failed to converge or if there was singularity due to random effect(s) explaining negligible variance (<0.001), we excluded those random effects and tested fixed-effects models using *lm* function of *lme4* package and ran the best-subset selection again using *dredge*. The analyses were carried out separately on the (individual-level within-clan) rate of agonism per female and the dyadic rate of agonism.

We also examined the effect of female group size on the within-clan rate of agonism per female in more detail and performed a piece-wise regression analysis on the dataset since there visually appeared to be a non-linear relationship.

4. Is the rate of individual-level between-clan agonistic interactions explained by variation in grass abundance, grass dispersion, and group size?

We used the same independent focal observations of between-clan encounters during which the groups' predominant activity was foraging, and which occurred within 100 m of the centre of one of the four plot-clusters that had been sampled for grass abundance. Since the random effect of year explained negligible variance and resulted in singularity in mixed-effects models, we used linear fixed-effects models (*lm* function in *lme4* package in R) to look at the effects of month, zone, within-plot-cluster grass abundance (biomass, cover, and height), within-zone grass abundance, within-zone grass variability (CV), and sum of female group sizes of the two groups (all fixed effects). We chose the best-subset model based on AICc as described in the previous section.

5. Are the rate of clan-level between-clan agonistic encounters and the duration of such encounters related to grass abundance/distribution and group size or the number of clans?

We divided each sampling day in a focal zone into four 2.5-hour intervals (08:30-11:00, 11:00-13:30, 13:30-16:00, 16:00-18:30) and counted the number of clans present and number of between-clan agonistic encounters (at the clan-level) occurring within each 2.5-hour interval. The temporal resolution (2.5 hours) is meaningful because, as mentioned above, more than 95% of between-clan agonistic encounters lasted less than or up to 2.5 hours (Supplementary Material 3). For each 2.5 hour interval with two or more clans (intervals with 0 or 1 clans in the focal zone were excluded because there was no potential for between-clan contest in such cases), we calculated the rate of between-clan agonistic encounters per clan using the formula given in Table 1, wherein the count of clans reflects the number of potential competing parties at the clan level. We explored the effects of month, zone, within-zone grass abundance (biomass, cover, and height) and within-zone variability (CV) in grass abundance, the number of clans present, area of the focal zone (all fixed effects), and year (random effect) using linear mixed-effects models (as described in a section above) and selected the best subsets based on AICc, to explain the rate of between-clan agonistic encounters. The number of clans would reflect the local density of competing parties during between-clan contest and area of the focal zone would take into account any confounding effect of a greater number of clans being found in larger focal zones. It turned out that the random effect of year explained negligible variance (<0.001); therefore, we excluded it and explored only fixed-effects models using *lm* function of *lme4*package and ran the best-subset selection again using *dredge*.

To analyse the durations of clan-level between-clan agonistic encounters, we excluded the clan-level encounters for which the complete durations were not known, for example those that began at the end of the day or extended beyond the permitted sampling time or those for which the exact time was not known. We then used fixed-effects models and subsequently selected best-subsets (based on AICc) to find out which variables among within-plot-cluster grass abundance, within-zone grass abundance and variability (CV) variables, sum of female group sizes (from the two competing clans), and difference in female group sizes of the two groups could explain the duration of agonistic between-clan encounters. Including the sum of group size in the analysis would reveal if the presence of a larger number of females prolonged the duration of between-clan encounters, whereas including the difference in group sizes in the analysis would help in testing whether between-clan encounters last longer when competing groups are of similar strength. Best subsets selection approach was used since most analyses had multiple independent variables which could lead to the problem of overfitting in the whole model. For GLMs, although we make our inferences largely based on the best model obtained from AIC-based model-selection, we also provide *P* values for reference and do not make inferences from the models whose *P*-values are very large. We did not use month and zone because the sample sizes of some of the levels within them was very small. We found that two grass abundance variables in the best model showed Wald statistic (*t*) in opposite directions (see Results). Therefore, we partitioned the variances using the ANOVA tables obtained from *anova()* function and obtained η^2 to infer which variable had a stronger effect.

Software

All ANOVAs on grass abundance were carried out using Statistica 7.0 (StatSoft Inc. 2004) but the appropriate *F* test calculations were done based on Neter *et al.* (1990, Chapter 27, pgs. 1010-1029), and η^2 (percentage variance explained by the variable) was calculated to measure effect size for each term ($SS_{effect}/SS_{corrected\ total}$, see Fritz *et al.* 2012). For comparing the means of two groups, we used Cohen's *d* (*d*=difference in means/pooled standard deviation, Cohen 1988) as the effect size. For mixed-effects models of rates of agonism, multiple R^2 was obtained from the *lm* output, while for the mixed models we used *r.squaredGLMM* function of R package *MuMIN*. The latter provides R^2 (marginal), which includes only the fixed effects, and R^2 (conditional), which also includes the variance explained by random effects (Nakagawa and Schielzeth 2013). All plots were made in Statistica 7.0 (StatSoft Inc. 2004).

Results

1. How does grass abundance in the Kabini grassland compare with that in the neighbouring forest habitat, and what is its distribution across and within different areas (focal zones) in the grassland?

1a. *Difference in grass abundance between grassland and forest habitat*

Grass biomass in the grassland habitat from both 2015 (*t*=14.187, *P* (one-tailed) <0.001) and 2016 (*t*=15.300, *P* (one-tailed) <0.001) were higher than that in the Nagarahole forest habitat (Figure 2a). The average grass biomass in the grassland habitat (2015: mean=704.78, 95% CI: 646.04—763.51 g/m^2, *N*=95 plot-clusters; 2016: mean=583.46, 95% CI: 546.58—620.34 g/m^2, *N*=96 plot-clusters), despite being sampled during the dry season, was about or over three times greater than that in the forest habitat (that was sampled at the end of the wet season) (mean=202.24, 95% CI: 165.22—239.26 g/m^2, *N*=40 plots). The mean grass biomass in Kabini, in both 2015 (mean=706.20 g/m^2, SD=254.302, *N*=4 months; Welch's *U*=3.715, *df*=3.115, *P*=0.034) and 2016 (mean=583.46 g/m^2, SD=49.752, *N*=4 months; Welch's *U*=11.616, *df*=5.691, *P*<0.001) was also greater than the mean grass biomass in the adjacent Bandipur National Park (229.4 g/m^2, SD=39.403, *N*=4 months), reported previously (Devidas 1995, Supplementary Material 4). Although a formal test could not be carried out (Nagarahole forest was sampled within two months), the grass biomass in the forest habitats of the two parks were similar to each other despite being sampled in very different years (Figure 2a, Supplementary Material 4).

1b. *Variation in grass abundance across and within focal zones*

The mixed-effects model explained more than 75% variation in grass biomass, which was found to be unevenly distributed across space and time (Figure 2b). Zone and year x month interaction had moderately large effects on grass biomass, while other factors had low effects if significant (Table 2). Similar trends were obtained for grass cover also (Supplementary Material 4). In the case of grass height, the effect of zone was very large, explaining 47% of the variation, while the effects of year, month x year, zone x year, and zone x year x month interaction were small to moderate (see Supplementary Material 4).

The average within-zone coefficient of variation (CV) was 21% (95% CI: 18.99—23.54, Figure 2c) and average within-plot-cluster CV in grass biomass was 28% (95% CI: 26.13—29.80%, Figure 2d). Similarly, based on grass height, within-zone CV was 22% (95% CI: 18.39—26.06) and within-plot-clusters CV was 30% (95% CI: 28.44—32.30).

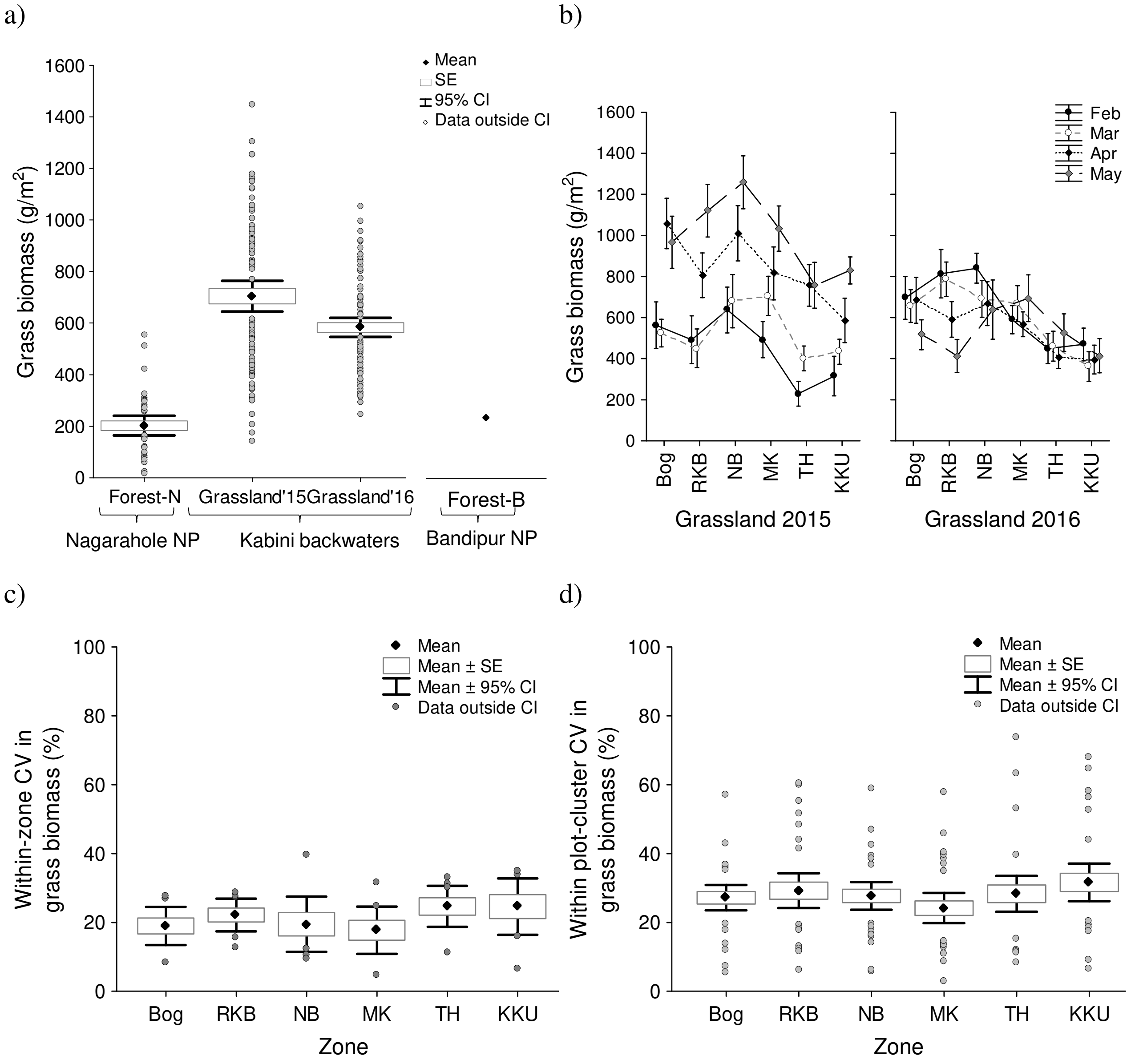

Figure 2. Grass biomass and distribution at different scales: a) grass abundance in the forest (Forest-N refers to Nagarahole National Park and Forest-B refers to Bandipur National Park) and grassland habitats around the backwaters, b) grass abundance (mean ± 95% CI estimated from averages of 4 plot-clusters) in different focal zones of the grassland habitat in different months of 2015 and 2016, c) within-zone CV in grass biomass (estimated from four plot-clusters) indicating variability across different plot-clusters within the focal zones, and d) within-plot-cluster CV in grass biomass (estimated from five quadrats), indicating local variability in grass abundance.

Table 2. Results from the mixed-effects GLM showing the effects of year (random factor), month and zones (both fixed factors), and their interactions on grass biomass (g/m^2). Significant (<0.05) *P* values and effect sizes above 0.2 are marked in bold.

Effect (Fixed/ Random)	SS	df_1	MS (effect)	df_2	MS (denom.)	*F*	*P*	Effect size (η^2)
Intercept	79717697.606	1	79717697.606	1	712018.848	111.960	0.060	
Year (R)	712018.848	1	712018.848	144	18548.337	38.387	**<0.001**	0.060
Month (F)	1519393.630	3	506464.543	3	1096869.867	0.462	0.729	0.127
Zone (F)	2687043.475	5	537408.695	5	15744.631	34.133	**<0.001**	**0.225**
Month x Year (R)	3290609.600	3	1096869.867	144	18548.337	59.136	**<0.001**	**0.275**
Zone x Year (R)	78723.155	5	15744.631	144	18548.337	0.849	0.517	0.007
Month x Zone (F)	432191.377	15	28812.758	15	38093.637	0.756	0.702	0.036
Zone x Month x Year (R)	571404.559	15	38093.637	144	18548.337	2.054	**0.015**	0.048
Error	2670960.468	144	18548.337					**0.223**
Corrected Total SS	11962345.112							

2. How do the rates and intensities of individual-level agonism among females compare within and between clans?

We recorded a total of 277 within-clan (duration=173 hours of focal group observations; number of individual-level interactions=459 independent and 267 non-independent interactions) and 96 between-clan (total duration=73 hours of focal group observations; number of individual-level interactions=377 independent and 579 non-independent interactions; no agonism seen in only 8 out of 96 between-clan encounters) focal group observations. Out of these, 180 within-clan (134 hours of focal group observations; 345 independent and 188 non-independent interactions) and 55 between-clan (50 hours of focal group observations; 213 independent and 318 non-independent individual-level interactions; no agonism seen in only 6 out of 55 between-clan encounters) focal group observations were completely inside the focal zones, were at least 15 minutes long, were independent focal observations (at least 15 minutes apart for within-clan and 2.5 hours apart for between-clan focal group observations), and included feeding as the primary group activity. The frequency distribution plots for different agonistic behaviours observed are presented separately for within-clan and between-clan agonism in Supplementary Material 3, Figure 2. Therefore, the results on the rate and intensity of individual-level agonism reported below are based on these focal group observations.

The top five commonly observed clans were observed in 39 between-clan and 142 within-clan focal observations, for which we present the results from the mixed-effects models. We found the rate of individual-level agonism per female per hour to be significantly higher during between-clan agonism than in within-clan agonism, and clan identity did not have an appreciable effect (Table 3a, Figure 3a). Similar mixed-effects model based on dyadic rate of agonism also showed that between-clan agonism was more frequent than within-clan agonism (Table 3b).

The rate of individual-level agonism was significantly higher during between-clan agonism than within-clan agonism based on focal observations of all clans also (Figure 3). Based on focal observations from all clans, the average rate of agonism per female during between-clan encounters was 2.441 agonistic interactions/female/hour (95% CI: 1.890—2.993, N=55focal group observations) while that within clans was 1.152 agonistic interactions/female/hour (95% CI=0.988—1.316, N=180 focal group observations) (Figure 3). The average dyadic rate of agonism during between-clan encounters was 1.069 agonistic interactions/dyad/hour (95% CI=0.827—1.311, N=55 focal group observations), while that within clans was 0.414 agonistic interactions/dyad/hour (95% CI=0.343—0.486, N=180 focal group observations). The effect sizes of the differences in rates of individual-level agonism between and within clans were large (Cohen's d=0.856 for rate of agonism per female, 0.972 for dyadic rate of agonism). In addition, the comparison of the effect of local competitor density on between-clan and within-clan rates of individual-level agonism showed a significantly steeper slope in the case of between-clan agonism than within-clan inter-individual agonism (Homogeneity of slopes test: type of agonism x number of females effect: $F_{1,\ 231}$=7.635, P=0.006; β=0.416, 95% CI of β=0.119—0.712, Figure 4, see Supplementary Material 5).

The intensity of individual-level agonism, measured as the number of non-independent interactions per independent interaction (NI/I ratio), was also higher during between-clan agonism in the fixed-effects model using the data for the five common clans (Table 3c). The average NI/I ratio during between-clan agonism, calculated from data from all clans was

1.757 (95% CI=1.296—2.218, *N*=49 focal group observations with at least one individual-level agonistic interaction) while the average NI/I ratio during within-clan agonism was 0.457 (95% CI=0.328—0.587, *N*=128 focal group observations with at least one individual-level agonistic interaction). The effect size was large (Cohen's *d*=1.057, Figure 3b).

Table 3. Results from a) mixed-effects model testing the effect of type of agonism (between-clan/within-clan, fixed effect) and clan identity (random effect) on the rate of individual-level agonism per female per hour, b) mixed-effects model testing the effect of type of agonism (between-clan/within-clan, fixed effect) and clan identity (random effect) on the dyadic rate of individual-level agonism per female per hour, and c) fixed-effects model testing the effect of type of agonism (between-clan/within-clan) on NI/I ratio. These results are for five common clans. Significant *P* values are marked in bold. In mixed-effects models, R^2 (marginal) includes only the fixed effects, while R^2 (conditional) also includes the variance explained by random effects.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
a)							
Fixed	Intercept	2.221	0.183	1.862	2.580	12.134	**<0.001**
Fixed	Type of agonism: within-clan	-1.217	0.207	-1.623	-0.810	-5.868	**<0.001**
Random variation							
Random effect (intercept)	Clan identity (*N*=5): variance = 0.031						
Residuals	Residual variance (*N*=218) = 2.110						
	R^2(m), R^2(c)	0.138, 0.150					
b)							
Fixed	Intercept	0.994	0.078	0.840	1.147	12.678	**<0.001**
Fixed	Type of agonism: within-clan	-0.620	0.093	-0.802	-0.438	-6.675	**<0.001**

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
Random variation							
Random effect (intercept)	Clan identity (N=5): variance = 0.003						
Residuals	Residual variance (N=218) = 0.427						
	R^2(m), R^2(c)	0.171, 0.177					
c)							
Fixed	Intercept	1.713	0.154	1.411	2.016	11.105	**<0.001**
Fixed	Type of agonism: within-clan	-1.267	0.203	-1.665	-0.870	-6.247	**<0.001**
Random variation							
Random effect	Clan identity: variance = NA						
Residual S.E. (*df*=164)			1.291				
	Multiple R^2	0.192					

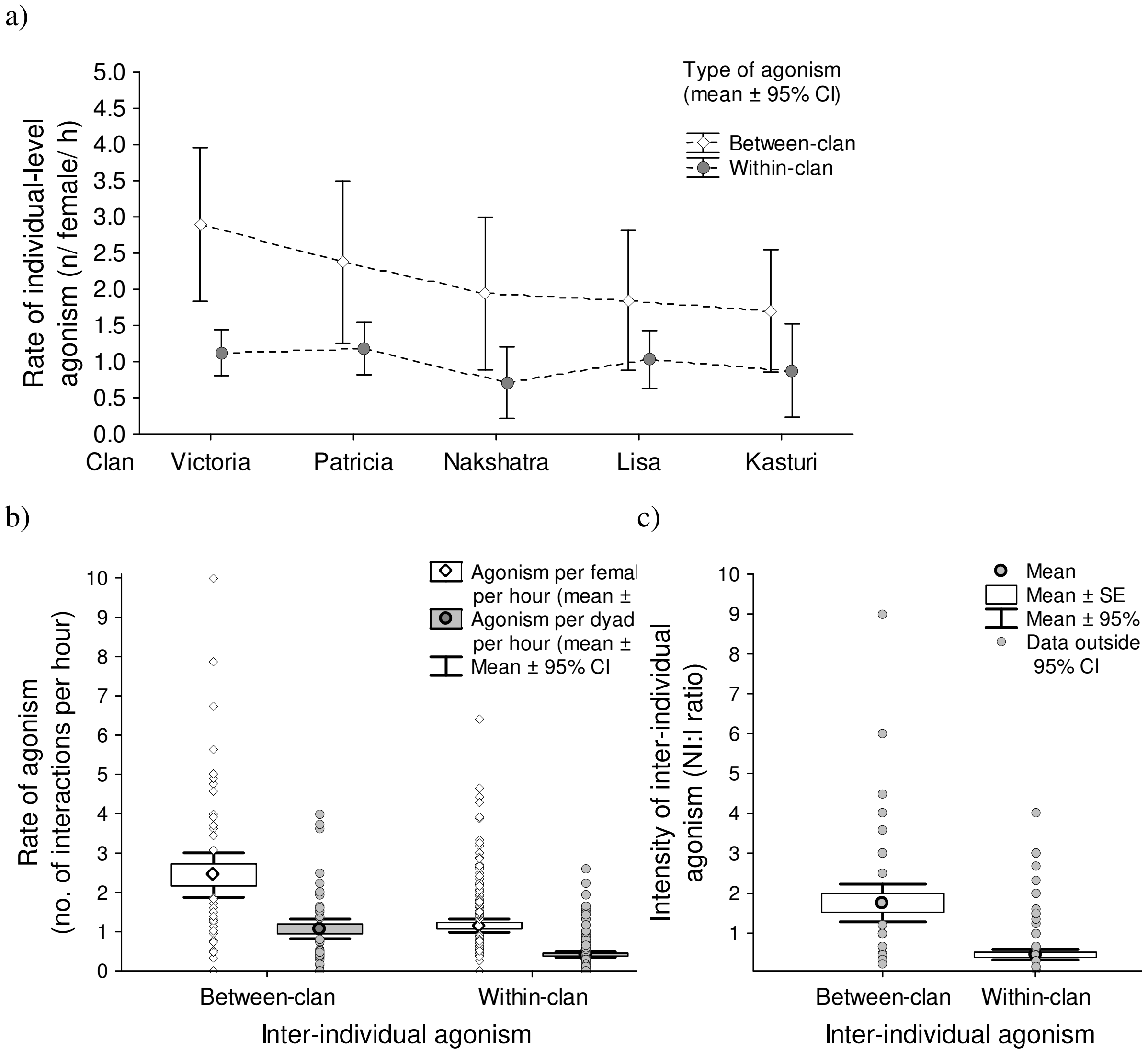

Figure 3. a) Rates of individual-level agonism per female per hour (mean and 95% CI) observed during between-clan and within-clan focal group observations of five common clans, b) rates of individual-level agonism (per female per hour and per dyad) observed during between-clan and within-clan focal group observations of all clans, and c) intensity of individual-level agonism (number of non-independent agonistic interactions per independent agonistic interaction between two females) during between- and within-clan interactions.

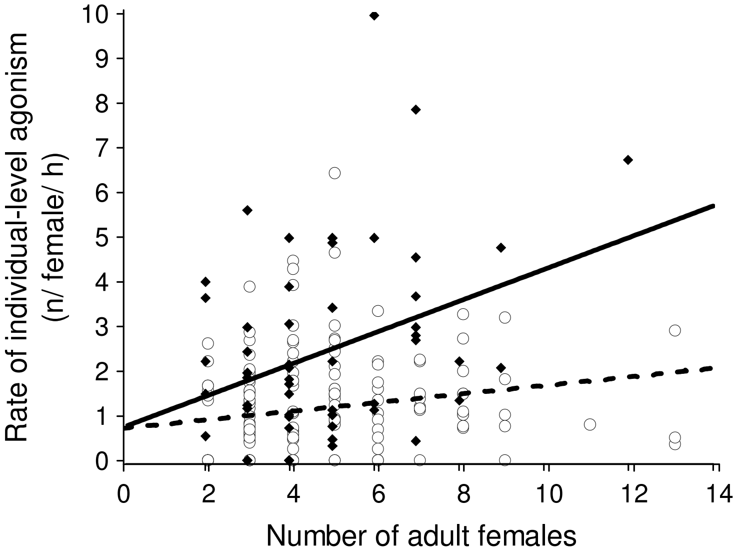

Figure 4. Overlaid scatterplots and slopes of rate of individual-level agonism during within-clan (open circles, dashed line) and between-clan (filled diamonds, solid line) focal group observations with respect to the number of female competitors (group size in the case of within-clan and sum of group sizes in the case of between-clan agonism).

3. Is the rate of within-clan agonism explained by variation in grass abundance, grass dispersion, and group size?

Since the random effects of clan identity and year explained negligible variance and resulted in singularity, we present results from fixed-effects models. The best-subset model of within-clan rate of agonism per female per hour included female group size, within-plot-cluster grass height, and zone as predictor variables, but explained only about 11% of the variation (Table 4, top models shown in Supplementary Material 6). Female group size and within-plot-cluster height had small effects and were positively related to within-clan rate of agonism (Table 4). A similar examination of the dyadic rate of within-clan agonism also yielded a weak fixed-effects model, explaining only 13% variation, with negative effects of female group size and a positive effect of within-plot-cluster grass biomass, in addition to significant effect of zones (Supplementary Material 7, top models shown in Supplementary Material 6).

The piece-wise regression of within-clan rate of agonism per female on female group size showed a moderate positive effect until female group size 5 ($F_{1,\ 136}$=19.651, R^2=0.126, P<0.001), and slope not different from zero for the remaining segment ($F_{1,\ 40}$=0.041, R^2=0.001, P=0.841) (Figure 5).

Table 4. Results from the best-subset fixed-effects model explaining within-clan rate of individual-level agonism per female per hour. Significant *P* values are marked in bold.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
Fixed	Intercept	-0.035	0.383	-0.781	0.711	-0.091	0.927
Fixed	Group size	0.106	0.039	0.029	0.182	2.703	**0.008**
Fixed	Within-plot-cluster height	0.134	0.051	0.035	0.233	2.634	**0.009**
Fixed	Zone- KKU	0.462	0.366	-0.252	1.176	1.261	0.209
Fixed	Zone- MK	-0.492	0.299	-1.075	0.091	-1.646	0.102
Fixed	Zone- NB	-0.354	0.328	-0.993	0.286	-1.078	0.283
Fixed	Zone- RKB	-0.071	0.223	-0.505	0.364	-0.317	0.751
Fixed	Zone- TH	0.687	0.306	0.090	1.283	2.245	**0.026**
Residual S.E. (*df*=166)			1.090				
	Multiple R^2	0.111					

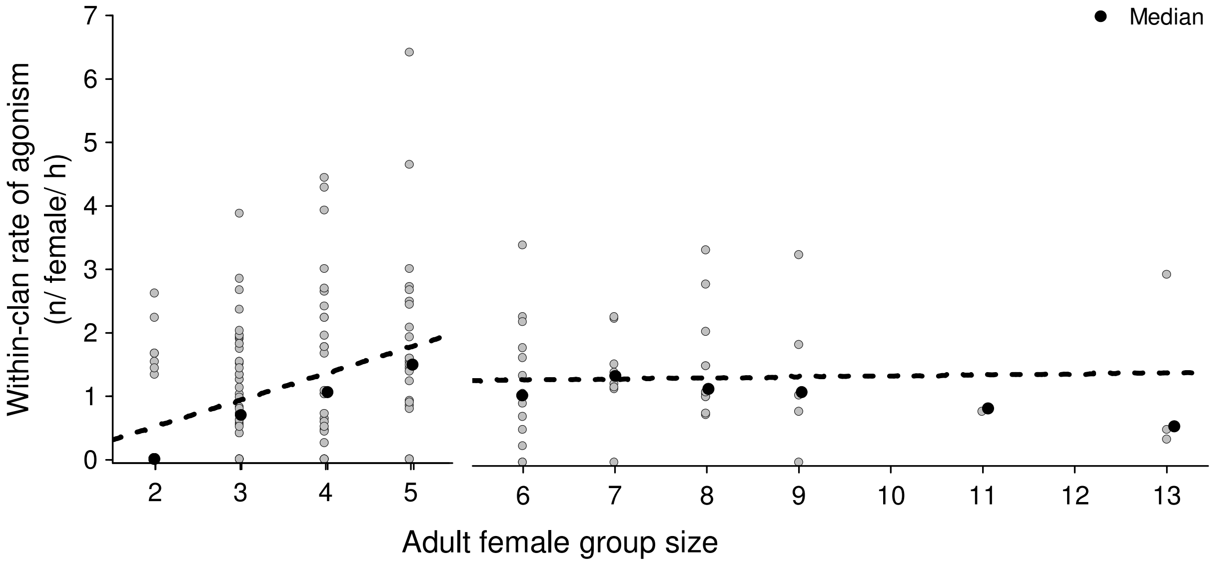

Figure 5. Piece-wise regression to show the relationship between female group size and within-clan rate of agonism per female for group size segments 2-5 and greater than five. Each data point in the graph is a focal group observation. Since many data points overlap on the graph, the median within-clan rate of agonism corresponding to each group size is also shown.

4. Is the rate of individual-level between-clan agonistic interactions explained by variation in grass abundance, grass dispersion, and group size?

The best-subset model of individual-level agonism during between-clan encounters was explained well (*Multiple* R^2=0.517) by month, zone, sum of group sizes of the contesting groups, and within-plot-cluster grass height (Table 5, scatter-plots in Supplementary Material 7, see Supplementary Material 6 for top models). While sum of group sizes was positively related, within-plot-cluster height was negatively related to rate of individual-level agonism during between-clan encounters (Figure 6).

Table 5. Results from the best-subset fixed-effects model explaining the rate of individual-level between-clan agonistic interactions. Significant *P* values are marked in bold.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI for estimate		*t*	*P*
Fixed	Intercept	2.906	1.214	0.539	5.273	2.394	**0.021**
Fixed	Sum of group sizes	0.382	0.109	0.169	0.596	3.499	**0.001**
Fixed	Within-plot-cluster height	-0.408	0.176	-0.751	-0.064	-2.315	**0.025**
Fixed	Zone- KKU	-4.527	1.302	-7.065	-1.988	-3.478	**0.001**
Fixed	Zone-MK	-0.811	1.274	-3.295	1.673	-0.637	0.528
Fixed	Zone- NB	-2.137	1.229	-4.533	0.259	-1.739	0.089
Fixed	Zone- RKB	-0.299	0.586	-1.442	0.843	-0.511	0.612
Fixed	Month- Feb	-0.570	0.552	-1.646	0.506	-1.033	0.308
Fixed	Month- Mar	1.253	0.754	-0.217	2.723	1.662	0.104
Fixed	Month- May	4.378	0.889	2.644	6.111	4.925	**<0.001**
Residual S.E. (*df*=43)			1.525				
	Multiple R^2	0.517					

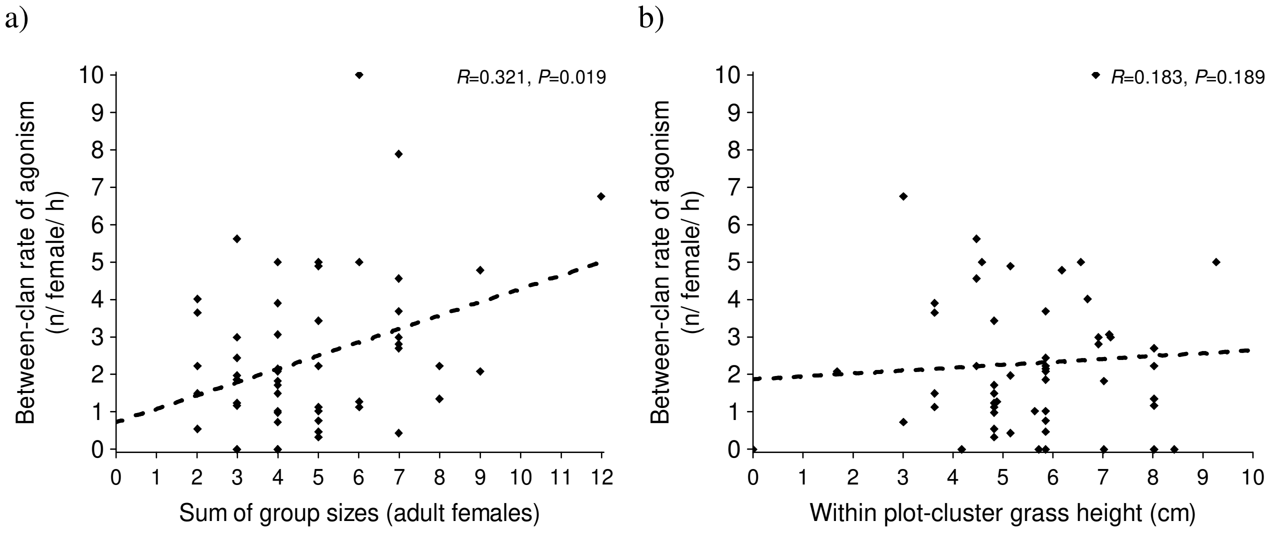

Figure 6. Scatterplots showing the effects of a) the sum of group sizes and b) within-plot-cluster grass height on individual-level agonism per female per hour during between-clan agonism. The correlation line and statistics shown are based on simple correlations.

5. Are the rate of clan-level between-clan agonistic encounters and the duration of such encounters related to grass abundance/distribution and group size or the number of clans?

Out of 672 intervals (168 days x 4 intervals, each interval 2.5 hour long), two or more clans were simultaneously present in the focal zone during 91 such intervals (from 56 sampling days), creating the potential for clan-level agonistic encounters. Of these 91 intervals, we observed between-clan agonistic encounters in 30 intervals. The average rate of between-clan agonistic encounters was found to be 0.409 per clan per 2.5-hour interval (95% CI=0.244-0.574), based on 91 intervals. The best-subset model explained 35% of the variation ($F_{1,89}$=47.93, *Multiple* R^2=0.350, P<0.001) in the rate of between-clan agonistic encounters, and showed a strong positive effect of only the number of clans (Table 6, top models shown in Supplementary Material 6, Figure 7a, see Supplementary Material 7 for other scatterplots).

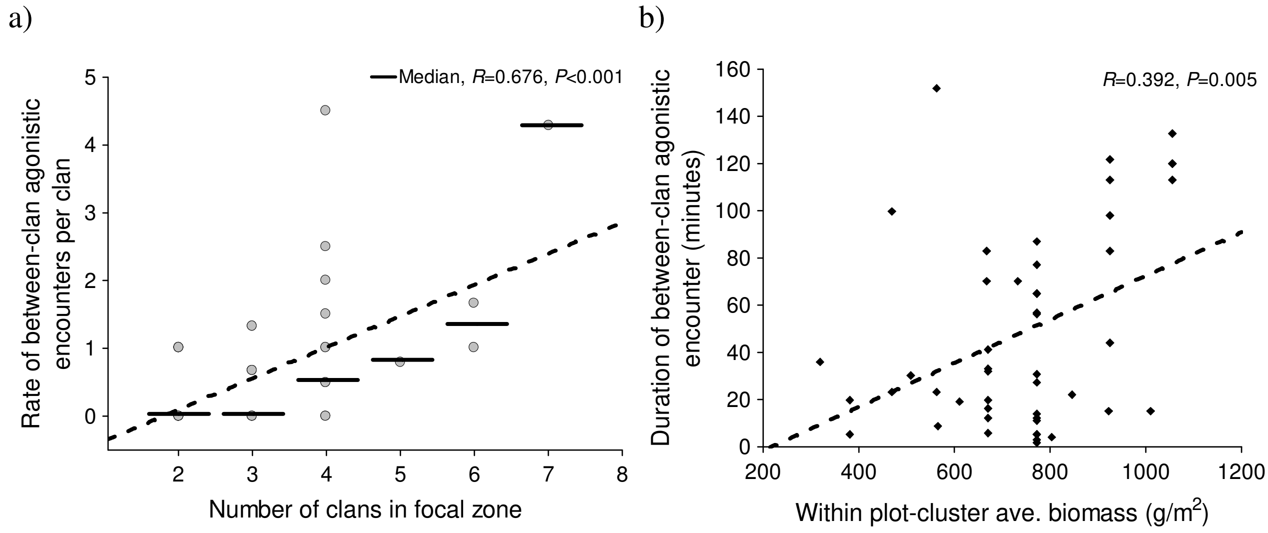

Figure 7. Scatterplots showing the effects of a) the number of clans on clan-level between-clan agonistic encounters, and d) within-plot-cluster grass biomass on the duration of clan-level between-clan agonistic encounters. The correlation line and statistics shown are based on simple correlations.

Table 6. Results from the best-subset linear model (all fixed effects) explaining the rate of clan-level between-clan agonistic encounters per clan per 2.5-hour interval. Significant *P* values are marked in bold.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI for estimate		*t*	*P*
Fixed	Intercept	-0.826	0.191	-1.198	-0.453	-4.323	**<0.001**
Fixed	No. of clans	0.461	0.067	0.331	0.590	6.923	**<0.001**
Residual S.E. (*df*=89)			0.651				
	Multiple R^2	0.350					

The best-subset regression model of duration of between-clan agonistic encounters (clan level) explained 31% variation (*Multiple* R^2=0.306), with a positive effect of within-plot-cluster average grass biomass and a negative effect of within-plot-cluster average grass cover (Table 7, top models shown in Supplementary Material 6, Figure 7b, see Supplementary Material 7 for other scatter-plots). The partitioning of variances showed that within plot-cluster grass biomass explained 30% of the variation while grass cover explained less than 1% variation in duration of between-clan agonistic encounters (Supplementary Material 6).

Table 7. Results from the best-subset model explaining the duration of between-clan agonistic encounters. Significant *P* values are marked in bold.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI for estimate		*t*	*P*	η^2
Fixed	Intercept	289.871	99.776	95.307	484.435	2.905	0.006	-
Fixed	Within-plot-cluster biomass	0.161	0.036	0.091	0.232	4.459	0.000	0.300
Fixed	Within-plot-cluster cover	-3.813	1.197	-6.147	-1.479	-3.186	0.003	0.007
Residual S.E. (*df*=46)			35.51					
	Multiple R^2	0.306						

Discussion

Despite the ecological model of female social relationships (EMFSR, Wrangham 1980, van Schaik 1989, Isbell 1991) conceptually not being restricted to any taxonomic group, studies on the relationship between food distribution and contest competition in non-primate mammals are almost non-existent. In this study, in a first such test of EMFSR in elephants, we monitored the agonistic interactions among individually identified female Asian elephants to understand the proximate ecological basis of agonistic interactions in the grassland habitat of Kabini. We set out to quantify the relationship between within- and between-clan agonism and food abundance, food distribution, and competitor density effects of group size and number of clans by directly measuring these variables. Since this population showed the occurrence of both between-clan and within-clan agonism despite relying on a graminivorous diet, which is classified as low quality subsistence food, widely distributed, and assumed not to elicit frequent contests (Wrangham 1980, Archie *et al.* 2006), spatial distribution of food was one of the possible drivers of contest competition. Although forest habitats may have high primary productivity and the forest understorey in the wider landscape has tall-grass areas (Sivaganesan 1991), we found that the grassland in Kabini had about three times the grass biomass as the neighbouring forest habitat of Nagarahole and Bandipur National Parks (data from Bandipur from Devidas 1995). As expected from EMFSR's prediction of between-group contest in high quality patches, we observed frequent occurrence of agonistic between-clan encounters, which was rarely seen in forest habitats previously (Baskaran 1998). Further, consistent with the expectation of EMFSR that high quality resource patches would elicit stronger between-group contest than within-group contest, we found that individual-level agonism was more frequent and intense during between-clan agonism than within-clan agonism. However, in contradiction to EMFSR's prediction of a positive relationship between within-group contest and patchiness of feeding sites, within-clan rate of agonism in our study was not explained by either grass abundance or dispersion at the local level, although we found that female group size (up to intermediate group sizes) positively explained some variation in within-clan agonism, consistent with simplistic models of resource competition. The rate of between-clan agonistic encounters, too, was positively explained by the number of clans present, and the duration of between-clan agonistic encounters was longer when the contest site had greater grass biomass. We discuss our findings on within-clan and between-clan agonism, in the context of their role in shaping the social organisation of elephants, as expected from socioecological theory.

Diet and agonism in elephants

We found high between-clan and within-clan agonistic contests among females (see also Nandini 2016) although only grasses were available as food in the Kabini grassland. The usefulness of diet type as a predictor of contest competition (Wrangham 1980, Isbell 1991, Clutton-Brock and Janson 2012) has been contradicted by observations of within-group and between-group dominance in folivorous primates (for example, Koenig *et al.* 1998, Harris 2006), whose diet was assumed to result in weak contest competition previously (reviewed in Snaith and Chapman 2007). In African savannah elephants also, strong dominance had been observed (Archie *et al.* 2006, Wittemyer and Getz 2007), despite the expectation that contest in elephants would be weak due to their flexible and generalist diet dominated by grasses that were assumed to be widely dispersed (Archie *et al.* 2006). However, Wittemyer and Getz (2007) found that contests among female African savannah elephants were common at point resources such as water holes, trees, and shade. De Silva *et al.* (2017), who found less frequent contests and weaker dominance expression among female Asian elephants in Uda Walawe (Sri Lanka) compared to African elephants of Samburu, argued that higher resource availability in the more mesic habitats of Asian elephants, along with their generalist diet, may facilitate more flexible associations and result in infrequent agonism. Although our study population of Asian elephants also shows flexible associations (discussed below), we found frequent occurrence of agonistic contests in the open grassland (and not for waterholes, trees or shade), which counter earlier interpretations of food distribution from dietary categories as questioned before in the context of primates (Snaith and Chapman 2007, Koenig *et al.* 2009, Wheeler *et al.* 2013). The difference between the Uda Walawe and Kabini populations of Asian elephants in the frequency of agonism is interesting, and it would be interesting to study both the causes (resource distribution) and social consequences (dominance structure) of these differences.

Individual-level agonism within and between clans

Our findings of individual-level between-clan agonism being twice as frequent as within-clan agonism during the observations made when groups were feeding, along with the findings of frequent between-clan agonistic encounters (discussed below), indicate that between-clan contest is strong in the study habitat. Since increased agonism results in the reduction of foraging time and food intake (for example, Janson 1985, Vogel 2005), frequent between-clan agonism, in addition to greater intensity of agonism (higher NI/I ratio), implies that females incur greater foraging costs during between-clan contests as compared to the usual contest competition faced within the clan. The greater slope of the relationship between agonism rates and the number of female competitors implies that greater agonism observed during between-clan encounters is more than what would be expected if an equal number of females from the same clan were present. Moreover, since over 50% of between-clan agonistic encounters in Kabini result in the exclusion of the losing group from the foraging site (Nandini 2016, Gautam and Vidya *unpublished*), there are clear foraging consequences of between-clan agonism, in addition to time lost from such interactions. Greater agonism among females from different clans rather than within the same clans also suggests that females Asian elephants may effectively use agonism as a signal of group membership, which demands advanced cognitive abilities, in addition to the requirements of effective recognition systems in maintaining fission-fusion societies (see Aureli *et al.* 2008).

Clan-level between-clan encounters and Kabini as a resource-rich habitat patch

Although opportunities for between-group competition are high in species with extensively overlapping home ranges, aggressive between-group encounters are thought to be rare in such species, perhaps due to large overlap being associated with low incentives from aggressive defense of territory/ranges (Cheney 1987, Pisor and Surbeck 2019, but see Wrangham 1980 for dominance-based avoidance as a reason for rare between-group aggression), in contrast to species wherein groups show more exclusive ranging that is associated with stronger territorial expression (for example, Willems and van Schaik 2015, see also Brown 2013). Interestingly, our findings of frequent between-clan agonistic encounters suggest that the Kabini grassland has an unusual competition regime. Clans of female Asian elephants are known to have extensively overlapping home ranges (Fernando *et al.* 2008, Baskaran and Desai 1996) and a previous long-term study in the nearby Mudumalai forest in the Nilgiri Biosphere Reserve in southern India (Baskaran 1998, Baskaran *et al.* 2018 discussed below) and in Sri Lanka (Prithiviraj Fernando, *personal communication*, see also de Silva *et al.* 2017) have rarely observed between-clan agonistic encounters. The high percentage (91.7%) of aggressive between-clan encounters (88 out of 96 between-clan encounters were agonistic) observed in Kabini is also higher than that reported in primates that show extensive home range overlap (between-group encounters are rarely aggressive, but occasionally, up to 69% of between-group encounters may be aggressive in species with ~50% or more overlap, reviewed in Cheney 1987, see also Cooper *et al.* 2004, Mirville *et al.* 2018), although the consequences of aggression can be more lethal in primates. This strong between-clan contest competition in Kabini can be explained by the peculiar food distribution in our study area. We found that the small Kabini grassland is a food-rich habitat compared to forests in Nagarahole, where grass is scarce in the lean season, and savanna-woodland/forest in Bandipur National Park based on previous data (Devidas 1995) (Supplementary Material 4). This concentration of resources (including water) in Kabini is reflected in the exceptionally high elephant density observed in Kabini during the sampling period (Supplementary Material 4). Given the high-quality nature of the grassland habitat at Kabini, frequent between-clan agonism is consistent with the expectations of strong between-group contest for high quality resource patches for species with extensive home range overlap (Wrangham 1980, see also Brown 2013). Strong between-group contest is thought to have implications for sociality as EMFSR predicts larger groups to be advantageous. Consequently, greater within-clan tolerance of subordinates by the dominant females is required to maintain large groups (Sterck *et al.* 1997). Data from the Kabini Elephant Project suggests that larger groups are more likely to win between-clan contests (Nandini 2016, Gautam and Vidya *unpublished*) and, in the future, it would be interesting to see if, due to strong between-clan contest, within-clan tolerance and social cohesion are greater in the Kabini grassland than in forests.

Correlates of within-clan agonism

Although we observed within-clan agonism frequently, it did not conform to EMFSR's classical prediction of more frequent agonistic contests in places with more heterogeneous food distribution, as the rate of agonism was not positively correlated with local variability (within-plot-cluster CV) in grass biomass. One explanation for this could be that feeding competition in our study area is very intense, arising due to the unusual nature of resource distribution at a larger spatial scale as explained in the section above. Female density in the grassland habitat is also much higher than the overall female density in Nagarahole and Bandipur National Parks (Supplementary Material 4), indicating a temporary habitat saturation during the dry season. Resource concentration in this small grassland habitat in the lean season, along with high elephant density, could result in very high overall feeding competition in the grassland to the point where local variations in food dispersion do not have much influence on within-clan agonism. Individuals might be adopting a tactic of maximising the access to any feeding site through agonistic contests under extreme competition. Such high competition in the unusual habitat setting created due to construction of a reservoir reinforces previous concerns about human interferences affecting social systems of wild populations (see Sterck *et al.* 1997, Halliwell *et al.* 2017, He *et al.* 2019, see also Robbins and Robbins 2018). Collared clans would have to be followed in order to find out what the patterns of agonism are in forest habitat. We also found more frequent agonism in localities with greater grass height, which is interesting given that local differences in biomass rather than height seem to be detected better in feeding site selection by individuals (Chapter 5 in this thesis). One possible explanation could be that height may be correlated with certain phenological (eg. flowering/fruiting) or physiological (eg.

nutrient/silica content) states, for which competition could occur, although the effect of height is small.

One cannot rule out the possibility that the methodology with respect to measuring grass dispersion could have resulted in the absence of a positive association between within-clan agonism and food distribution in the grassland habitat. Although the spatial extent of measurement of grass dispersion within plot-clusters (inter-quadrat distances from random sampling) was of the same order of magnitude as elephant group spread, it is possible that the distances used are not the best suited to the scale at which feeding competition operates between individual elephants. Future studies could develop consumer-defined measures of food dispersion (for example, focal tree sampling, Vogel and Janson 2011), although this might be challenging in grassland habitats where food is continuously spread with no reference points, unlike in the case of most primates whose foraging patches may be more distinguishable (canopy spread and trunk position used as reference points). Relevant aspects of elephant foraging such as average group spread and inter-individual distances during foraging would also have to be considered during such sampling. One of our future objectives is to explore consumer-based measures of food distribution such as food-site depletion and residence time to understand contest competition (for example, Chapman *et al.* 1995, Chancellor and Isbell 2009). Further, it is also possible that some of the observed agonistic interactions may not be occurring in the context of immediate acquisition of food but could represent social dominance, which is driven by motivations to advance or maintain one’s social status over a longer time scale. Such social dominance might be responsible for some of the unexplained variation in agonism.

The observed positive relationship between within-clan agonism rate and female group size was expected from simple models of competition. Since group size represents local density of competitors for a focal individual, larger groups face greater within-group contest when feeding sites are limited (Koenig and Borries 2006). This has been reported many times before in primates (see van Schaik *et al.* 1983, Wittig and Boesch 2003, Klass and Cords 2015, Wheeler *et al.* 2013) although not in elephants. Increase in agonism with group size suggests ecological constraints on larger groups, which had also been suggested previously in this population based on average group sizes not differing across clans despite differences in clan sizes and reduced average association strength in larger clans (Nandini *et al.* 2018). Higher agonism in larger groups implies that, although larger group size may confer feeding benefits in this habitat with strong between-clan contest regime (see above), a part of such foraging benefits accruing from larger group size are offset by the costs of higher within-clan contest as group size increases, possibly in addition to the usual expectation of increased within-group scramble (ecological constraints model, Wrangham *et al.* 1993, Chapman *et al.* 1995).

While dealing with the proximate costs of larger group size, previous studies have looked at the feeding (faster food depletion) and energetic (movement costs) consequences arising largely from exploitative (scramble) competition, as evident from the literature on ecological constraints models (Wrangham *et al.* 1993, Chapman *et al.* 1995, see also Snaith and Chapman 2007, Smith *et al.* 2008). However, within-group contest, too, can have non-trivial consequences such as loss in foraging opportunities and physiological (stress) costs that can influence sociality (reduced within-group tolerance and cooperation, permanent group fissions, see Sterck *et al.* 1997). Thus, studies that account for the effects of both scramble and contest competition could add to our understanding of proximate mechanisms governing group size, which has shown different relationships with foraging efficiency, travel costs and stress in different populations (Markham *et al.* 2015, Grueter *et al.* 2018). In our results from piece-wise regression of rate of agonism on group size, while the absence of a positive relationship in the segment after group size of 5 could be seen as conforming to a non-linear relationship (for example, Grueter *et al.* 2018 on gorillas) in a strong between-clan competition regime, our sample size for large group sizes was low. In the future, it might be worth exploring such non-linearity in the foraging costs and benefits of larger group size in this habitat. The dyadic rates of agonism showing a negative effect of group size is consistent with the comparative study on primates by Cowl and Shultz (2016). Cowl and Shultz (2016) found a positive relationship between dyadic agonism and collective action, and suggested that the negative relationship between dyadic rates of agonism and group size (from reducing agonism towards other group-mates) could mediate the maintenance of prosocial relationships.

Correlates of clan-level between-clan agonism

The rate of (clan-level) between-clan agonistic encounters showed a strong positive effect of the number of clans but was not related to within-zone grass biomass even though zones differed greatly in grass biomass. However, the duration of between-clan agonistic encounters, a variable that may reflect intensity of contest (Roth and Cords 2016), was positively explained by local grass biomass, which is consistent with game theory explanations of contests becoming longer when the resource value of contest location is high (Smith and Parker 1976). In the socioecological framework, whether food abundance or patchiness shapes between-group contest has been a topic of interest, the answer to which has remained elusive due to scarcity of empirical data (Koenig 2002). Our study provides positive results with respect to food abundance, which explained the duration of agonistic between-clan encounters, in addition to habitat-level differences in grass biomass explaining strong between-clan contest. Studies on primates have found more between-group contests when food abundance was high or when intensity of feeding at a location was high (Wilson *et al.* 2012, Brown 2013, Pal *et al.* 2018), suggesting the role of food abundance in between-group contest (see also Harris 2006, Roth and Cords 2016). In addition to the effect of the resource value of contest site, the resource holding potential of the contestants is also thought (Smith and Parker 1976) to determine the duration and intensity of contests, which can be applied to group-level contests also (for example, Markham *et al.* 2012). While previous studies on primates (for example, Roth and Cords 2016, Mirville *et al.* 2018) have found that between-group contests last longer and are more intense if competing groups are evenly matched in group size (a proxy for groups' resource holding potential), we did not find any effect of the difference in group size on contest duration. It is possible that this could result from the participation of sub-adult females or males in between-clan contests, which was not explored in this study, or because of non-participation by some group members, which could affect the collective defense of resources. These remain to be explored in the future.

Fission-fusion sociality and within-clan agonism

Fission-fusion sociality is expected to confer flexibility in grouping behaviour to balance the costs and benefits of large social groups in response to environmental variability across space and time (Aureli *et al.* 2008, see also Sueur *et al.* 2011). Interestingly, our study found frequent within-clan agonism, which would seem surprising since there is flexibility in associations among females in the Kabini population (Nandini *et al.* 2017, 2018). An explanation for high within-clan contest in Kabini could be the need to be in larger groups due to between-clan contest being strong, as discussed above. The advantage of larger groups is supported by the previous findings on the observed female group size being higher in the grassland than in the adjacent forests (Vidya *et al. unpublished*). In another study, de Silva *et al.* (2017) had ascribed lower agonism among female Asian elephants observed in

Uda Walawe, in contrast to African savannah elephants in Samburu (Wittemyer and Getz 2007), to conditions that facilitate greater fission-fusion, namely higher resource availability due to mesic environment and lower predation risk in Asian elephant habitats. A testable hypothesis to explain lower agonism found by de Silva *et al.* (2017) would be the expectation of greater resource availability in the tall-grass grassland habitat of Uda Walawe and more similarity between that grassland and the neighbouring forest, in comparison to Kabini grassland and Nagarahole forests.

Lastly, the findings of our study must be seen in the light of such grassland habitats around the man-made reservoirs being recently created habitats, and not the natural habitat (forests/savannah woodlands) of Asian elephants. Hence, the patterns of high within-clan and between-clan contest reflect plastic responses to such novel environments, and may not reflect the basal or adaptive behaviour in more pristine natural habitats. For the latter, similar quantitative studies of agonistic interactions in the forest habitats will be crucial to understanding sociality in female Asian elephants.

Conclusion

A consistent trend in our study was that local competitor density positively affected the rate of agonism at both individual (female) and clan level. This suggests that despite higher abundance of grass, feeding competition is very high in Kabini. These results conform to the broader socioecological framework (van Schaik 1989) where between-group contest is expected to be stronger at higher animal density, which is supported by few studies (for example, Kumara *et al.* 2014). Another implication of high within-clan agonism on social relationships, according to predictions of EMFSR, would be a strongly expressed dominance hierarchy, and consequently, strong rank-related skew in foraging success within groups (Janson and van Schaik 1988). De Silva *et al.* (2017) found agonism to be rare in the Uda Walawe population in Sri Lanka and found a weak expression of dominance relationships. But, interestingly in our population, despite frequent occurrence of agonism, our analyses of the dominance structure (see also Nandini 2016) and a test of the relationship between dominance rank and grass abundance at foraging sites in this habitat during the same period does not support this prediction (Gautam and Vidya 2019). This makes the Kabini population an interesting contradiction to predictions of EMFSR, which may require alternative explanations (Gautam and Vidya 2019, see also Koenig and Borries 2009).

In conclusion, our tests of some predictions of EMFSR in female Asian elephants show that food distribution explains between-clan contest better than within-clan contest and that competitor density increases both within-clan and between-clan contest. While between-clan agonism conforms to EMFSR, we had limited success in explaining within-clan agonism, which might also be examined profitably using alternate methods of measuring food dispersion and usurpability in future. We call for more field-based studies of proximate ecological basis of agonistic contests, dominance relationships, and their proximate (food/energy/time) and ultimate (reproduction) consequences in other populations of elephants to tests the generality of socioecological models in the Proboscidean clade and other mammal species.

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Supplementary Material

Supplementary Material 1. Pictures of the grassland habitat around the Kabini backwaters, foraging elephant groups, and agonistic interactions.

Supplementary Material 1, Figure 1. Elephants foraging in the grassland habitat around the Kabini backwaters.

Supplementary Material 1, Figure 2. An elephant group feeding in the RKB (Rajamanakere backwaters) focal zone of the grassland habitat in Kabini. The background shows the edge of the forest.

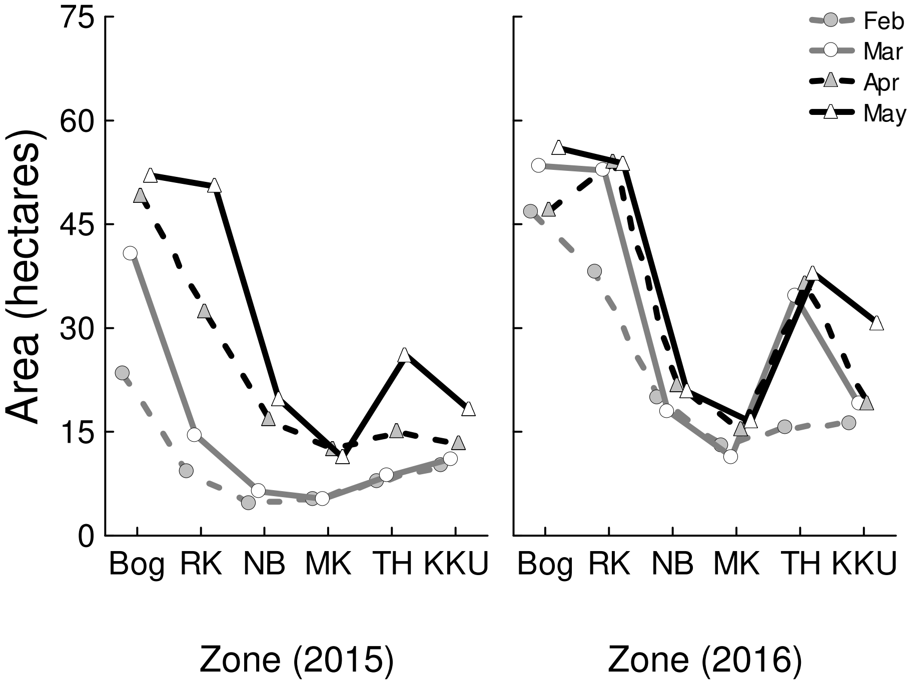
Supplementary Material 1, Figure 3. An agonistic interaction (hit) during a between-clan agonistic encounter involving Sunetra (initiator of agonism) and other members of Victoria's clan, and Nandini (recipient) and other members of Nakshatra's clan.

Supplementary Material 1, Figure 4. Another individual-level agonistic interaction (trunk on head) during a between-clan agonistic encounter, involving Sunetra (initiator of agonism) from Victoria’s clan and Nandini (recipient) from Nakshatra’s clan.

Supplementary Material 1, Figure 5. A 1 m x 1 m quadrat, from which grass biomass has been harvested from the ground level.

Supplementary Material 2. Areas of focal zones sampled.

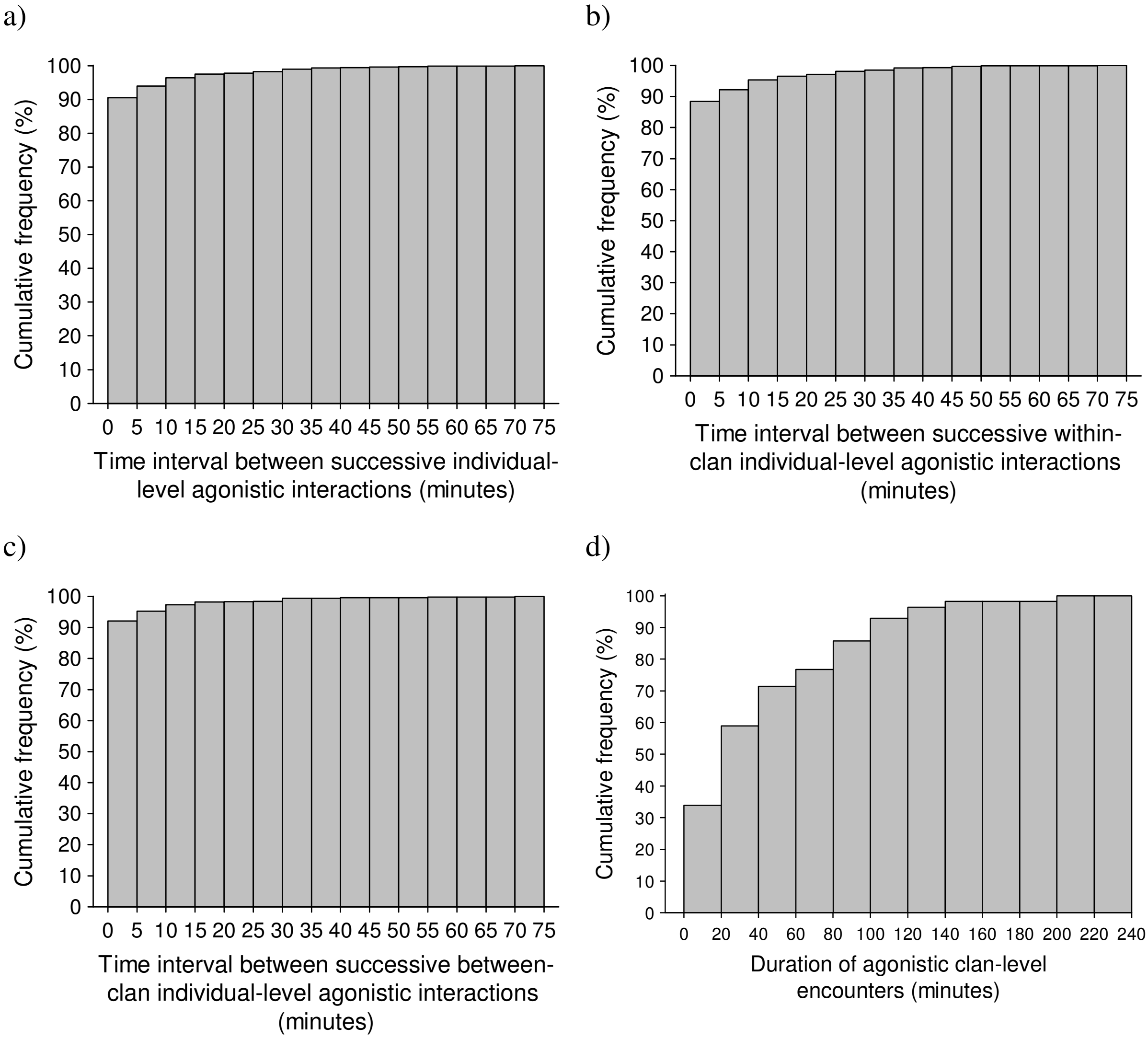
We calculated the area of each focal zone by delineating water and forest boundaries of the focal zone using monthly Landsat 8 satellite images. The areas varied across months due to fluctuations in the reservoir's water level. The monthly areas of focal zones are shown in Figure 1 below.



Supplementary Material 2, Figure 1. Areas of focal zones during different dry season months of 2015 and 2016.

Supplementary Material 3. Time interval between successive individual-level agonistic interactions, duration of clan-level agonistic encounters, and different types of agonistic interactions.

We calculated the time intervals between successive individual-level agonistic interactions by subtracting the time of occurrence of each interaction occurring between two females in the focal duration from that of the subsequent interaction involving the same females during that focal observation. Since over 95% of successive interactions (during both within-clan and between-clan agonism) occurred within 15 minutes (see Figure 1 below), we eventually used 15 minutes as the cutoff to define an independent interaction for data analyses.



Supplementary Material 3, Figure 1. a) Cumulative frequency distribution of the time interval between successive individual-level agonistic interactions for all (within-clan and between-clan) individual-level agonistic interactions (*N*=1682). Data from the first figure were further divided into b) time interval between successive within-clan individual-level agonistic interactions (*N*=726) and c) time interval between successive between-clan agonistic interactions (*N*=956). The last column in a), b), and c) represents an interval of 75 minutes or more. d) Cumulative frequency distribution of the duration of between-clan agonistic encounters (at the clan-level).

We also calculated the durations of between-clan agonistic encounters (at the clan-level), from the start and end time of each agonistic encounter. The cumulative frequency distribution of the durations is shown in Figure 1 above. Based on this, we used a 2.5 hour cut off to demarcate consecutive encounters between the same groups as independent focal observations for the purpose of calculating the rate of individual-level agonistic interactions during between-clan agonism. We also divided the sampling day into 2.5-hour intervals to count the occurrence of between-clan encounters in a focal zone and calculate the rate of between-clan agonistic encounters (clan-level rate).

We recorded different types of agonistic behaviours (Table 1 below). The frequency distribution of different agonistic behaviours is shown in Figure 2 below.

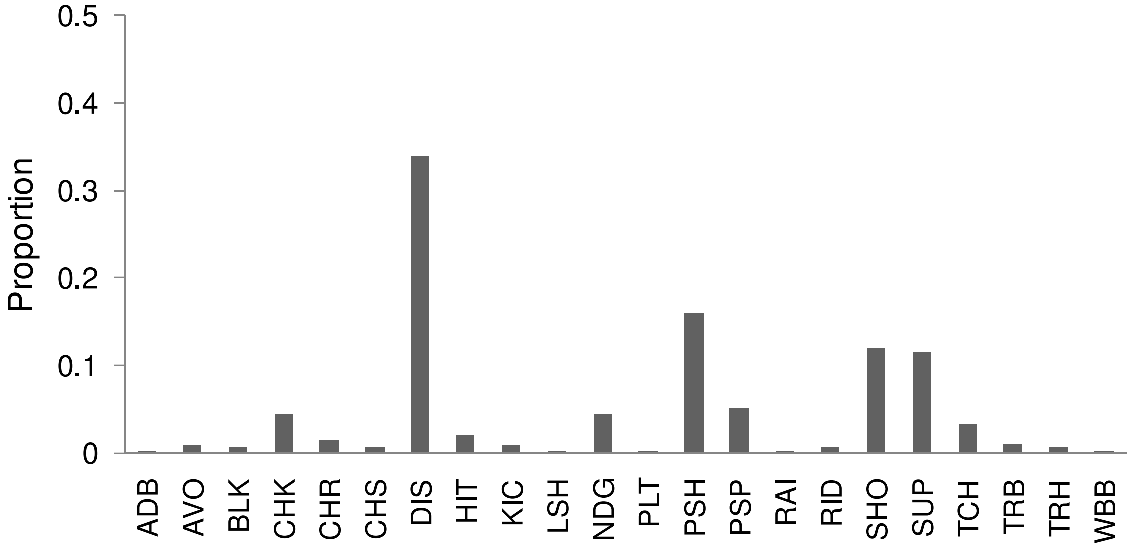
Supplementary Material 3, Table 1. Different behaviours shown during agonistic interactions. A and B are used as examples of initiator and recipient individuals.

S.No.	Behaviour code	Behaviour	Brief description
1.	ADB	Avoid and show back	Upon advance by another individual, turn away from it and present the back, including standing still to be checked (subordinate behaviour).
2.	ADS	Avoid and shake head	Upon advance by another individual, turn away from it and shake head (subordinate behaviour).
3.	AVO	Avoid	While moving in B's direction, A suddenly seems to register the presence of B and turns away and walks/runs away from B (subordinate behaviour).

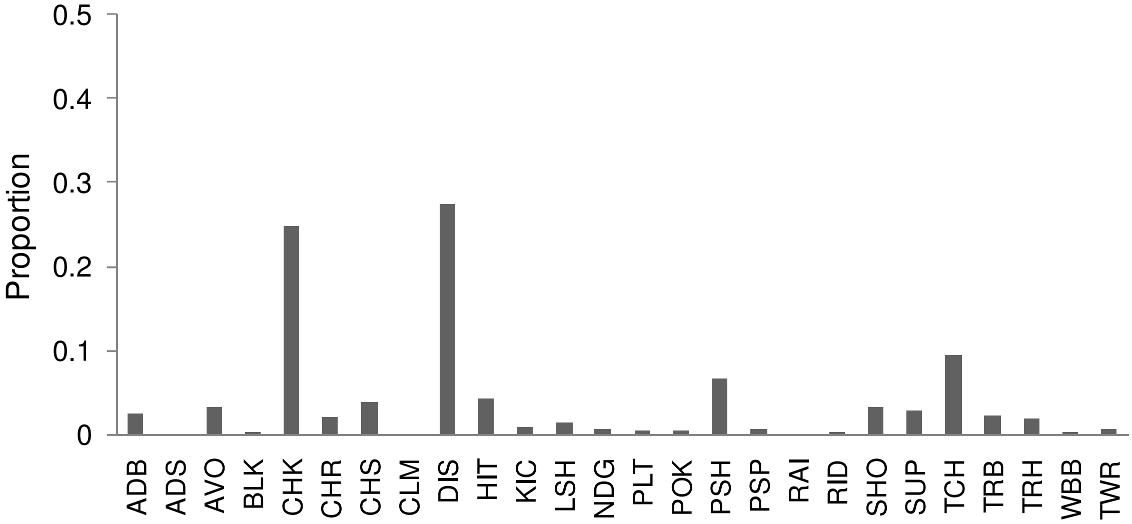
S.No.	Behaviour code	Behaviour	Brief description
4.	BLK	Block	Blocking the activity (movement/feeding) of the other individual with trunk or body.
5.	CHK	Check	Check another individual's genitalia with trunk tip during dominance. This appears more aggressive than when individuals check in other contexts.
6.	CHR	Charge	Run suddenly or move fast towards another individual in aggression.
7.	CHS	Chase	Chase another individual (both individuals move).
8.	CLM	Climb	Climb on to another animal (head on the back of the other animal and lifting forelegs off the ground) in dominance.
9.	DIS	Displace	Movement by A towards B leading to the removal (displacement) of B from its feeding position or resource.
10.	HIT	Hit	Hit another individual's head by aggressively using the head.
11.	KIC	Kick	Kick at another individual.
12.	LSH	Lash	Lash out at an individual using the trunk.
13.	NDG	Nudge	When feeding very close to a conspecific, nudge the (head of the) other individual away and gradually occupy its feeding position.
14.	PLT	Pull tail	Pull the tail of another individual.
15.	POK	Poke	Poke another individual with the tush (in the case of females).
16.	PSH	Push	Push the body of another individual using the head.
17.	PSP	Push/shove-occupy	Push (or sometimes shove) and, thereby, occupy the position of another animal, usually while feeding.
18.	RAI	Raise head	Raise head in aggression towards the recipient.
19.	RID	Rub in dominance	Rub the body against another's in dominance.

S.No.	Behaviour code	Behaviour	Brief description
20.	SHO	Shove	Push another individual's body using the side of the body.
21.	SUP	Supplant	Move towards the recipient and, effecting the removal of that individual (without touching it, which would otherwise be PSP), occupy that individual's position.
22.	TCH	Touch	Touch the face of another individual with the trunk tip in dominance. This is a rough touch or prodding, unlike that shown during affiliative behaviour.
23.	TRB	Trunk on body	Place the trunk on recipient's body in dominance. Again, different from that in an affiliative context.
24.	TRH	Trunk on head	Place trunk on the recipient's head in dominance.
25.	TWR	Trunk wrestle	Intertwine trunks and push back and forth in dominance.
26.	WBB	Walk backwards	Walk backwards with the back towards the recipient (subordinate behaviour).

a.



b.

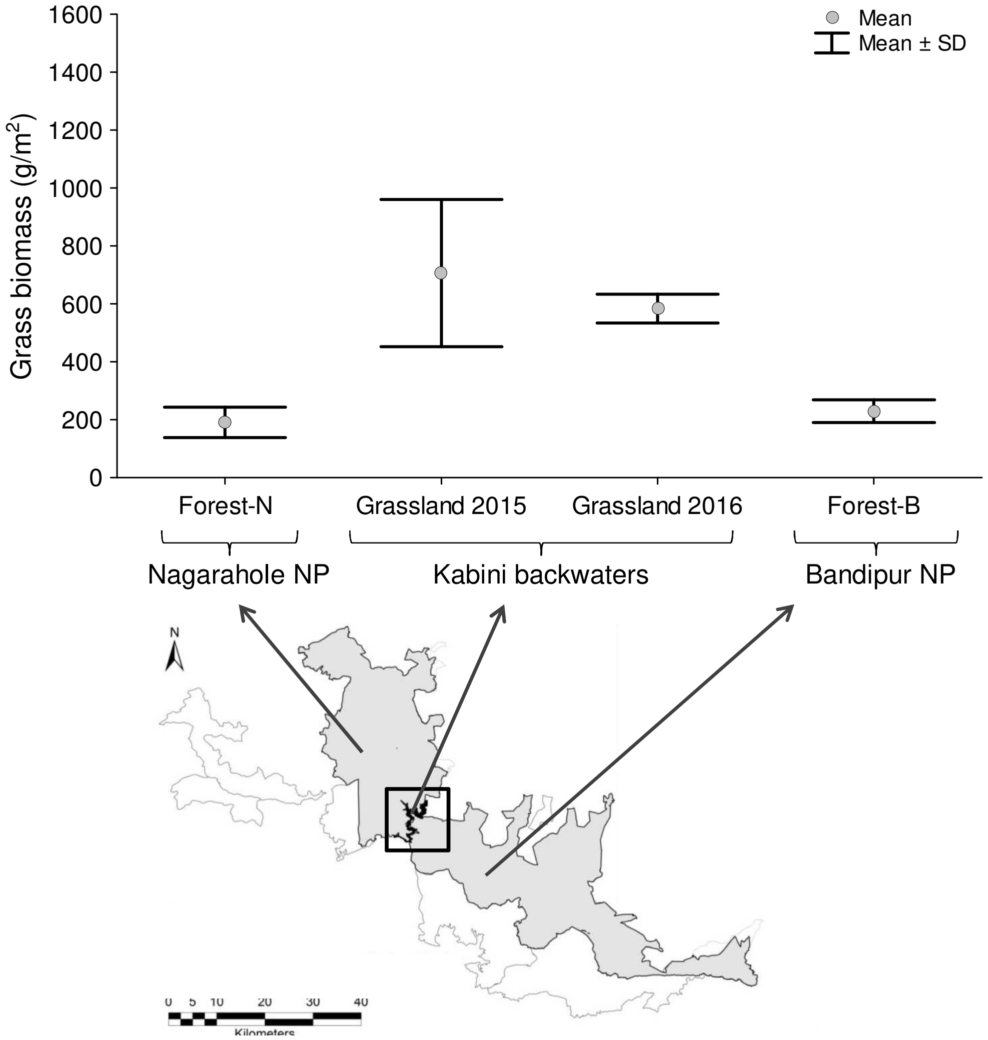


Supplementary Material 3, Figure 2. Frequency distribution plots showing different agonistic behaviours seen during a) within-clan agonism as a proportion of the total 726 (independent and non-independent) agonistic interactions observed, and b) between-clan agonism as a proportion of the total 956 (independent and non-independent) agonistic interactions observed. All behaviour codes shown on the X-axes of the two figures have been observed at least once.

Supplementary Material 4. Grass biomass in the grassland habitat in Kabini and in the neighbouring forest/savannah woodland habitats of Nagarahole and Bandipur National Parks, and variability in grass cover, grass height, and density of elephants around the Kabini backwaters.

As mentioned in the main text, we compared the grass biomass in the grassland habitat in Kabini with that in the neighbouring forest/savannah woodland habitats of Nagarahole and Bandipur National Parks. The mean and SD of monthly values in the four cases, which were used to perform the Welch's test, are shown in Figure 1 below. In Bandipur, the savannah-woodland habitat of Ainurmarigudi Range had been sampled and grass biomass values averaged from the monthly wet phytomass of grasses from February to June of 1993 by Devidas (1995, pp.71). The monthly values of wet grass phytomass were 261.61 g/m^2 in February, 180.25 g/m^2 in March, 198.61 g/m^2 in April, 234.72 g/m^2 in May, and 271.6 g/m^2 in June.

The results of the GLMs to examine the variability in grass cover and grass height in the Kabini grassland, and the within-day temporal profile of the density of adult females in the focal zones are also shown in this Supplementary Material.



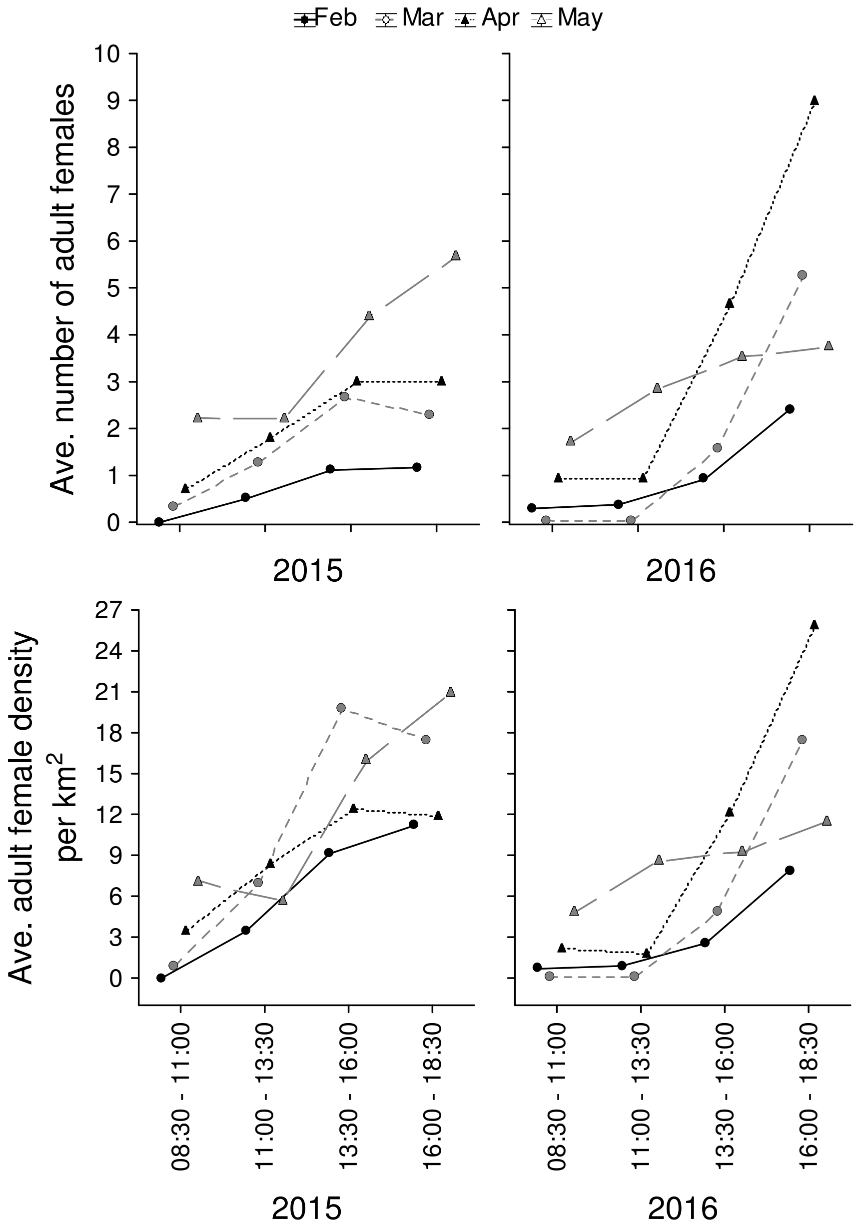
Supplementary Material 4, Figure 1. Grass biomass in the forest habitat of Nagarahole National Park, grassland habitat in Kabini, and forest/savannah-woodland habitat of Bandipur National Park. The values shown are the mean and SD of monthly values (*N*=2 months for Nagarahole forest, 4 months for Kabini grassland, and 5 months for Bandipur forest).

Supplementary Material 4, Table 1. Results from the GLM showing the effects of year (random effect) and month and zones (both fixed effects), and their interactions on grass cover (%). Significant (<0.05) *P* values and effect sizes above 0.2 are marked in bold.

Effect (Fixed/Random)	SS	df_1	MS (effect)	df_2	MS (denom.)	*F*	*P*	Effect size (η^2)
Intercept	1538958.626	1	1538958.626	1	548.326	2806.648	**0.012**	
Year (R)	548.326	1	548.326	144	49.729	11.026	**0.001**	0.027
Month (F)	992.995	3	330.998	3	1495.422	0.221	0.876	0.048
Zone (F)	3153.179	5	630.636	5	104.917	6.011	**0.036**	0.154
Month x Year (R)	4486.267	3	1495.422	144	49.729	30.071	**<.001**	**0.219**
Zone x Year (R)	524.584	5	104.917	144	49.729	2.110	0.068	0.026
Month x Zone (F)	1913.959	15	127.597	15	114.153	1.118	0.416	0.093
Zone x Month x Year (R)	1712.291	15	114.153	144	49.729	2.295	**0.006**	0.084
Error	7160.997	144	49.729					**0.349**
Corrected Total SS	20493							

Supplementary Material 4, Table 2. Results from GLM showing the effects of year (random effect) and month and zones (both fixed effects), and their interactions on grass height (cm). Significant (<0.05) *P* values and effect sizes above 0.2 are marked in bold.

Effect (Fixed/Random)	SS	df_1	MS (effect)	df_2	MS (denom.)	*F*	*P*	Effect size (η^2)
Intercept	5351.984	1	5351.984	1	81.090	66.001	0.078	
Year (R)	81.090	1	81.090	144	1.386	58.513	**<0.001**	0.087
Month (F)	48.443	3	16.148	3	21.540	0.750	0.591	0.052
Zone (F)	439.624	5	87.925	5	4.855	18.109	**0.003**	**0.471**
Month x Year (R)	64.621	3	21.540	144	1.386	15.543	**<0.001**	0.069
Zone x Year (R)	24.276	5	4.855	144	1.386	3.504	**0.005**	0.026
Month x Zone (F)	31.778	15	2.119	15	2.946	0.719	0.735	0.034
Zone x Month x Year (R)	44.195	15	2.946	144	1.386	2.126	**0.012**	0.047
Error	199.560	144	1.386					**0.214**
Corrected Total SS	934							



Supplementary Material 4, Figure 2. Temporal profile showing count and density (accounts for area of the focal zone) of unique adult females in the focal zones during 2.5-hour intervals within a sampling day for different months. Each data point is the average obtained from six focal zones sampled on three sampling days in each month in 2015 and four sampling days in each month in 2016. The elephant density around the Kabini backwaters is higher than that reported (less than 2 elephants/km^2) in forests in Nagarahole and Bandipur National Parks (Baskaran and Sukumar 2011).

References

1. Devidas S (1995). *Dynamics of the Herbaceous Layer in a Dry Deciduous Forest of South India (Bandipur National Park)*. Ph.D. thesis, Pondicherry University, Pondicherry, India.
2. Baskaran N and Sukumar R (2011). *Karnataka Elephant Census 2010.* Asian Nature Conservation Foundation and Centre for Ecological Sciences, Indian Institute of Science Technical report to the Karnataka Forest Department, Bangalore, India.

Supplementary Material 5. Homogeneity of slopes test for effect of competitor number on rate of individual-level agonism between and within clans.

Supplementary Material 5, Table 1. Results from homogeneity of slopes test to examine the slopes of the relationship between rate of individual-level agonism and number of female competitors (group size for within-clan agonism and sum of group size for between-clan agonism) during between- and within-clan agonism. Significant *P* values are marked in bold. Whole model statistics: *Multiple* R^2=0.208, $F_{3,\,231}$=20.196, *P*<0.001.

Effect	SS	*df*	MS	*F*	*P*
Intercept	12.850	1	12.850	7.060	0.008
Type of agonism (between-clan/ within-clan)	0.041	1	0.041	0.023	0.881
Number of females	40.257	1	40.257	22.116	**<0.001**
Type of agonism x Number of females	13.898	1	13.898	7.635	**0.006**
Error	420.481	231	1.820		

Supplementary Material 6. Top best-subset models from linear mixed-model analyses of rates of agonism and partitioning of variances in the models explaining the duration of clan-level between-clan encounters.

Supplementary Material 6, Table 1. Top best-subset fixed-effects models explaining the rate of within-clan individual-level agonism per female. Since random effects resulted in singularity due to negligible variance explained by them, mixed-effects models were not explored further. Code descriptions are provided at the end. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model

Model no.	Intercept	biomass_plot	cover_plot	CV_biomass_plot	CV_cover_plot	CV_height_plot	height_plot	month	no._AF	zone	AIC	BIC	df	logLik	AICc	delta	weight
417	-0.035	-	-	-	-	-	0.134	-	0.106	+	533.505	561.936	9	-257.752	534.602	0.000	0.051
133	1.107	-	-	-0.015	-	-	-	-	0.100	-	534.799	547.435	4	-263.399	535.035	0.433	0.041
418	-0.233	0.001	-	-	-	-	0.094	-	0.112	+	534.368	565.959	10	-257.184	535.718	1.115	0.029
386	-0.053	0.001	-	-	-	-	-	-	0.112	+	534.632	563.063	9	-258.316	535.730	1.127	0.029
419	-1.044	-	0.012	-	-	-	0.117	-	0.110	+	534.584	566.175	10	-257.292	535.934	1.331	0.026
129	0.746	-	-	-	-	-	-	-	0.095	-	535.838	545.315	3	-264.919	535.979	1.377	0.025
425	0.094	-	-	-	-0.009	-	0.120	-	0.111	+	534.687	566.278	10	-257.343	536.037	1.434	0.025
421	0.276	-	-	-0.008	-	-	0.115	-	0.107	+	534.730	566.321	10	-257.365	536.080	1.477	0.024
433	-0.065	-	-	-	-	0.000	0.135	-	0.106	+	535.484	567.074	10	-257.742	536.834	2.232	0.017
165	0.936	-	-	-0.013	-	-	0.024	-	0.100	-	536.496	552.292	5	-263.248	536.853	2.251	0.016

Supplementary Material 6, Table 2. Top best-subset fixed-effects models explaining the rate of within-clan individual-level agonism per dyad. Since random effects (year and clan identity) resulted in singularity due to negligible variance explained from them, mixed-effects models were not explored further. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model.

Model no.	Intercept	biomass_ plot	cover_ plot	CV_ biomass_ plot	CV_cover _plot	CV_ height_ plot	height_ plot	month	no._AF	zone	AIC	BIC	df	logLik	AICc	delta	weight
386	0.325	0.000	-	-	-	-	-	-	-0.043	+	241.464	269.896	9	-111.732	242.562	0.000	0.047
417	0.362	-	-	-	-	-	0.047	-	-0.046	+	241.675	270.106	9	-111.837	242.772	0.211	0.042
418	0.271	0.000	-	-	-	-	0.028	-	-0.043	+	242.376	273.967	10	-111.188	243.726	1.164	0.026
402	0.231	0.000	-	-	-	0.003	-	-	-0.041	+	242.590	274.181	10	-111.295	243.940	1.378	0.023
390	0.468	0.000	-	-0.003	-	-	-	-	-0.043	+	242.699	274.290	10	-111.350	244.049	1.487	0.022
421	0.506	-	-	-0.004	-	-	0.038	-	-0.045	+	242.787	274.377	10	-111.393	244.136	1.575	0.021
406	0.414	0.000	-	-0.006	-	0.004	-	-	-0.040	+	242.766	277.515	11	-110.383	244.395	1.834	0.019
433	0.291	-	-	-	-	0.002	0.049	-	-0.045	+	243.049	274.639	10	-111.524	244.398	1.837	0.019
389	0.790	-	-	-0.006	-	-	-	-	-0.047	+	243.360	271.792	9	-112.680	244.458	1.896	0.018
425	0.397	-	-	-	-0.002	-	0.043	-	-0.044	+	243.356	274.946	10	-111.678	244.705	2.144	0.016

Supplementary Material 6, Table 3. Top best-subset fixed-effects models explaining the rate of between-clan individual-level agonism per female per hour. Since random effect of year resulted in singularity due to negligible variance explained by year, mixed-effects models were not explored further. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model.

Model no.	Intercept	biomass _plot	biomass _zone	cover _plot	cover_ zone	CV_ biomass _zone	CV_ cover_ zone	CV_ height_ zone	diff_ AF	height_ plot	height_ zone	month	sum_ AF	zone	AIC	BIC	df	logLik	AICc	delta	Weight
7425	2.906	-	-	-	-	-	-	-	-	-0.408	-	+	0.382	+	206.050	227.723	11	-92.025	212.489	0.000	0.034
7429	8.336	-	-	-0.059	-	-	-	-	-	-0.371	-	+	0.341	+	205.787	229.430	12	-90.893	213.587	1.098	0.019
3073	0.183	-	-	-	-	-	-	-	-	-	-	+	0.355	-	212.294	224.116	6	-100.147	214.120	1.631	0.015
7426	3.783	-0.001	-	-	-	-	-	-	-	-0.368	-	+	0.346	+	206.837	230.480	12	-91.418	214.637	2.148	0.011
3841	-0.359	-	-	-	-	-	-	-	-	-0.441	0.525	+	0.383	-	211.510	227.273	8	-97.755	214.783	2.294	0.011
7553	2.638	-	-	-	-	-	-	-	-0.191	-0.398	-	+	0.501	+	207.152	230.795	12	-91.576	214.952	2.463	0.010
7183	0.053	-	-0.005	-0.135	0.184	-	-	-	-	-	-	+	0.345	+	205.889	231.503	13	-89.944	215.222	2.733	0.009
3074	1.620	-0.002	-	-	-	-	-	-	-	-	-	+	0.304	-	212.834	226.626	7	-99.417	215.323	2.834	0.008
3329	1.315	-	-	-	-	-	-	-	-	-0.187	-	+	0.340	-	212.907	226.699	7	-99.453	215.395	2.906	0.008
7441	3.995	-	-	-	-	-0.049	-	-	-	-0.467	-	+	0.416	+	207.635	231.278	12	-91.817	215.435	2.946	0.008

Supplementary Material 6, Table 4. Top best-subset fixed-effects models explaining the rate of between-clan agonistic encounters per clan per 2.5-hour interval. Since random effect of year resulted in singularity due to negligible variance explained by year, mixed-effects models were not explored further. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model.

Model no.	Intercept	area_zone	clan_count	month	zone	zone_biomass	zone_cover	CV_biomass_zone	CV_cover_zone	CV_height_zone	zone_height	AIC	BIC	df	logLik	AICc	delta	weight
3	-0.826	-	0.461	-	-	-	-	-	-	-	-	193.289	203.333	4	-92.645	193.755	0.000	0.623
4	-0.866	0.139	0.458	-	-	-	-	-	-	-	-	194.781	207.336	5	-92.391	195.487	1.733	0.262
515	-0.686	-	0.460	-	-	-	-	-	-	-	-0.023	199.530	212.084	5	-94.765	200.236	6.481	0.024
7	-0.501	-	0.420	+	-	-	-	-	-	-	-	199.027	216.603	7	-92.514	200.377	6.622	0.023
131	-0.922	-	0.458	-	-	-	-	-	0.016	-	-	200.722	213.276	5	-95.361	201.428	7.673	0.013
516	-0.727	0.155	0.456	-	-	-	-	-	-	-	-0.024	200.993	216.058	6	-94.497	201.993	8.239	0.010
8	-0.517	0.048	0.419	+	-	-	-	-	-	-	-	200.604	220.691	8	-92.302	202.361	8.606	0.008
132	-0.998	0.235	0.453	-	-	-	-	-	0.017	-	-	202.043	217.108	6	-95.022	203.043	9.289	0.006
35	-1.096	-	0.460	-	-	-	0.003	-	-	-	-	202.464	215.018	5	-96.232	203.170	9.415	0.006
67	-0.751	-	0.463	-	-	-	-	-0.004	-	-	-	202.586	215.141	5	-96.293	203.292	9.538	0.005

Supplementary Material 6, Table 5a. Top best-subset fixed-effects models explaining the duration of between-clan agonistic encounters per clan per 2.5-hour interval. Since random effect of year resulted in singularity due to negligible variance explained by year, mixed-effects models were not explored further. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model.

Model no.	(Intercept)	biomass_plot	biomass_zone	cover_plot	cover_zone	CV_biomass_zone	CV_cover_zone	CV_height_zone	diff_AF	height_plot	height_zone	sum_AF	AIC	BIC	df	logLik	AICc	delta	weight
6	289.871	0.161	-	-3.813	-	-	-	-	-	-	-	-	493.801	501.369	4	-242.901	494.711	0.000	0.050
38	337.073	0.145	-	-4.031	-	-	-2.338	-	-	-	-	-	493.852	503.311	5	-241.926	495.248	0.537	0.038
70	285.929	0.154	-	-3.646	-	-	-	-0.378	-	-	-	-	495.196	504.655	5	-242.598	496.591	1.881	0.020
22	280.526	0.172	-	-3.954	-	0.675	-	-	-	-	-	-	495.200	504.659	5	-242.600	496.595	1.884	0.020
14	227.728	0.151	-	-4.105	1.044	-	-	-	-	-	-	-	495.421	504.880	5	-242.710	496.816	2.106	0.017
54	329.991	0.158	-	-4.235	-	0.870	-2.583	-	-	-	-	-	494.832	506.183	6	-241.416	496.832	2.121	0.017
262	311.867	0.174	-	-4.031	-	-	-	-	-	-1.925	-	-	495.526	504.985	5	-242.763	496.921	2.210	0.017
8	269.919	0.146	0.017	-3.607	-	-	-	-	-	-	-	-	495.627	505.086	5	-242.814	497.023	2.312	0.016
518	274.281	0.153	-	-3.687	-	-	-	-	-	-	1.692	-	495.649	505.108	5	-242.825	497.045	2.334	0.016
1030	273.112	0.156	-	-3.618	-	-	-	-	-	-	-	0.382	495.675	505.134	5	-242.838	497.071	2.360	0.015

Supplementary Material 6, Table 5b. Partitioning of variances for the fixed effects of within-plot-cluster biomass and cover on duration of between-clan agonistic encounters. The effect size (η^2) was calculated from the ANOVA table which was obtained after running the function *anova()* in R.

Effect	SS	*df*	MS (effect)	*F*	*P*	η^2
Within-plot-cluster biomass	25067	1	25066.6	19.879	**<0.001**	0.300
Within-plot-cluster cover	547	1	547.1	0.4339	0.513	0.007
Residuals	58003	46	1260.9	-	-	0.694

Code descriptions

zone: focal zone (*N*=6) of sampling.

month: month (*N*=4) of sampling.

year: year (*N*=2) of sampling.

clan_id: name of clan of the group on which focal group observation was taken.

biomass_plot: within-plot grass biomass.

cover_plot: within-plot grass cover.

height_plot: within-plot grass height.

CV_biomass_plot: within plot-cluster coefficient of variation in grass biomass.

CV_biomass_cover: within plot-cluster coefficient of variation in grass cover.

CV_biomass_height: within plot-cluster coefficient of variation in grass height.

no._AF: number of adult females in the group.

sum_AF: total number of adult females (group size in the case of within-clan agonism and sum of group sizes in the case of between-clan agonism).

diff_AF: absolute difference in adult female group sizes of the two competing groups.

zone_area: area of the focal zone in the month of sampling.

cover_zone: within-zone average grass cover.

biomass_zone: within-zone average grass biomass.

height_zone: within-zone average grass height.

CV_cover_zone: within-zone coefficient of variation in average grass cover.

CV_biomass_zone: within-zone coefficient of variation in average grass biomass.

CV_height_zone: within-zone coefficient of variation in average grass height.

Supplementary Material 7. Best-subset model of within-clan agonism, and scatter-plots of the relationships between ecological variables (grass abundance, distribution, and number of competitors) and within-clan and individual-level between-clan agonism.

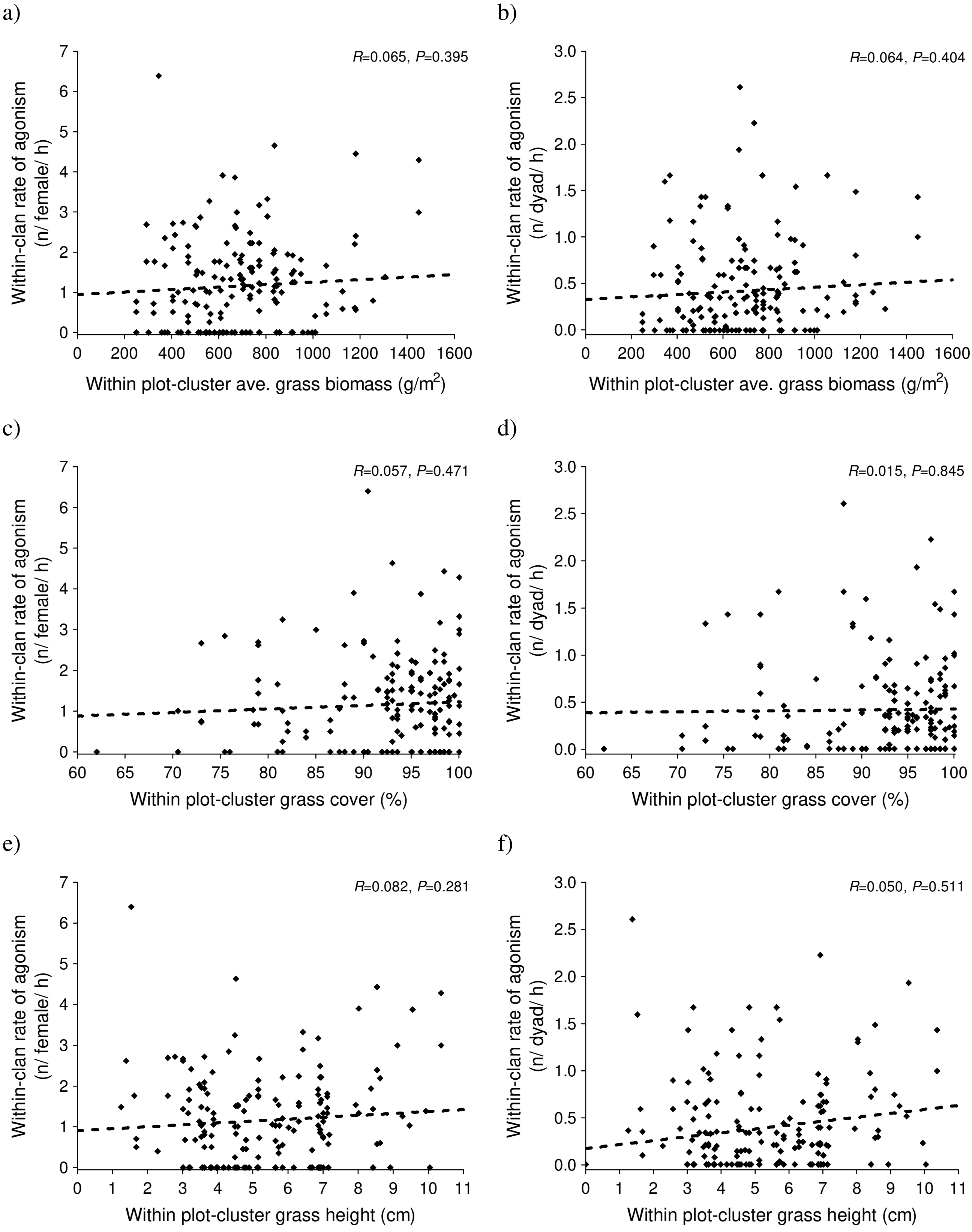
Results from the best-subset model explaining within-clan rate of individual-level agonism per female had been shown in the main text. The results from the best-subset model for within-clan rate of inter-individual agonism per dyad is shown in the table below. Scatterplots showing how within-clan agonism, individual-level between-clan agonism, and duration of clan-level between-clan agonism vary with the independent variables explored, i.e. grass biomass, cover, and height, CV in grass biomass, cover, and height, group size (for within-clan agonism), sum of group size, difference in group size (for between-clan individual-level agonism), and number of clans, are shown in figures below.

Supplementary Material 7, Table 1. Results from the best-subset fixed-effects model explaining dyadic rate (per female dyad per hour) of within-clan agonism.

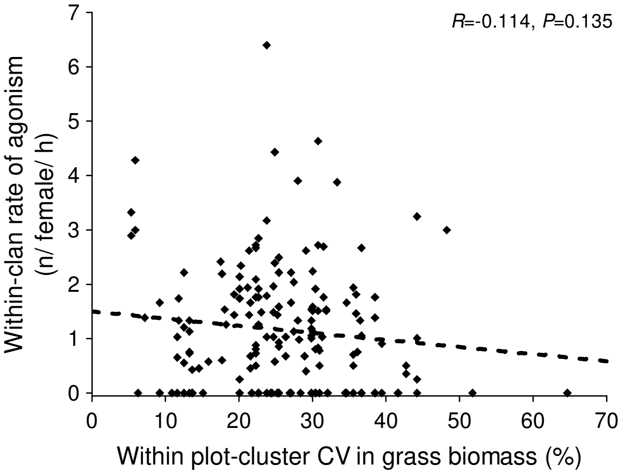
Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
	Intercept	0.325	0.177	-0.021	0.670	1.833	0.069
Fixed	Group size	-0.043	0.017	-0.076	-0.009	-2.501	0.013
Fixed	Within-plot-cluster biomass	0.000	0.000	0.000	0.001	-2.167	0.032
Fixed	Zone- KKU	0.285	0.158	-0.024	0.593	1.798	0.074
Fixed	Zone- MK	-0.292	0.129	-0.544	-0.040	-2.257	0.025
Fixed	Zone- NB	-0.138	0.143	-0.417	0.141	-0.963	0.337
Fixed	Zone- RKB	0.045	0.096	-0.142	0.231	0.465	0.642
Fixed	Zone- TH	0.196	0.128	-0.053	0.446	1.537	0.126
	Multiple R^2	0.128					

Within-clan rate of individual-level agonism per female per hour

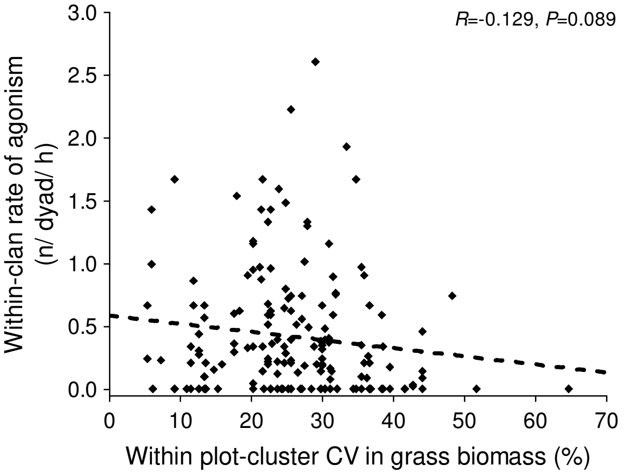
Within-clan rate of individual-level agonism per dyad per hour



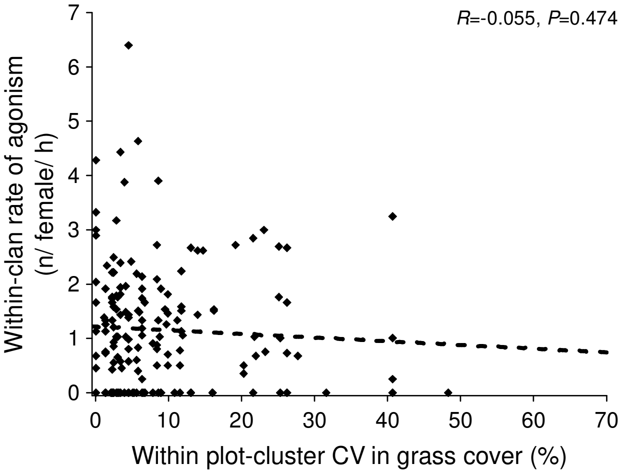
g)


R=-0.114, P=0.135
Within-clan rate of agonism (n/ female/ h)
0
1
2
3
4
5
6
7
0
10
20
30
40
50
60
70
Within plot-cluster CV in grass biomass (%)

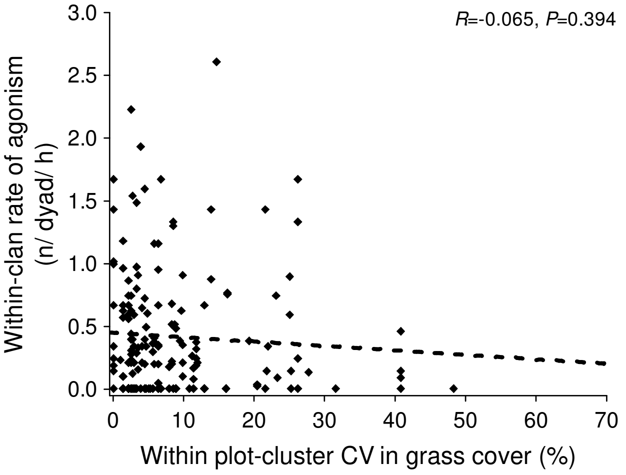
h)


R=-0.129, P=0.089
Within-clan rate of agonism (n/ dyad/ h)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
10
20
30
40
50
60
70
Within plot-cluster CV in grass biomass (%)

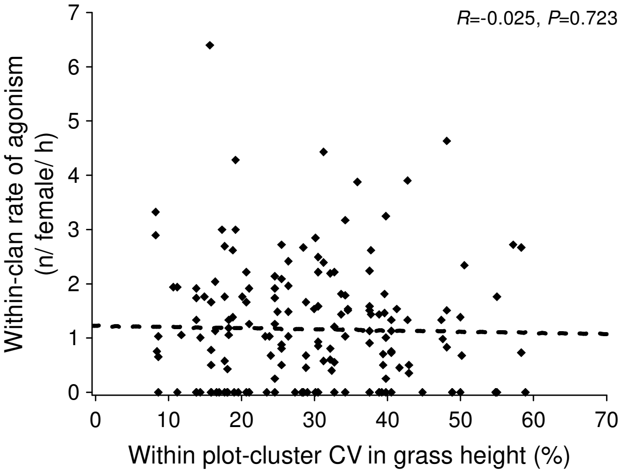
i)


R=-0.055, P=0.474
Within-clan rate of agonism (n/ female/ h)
0
1
2
3
4
5
6
7
0
10
20
30
40
50
60
70
Within plot-cluster CV in grass cover (%)

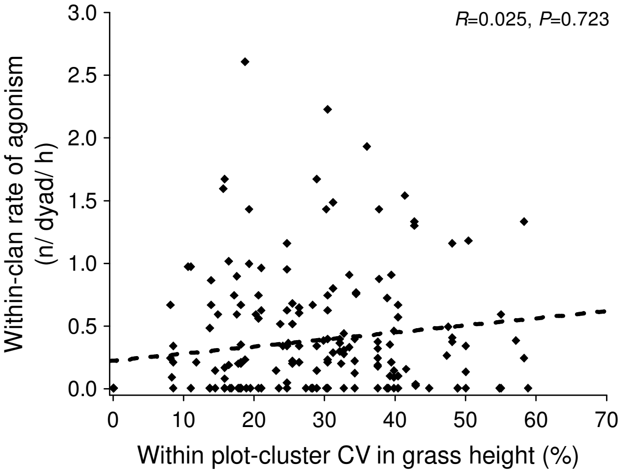
j)

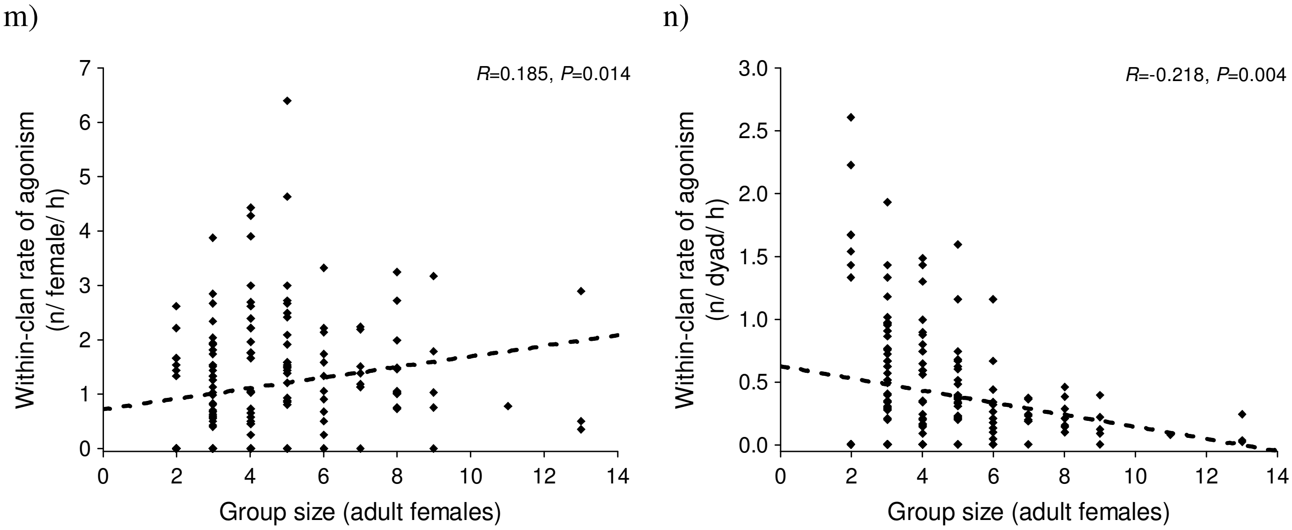

R=-0.065, P=0.394
Within-clan rate of agonism (n/ dyad/ h)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
10
20
30
40
50
60
70
Within plot-cluster CV in grass cover (%)

k)


R=-0.025, P=0.723
Within-clan rate of agonism (n/ female/ h)
0
1
2
3
4
5
6
7
0
10
20
30
40
50
60
70
Within plot-cluster CV in grass height (%)

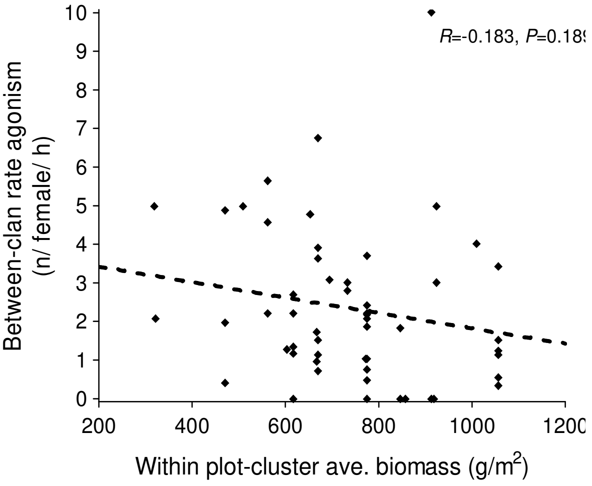
l)


R=0.025, P=0.723
Within-clan rate of agonism (n/ dyad/ h)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
10
20
30
40
50
60
70
Within plot-cluster CV in grass height (%)

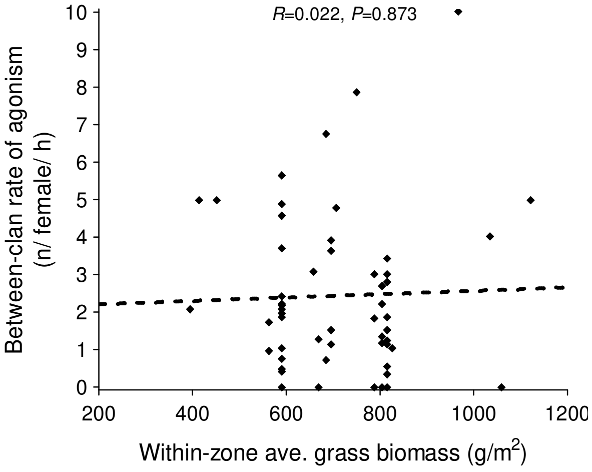


Supplementary Material 7, Figure 1. Scatterplots showing the relationship between within-clan agonism and grass abundance (biomass, grass cover, and grass height), CV in grass abundance, and group size. Correlation line and statistics given in these plots are for simple correlation.

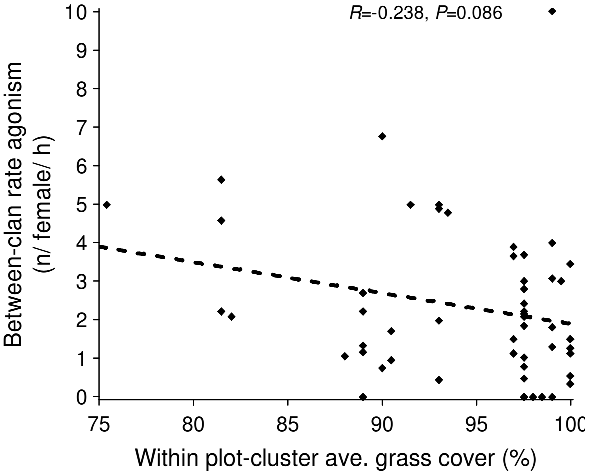
a)


R=-0.183, P=0.18
Between-clan rate agonism
(n/ female/ h)
0
1
2
3
4
5
6
7
8
9
10
200
400
600
800
1000
1200
Within plot-cluster ave. biomass (g/m^2)

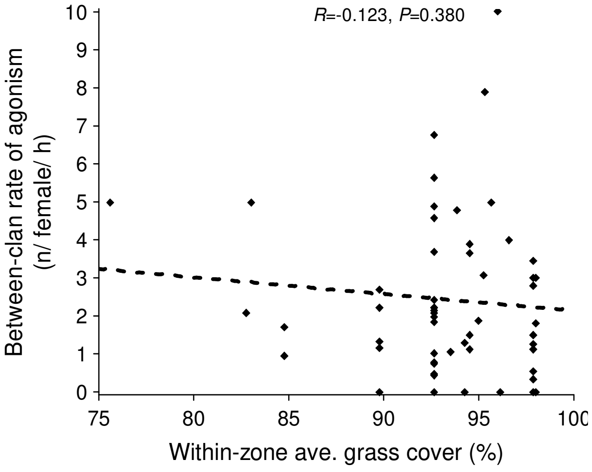
b)


R=0.022, P=0.873
Between-clan rate of agonism
(n/ female/ h)
0
1
2
3
4
5
6
7
8
9
10
200
400
600
800
1000
1200
Within-zone ave. grass biomass (g/m^2)

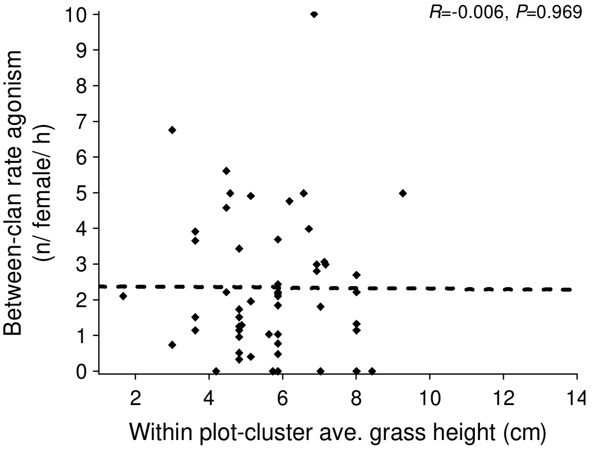
c)


R=-0.238, P=0.086
Between-clan rate agonism
(n/ female/ h)
0
1
2
3
4
5
6
7
8
9
10
75
80
85
90
95
100
Within plot-cluster ave. grass cover (%)

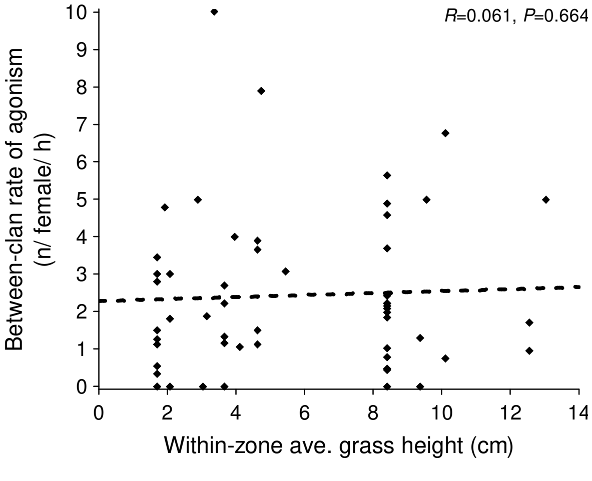
d)

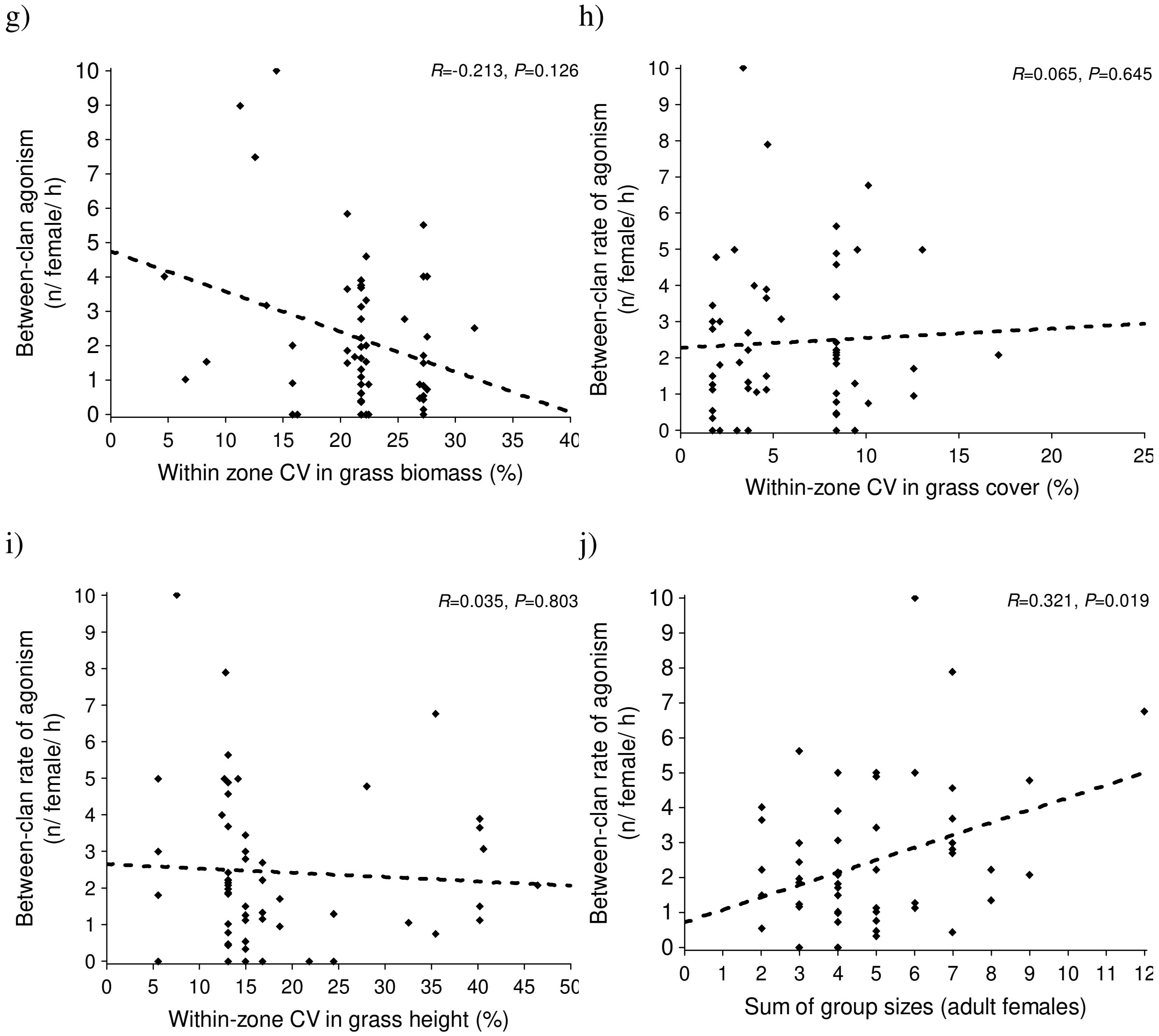

R=-0.123, P=0.380
Between-clan rate of agonism
(n/ female/ h)
0
1
2
3
4
5
6
7
8
9
10
75
80
85
90
95
100
Within-zone ave. grass cover (%)

e)


R=-0.006, P=0.969
Between-clan rate agonism
(n/ female/ h)
0
1
2
3
4
5
6
7
8
9
10
2
4
6
8
10
12
14
Within plot-cluster ave. grass height (cm)

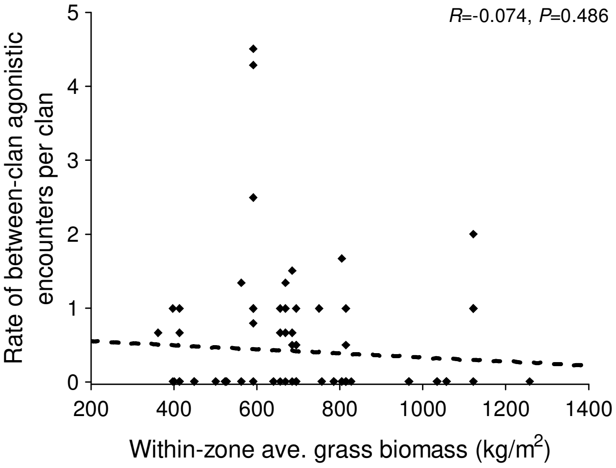
f)


R=0.061, P=0.664
Between-clan rate of agonism
(n/ female/ h)
0
1
2
3
4
5
6
7
8
9
10
0
2
4
6
8
10
12
14
Within-zone ave. grass height (cm)

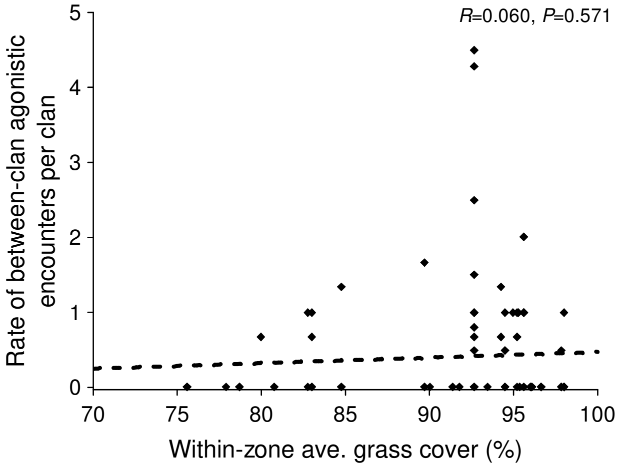


Supplementary Material 7, Figure 2. Scatterplots showing how the rate of individual-level between-clan agonism is related to grass abundance, grass distribution, average group size, and sum of group sizes of the contestant groups. Some data points in panel j mask others due to overlap. Correlation line and statistics given in the plots are for simple correlation.

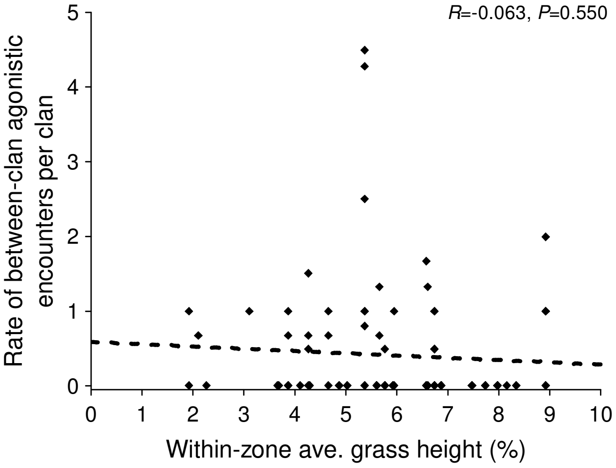
a)


R=-0.074, P=0.486
Rate of between-clan agonistic encounters per clan
0
1
2
3
4
5
200
400
600
800
1000
1200
1400
Within-zone ave. grass biomass (kg/m2)

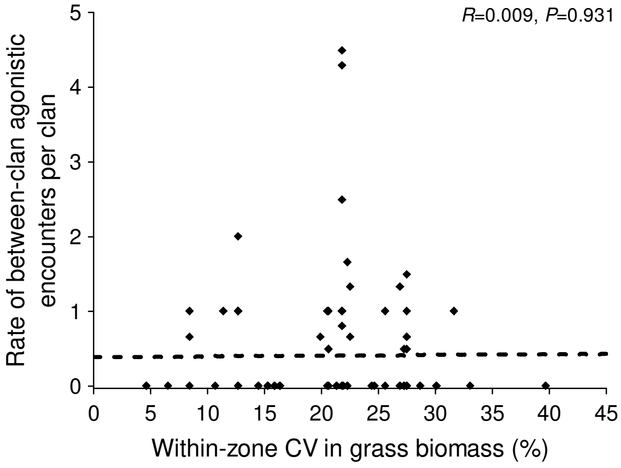
b)


R=0.060, P=0.571
Rate of between-clan agonistic encounters per clan
0
1
2
3
4
5
70
75
80
85
90
95
100
Within-zone ave. grass cover (%)

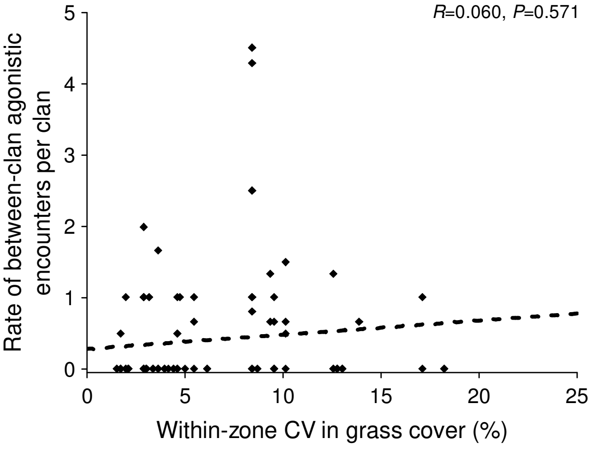
c)


R=-0.063, P=0.550
Rate of between-clan agonistic encounters per clan
0
1
2
3
4
5
0
1
2
3
4
5
6
7
8
9
10
Within-zone ave. grass height (%)

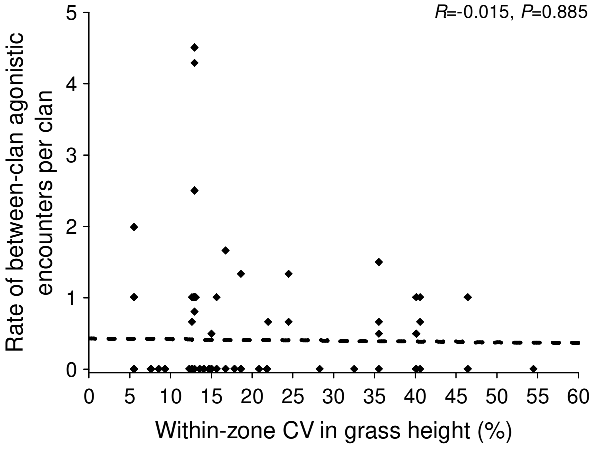
d)

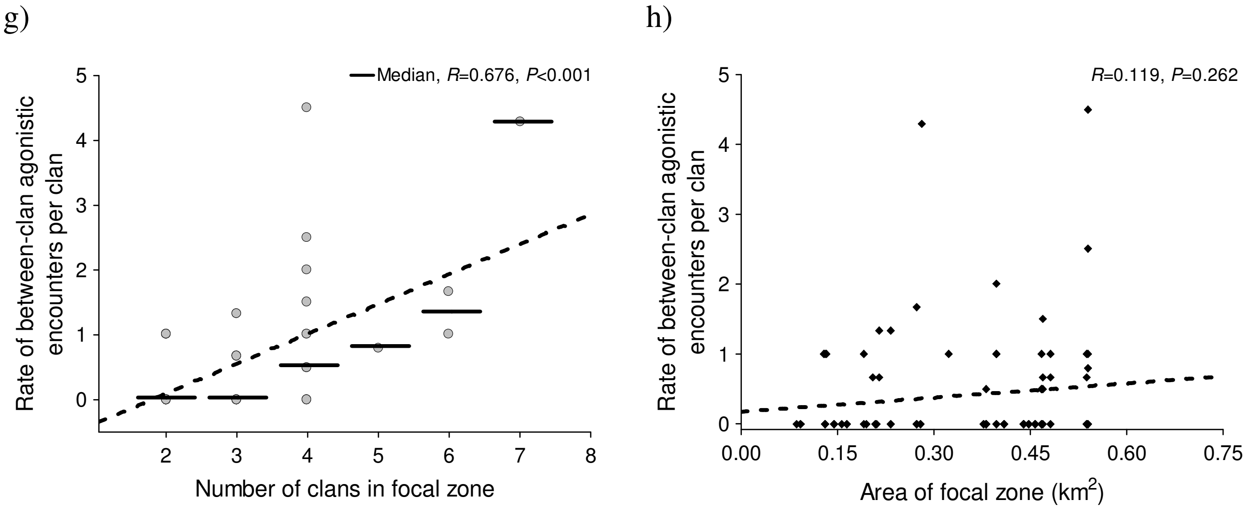

R=0.009, P=0.931
Rate of between-clan agonistic encounters per clan
0
1
2
3
4
5
0
5
10
15
20
25
30
35
40
45
Within-zone CV in grass biomass (%)

e)


R=0.060, P=0.571
Rate of between-clan agonistic encounters per clan
0
1
2
3
4
5
0
5
10
15
20
25
Within-zone CV in grass cover (%)

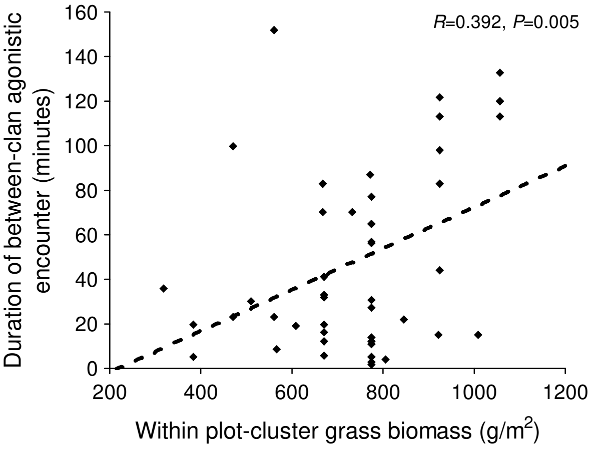
f)


R=-0.015, P=0.885
Rate of between-clan agonistic encounters per clan
0
1
2
3
4
5
0
5
10
15
20
25
30
35
40
45
50
55
60
Within-zone CV in grass height (%)

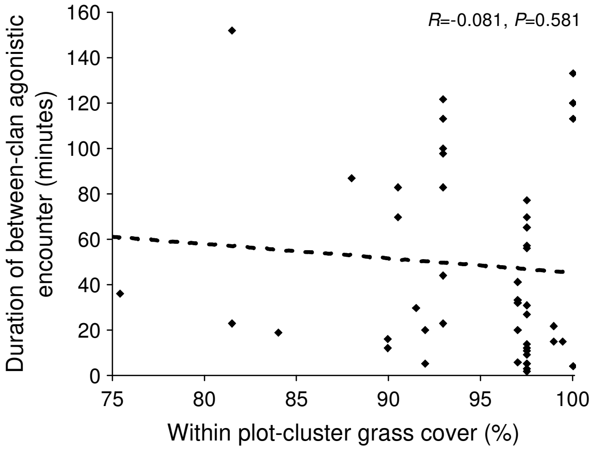


Supplementary Material 7, Figure 3. Scatterplots showing how the rate of (clan-level) between-clan agonistic encounters per clan per 2.5-hour interval varies with grass abundance (biomass, cover, height), grass distribution (CV in grass biomass, cover, and height), number of clans in focal zones, and area of the focal zone. Each data point is a 2.5-hour interval during which two or more clans were present in the focal zone. In g), since data points may be masked due to overlap, medians are also plotted against each value of the number of clans. Correlation line and statistics given in the plots are for simple correlation.

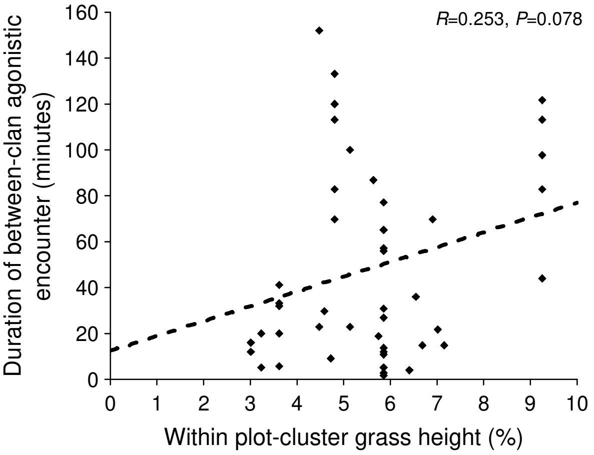
a)


R=0.392, P=0.005
Duration of between-clan agonistic encounter (minutes)
0
20
40
60
80
100
120
140
160
200
400
600
800
1000
1200
Within plot-cluster grass biomass (g/m2)

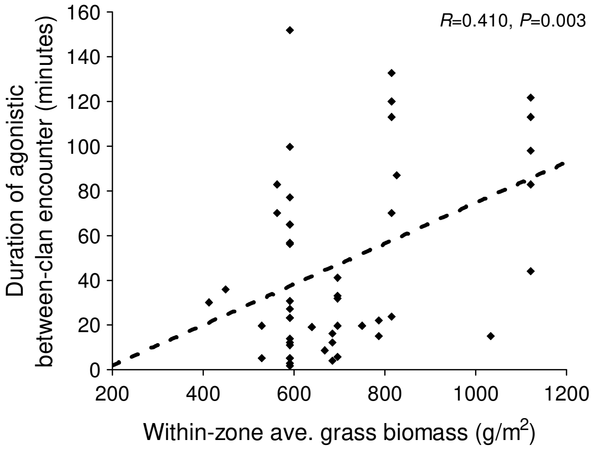
b)


R=-0.081, P=0.581
Duration of between-clan agonistic encounter (minutes)
0
20
40
60
80
100
120
140
160
75
80
85
90
95
100
Within plot-cluster grass cover (%)

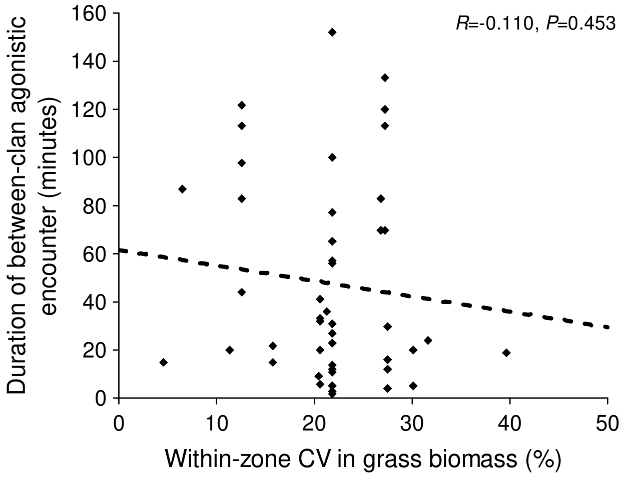
c)


R=0.253, P=0.078
Duration of between-clan agonistic encounter (minutes)
0
20
40
60
80
100
120
140
160
0
1
2
3
4
5
6
7
8
9
10
Within plot-cluster grass height (%)

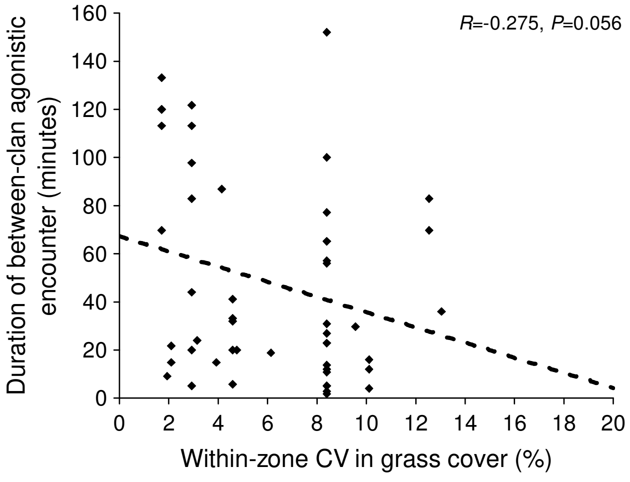
d)

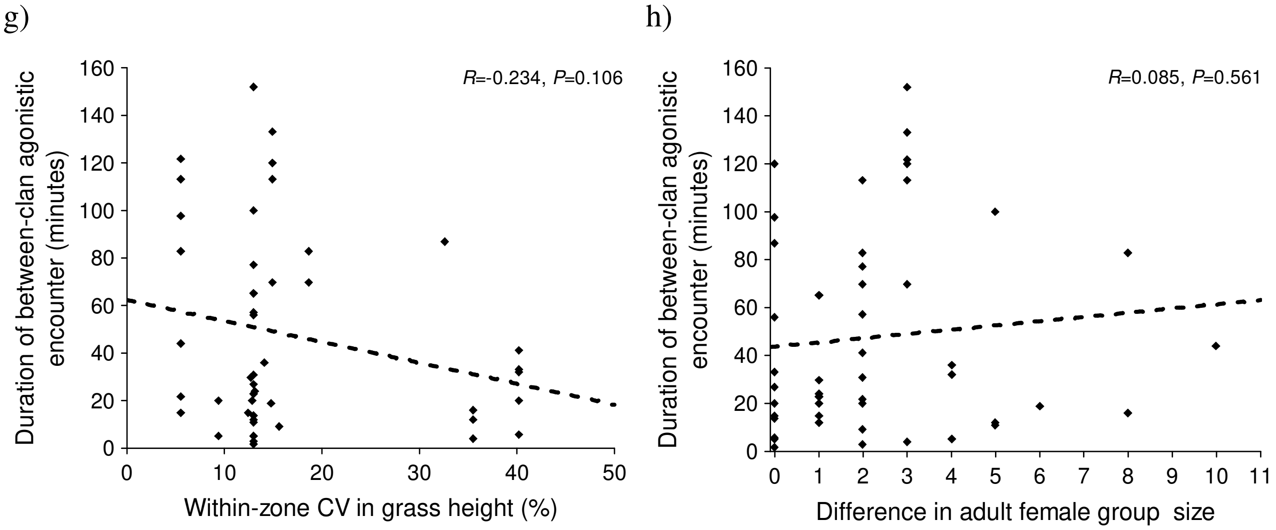

R=0.410, P=0.003
Duration of agonistic between-clan encounter (minutes)
0
20
40
60
80
100
120
140
160
200
400
600
800
1000
1200
Within-zone ave. grass biomass (g/m2)

e)


R=-0.110, P=0.453
Duration of between-clan agonistic encounter (minutes)
0
20
40
60
80
100
120
140
160
0
10
20
30
40
50
Within-zone CV in grass biomass (%)

f)


R=-0.275, P=0.056
Duration of between-clan agonistic encounter (minutes)
0
20
40
60
80
100
120
140
160
0
2
4
6
8
10
12
14
16
18
20
Within-zone CV in grass cover (%)



Supplementary Material 7, Figure 4. Scatterplots showing how the duration of clan-level between-clan agonistic encounters varies with within plot-cluster and within-zone grass abundance (biomass, cover, and height), within-zone grass distribution (CV in grass biomass, cover, and height), and difference in group sizes of the competing clans. Correlation line and statistics given in the plots are for simple correlation.

CHAPTER 5

Dominance Relationships are not Well-Resolved and do not Ensure Access to Better Feeding Sites in Female Asian Elephant Groups in a Grass-Rich Habitat

Title: Dominance relationships are not well resolved and do not ensure access to better feeding sites in female Asian elephant groups in a grass-rich habitat

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Author contributions

HG and TNCV conceived this work. HG collected field data and carried out the analyses. HG, primarily, and TNCV wrote the manuscript.

Abstract

Socioecological models posit that frequent agonistic interactions resulting from strong contest competition lead to resolved dominance relationships in stable groups, whereas weakly-expressed dominance is expected in fission-fusion societies, which have evolved to reduce within-group contest. In this study on individually identified wild female Asian elephants showing fission-fusion sociality, we assessed the structure of dominance relationships in eight clans, and examined the feeding consequences of dominance relationships in a small food-rich habitat for the first time in elephants. Analysing the outcomes of agonistic interactions between adult females, we found that the initiators of dominance were more likely to win and also tended to be older than the recipients. Dominance hierarchies were weak or not significant in all the clans tested for linearity, perhaps due to many unknown relationships. However, significant unidirectionality was observed in most clans, although the directional consistency index was not very high overall (~0.74), in contrast to female societies in African savannah elephants. The strength of dominance expression in a clan, measured by directional consistency, was positively related to the rate of agonism, but this effect was non-significant due to small sample size. Analysis of feeding areas/sites selected by groups and individuals revealed that sites selected by individuals had slightly higher grass abundance than available sites nearby, and feeding site selection was more pronounced when grass availability was low. However, we did not find rank-related benefits of access to better feeding sites based on dominance status within groups. These results conform to the socioecological models that do not expect strong effects of dominance rank on feeding benefits in societies with weakly expressed dominance structure. We discuss our results in the context of the existing understanding of sociality in other elephant populations and suggest that a Red Queen effect type of feeding competition might be operating in the Kabini population.

Keywords

Socioecological theory, within-group contest competition, agonism, fission-fusion, dominance relationships, feeding site selection, rank-related foraging benefits, priority of access, female Asian elephants, Kabini Elephant Project.

Introduction

Within-group feeding competition is an unavoidable cost of group living (Crook and Gartlan 1966, Alexander 1974, Caraco and Wolf 1975, Terborgh and Janson 1986, Janson and van Schaik 1988, Wrangham *et al.* 1993, Isbell 1991, Chapman *et al.* 1995, Smith *et al.* 2008) and has social and energetic/reproductive consequences (for example, van Schaik *et al.* 1983, Monaghan and Metcalfe 1985, Janson 1985, Borries 1993, Holekamp *et al.* 1996, Koenig 2000, Schmidt and Mech 1997, Vogel 2005, Snaith and Chapman 2008, Markham *et al.* 2015). Within-group competition can be of scramble or contest type: scramble or non-interference competition occurs over non-monopolisable resources with usually no clear winner and loser, while contest or interference competition occurs over monopolisable resources and usually has clear winners and losers and results in asymmetric resource intake among competitors in the long term (Nicholson 1954, see Janson and van Schaik 1988). The asymmetry or skew in resource gains is effected through some individuals (dominants) gaining at the expense of others (subordinates), via consistent aggression directed by dominants towards subordinates to control high quality resources, or via avoidance of dominants by subordinates (Janson and van Schaik 1988, Koenig 2002). Thus, the ecological model of female social relationships (EMFSR), which was developed to understand the evolution of gregariousness in females and variations in their social systems as a function of feeding competition and predation risk (Wrangham 1980, Janson and van Schaik 1988, van Schaik 1989, Isbell 1991, Sterck *et al.* 1997), expects that when food is evenly distributed and cannot be usurped, the predominant feeding competition would be of scramble type, while if food is clumped such that it can be usurped by individuals, feeding competition within groups would be of contest type. Scramble competition can constrain group size since foraging efficiency decreases and travel costs increase in larger groups (for example, Caraco and Wolf 1975, van Schaik *et al.* 1983, Isbell 1991, Wrangham *et al.* 1993, Chapman *et al.* 1995, Schmidt and Mech 1997). When food is usurpable, feeding benefits maybe unequally distributed within groups (for example, Whitten 1983, Janson 1985, van Noordwijk and van Schaik 1987, Robbins *et al.* 2007, Smith *et al.* 2008) since subordinate individuals may get excluded from limited food patches (Janson and van Schaik 1988, van Schaik 1989, Sterck *et al.* 1997, Koenig 2002). It is expected that frequent agonistic interactions should lead to consistent dominance relationships and strong dominance hierarchies (van Schaik 1989, Sterck *et al.* 1997, Koenig *et al.* 2013). This is because frequent contests allow for assessments of competitive ability within stable groups and, consequently, in order to minimise the costs of frequent aggressive interactions, lead to the development of resolved dominance relationships (Smith and Parker 1976, Hemelrijk 2000, see Kokko 2013) that lead to differential sharing of foraging benefits through priority of access to dominants (for example, Whitten 1983, Monaghan and Metcalfe 1985, Janson 1985, Koenig 2000, Vogel 2005, Wright et al. 2014, Grueter *et al.* 2016, see Koenig 2002). However, there have been few studies (Koenig *et al.* 2013, Wikberg *et al.* 2013) examining the link between agonism and the expression of dominance (i.e., directional consistency, van Hooff and Wensing 1987), and data-based understanding of the proximate mechanisms shaping dominance structure within- as well as between-species remains of interest (for example, Hemelrijk 2000, Chase *et al.* 2002, Dugatkin and Earley 2004, Wikberg *et al.* 2013, Koenig *et al.* 2013).

Dominance systems vary in strength, ranging from egalitarian societies, showing high inconsistency and unresolved dominance relationships, to strong dominance hierarchies with highly consistent and linear rank relationships (Chase 1980, Sterck *et al.* 1997, see Hemelrijk 2000). Dominance hierarchies may also be individualistic, based on attributes such as strength, age, and body condition, or may be nepotistic, in which relatives of dominant individuals are ranked closely in the dominance hierarchy (Vehrencamp 1983, see Sterck *et al.* 1997). The EMFSR expects that dominance hierarchies should range from individualistic to nepotistic depending on the strength of within-group contest and quality of feeding benefits ensuing from it. A greater nepotistic bias is expected in dominance relationships when contested usurpable foods yield high benefits, because of inclusive benefits gained from access to food patches through kin-based intra-group coalitions, whereas individualistic hierarchies are expected under weak contest competition (Wrangham 1980, van Schaik 1989, Sterck *et al.* 1997). In addition, patchiness of food at larger scales is expected to elicit between-group contest, which may have a bearing on within-group relationships, due to the advantage of large group size in between-group contests. In such cases, dominants are expected to show tolerance towards subordinate individuals, in groups that might otherwise exhibit strong within-group competition and exclusion of subordinates (Sterck *et al.* 1997, reviewed in Isbell and Young 2002).

Socioecological models expect the relationship between foraging success and dominance rank to be strong when within-group contest competition is strong (Janson and van Schaik 1988, van Schaik 1989, see also Koenig and Borries 2009). Such proximate foraging benefits related to dominant rank may translate into differential energetic and reproductive gains among group members (Janson and van Schaik 1988, Koenig 2002). This has been demonstrated in many species in which dominant group members show signs of better reproduction (for example, van Noordwijk and van Schaik 1987, Holekamp *et al.* 1996, Robbins *et al.* 2007, but see Roberts and Cords 2013), and more proximate investigations have also found greater foraging benefits to dominant individuals (for example, Janson 1985, van Noordwijk and van Schaik 1987, Wright *et al.* 2014, Grueter *et al.* 2016) and/or costs to subordinates (for example, Pazol and Cords 2005, Wright *et al.* 2014), which can impact overall energetic gains (for example, Janson 1985, see Janson and van Schaik 1988, Vogel 2005, but see Grueter *et al.* 2016). However, in contrast to stable groups that show the above patterns, fission-fusion societies allow subordinate individuals to minimise the costs of high within-group feeding competition by moving away from the main group through fissioning into subgroups (see van Schaik *et al.* 1983, Aureli *et al.* 2008). They may coalesce to form larger groups to maintain social bonds (Aureli and Schaffner 2007) when food abundance permits it (for example, Chapman *et al.* 1995, Snaith and Chapman 2008, Sugiura *et al.* 2011) or when between-group contests demand large groups. Thus, fission-fusion societies may have inconsistent relationships and dampened expression of dominance (but see Wittig and Boesch 2003) due to weakened feeding competition (de Silva *et al.* 2017), which can reduce the frequency of agonistic contests, or because reduced association may prevent proper assessments of competitive abilities among the contestants (*sensu* Smith and Parker 1976, see Kokko 2013). These possibilities make species with fluid sociality an interesting system to test the inter-linked predictions of EMFSR which can be helpful in understanding the costs and benefits of sociality.

In this paper, we examine the structure of dominance relationships and foraging consequences of dominance among adult female Asian elephants (*Elephas maximus*) in a grassland habitat (around the backwaters of the Beechanahalli Dam built on River Kabini) in Nagarahole National Park (Kabini elephant population), southern India. Female Asian elephants live in fission-fusion societies (de Silva *et al.* 2012, Nandini *et al.* 2018). The most inclusive female social unit is the clan, within which females show fluid associations, changing their groupings over time (Nandini *et al.* 2017, 2018). Although a large part of the diet of Asian elephants and African savannah elephants comprises grass (Owen-Smith 1988, Baskaran *et al.* 2010), a food type considered to be continuously distributed and of low quality and not expected to elicit contest (see Wrangham 1980, Archie *et al.* 2006, de Silva *et al.* 2017), African savannah elephant family groups show signs of strong dominance structure that is age-based (Archie *et al.* 2006) and dominance between matriarchs of family groups that is also age-based (Wittemyer and Getz 2007). A study comparing the dominance structures of Asian and African savannah elephants attributed weaker expression of dominance hierarchy in Asian elephants (in Uda Walawe, Sri Lanka) to reduction in competition due to fission-fusion processes and greater productivity in Asian elephant habitats in contrast to African savannahs (de Silva *et al.* 2017). In our study area, due to the concentration of resources (food and water) around the Kabini backwaters, there is strong between-clan contest indicated by the high frequency and intensity of agonistic interactions (Nandini 2016, Gautam and Vidya 2019) as compared to other habitats (Baskaran 1998). Due to strong between-clan contest, larger group size is advantageous in winning between-group contests (Nandini 2016, Gautam and Vidya *unpublished*). However, group size in this population was also found to be constrained (Nandini *et al.* 2018): group sizes were generally smaller than clan sizes, which is expected in fission-fusion societies, but the average group sizes of different clans did not increase with clan sizes and were similar instead, giving rise to reduced associations between clan-mates in larger clans (Nandini *et al.* 2017). Moreover, greater within-clan interference competition with increasing group size shows that these constraints are ecological (Gautam and Vidya 2019). These patterns suggest that although fission-fusion dynamics may allow for an increase in group size when between-group contest is strong, an increase in group size is not free of within-group contest competition even in this resource-rich habitat. Moreover, the frequency of agonistic contests in our study population seems to be higher (Nandini 2016, Gautam and Vidya 2019) than that reported for the Asian elephant population in Uda Walawe, Sri Lanka (de Silva *et al.* 2017). From classic socioecological models, stronger contest competition is expected to result in stronger expression of dominance (linearity and directional consistency), which may translate into dominance-based differential foraging consequences of within-group contest (Janson and van Schaik 1988, van Schaik 1989). With this framework in mind, we addressed the following questions about the structure of within-clan dominance and its correlates, and on foraging site selection and the relationship of feeding site selection to dominance ranks of females.

1) What are the effects of age and initiator/recipient category on dominance outcomes, and how are dominance relationships structured with respect to linearity, reciprocity, and directional consistency?

Since age is often a correlate of dominance status, we expected older females to initiate and win dominance interactions more frequently. Moreover, since individuals are expected to assess the opponents' competitive ability and possible outcome of an agonistic interaction before initiating it, we expected initiators to win more frequently than recipients. Two contrasting expectations could be rationalised about the dominance hierarchy. Since fluid associations might prevent the assessment of dominance status among clan members and since the only food available in Kabini is grass, which is assumed to be a low quality resource (Wrangham 1980, Archie *et al.* 2006, de Silva *et al.* 2017), we expected a weakly expressed hierarchy, characterised by low linearity, high reciprocity and low consistency in dominance relationships (see Methods). However, in keeping with the EMFSR's prediction (Koenig *et al.* 2013), since we had previously found overall frequent within-clan agonism (Gautam and Vidya 2019), it would not be surprising if we found a stronger expression of dominance compared to previous findings in Asian elephants in Sri Lanka (de Silva *et al.* 2017) and African savannah elephants in Amboseli (Kenya) and Tarangire (Tanzania) National Parks (Archie *et al.* 2006).

2) Is the rate of agonism related to the directional consistency of dominance within clans?

The EMFSR predicts that frequent agonistic contests should result in strongly expressed dominance structure (Koenig *et al.* 2013, Wikberg *et al.* 2013). We expected this relationship to hold within a population, and expected the clans showing more frequent agonism to have greater directional consistency in dominance relationships.

3) Are the feeding areas/sites selected by elephants at the level of groups or individual females better than control sites?

We expected elephant groups, as well as females within groups, to select better feeding areas/sites than nearby control sites.

4) Are differences in food abundance at feeding sites selected by females within groups explained by their dominance ranks?

If a dominance hierarchy is linear and strongly expressed, a steep rank-related skew in access to feeding opportunities is expected in favour of dominants, whereas if a dominance hierarchy is weak, rank-related skew is expected to flatten out (Janson and van Schaik 1988, Koenig 2002). Accordingly, we expected higher ranking females to occupy feeding sites with greater food abundance than lower ranking females if the hierarchy was linear, but expected a weak or no correlation between the rank of a female and food abundance at her selected site if the dominance hierarchy was weakly expressed.

Methods

Study area and population

The study was carried out in the grassland habitat around the backwaters of the River Kabini that flows between Nagarahole and Bandipur National Parks and Tiger Reserves (Figure 1). The elephants visiting the Kabini backwaters are part of the world's largest connected population of Asian elephants. Elephants using this habitat and its surrounding forests have been individually identified and monitored since 2009 as part of a long-term programme (Kabini Elephant Project) to understand the ecology and behaviour of Asian elephants. Based on natural physical characteristics, over 460 adult females (>10 years of age) and 135 adult males (>15 years of age) were identified till the end of this study (see Vidya *et al.* 2014 for methods of identification of individual elephants). As mentioned above, female elephants show fluid associations within clans (Nandini *et al.* 2017, 2018). There is substantial within- and between-clan dominance, the latter being more intense (Nandini 2016, Gautam and Vidya 2019). The grassland habitat where this study was conducted attracts a very high density of elephants in the dry season since this area is a rich source of water and grass, whereas the surrounding forest habitat has less abundant grass (Gautam and Vidya 2019), although browse food plants are available (Gautam *et al.* 2019).

Field sampling

The grassland habitat around the Kabini backwaters of Nagarahole National Park and Tiger Reserve was demarcated into six different large stretches, henceforth called focal zones (see Figure 1) for sampling dominance interactions, foraging site selection, and grass abundance and distribution. The focal zones were sampled in a nearly systematic rotational basis such that each zone was sampled for one day in a cycle of 6 sampling days. Three such cycles were sampled per 30-day period (month) for three such periods in 2015 and four in 2016. Additionally, sampling of foraging site selection and dominance interactions was also carried out on the remaining days of each month through opportunistic sampling, which could sometimes be outside these zones but in the same general area. Data presented, on both dominance and foraging, in this study are from adult females (10 years or above, see

Nandini *et al*. 2018).

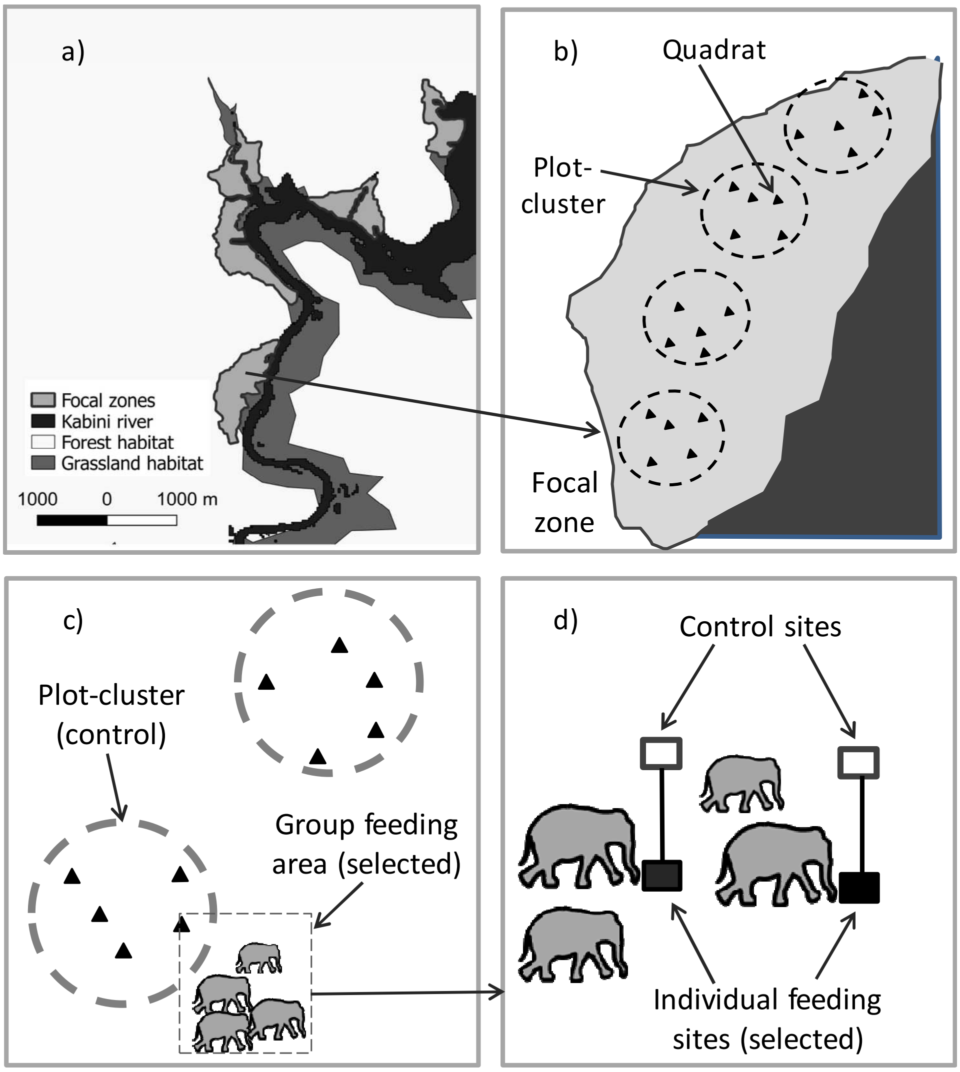


Figure 1. a) A map of the Kabini area showing the outlines of focal zones sampled in the grassland habitat, b) an illustration of the sampling scheme used to sample grass abundance, showing five quadrats each in four plot-clusters in a focal zone, c) an illustration of a sampled group feeding area (comprising of feeding sites of multiple individuals, shown as a dashed box) and the nearest plot-cluster used as control for the group feeding area, and d) a zoomed-in illustration of feeding sites of individuals within a group feeding area and their respective control sites.

Sampling dominance interactions

Dominance interactions were sampled between approximately 6:30 AM and 06:30 PM. Dominance data were recorded through focal group sampling as the grassland habitat allows good visibility (Altmann 1974). Dominance observations were video recorded using a Sony HDR-XR100E video camera when a group had settled down to feed or to use puddles or the river. The videos were focused in a way to attempt recording all females, and in cases when interactions involved females who were outside the video frame, details were written down in field notes. Most (>95%) of the data used were from focal group samples of 15 minutes or more, which were used to calculate rates of agonism (see below), although we also used interactions which were recorded in the field notes as mentioned above or were opportunistically recorded as short videos. The within-clan dominance data obtained through focal sampling that were used in this study largely overlap with a previous study (Gautam and Vidya 2019) on the relationship between food distribution and the occurrence of agonistic interactions between- and within- clans, rather than on the outcomes of agonism within clans, as in this study. However, some focal observations that were taken when groups were not feeding and short videos had not been used previously. They were included in this study to analyse dominance structure. The rates of agonism here are based on data from Gautam and Vidya (2019). Clan membership of the interacting individuals was based on the modularity classes identified previously (Nandini *et al.* 2018).

We observed videos to score within-clan agonistic interactions as different types of aggressive (for example, displacement, supplant, push, shove, trunk wrestle, hit, kick, chase, charge, place trunk over opponent's head/body to dominate, pull tail) and submissive (for example, turn away and show one's back/ urinate/ shake head after advancing towards opponent, submissively walk backwards towards opponent, and avoidance) behaviours. We recorded details such as the time of interaction, identity of the initiator, recipient, winner and loser. Based on the observed durations of dominance interactions, dominance interactions separated by a gap of 15 minutes or more were classified as independent interactions, whereas dominance interactions that occurred at shorter intervals were classified as non-independent (cumulative distribution of time intervals between subsequent interactions available in Gautam and Vidya 2019). The initiator of the interaction was the individual who started an approach or contact-based dominant or submissive action towards the opponent (called recipient). We recorded the winner and loser in independent interactions as well as non-independent interactions. In a non-independent interaction, the initiator was said to be the perceived winner if the recipient moved away or flinched its body immediately in response to the received agonism. There was no perceived winner when the recipient did not respond or when it retaliated slightly but could not move the initiator away, whereas the recipient was said to be the winner if its retaliation resulted in the initiator moving away or if the initiator moved away by itself within a few seconds (in the case of submissive or avoidance behaviours). In the case of independent dominance interactions with multiple non-independent interactions, the initiator was the eventual winner if the recipient moved away by about three or more steps from its position at the end of the independent interaction. In case a winner could not be clearly ascertained, the interaction was said to have no winner or loser.

Sampling feeding sites and food availability

When an elephant group fed in a location for some time (about ten or more continuous minutes), multiple adult females were photographed at the same time to take a single snap-shot record of their feeding positions. We refer to this collection of individual feeding sites as a group feeding area. After the group had moved away, we laid 1 m x 1 m quadrats at the feeding sites of different individuals recorded in the photograph in order to measure grass abundance. We also sampled another 1 m x 1 m quadrat, placed 3 m (approximately one adult female elephant body length) away from each feeding site and perpendicular to the direction the individual was facing, as a control site to compare with each feeding site (Figure 1). This distance was chosen as it would require an elephant to make an effort greater than just extending the trunk (~2 m) and thus such a site one body length away is not likely to be part of the same feeding site. In each 1 m x 1 m quadrat, we first visually estimated grass cover and measured the average height of grass (from 10 different grass stems in the quadrat), after which all the grass was clip-harvested from the ground and the fresh biomass measured with a digital balance. For a few feeding sites, data on grass heights could not be collected due to permit times or other logistical constraints.

The average grass abundance of the group feeding area was taken as the average of the abundances of individual feeding sites. We estimated the average grass abundance available near the group feeding area from data on grass abundance in the focal zones, collected during the same time period (Gautam and Vidya 2019) as follows. We had previously sampled grass abundance (cover, average height, and biomass) in five random 1 m x 1 m quadrats in each of four plot-clusters in each focal zone in the middle of each month (see

Gautam and Vidya 2019, Figure 1). We calculated the average grass abundance of the quadrats in the nearest plot-cluster (sampled within two weeks of the behavioural observations) as the representative value of average grass availability for the group. Female groups were usually spread within about 50 m. If the sampled group feeding area was more than 100 m away from the centre of the nearest plot-cluster, we did not use the data on grass availability for that group-level analysis (see below).

Data processing and analyses

Analyses of dominance were carried out only using interactions wherein both contestants were adult females. Similarly, feeding site data were also from adult females.

Effect of initiator/recipient category and age on dominance outcomes and dominance status

We calculated the percentages of independent dominance interactions in which the initiators and the recipients won agonistic interactions, those in which the eventual winner was older or younger than the eventual loser. To find out whether age was related to the initiation of dominance interactions, we compared the ages of initiators and recipients of independent dominance interactions using a linear mixed-effects model, considering initiator/recipient as a fixed factor and interaction number and dyad identity (dyadic combination of the two participating females) as random factors. To find out whether age was associated with the final outcome of independent dominance interactions, we used a similar linear mixed-effects model again, considering winner/loser as a fixed factor, and interaction number and dyad identity as random factors. In both mixed-effects models described above, since the inclusion of interaction number resulted in models with singularity due to no variance explained by it, this variable was subsequently dropped and only dyad identity used as a random effect. These tests were done using *lmer* function of *lme4* (Bates *et al.* 2011) package in R (R Core Team 2018).

We also examined how age was related to the dominance scores of individuals, namely the Proportion of Contests Won (PCW), David's Score (DS, David 1987), and Modified David's Score (MDS, de Vries *et al.* 1998), obtained from the analyses of outcomes of dominance interactions from each clan, using SOCPROG 2.6 (Whitehead 2009). Supplement 1 gives an overview of these dominance scores. To test this, we performed separate linear regressions of each of these dominance scores against the ages of individuals, for the clans for which we had data on at least 10 adult females. We used data on age from the Kabini Elephant Project and the ages were estimated by considering physical characteristics like shoulder height, skull and body size, and loose skin folds, taking semi-captive elephants of known age as reference (Vidya *et al.* 2014). We base our inferences on the results using modified David's score (MDS), which is an improved version of David's score (DS) that takes into account the number of interactions in the dyads in addition to the proportion of wins for an individual (see Briffa *et al.* 2017). However, we also present results based on PCW and DS in the Supplementary Material.

Structure of dominance hierarchies and relationships

We analysed dominance structures separately for different clans and used only those clans in which clear winners were known in at least 15 independent dominance interactions. We tested for linearity of dominance hierarchies using Landau's index h (Landau 1951) and de Vries' corrected index h' (de Vries 1995). We tested for reciprocity of dominance relationships by comparing the dominance matrix with its inverse matrix using a Mantel Z test, and used non-significance of reciprocity to detect unidirectionality in dominance (Hemelrijk 1990). We carried out these analyses using SOCPROG 2.6 (Whitehead 2009). Since the two indices of linearity mentioned above are sensitive to group size, inconsistencies, and unknown relationships, we also calculated the directional consistency index, which is not affected by group size or unknown relationships, unlike the h index (Koenig and Borries 2006, Klass and Cords 2011, Koenig *et al.* 2013). We calculated directional consistency index (DCI, van Hooff and Wensing 1987), taking average of DC from all known dyads, using the formula $DC=(H-L)/(H+L)$, where H is the number of wins in the higher frequency direction and L is the number of wins in the lower frequency direction for each dyad. DCI for each clan was calculated using only those dyads in which two or more decided dominance interactions were seen. Supplement 1 gives an overview of these measures of dominance structure in groups.

Relationship between rate of agonism and directional consistency

We used previous data on clan-wise rates of agonism obtained from focal samples (Gautam and Vidya 2019) and performed a linear regression of DCI (from dyads with two or more interactions) on agonism to test if clans with more frequent agonism showed greater directional consistency.

Comparison of feeding areas/sites of groups/individuals with control sites

We compared the average grass abundance (cover, height, and biomass) in group feeding areas (average of the grass abundance in 1 m x 1 m quadrats at the feeding sites of different individuals sampled in the group) with the average grass availability for the group from the nearest plot-cluster (average of the grass abundance in 1 m x 1 m quadrats of the nearest plot-cluster as explained above), which we call a control plot-cluster, using a linear mixed-effects model. We used selected/control as a fixed effect and clan identity and the identity of the group feeding area (i.e., the group feeding area number among the 63 group feeding areas) as random effects. The null hypothesis was that there would be no difference between the average grass abundance in the group feeding area and the control plot-cluster.

Further, using the concept of resource selection functions (Thomas and Taylor 1990), we tested whether group foraging selection was dependent on grass abundance and variability by calculating the relative margin of foraging selection by the group. We used the formula, relative margin of selection = (average grass abundance in group feeding area – average grass availability at control plot-cluster) / average grass availability at control plot-cluster. A positive value of the relative margin of selection would mean that the group feeding area had more abundant grass than average availability, whereas a negative value would imply that the selected area had less than average available grass abundance. We used a linear mixed-effects model to test the effects of mean and variability (CV, coefficient of variation) in grass biomass (both fixed effects) and clan identity (random effect) on the relative margin of foraging selection for grass biomass (dependent variable). These analyses were also carried out on grass cover and grass height as grass abundance variables.

We also compared the grass abundance of individual feeding sites with their respective control sites using a mixed-effects model, with selected/control as fixed effect and individual identity, clan identity and group feeding area identity (number) as random effects. The null hypothesis was that there would be no difference between grass abundance in the individual feeding site and the control site.

Relationship between dominance status and feeding site grass abundance

In order to examine the relationship between dominance status and grass abundance at the feeding site, we used data only from those groups for which feeding site data were collected on at least two individuals, and then selected clans for which we had data on at least 10 individual feeding sites. We primarily used the modified David's score (MDS) as the dominance score for the individual (although we also present results based on PCW and DS). To ensure that the spatio-temporal context was considered in the analyses, we carried out relative scoring of feeding site data and dominance scores for the individuals and their feeding sites that were sampled at the same time, within the same group foraging area. Such relative scoring was necessary because an individual's feeding site at one location/time may not be comparable to another clan-member's feeding site at a different place and time due to spatio-temporal differences in food availability. Similarly, relative scoring of dominance scores was required for individuals sampled at that instant because different sets of individuals could be present in different group feeding areas due to fission-fusion sociality. We used z-transformation (mean z score=0, standard deviation=1, values greater than or smaller than mean z being positive or negative scores) for standardising data for relative scoring. We calculated z-scores ($z=[x_i - \bar{x}]/s]$, where x_i is the grass abundance at feeding site of individual i, and $\bar{x}$ and s are the average and standard deviation, respectively, of such feeding sites in each group feeding area) of grass abundance at feeding sites of individuals sampled in each group feeding area. A positive z-score value would mean that the individual was feeding at a site better than the average of the individuals sampled at that time, while a negative value would mean that the feeding site was poorer than average. Similarly, we z-transformed the dominance scores of the individuals sampled at each group feeding area. We used a mixed-effects model to test if dominance scores could predict food abundance at feeding sites. Grass biomass (z-transformed) at the feeding sites was the dependent variable, MDS (z-transformed) was the fixed effect predictor, and clan identity was the random effect in this model. While we primarily relied on grass biomass as the measure of grass abundance, similar tests done using grass cover and average height at feeding sites are also shown in the Supplementary Material.

Software

We used *lmer* and *lm* functions of *lme4* package (Bates *et al.* 2011) of R (R Core Team, 2018) to test linear mixed-effects models and linear fixed-effects models, respectively. For fixed-effects models, multiple R^2 was obtained from the *lm* output, while for the mixed models we used *r.squaredGLMM* function of R package *MuMIN*. The latter provides R^2 (marginal), which includes only the fixed effects, and R^2 (conditional), which also includes the variance explained by random effects (Nakagawa and Schielzeth 2013). All plots were made in Statistica 7.0 (StatSoft Inc. 2004). Simple correlation and regression tests were done in Statistica 7 (StatSoft Inc. 2004).

Results

Dominance relationships

We collected dominance data from 282 focal group and *ad-libitum* observations for a total of 175 hours. During these focal and *ad-libitum* observations, we observed 726 agonistic interactions, out of which 459 were independent agonistic interactions and 267 were non-independent interactions. These agonistic interactions involved 128 adult females. The average duration of the focal group observations was about 37 minutes, and 40 of these observations were less than 15 minutes long.

1. *What are the effects of age and initiator/recipient category on dominance outcomes, and how are dominance relationships structured with respect to linearity, reciprocity, and directional consistency?*

Effect of age and initiator/recipient category

Considering all the 459 independent agonistic interactions, the initiator was the winner in about 91% of the interactions, and the recipient was the winner in 7% of the interactions, while there was no winner in 2% of the interactions. The ages of initiators (mean=35.65 years, 1.96 SE=1.368) of independent dominance interactions were greater than those of the recipients (mean=23.65 years, 1.96 SE=1.317) and dyad identity (random effect) contributed significantly to the variation explained by the mixed-effects model (Table 1a, Figure 2a).

Of the 432 interactions with clear outcomes, the winner was older than the loser in 314 (73%) independent dominance interactions, while reversal against age (winner was younger) was seen in 118 (~27%) independent interactions. Six percent (27 out of 459) of all interactions had no decided winner. Winners were significantly older (mean=35.53 years, 1.96 SE=1.428) than losers (23.61 years, 1.96 SE=1.354, Table 1b, Figure 2b), and the random effect of dyad identity had large contribution to the variation explained by the mixed-effects model. However, in a regression of dominance scores of individuals against age within clans, the positive effect of age on the dominance scores of adult females varied from being non-significant in one (Lisa's) clan to moderate in two (Patricia's and

Victoria's) clans, to large in one (Nakshatra's) clan, among the clans for which we had data on 10 or more adult females (Figure 3, see Supplementary Material 1 for regression test results). Moreover, despite the positive relationship between age and dominance scores, the oldest female was not the most dominant female in three out of four such clans.

Table 1. Results from linear mixed-effects models testing a) the differences in the age of initiators and recipients in independent agonistic interactions (initiator/recipient was a fixed effect and dyad identity was a random effect), and b) the differences in the age of eventual winners and losers in the independent interactions with clear winners (winner/loser was a fixed effect and dyad identity was a random effect). Significant *P* values are marked in bold. In mixed-effects models, R^2 (marginal) includes only the fixed effects, while R^2 (conditional) also includes the variance explained by random effects.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
a)							
Fixed	Intercept	35.064	0.820	33.458	36.670	42.78	**<0.001**
Fixed	Initiator/recipient: recipient	-12.002	0.744	-13.460	-10.544	-16.130	**<0.001**
Random variation							
Random effect (intercept)	Dyad identity (*N*=245): variance=85.17						
Residuals	Residual variance (*N*=918) = 127.03						
	R^2(m), R^2(c)	0.145, 0.489					
b)							
Fixed	Intercept	23.007	0.846	21.349	24.665	27.2	**<0.001**
Fixed	Winner/loser: winner	11.913	0.773	10.398	13.428	15.41	**<0.001**
Random variation							

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate	*t*	*P*
Random effect (intercept)	Dyad identity (*N*=233): variance=86.54					
Residuals	Residual variance (*N*=864) = 233					
	R^2(m), R^2(c)	0.141, 0.486				

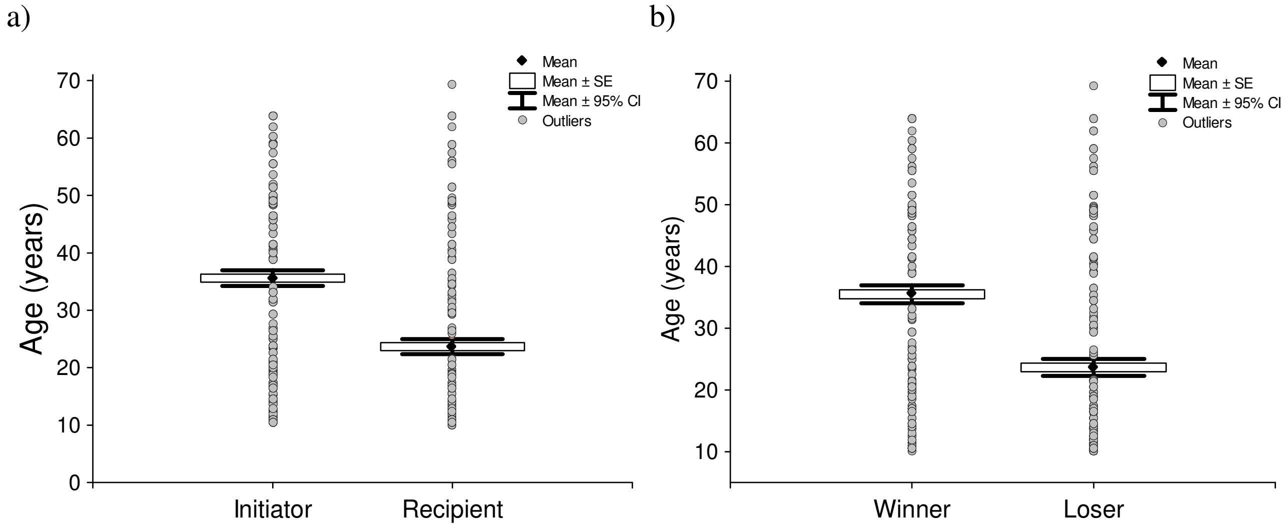


Figure 2. Ages of a) initiators and recipients, and b) winners and losers, of independent agonistic interactions.

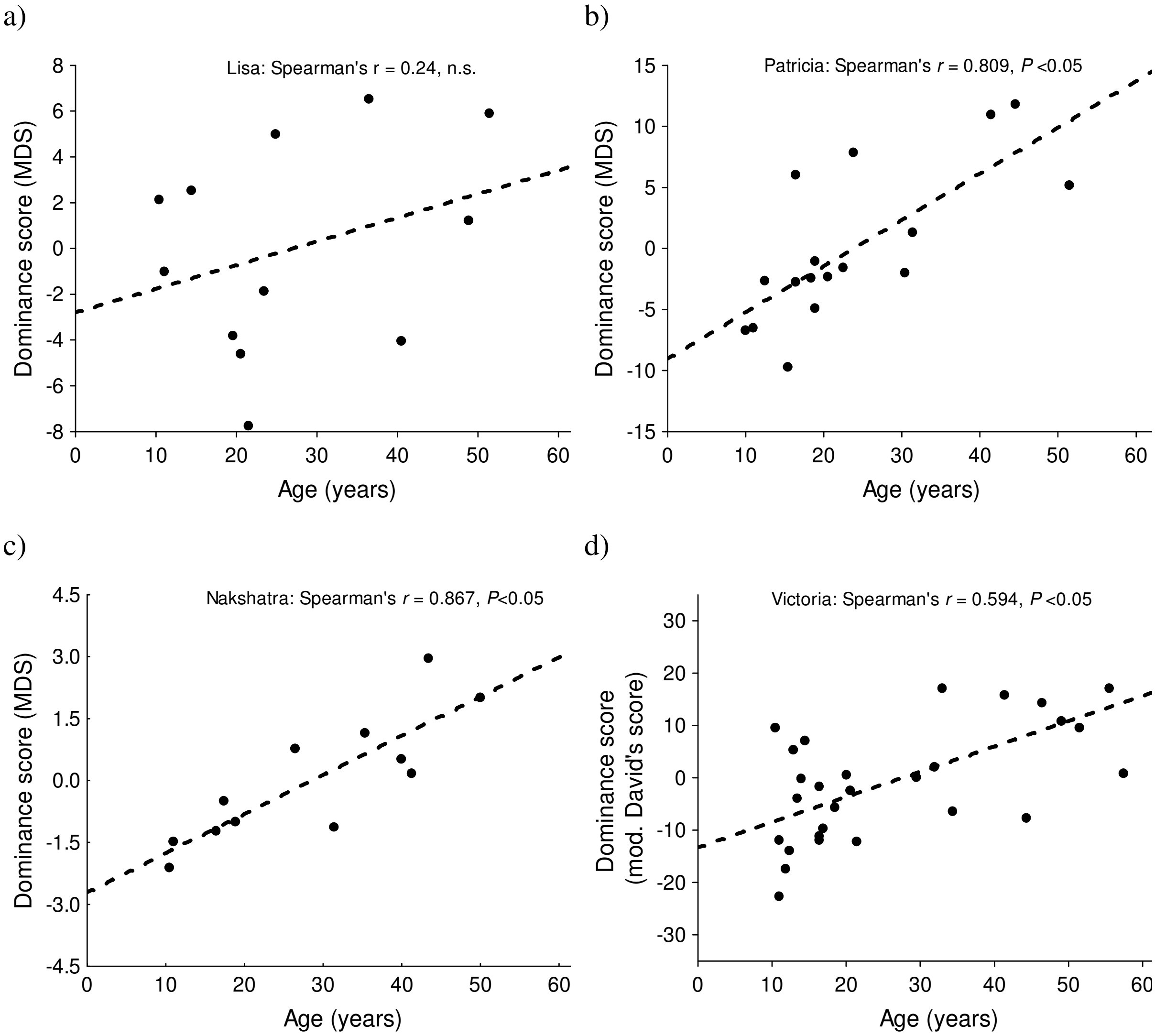


Figure 3. Scatterplots showing the relationship between age and dominance score (modified David's score) of individuals from clans for which dominance data were available on at least 10 individuals: a) Lisa, b) Patricia, c) Nakshatra, d) Victoria.

Structure of dominance relationships and hierarchies

Overall, we did not find linear dominance hierarchies within clans. A summary of statistics on linearity and reciprocity in the eight clans with 15 or more interactions is shown in Table 2. Landau's index of linearity (*h*) was not significant in five of the eight clans tested for linearity whereas it exceeded the expected random value in three clans; however, de Vries' corrected index *h'* was not significant in any clan. The former was significant in the three smaller clans, although two of these clans had group sizes less than six (Table 2). Despite no linear dominance hierarchy, all clans exhibited unidirectionality (although one clan showed unidirectionality through the test of absolute reciprocity, but reciprocity with Hemelrijk's relative Rr test; Table 2). The directional consistency index values were variable, but not very high (mean DCI=0.740, SD=0.069, *N*=8 clans).

Table 2. Measures of linearity (*h*- Landau 1951; *h'*- de Vries *et al.* 1995), reciprocity (Mantel *Z* matrix correlation test and Hemelrijk *Rr* test), and directional consistency (DCI) in focal clans. Significant values are marked in bold.

Clan name (no. of adult females, no. of interactions)	Landau's *h* / expected random *h* value	de Vries' *h*', *P*	Mantel test for absolute reciprocity: *Z, P*	Hemelrijk test for relative reciprocity: *Rr, P*	DCI (no. of dyads with >1 wins)
Katrina (6, 22)	0.286 / 0.429	0.429, *P*=0.495	-0.227, *P*=0.916	-0.078, *P*=0.658	0.786 (7)
Lisa (12, 46)	0.098 / 0.231	0.245, *P*=0.423	0.156, *P*=0.075	0.129, *P*=0.081	0.648 (9)
Menaka (3, 15)	**1.0 / 0.750**	1.000, *P*=0.750	-0.583, *P*=1.000	-0.500, *P*=1.000	0.778 (3)
Mridula (6, 21)	**0.486 / 0.429**	0.600, *P*=0.338	-0.179, *P*=0.849	-0.125, *P*=0.754	0.806 (6)
Nakshatra (12, 16)	0.052 / 0.231	0.241, P=0.488	0.003, *P*=0.483	0.124, *P*=0.081	0.667 (3)
Patricia (17, 99)	0.075 / 0.167	0.196, *P*=0.350	0.010, *P*=0.334	0.190, ***P*=0.003**	0.799 (23)
Tilottama (5, 19)	**0.650 / 0.500**	0.750, *P*=0.306	-0.373, *P*=0.873	0.053, *P*=0.333	0.778 (6)
Victoria (29, 148)	0.059 / 0.100	0.137, *P*=0.164	0.287, *P*=0.999	0.156, *P*=0.999	0.660 (30)

2) Is the rate of agonism related to directional consistency of dominance?

The rate of agonism was positively related to and explained 37% percent of the variation in directional consistency index, although the relationship was not statistically significant ($F_{1,6}$=3.484, r=0.606, R^2=0.367, P=0.111, Figure 4) possibly due to small sample size (N=8 clans).

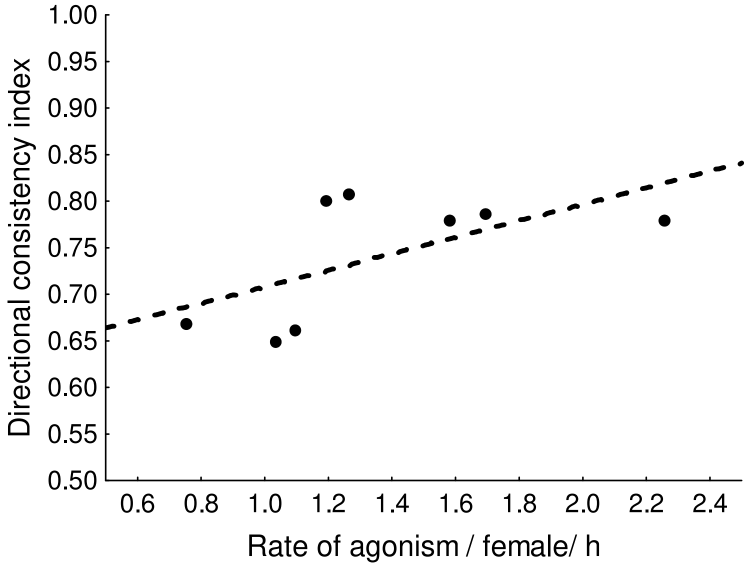


Figure 4. Scatterplot showing the relationship between directional consistency index (a measure of despotism) and the rate of agonistic interactions. Each data point corresponds to a clan. DCI was measured from dyads with two or more interactions. The rate of agonism was calculated from focal sampling.

Feeding sites

We sampled grass biomass from 176 individual feeding sites, representing 71 females from 10 different clans, although the number of feeding sites sampled varied across clans. These individual feeding sites were from 63 group feeding areas. Data on average available grass abundance and variability from the nearest plot-clusters were available for 59 of these group feeding areas (the others were >100 m away from the plot-clusters). We were able to sample control sites for 152 individual feeding sites from 56 group feeding areas.

3) Are the feeding areas/sites selected by elephants at the level of groups or individual females better than control sites?

Feeding areas selected by groups

Although there was a trend of average grass biomass at the selected group feeding areas (mean=733.811 g/m^2, 1.96 SE=54.630, N=63 group feeding areas) being higher than in the control plot-clusters (mean=687.207 g/m^2, 1.96 SE=51.748) (Figure 5), this difference was not statistically significant (Table 3). Average grass cover in the group feeding areas (mean=94.48%, 1.96 SE=1.401, N=63 group feeding areas) was higher than the average cover in the control plot-clusters (mean=91.31%, 1.96 SE=2.256) but the R^2 from the fixed effect was very low (Figure 5, Supplementary Material 2). Similarly, the average grass height was also higher at the selected group feeding areas (mean=5.80 cm, 1.96 SE=0.662, N=63 group feeding areas) than the control plot-clusters (mean=5.04 cm, 1.96 SE=0.470) but the R^2 from the fixed-effect was very low (Figure 5, Supplementary Material 2).

The mixed-effects model of relative margin of selection (biomass) at group feeding areas showed a strong negative relationship of the relative margin of selection with average grass biomass at control plot-clusters (Figure 6, results from mixed-effects model in Supplementary Material 3). Negative relationships between relative margins of selection at group feeding sites and average grass abundance at control plot-clusters were also obtained based on grass cover and grass height (Figure 6, see Supplementary Material 3). Although CV in biomass and cover were positively related to the respective relative margins of selection in simple correlation tests, CV in biomass was not included the top three models (Figure 6, Supplementary Material 3).

Table 3. Results from linear mixed-effects model for a) comparison of average grass biomass (dependent variable) at selected group feeding areas and their control plot-clusters. Selected/control was a fixed effect and clan identity was a random effect. Significant *P* values are marked in bold. In mixed-effects models, R^2 (marginal) includes only the fixed effects, while R^2 (conditional) also includes the variance explained by random effects.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
Fixed	Intercept	698.25	37.650	624.456	772.044	18.546	**<0.001**
Fixed	Selected/Control: Selected	50.02	32.000	-12.7	112.74	1.563	0.123
Random variation							
Random effect (intercept)	Clan identity (*N*=10): variance = 5313						
Random effect (intercept)	Group feeding area no. (*N*=63): variance = 10512						
Residuals	Residual variance (*N*=122) = 30897						
	R^2(m), R^2(c)	0.013, 0.348					

Group feeding area vs control plot-cluster

Individual feeding site vs control site

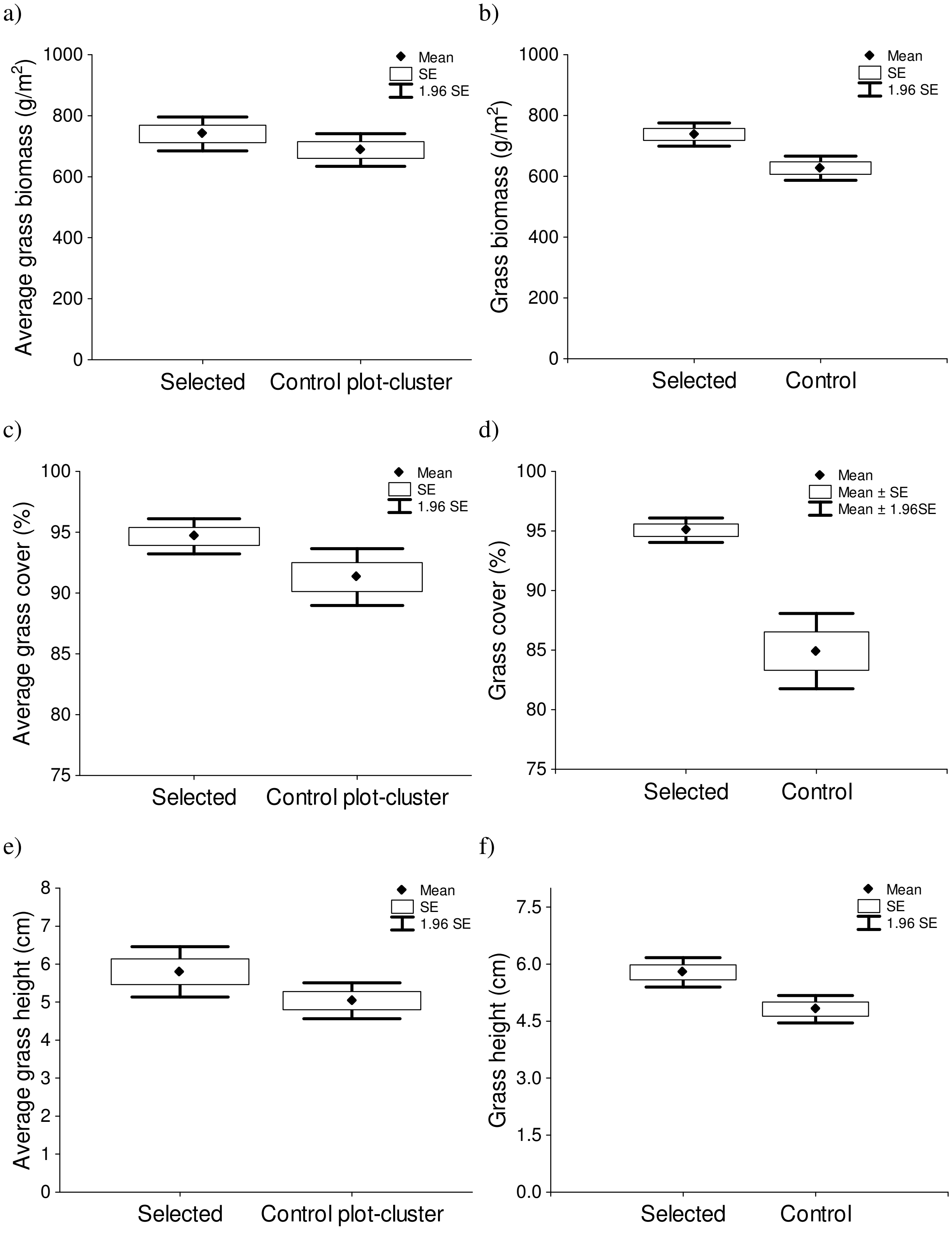
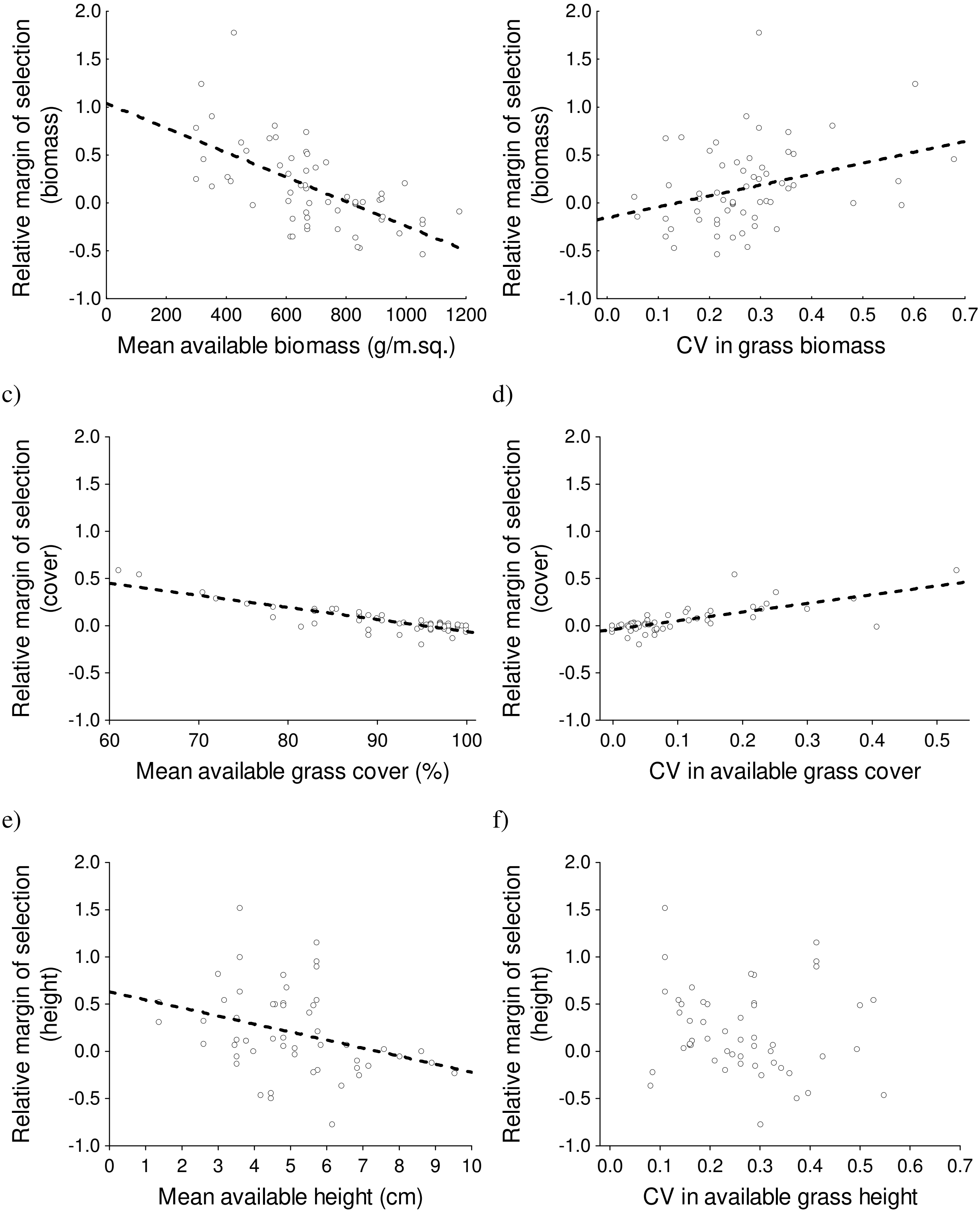


Figure 5. Plots of mean, standard error, and 95% confidence intervals of a) average grass biomass, c) average grass cover, and e) average grass height at group foraging areas (selected) and control plot-clusters, and b) grass biomass, d) grass cover, and f) grass height at individual feeding sites (selected) and nearby control sites.

Relative margin of selection vs average available grass abundance at control plot-clusters

Relative margin of selection vs CV in available grass abundance at control plot-cluster



a)

b)

c)

d)

e)

f)

Figure 6. Scatter-plots of the relationship between the relative margins of selection

(difference between average grass abundance at group feeding area and average available grass abundance at control plot-cluster) and a) average available grass biomass, b) CV of available grass biomass, c) average available grass cover, d) CV of available grass cover, e) average available grass height, and f) CV of available grass height. The average available grass abundance and CV in grass abundance were calculated for the nearest plot-cluster from five quadrats. Scatter-plots are for simple correlations and trend-lines are shown if simple correlation tests were significant.

Feeding sites selected by individuals

Grass biomass at the feeding sites selected by individual females (mean=731.658 g/m^2, 1.96 SE=38.252, *N*=152 individual feeding sites) was significantly higher than that at the nearby control sites (mean=626.882 g/m^2, 1.96 SE=39.841) (Table 4, Figure 5), but the R^2 value based on the fixed effect was very small and there were large contributions of random effects. Similarly, we also found significantly greater grass cover at feeding sites (mean=95.04%, 1.96 SE=1.039, *N*=152 individual feeding sites) than the control sites (mean=84.91%, 1.96 SE=3.182, *N*=152 control sites, Figure 5, see Supplementary Material 4) and grass height at the feeding sites (mean=5.77 cm, 1.96 SE=0.373, *N*=140 individual feeding sites) than at nearby control sites (mean=4.81 cm, 1.96 SE=0.349) but their effect sizes were very low (Figure 5, see Supplementary Material 4).

Table 4. Results from a linear mixed-effects model of grass biomass (dependent variable) at individual feeding sites and control sites. Selected/control was the fixed effect and clan identity, individual identity, and group feeding area identity were the random effects. Significant P values are marked in bold. In mixed-effects models, R^2 (marginal) includes only the fixed effects, while R^2 (conditional) also includes the variance explained by random effects.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		t	P
a)							
Fixed	Intercept	653.799	42.199	571.089	736.509	15.493	**<0.001**
Fixed	Selected/Control: Selected	104.776	17.525	70.427	139.125	5.979	**<0.001**
Random variation							
Random effect (intercept)	Individual identity (N=71): variance = 3226						
Random effect (intercept)	Clan identity (N=10): variance = 7756						
Random effect (intercept)	Group feeding site no. (N=56): variance = 29114						
Residuals	Residual variance (N=304) = 23314						
	R^2(m), R^2(c)	0.042, 0.647					

4) Can dominance ranks of individuals within groups explain the differences in food abundance at their respective feeding sites?

The mixed-effects model did not show a significant effect of dominance score of the individual (z-transformed MDS) on the abundance of grass (z-transformed grass biomass) at its feeding site (Table 5). Similar results were also obtained based on grass cover and grass height at the feeding sites (Supplementary Material 5). Scatter-plots of dominance scores and grass abundance at feedings sites of individuals are shown in Supplementary Material 6, and do not suggest any effect of other dominance scores (PCW and DS) either. Supplementary Material 7 provides separate tables for each clan, showing the results from simple correlation tests between dominance scores and grass abundance at individual feedings sites.

Table 5. Results from the mixed-effects model testing the effect of dominance score of the individual (*z*-transformed MDS, fixed effect) and individual identity (random effect) on the grass abundance at its feeding site (*z*-transformed grass biomass, dependent variable). The results are from the feedings sites of individuals from 5 clans on which data were available on at least 10 individual feeding sites.

Fixed/ Random	Effect	Estimate	S.E. of estimate	Mean - 1.96SE	Mean +1.96SE	*t*	*P*
Fixed	Intercept (fixed)	-0.011	0.078	-0.163	0.141	-0.144	0.886
Fixed	*z*-transformed MDS (fixed)	0.011	0.094	-0.173	0.195	0.117	0.908
Random effects							
Random	Individual identity: variance=0.012 Residuals: variance=0.689 R^2 *(m)*= 0.000, R^2 *(c)*= 0.018						

Discussion

In this quantitative assessment of the socioecological model in female Asian elephant societies, we set out to characterise the dominance structure, and to quantify its proximate foraging consequences by sampling feeding sites used by adult females. Analysis of dominance outcomes showed an advantage of age, which positively explained dominance scores of females. Initiators were older than recipients and were more likely to win, and winners were older than losers. However, linearity in dominance hierarchies was low and non-significant for all clans, and directional consistency was low compared to African savannah elephants as well as many primate species known to have resolved hierarchies (discussed below). Clans with higher rates of agonism seemed to have more consistent dominance relationships. In keeping with the expectation for a society showing unresolved and inconsistent dominance relationships, we found weak or no support for dominant individuals occupying better feeding sites than less dominant individuals. While the findings in this study largely conform to classical predictions of the socioecological model, on which studies on non primate-species have been rare (Clutton-Brock and Janson 2012, see also Silk *et al.* 2007), there were also some inconsistencies, and we discuss both below.

Structure of dominance relationships

The effect of age and initiator/recipient category on winning agonistic interactions was consistent with a previous study in the same population (Nandini 2016), in which initiators won most of the interactions, initiators were older than recipients, and winners were usually (78% interactions, 73% in this study) older than losers. We also found that the oldest female in the clan was not necessarily the most dominant, despite dominance scores of individuals being positively related to age, similar to the findings of Nandini (2016). The two non-overlapping studies, thus, demonstrate persistence and replicability of the effect of age and initiator/recipient category in this population. The effect of age on dominance order was also seen in the Uda Walawe Asian elephant population (de Silva *et al.* 2016). African savannah elephants have been observed to show even stronger effects of age on dominance outcomes, with older females within family groups winning 95% and 98% of the interactions in Amboseli and Tarangire National Parks, respectively (Archie *et al.* 2006). Additionally, Wittemyer and Getz (2007) found that the age of the matriarch of family group positively explained the dominance status of matriarchs as well as the individuals within the family groups, the latter suggesting kin-based dominance structure. While findings from our study population show the age-based individualistic nature of within-clan dominance, we do not yet know if there is any nepotistic bias in dominance rankings. Due to their larger group sizes and more stable social structure than Asian elephants, resulting in greater association strengths between associating females (see de Silva and Wittemyer 2012, Nandini *et al.* 2018), African savannah elephants possibly experience a greater number of interactions within family groups, resulting in consistent relationships. Archie *et al.* (2006) suggest that the presence of lethal weaponry (tusks) and large age-based differences in tusk size could be a factor in reducing the overall frequency of aggression. The presence of tusks could thus be an additional factor explaining more consistent dominance in African savannah elephants.

Despite age-based dominance outcomes as described above, and significant unidirectionality in dominance relationships, we did not find a significant linear dominance hierarchy in the majority of clans examined. Low or non-significant linearity has also been previously reported in the Kabini and Uda Walawe (Sri Lanka) populations (Nandini 2016, de Silva *et al.* 2016). It should be noted, however, that linearity indices (Landau's *h* and de Vries' corrected *h*') are highly sensitive to inconsistencies and unknown relationships and tend to undermine dominance relationships in such datasets (Koenig and Borries 2006, Klass and Cords 2011). Further, given the fission-fusion nature of grouping which limits longer observation for certain within-clan dyads and also due to limited number of the dominance interactions observed, many dyads in our datasets for different clans have single interactions, which could have been a random outcome instead of showing the actual direction of dominance between the individuals, and hence could be responsible for non-significance of linearity. Although we found higher Landau's *h* than the random expected value in three clans, their effective community size (number of females for which we had dominance data) was less than six, for which linearity cannot be assessed properly (Appleby 1983, see Koenig and Borries 2006). However, given that there is significant unidirectionality in dominance relationships, there is a possibility of the larger clans showing significant linearity if more dominance interactions are recorded in the future.

In contrast to linearity indices, the directional consistency index (DCI) is not sensitive to unknown relationships, intransitivity or group size (Koenig and Borries 2006), and has been thought of as a more promising index to compare dominance structure (Koenig *et al.* 2013) across field datasets where sparse dominance matrices are common. Directional consistency in our study population was overall low compared to the 0.95 cut-off used in some studies of primates (for example, Wikberg *et al.* 2013, Michel *et al.* 2016) to qualify strong dominance structure, although others have stressed that dominance expression should be seen as having a continuous rather than discrete nature (*sensu* Isbell and Young 2002, Clutton-Brock and Janson 2012). The average DCI (DCI=0.74) observed in our study population was lower than those of many primates (for example, 0.93 in Hanuman langurs- Koenig 2000, 0.99 in blue monkeys- Cords 2002, >0.90 in black and white colobus- Wikberg *et al.* 2013, see also Koenig *et al.* 2013) that showed significant linear dominance hierarchies. However, in a few other primates that showed significantly linearity, the DCI was similar to our estimates (for example, 0.76 in Phayre's leaf monkey- Koenig *et al.* 2004, 0.75 in the black and white colobus- Koenig *et al.* 2013 based on Korstjens *et al.* 2002). The DCI of focal clans in the Kabini population was lower than those in the family groups (Archie *et al.* 2006) observed in the African savannah elephant populations in Amboseli (DCI=0.90) and Tarangire (DCI=0.97) and across matriarchs of different family groups of higher-order communities in Samburu (DCI=0.88) (Figure 7). There are no DCI values available for entire clans in the African savannah elephant. These observations of greater consistency in dominance in African savannah elephants than in Asian elephants conform to similar inferences made using linearity and transitivity which was greater in the African savannah elephants of Samburu than in Asian elephants of Uda Walawe, Sri Lanka (de Silva *et al.* 2017). Thus, based on DCI values and tests of linearity, on a continuum of dominance expression, the Kabini Asian elephant population would seem to fall towards the side of weaker expression of dominance than the African savannah elephants of Amboseli, Tarangire, and Samburu.

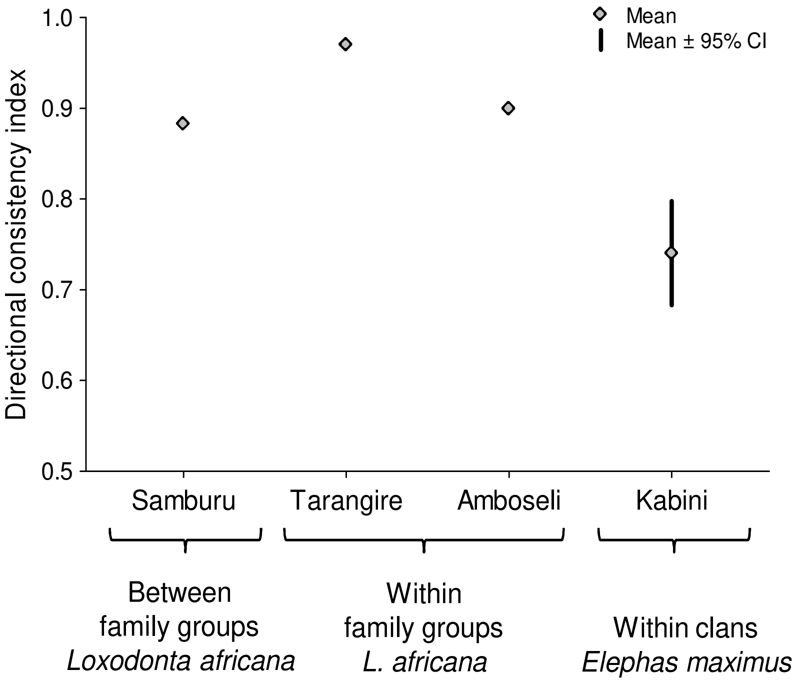


Figure 7. Comparison of average directional consistency index of dominance within clans in the Kabini Asian elephant population with those of African savannah elephant populations in Samburu (dominance between family groups, Wittemyer and Getz 2007) and in Tarangire and Amboseli (dominance within family groups, from Archie *et al.* 2006). The vertical spread around average DCI for Kabini population is the 95% confidence interval obtained from eight clans.

Dominance structure and its relationship with the rate of agonism

Although the socioecological model was developed to primarily explain inter-specific variations in social relationships (Wrangham 1980, Isbell 1991, for example, Pruetz and Isbell 2000, Wheeler *et al.* 2013, Koenig *et al.* 2013), its interlinked predictions have also been explored within species to understand how similar proximate mechanisms may explain intra-specific variations (for example, van Noordwijk and van Schaik 1987, Koenig 2000, Balasubramaniam *et al.* 2012). Our finding of a positive and moderate effect of clan-level rate of agonism on directional consistency conforms to a core assumption of EMFSR, that frequent within-group agonistic contests result in greater despotism (van Schaik 1989, Koenig *et al.* 2013). However, although the R^2 was 36%, this positive relationship in our data was not statistically significant, perhaps because of the small number of clans (N=8) for which had sufficient data. Paucity of data occurred either due to infrequent agonism in some clans (preventing the calculation of DCI because of unavailability of dyads with multiple interactions) or infrequent or short visitations to the study area by other clans (thus limiting observations of dominance). There have been mixed findings regarding the relationship between the rate of agonism and directional consistency in primates. Discussing conditions for the expression of dominance across primate species, the compilation of agonism and DCI data on primates by Wikberg *et al.* (2013) suggested that the rate of agonism was positively associated with despotism (DCI). Koenig *et al.* (2013) comprehensively assessed this assumption within and across phylogenetic groups of primates and found that while agonism was not significantly related to despotism (DCI) when considering all taxonomic groups, there was a positive relationship that interacted with phylogeny (the relationship was steeper within the Cercopithecine clade than in non-Cercopithecines).

Simultaneous data on the rate of agonism per female from focal samples and DCI are not available from any other elephant species/populations to our knowledge. However, some preliminary comparisons can be made between our study population and the Uda Walawe population. The number of agonistic interactions reported by de Silva *et al.* (2017) in their long sampling hours (1923 focal hours) was very small (75 interactions, majority between social classes, the equivalent of clans). In contrast, two independent assessments of agonism in our study population (Nandini 2016, Gautam and Vidya 2019) have reported a far greater number of agonistic interactions from fewer focal hours, which translates to higher frequencies of within-clan agonism per adult female. Curious as these inter-populational differences are, considering that the reservoir-affected habitats of Uda Walawe and Kabini seem to be similar, they are unlikely due to the omission of subordinate behaviours, which all three studies have included. While measures of DCI are not available for the Uda Walawe population, high reversal and low transitivity (de Silva *et al.* 2017) suggest that the observed dominance relationships are qualitatively not very different from those in our study population. The similarity in the dominance expression being weak despite differences in agonistic rates within the same species would seem puzzling in the context of the classical prediction of EMFSR that more frequent agonism shapes despotic societies. One possible testable hypothesis is that there may be greater overall abundance of food resources in Uda Walawe, giving rise to lower rates of agonism than in Kabini.

The conserved expression of dominance despite differences in within-group competition might be explained by some game theoretical models, as postulated by Koenig and Borries (2009) in their fusion of game theory with classical socioecological theory. The anthropogenic creation of the dam and reservoir on the river Kabini has resulted in a peculiar distribution of resources, which are abundant in the grassland habitat and limited in the vast forest habitat surrounding it during the dry season, resulting in an unusually high density of elephants in the grassland and increasing feeding competition (Gautam and Vidya 2019). Our data on high elephant density, frequent agonistic contests, low despotism, as well as absence of a strong rank-related skew in access to foraging sites (see below), point to the possible operation of the Red Queen effect type of feeding competition in this small grassland with high resource-incentive during the lean season- "*it takes all the feeding over food you can do just to gain the same as everyone else*" (Koenig and Borries 2009). Koenig and Borries (2009) postulated that this effect operates under rare situations. Abrupt anthropogenic creations (see also Sterck *et al.* 1997 for effects of habitat saturation on social structure) of unusual feeding competition regime as seen in our study area (where these conditions are also not perennial) could well fulfill such narrow conditions, although frequent agonism could most likely not be an adaptive but a plastic response to novel conditions.

To extend the above model to other elephant populations/species, a rough placement of the studied African and Asian elephant populations along the agonism x despotism matrix is shown in Table 6. Asian elephant societies may be expected to be qualitatively egalitarian (rare agonism and egalitarianism, de Silva *et al.* 2016, top-left panel) considering the absence of large cooperative predators (like lions in African savannahs), their grass-dominated generalist diet and abundant resources in the more mesic conditions (*sensu* de Silva *et al.* 2017, but see Gautam and Vidya 2019 for the current study's habitat), and fission-fusion sociality. Weak expression of dominance in an anthropogenically created novel habitat with high competition, like in Kabini, can be explained by the Red Queen effect type of feeding competition and phylogenetic constraints in a species where reversals may be common (bottom-left). In contrast, while the food is thought to be abundant and widely distributed for African savannah elephants (Archie *et al.* 2006), their dry savannah habitats may have temporally less predictability and there are contestable point resources like waterholes and fruit trees, in addition to risks from large cooperative predators which require formation of larger groups for cooperatively defense (Wittemyer and Getz 2007, de Silva *et al.* 2017). The latter conditions are known to facilitate the formation of large groups and, hence, also result in stronger within-group competition (van Schaik *et al.* 1983, van Schaik 1989, Wrangham *et al.* 1993, see also Smith *et al.* 2008). Further, in species with explicit weaponry, dominance relationships could serve to reduce escalated agonism in order to minimise high risks of potentially lethal injuries to contestants (Smith and Parker 1976). Archie *et al.* (2006) presented these arguments to explain why African savannah elephants, in which most females have long tusks and the differences in the tusk size can be large between old and young females (unlike in Asian elephants that lack tusks and may have tiny tushes), show highly consistent age/size-based dominance relationships (top-right panel, see also Wittemyer and Getz 2007). The effect of weaponry on agonism-despotism relationship in African elephants as a testable hypothesis can be explored in the future as recent, intensive, human-induced poaching for tusks has, unfortunately, created some populations where tuskedness is becoming rare. While not much is known about dominance structure in African forest elephants, their highly fluid associations and small group size (Fishlock *et al.* 2008, Turkalo *et al.* 2013) which, along with a very generalist diet in a wet tropical forest habitat (Blake 2002), is likely to result in low contest competition in tropical rainforest habitats. However, resource-rich patches such as forest clearings could create competition regimes similar to that in Kabini (see Turkalo 1995), apart from possible contests for fruiting trees (Blake 2002) in African forest elephants. Apart from competition-asssociated costs, ecology-based differences in the benefits of sociality (such as cooperative care and defense of claves, and the role of social play for young ones) may also lead to differences in sociality. In the absence of quantitative studies, this proposed explanation of elephant sociality remains speculative, and we call for more field studies and sharing of quantifiable aspects of resource distribution, contest competition, and despotism within and across the extant elephant species. Moreover, collaborative studies that minimise methodological differences can further help in a more comprehensive explanation of the social diversity seen in the Proboscideans.

Table 6. Placement of studied elephant populations along the axes of frequency of agonism and level of despotism, based on our data and from discussion in published studies on dominance. The placement is categorical here due to the paucity of quantitative measures of agonism and despotism from the same populations. This table was adapted from Koenig and Borries (2009) where variables in bold are sourced from game theory explanations. More speculative placements are followed by question marks. The placements are based on Archie *et al.* (2006) for the Amboseli and Tarangire populations and Wittemyer and Getz (2007) for the Samburu population of African savannah elephants, Turkalo (1995) for the Dzanga Bai forest clearing population of African forest elephants, and de Silva *et al.* (2017) for the Uda Walawe and Nandini (2016), Gautam and Vidya (2019), and this study for the Kabini population of Asian elephants.

	Low despotism	High despotism
Rare agonism	Classic socioecological model for fission-fusion societies with solitary predators, low quality diet and dispersed food - Asian elephants (e.g. Uda Walawe) - African forest elephants**?**	Socioecological theory (high predation and unpredictable resources) **+ effect of weaponry (tusks) and avoidance** - African savannah elephants (e.g. Amboseli, Tarangire)
Frequent agonism	Phylogenetic constraints (high retaliations due to weak hierarchy) + within-group contest and/or **Red Queen effect (high feeding competition in the lean season)** - Asian elephants (e.g. Kabini) - African forest elephants in forest clearings**?**	Classic socioecological model (high predation and unpredictable resources) - African savannah elephant populations with tuskless females**?**

Selection of feeding sites and the effect of dominance rank relationships

Our analyses of the feeding areas/sites selected by groups and individuals show that elephants exert some feeding selection even in this grassland habitat in which food seems to be continuously spread visually and is more abundant than in the adjacent forests of

Nagarahole and Bandipur (Gautam and Vidya 2019). Group feeding areas were found to have slightly greater grass abundance than the available grass abundance at the nearest plot-cluster. Feeding selection was stronger in areas where grass abundance was low, thus demonstrating that groups have to actively seek better foraging sites in low abundance areas. These results are in agreement with our previous study showing that grass is heterogeneously distributed at different scales within this grassland and that groups compete for longer duration when local grass availability is high (Gautam and Vidya 2019). The need to actively search for better foraging sites in areas with low grass abundance could enhance within-group competition through "pushing forward" effects of group size in such places as expected from the ecological constraints models (van Schaik *et al.* 1983, Wrangham *et al.* 1993, see also Snaith and Chapman 2007). One of our future objectives is to test this by studying how the relationship of group size with feeding rate or food searching effort varies with food availability.

A commonly observed drawback of most field-based tests of the socioecological model has been the lack of demonstration of association between dominance rank relationships resulting from contest competition and its foraging, energetic, or reproductive consequences (Isbell and Young 2002, Koenig 2002, Koenig and Borries 2009, Clutton-Brock and Janson 2012). We explored this here, albeit in a limited way and at a very proximate level, and studied the relationship between within-clan dominance status and grass abundance at feeding sites of different individuals. Analyses of foraging consequences of dominance rank relationships in five different clans showed no significant correlation between dominance scores and food abundance at feeding sites in any clan. One reason for the weak relationship between dominance and feeding success could be the small number of group feeding areas sampled for each clan (maximum number of group feeding areas was 13, for Patricia's clan). Further, the feeding sites that we sampled are only snap-shots of foraging by group members and, thus, represent feeding site occupancy for a very brief period of their foraging time. Therefore, our results might be influenced by random effects. In the future, we plan to examine food site residence time, which might be a better estimate of proximal benefits of dominance status (Chancellor and Isbell 2009, Grueter *et al.* 2016), foraging effort (in searching for feeding sites, Wright *et al.* 2014), and feeding rates calculated from longer durations of feeding (for example, Janson 1985, Wright *et al.* 2014). Another limitation of our feeding site data is that the quadrats placed next to the feeding sites do not exactly represent feeding sites and are approximations because food has already been consumed from the exact site. Therefore, once the group moves away from the site, only the site adjacent to that from which food has been consumed can be sampled. This limitation is unavoidable in such plot-sampling methods. Even though the sampled feeding sites had slightly greater grass abundance than the control sites (3 m away from the feeding sites), the sampled feeding sites may be underestimates of the actually used sites. This limitation of plot sampling may be avoided by behaviourally measured indicators of foraging success such as feeding rates and food site residence time (see above).

While keeping in mind the limitations acknowledged above, the finding that dominance rank relationships among female elephant clan members do not confer clear benefits of access to better feeding sites is consistent with socioecological theory which predicts flatter rank-related skew in energetic/reproductive benefits in egalitarian or weak dominance hierarchies (Janson and van Schaik 1988, Koenig 2002, Isbell and Young 2002). Studies on other species have found support for this prediction, with energetic and reproductive advantages to dominant individuals being observed in multiple species wherein dominance hierarchies are linear and dominance is strongly expressed (for example, Whitten 1983, Janson 1985, van Noordwijk and van Schaik 1987, Robbins *et al.* 2007, but see Roberts and Cords 2013), and species with unresolved or weak dominance hierarchies showing weak or non-significant advantages of dominance (Robbins *et al.* 2007, Grueter *et al.* 2016). More intensive data on foraging efficiency (feeding benefits and movement costs) in the future would help in better assessment of the consequences of dominance relationships in elephants, which could have energetic (Janson 1985, Vogel 2005), physiological (Grueter *et al.* 2018), physical (Koenig *et al.* 2000), or reproductive (van Noordwijk and van Schaik 1987) consequences for dominant and subordinate individuals in a fission-fusion society. It would also be interesting to examine the prediction of rank-related skew and energetic/reproductive benefits in the four quadrants of the agonism-despotism axes (Table 9) to better understand the socioecology of elephants.

Conclusion

In conclusion, our study demonstrates that dominance relationships in female Asian elephants are inconsistent, which seems to be related to rates of agonism, and translate into largely egalitarian patterns of occupancy of better feeding sites. While older individuals tend to be more dominant than subordinates, the effect of age relative to nepotistic bias remains to be examined. More field studies on different elephant populations and species are needed to examine the ultimate consequences of dominance relationships, such as foraging, energetic, and reproductive benefits, which can also help in understanding the sources of variation in sociality in elephants.

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Supplementary Material

Supplementary Material 1. An overview of different group-level dominance indices and individual-level dominance scores used in this chapter, and results from regressions of dominance scores on age.

We provide, here, an overview of different group-level dominance indices and individual-level dominance scores

Landau's dominance index (h)

Landau's *h* index (Landau 1951) is a measure of the strength of a dominance hierarchy and was developed to measure the extent to which the contestants are placed linearly in a dominance hierarchy. In a strongly linear dominance hierarchy, dominance relationships are mostly transitive (i.e., if A dominates B and B dominates C, then A also dominates C) whereas weaker linear dominance hierarchies contain more circular (A dominates B, B dominates C, but C dominates A, hence circular) relationships. Calculations for Landau's *h* are briefly described below with the example of Mridula's clan (see Table 1 below). In this table, the cell entries represent the number of times the row individual won over the column individuals. *N* is the group size in the matrix. Highlighted cells represent dyads for which dominance interactions were not observed.

Supplementary Material 1, Table 1. Data on dominance interactions from Mridula's clan. The cell entries represent the number of times the row individual won over the column individuals. *N* is the group size in the matrix. Highlighted cells represent dyads for which dominance interactions were not observed.

N=6	Midhuna	Mihika	Mihira	Mili	Mitali	Mridula_2003_F
Midhuna	X	1	1	2	0	1
Mihika	0	X	0	0	0	0
Mihira	3	1	X	0	1	1
Mili	0	0	1	X	0	3
Mitali	0	0	2	2	X	2
Mridula_2003_F	0	0	0	0	0	X

Based on the data in Table 1, another table is constructed in which cell entries for each dyad contain 1 if an individual won more interactions in the dyad and 0 if it won fewer interactions (see Table 2 below). In case a dyad had no observed interaction (the highlighted cells in Table 1), 0.5 is entered in both cells of that dyad. Landau's *h* is calculated as

$$\left[\frac{12}{N^3 - N}\right] \times \sum_{i=1}^{N} \left[V_i - \frac{N-1}{2}\right]^2$$

where N is the group size and V_i is the sum of cell values in the row for individual *i*. The first term within the brackets is constant and sets the range of *h* from 0 to 1, where 0 corresponds to absolute egalitarianism and 1 corresponds to a completely linear dominance hierarchy.

Supplementary Material 1, Table 2. Table to calculate Landau's *h*.

N=6	Midhuna	Mihika	Mihira	Mili	Mitali	Mridula_ 2003_F	V_i	(*N*-1)/2	[V_i - ((*N*-1)/ 2)] ^2
Midhuna	X	1	0	1	0.5	1	3.5	2.5	1
Mihika	0	X	0	0.5	0.5	0.5	1.5	2.5	1
Mihira	1	1	X	0	0	1	3	2.5	0.25
Mili	0	0.5	1	X	0	1	2.5	2.5	0
Mitali	0.5	0.5	1	1	X	1	4	2.5	2.25
Mridula_20	0	0.5	0	0	0	X	0.5	2.5	4
							15		Sum = 8.5
								h	**0.486**

de Vries (1995) proposed a method to check the significance of this linearity index by randomly assigning 1 and 0 to individuals within each dyad and calculating *h* for each randomization, and then calculating the one-tailed null probability by calculating the number of times the randomized *h* exceeded observed *h*. Further, for matrices with unknown relationships (usually the case with most field data), de Vries (1995) proposed an unbiased estimate of *h* (*h*'). For this, we first calculate h_0, which is obtained by randomly assigning 1 and 0 to the number of wins by individuals within unknown dyads and then calculating Landau's *h* (see above formula). Such randomization is performed several times (1000 in SOCPROG) and an unbiased estimate of *h* (*h'*) is obtained after averaging these values.

Directional consistency

Directional consistency index (DCI) was proposed first by van Hooff and Wensing (1987). It captures whether there is directionality or equality in the outcomes of interactions within dyads. It first calculates directional consistency (DC) within each dyad, using the formula DC=(H-L)/(H+L), where H is the number of wins in the higher frequency direction and L is the number of wins in the lower frequency direction for each dyad. An average of DCs from all the dyads is then calculated and used as DCI for the group, indicating how consistent the dominance relationships within dyads of the group. Like many other dominance indices, DCI too may be biased if there are many dyads with single interactions because, in such dyads, even a random outcome could bias DC. In our calculations, we avoided this in a limited way by excluding such single-interaction dyads.

Individual dominance scores

We report three dominance scores for individuals in this chapter.

Proportion of contests won (*PCW*) is simply the number of contests won by an individual divided by the number of contests it engaged in. However PCW could be unrepresentative of the actual dominance status of an individual if it defeats weaker individuals and avoids and does not interact with other individuals.

David's score (*DS*) takes care of this and takes into account the relative dominance status of the individuals against whom it won. The first step in the calculation of *DS* is to convert the number of wins for each individual into proportions (*Pij*) within each dyad of the dominance matrix. After this, *DS* is calculated as $DS = w + w_2 - l - l_2$, where w is the sum of P_{ij} (wins as proportions in each dyad) for each individual and l is the sum of P_{ji} (losses as proportions in each dyad), whereas w_2 is the sum of weighted (by P_{ij}) w values of the individuals defeated by i, and l_2 is the sum of weighted (by P_{ji}) l values of the individuals to whom i lost.

de Vries *et al.* (2006) developed another David's score based on D_{ij} (see below) as they pointed limitations with David's score if some dyads represented only few interactions or if some dyads had no interactions. They said that the relative dominance score for individuals of dyad *ij* with more (say n_{ij}=6) interactions were more reliable than another dyad *ik* with fewer (say n_{ik}=1) interactions when compared to the dominance scores if the outcomes were random i.e. each individual had an equal probability of winning. To overcome this problem, they proposed the use of D_{ij} instead of P_{ij}, where $D_{ij}= (a_{ij} + 0.5) / (n_{ij} +1)$. This overcomes the issue of unknown relationships (no interactions) since if n_{ij} is 0, then D_{ij} becomes 0. The corrected or *modified David's score* (*MDS*) is calculated after using *w* and *l* calculated from D_{ij} values instead of P_{ij} values in the case of DS mentioned above.

It should be noted, however, that most of the methods assume that the number of interactions observed per group as well as per dyad should be high so that the dominance observed is distinct from random outcomes. However, unlike observations on captive groups, observations on free-ranging groups may not yield sufficient interactions per dyad. This limitation may further be enhanced in fission-fusion societies like elephants, in which even if a clan is observed for many hours, one may not observe certain dyads long enough to obtain data on dominance. This can affect the reliability of the above mentioned dominance indices.

The results from regressions of dominance scores on age are shown below (Table 3).

Supplementary Material 1, Table 3. Results from simple regressions testing the relationship between age and dominance scores (PCW: proportion of contests won, *DS*: David's score, and *MDS*: modified David's score) of individuals in four different clans. *R* and R^2 are highlighted in bold if they were significant at $P<0.05$.

Clan name (no. of females)	Dominance score	$F_{\mathrm{df1,\,df2}}$ statistic	Pearson's *R*, Multiple R^2	*P*
Lisa (12)	*PCW*	$F_{1,10}=0.118$	0.108, 0.012	0.738
	DS	$F_{1,10}=0.829$	0.277, 0.077	0.384
	MDS	$F_{1,10}=1.117$	0.317, 0.101	0.315
Nakshatra (12)	*PCW*	$F_{1,10}=25.989$	**0.850, 0.694**	**<0.001**
	DS	$F_{1,10}=24.699$	**0.844, 0.683**	**<0.001**
	MDS	$F_{1,10}=24.563$	**0.843, 0.682**	**<0.001**

Clan name (no. of females)	Dominance score	$F_{\mathrm{df1,\,df2}}$ statistic	Pearson's *R*, Multiple R^2	*P*
Patricia (17)	*PCW*	$F_{1,\,15}=5.657$	**0.523, 0.274**	**0.031**
	DS	$F_{1,\,15}=14.005$	**0.695, 0.483**	**0.002**
	MDS	$F_{1,\,15}=17.667$	**0.735, 0.541**	**<0.001**
Victoria (29)	*PCW*	$F_{1,\,27}=13.258$	**0.574, 0.329**	**0.001**
	DS	$F_{1,\,27}=19.575$	**0.648, 0.420**	**<0.001**
	MDS	$F_{1,\,27}=21.274$	**0.664, 0.441**	**<0.001**

Supplementary Material 2. Linear mixed-effects models of average grass abundance at selected group feeding areas and control plot-clusters.

In the main text, the results from a linear mixed-effects model of average grass abundance at selected group feeding areas and control plot-clusters had been shown based on grass biomass. Here, in Table 1 below, results based on average grass cover and average grass height as the measures of grass abundance are shown.

Supplementary Material 2, Table 1. Results from linear mixed-effects models of average grass abundance (dependent variable) at selected group feeding areas and control plot-clusters for a) average grass cover and b) average grass height. Selected/control was a fixed effect and clan identity was a random effect. Significant *P* values are marked in bold. In mixed-effects models, R^2 (marginal) includes only the fixed effects, while R^2 (conditional) also includes the variance explained by random effects.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
a)							
Fixed	Intercept	91.528	1.257	89.064	93.992	72.793	**<0.001**
Fixed	Selected/Control-Selected	3.209	1.259	0.741	5.677	2.549	**0.013**
Random variation							
Random effect (intercept)	Clan identity (*N*=10): variance = 4.916						
Random effect (intercept)	Group feeding area no. (*N*=63): variance = 5.193						
Residuals	Residual variance (*N*=122) = 48.084						
	R^2(m), R^2(c)	0.043, 0.209					

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
b)							
Fixed	Intercept	5.371	0.424	4.541	6.201	12.68	**<0.001**
Fixed	Selected/Control-Selected	0.681	0.298	0.097	1.265	2.286	**0.026**
Random variation							
Random effect (intercept)	Clan identity (*N*=10): variance = 0.907						
Random effect (intercept)	Group feeding area no. (*N*=63): variance = 1.246						
Residuals	Residual variance (*N*=116) = 2.479						
	R^2(m), R^2(c)	0.025, 0.478					

Supplementary Material 3. Linear mixed-effects models of the relative margin of selection of grass abundance by groups.

Supplementary Material 3, Table 1. Results from linear mixed-effects models of the relative margin of selection for grass abundance (difference between average grass abundance at selected group feeding area and the average grass abundance at control plot-clusters; dependent variable) by groups. The models are based on a) grass biomass, b) grass cover, and c) grass height. Average grass abundance and CV in grass abundance at the control plot-cluster were fixed effects and clan identity was a random effect. Significant *P* values are marked in bold. In mixed-effects models, R^2 (marginal) includes only the fixed effects, while R^2 (conditional) also includes the variance explained by random effects.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
a)							
Fixed	Intercept	0.961	0.242	0.487	1.434	3.978	**<0.001**
Fixed	Average biomass (control)	-0.001	0.0002	-0.002	-0.001	-5.868	**<0.001**
Fixed	CV in biomass (control)	0.222	0.403	-0.567	1.011	0.551	0.584
Random variation							
Random effect (intercept)	Clan identity (*N*=9): variance = 0.007						
Residuals	Residual variance (*N*=59) = 0.114						
	R^2(m), R^2(c)	0.382, 0.419					
b)							
Fixed	Intercept	1.345	0.206	0.941	1.749	6.529	**<0.001**

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
Fixed	Average cover (control)		-0.014	-0.018	-0.010	-6.682	**<0.001**
Fixed	CV in cover (control)	-0.137	0.174	-0.478	0.203	-0.79	0.433
Random variation							
Random effect (intercept)	Clan identity (*N*=9): variance = 0.001						
Residuals	Residual variance (*N*=59) = 0.004						
	R^2(m), R^2(c)	0.718, 0.759					
c)							
Fixed	Intercept	0.762	0.207	0.355	1.168	3.672	**<0.001**
Fixed	Average height (control)	-0.115	0.038	-0.189	-0.040	-3.017	**0.004**
Fixed	CV in height (control)	0.219	0.553	-0.864	1.303	0.397	0.693
Random variation							
Random effect (intercept)	Clan identity (*N*=8): variance = 0.030						
Residuals	Residual variance (*N*=53) = 0.164						
	R^2(m), R^2(c)	0.158, 0.290					

Supplementary Material 4. Results from linear mixed-effects models for grass abundance at selected individual feeding sites and control sites.

In the main text, the results from a linear mixed-effects model of grass abundance at individual feeding sites and control sites had been shown based on grass biomass. Here, in Table 1 below, results based on average grass cover and average grass height as the measures of grass abundance are shown.

Supplementary Material 4, Table 1. Results from linear mixed-effects models for grass abundance (dependent variable) at feeding sites selected by individuals and control sites, based on a) grass cover and b) grass height. Selected/control was the fixed effect and clan identity, individual identity, and group feeding area identity were the random effects. Significant *P* values are marked in bold. In mixed-effects models, R^2 (marginal) includes only the fixed effects, while R^2 (conditional) also includes the variance explained by random effects.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
a)							
Fixed	Intercept	85.871	1.867	82.212	89.530	46.004	**<0.001**
Fixed	Selected/Control: Selected	10.14	1.504	7.192	13.088	6.743	**<0.001**
Random variation							
Random effect (intercept)	Individual identity (*N*=71): variance = 7.267						
Random effect (intercept)	Clan identity (*N*=10): variance = 11.807						
Random effect (intercept)	Group feeding area no. (*N*=56): variance = 30.707						

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
Residuals	Residual variance (*N*=304) = 171.848						
	R^2(m), R^2(c)	0.104, 0.305					
b)							
Fixed	Intercept	5.237	0.502	4.252	6.221	10.427	**<0.001**
Fixed	Selected/Control: Selected	0.961	0.154	0.660	1.263	6.248	**<0.001**
Random variation							
Random effect (intercept)	Individual identity (*N*=65): variance = 0.144						
Random effect (intercept)	Clan identity (*N*=9): variance = 1.294						
Random effect (intercept)	Group feeding area no. (*N*=51): variance = 3.146						
Residuals	Residual variance (*N*=280) = 1.657						
	R^2(m), R^2(c)	0.036, 0.744					

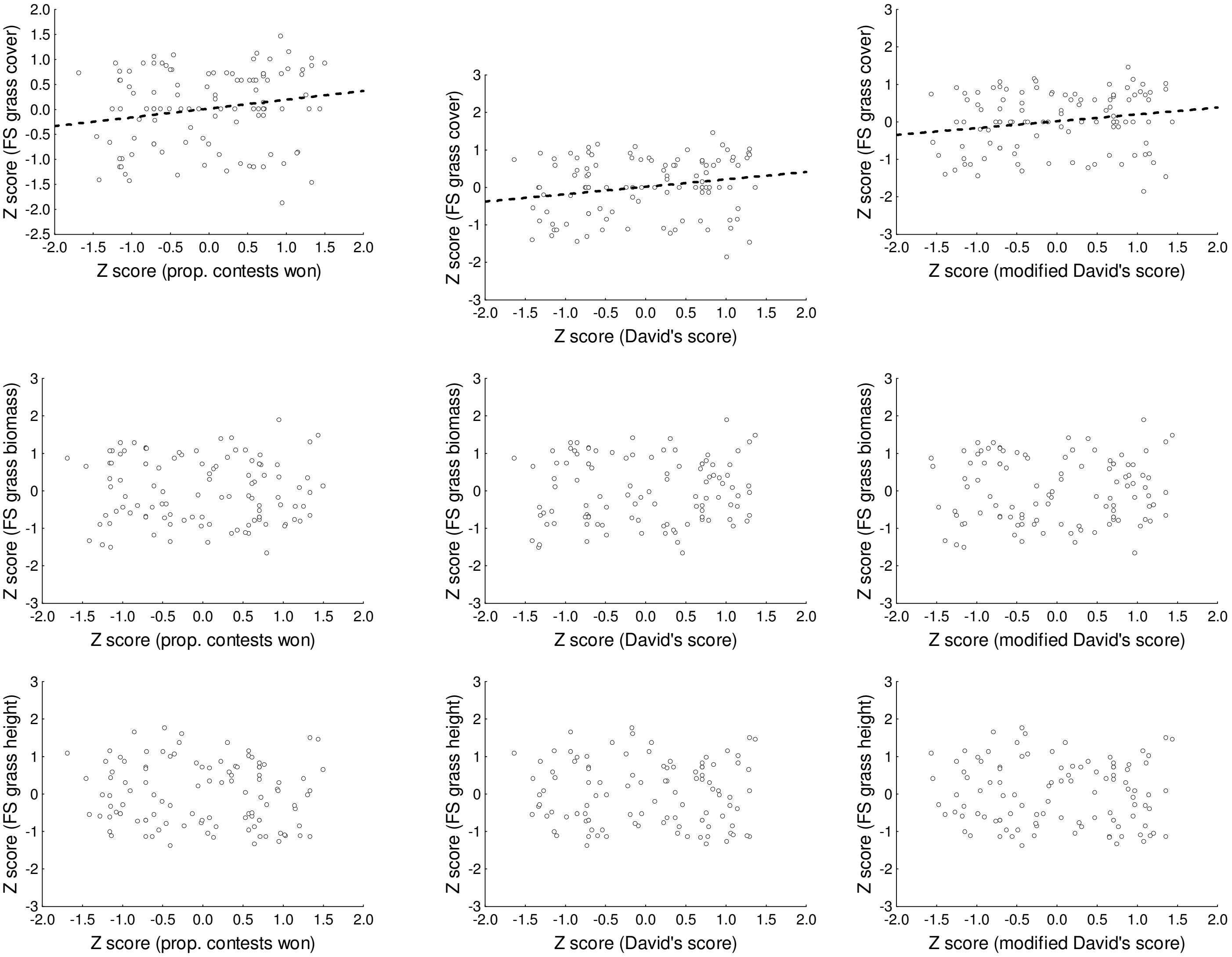
Supplementary Material 5. Fixed-effects models testing the effect of individual dominance score on grass abundance.

Mixed-effects models were used to test the effect of dominance score of the individual (*z*-transformed MDS, fixed effect) and individual identity (random effect) on grass abundance at its feeding site (*z*-transformed, dependent variable) for a) grass cover and b) grass height. However, individual identity did not explain any variation in the mixed models, and therefore, results from the fixed-effects models are shown below (Table 1).

Supplementary Material 5, Table 1. Fixed-effects models to test the effect of dominance score of the individual (*z*-transformed MDS) on grass abundance at its feeding site (*z*-transformed, dependent variable) for a) grass cover and b) grass height. The results are from the feedings sites of individuals from 5 clans on which data were available on at least 10 individual feeding sites. The *F*-test statistics for a) grass cover are: $F_{1,\ 120}$=3.999, *Multiple* R^2=0.032, P=0.048, and for b) grass height are $F_{1,\ 120}$=0.068, *Multiple* R^2=0.001, P=0.795.

Fixed/Random	Effect	Estimate	S.E. of estimate	Mean - 1.96 SE	Mean + 1.96 SE	*t*	*P*
a)							
Fixed	Intercept	0.017	0.067	-0.115	0.149	0.257	0.798
Fixed	*z*-transformed MDS (fixed)	0.163	0.082	0.003	0.324	2.0	0.048
	Multiple R^2 =0.032						
b)							
Fixed	Intercept	0.001	0.076	-0.149	0.151	0.013	0.989
Fixed	*z*-transformed MDS (fixed)	0.024	0.092	-0.157	0.205	0.260	0.795
	Multiple R^2 =0.001						

Supplementary Material 6. Relationship between grass abundance at individual feeding sites and dominance scores of individuals.



a) Proportion of contests won

b) David's score

c) Modified David's score

Supplementary Material 6. Scatter-plots showing the relationship between grass abundance at feeding sites (FS) and different dominance scores of individuals: a) proportion of contests won, b) David's score, and c) modified David's score.

Supplementary Material 7. Relationship between dominance scores and feeding site quality in different clans.

Supplementary Material 7, Table 1. Results of correlation tests to examine the relationship between dominance score and feeding site quality for Patricia's clan. All variables were *z*-transformed to allow inclusion of data from different group feeding areas and groups of different compositions.

Dominance score	Grass cover at feeding site	Grass biomass at feeding site	Grass height at feeding site
PCW	*R*=0.255 *N*=44 *P*=0.095	*R*=0.220 *N*=44 *P*=0.152	*R*=-0.040 *N*=42 *P*=0.803
David's score	*R*=0.272 *N*=44 *P*=0.074	*R*=0.299 *N*=44 *P*=0.049	*R*=-0.027 *N*=42 *P*=0.863
Modified David's score	*R*=0.259 *N*=44 *P*=0.090	*R*=0.268 *N*=44 *P*=0.078	*R*=-0.054 *N*=42 *P*=0.735

Supplementary Material 7, Table 2. Results of correlation tests to examine the relationship between dominance score and feeding site quality for Victoria's clan. All variables were *z*-transformed to allow inclusion of data from different group feeding areas and groups of different compositions.

Dominance score	Grass cover at feeding site	Grass biomass at feeding site	Grass height at feeding site
PCW	*R*=0.055 *N*=33 *P*=0.761	*R*=-0.127 *N*=33 *P*=0.480	*R*=-0.030 *N*=33 *P*=0.870
David's score	*R*=-0.062 *N*=33 *P*=0.730	*R*=-0.040 *N*=33 *P*=0.827	*R*=0.027 *N*=33 *P*=0.882
Modified David's score	*R*=0.065 *N*=33 *P*=0.721	*R*=-0.029 *N*=33 *P*=0.873	*R*=0.023 *N*=33 *P*=0.899

Supplementary Material 7, Table 3. Results of correlation tests to examine the relationship between dominance score and feeding site quality for Lisa's clan. All variables were *z*-transformed to allow inclusion of data from different group feeding areas and groups of different compositions.

Dominance score	Grass cover at feeding site	Grass biomass at feeding site	Grass height at feeding site
PCW	*R*=0.087 *N*=21 *P*=0.708	*R*=-0.194 *N*=21 *P*=0.398	*R*=-0.135 *N*=19 *P*=0.582
David's score	*R*=0.251 *N*=21 *P*=0.272	*R*=-0.124 *N*=21 *P*=0.591	*R*=-0.050 *N*=19 *P*=0.840
Modified David's score	*R*=0.202 *N*=21 *P*=0.379	*R*=-0.214 *N*=21 *P*=0.352	*R*=-0.100 *N*=19 *P*=0.685

Supplementary Material 7, Table 4. Results of correlation tests to examine the relationship between dominance score and feeding site quality for Mridula's clan. All variables were z-transformed to allow inclusion of data from different group feeding areas and groups of different compositions.

Dominance score	Grass cover at feeding site	Grass biomass at feeding site	Grass height at feeding site
PCW	$R=0.321$	$R=-0.118$	$R=0.402$
	$N=12$	$N=12$	$N=12$
	$P=0.308$	$P=0.715$	$P=0.195$
David's score	$R=0.357$	$R=-0.106$	$R=0.425$
	$N=12$	$N=12$	$N=12$
	$P=0.255$	$P=0.742$	$P=0.168$
Modified David's score	$R=0.334$	$R=-0.113$	$R=0.410$
	$N=12$	$N=12$	$N=12$
	$P=0.288$	$P=0.726$	$P=0.185$

Supplementary Material 7, Table 5. Results of correlation tests done to check the relation between dominance score and feeding site quality for Nakshatra's clan. All variables were z-transformed to allow inclusion of data from different group feeding areas and groups of different compositions.

Dominance score	Grass cover at feeding site	Grass biomass at feeding site	Grass height at feeding site
PCW	$R=0.232$	$R=-0.199$	$R=0.006$
	$N=12$	$N=12$	$N=12$
	$P=0.469$	$P=0.536$	$P=0.985$
David's score	$R=0.467$	$R=-0.410$	$R=0.212$
	$N=12$	$N=12$	$N=12$
	$P=0.126$	$P=0.536$	$P=0.507$
Modified David's score	$R=0.451$	$R=-0.335$	$R=0.243$
	$N=12$	$N=12$	$N=12$
	$P=0.141$	$P=0.288$	$P=0.446$

CHAPTER 6

Conclusions

Conclusions

In this thesis, I carried out field-based investigations to assess the reliability of methods of estimating elephant forage abundance, and then investigated the ecological model of female social relationships (EMFSR, Wrangham 1980, Janson and van Schaik 1988, van Schaik 1989, Sterck *et al.* 1997) in female Asian elephants in Nagarahole National Park. Here, I briefly discuss the findings from my thesis and point to some future directions for research on socioecology in elephants.

Visually-estimated cover and remotely-sensed NDVI in assessment of forage abundance for elephants

In the first part of my thesis, I studied methods of rapid assessment of abundance of forage availability for Asian elephants in forest and grassland habitats. I found that visual assessment of cover performed well in estimating graminoid biomass in both forest and grassland habitat but NDVI did not. In forest habitat, where multiple graminoid species existed, the sum of visually estimated covers of different species explained even greater variation in biomass than visually estimated total graminoid cover. This is likely to occur when the within-species leaf overlap is not as high as between-species leaf overlap (when self-shading is avoided), resulting in the sum of species covers incorporating some of the overlap that total cover does not. Thus, although the sum of species covers has been criticised for giving numbers exceeding 100% (Wilson 2011), it performs well empirically. Interestingly, the inclusion of height did not increase the explanatory power substantially beyond what was explained by cover, possibly because we did not encounter habitats with very tall grass in our sampling plots. In the grassland habitat also, total grass cover was useful in predicting grass biomass, but since cover was almost always near saturation levels (~90% or more), height served as useful additional information in predicting grass biomass. Thus, visual assessment can be potentially used by researchers in the future to rapidly and reliably assess forage abundance for elephants and other largely graminivorous animals, but it requires on-site validation.

On the other hand, while satellite-based remote sensing can potentially provide information about habitats at multiple spatial and temporal resolutions, facilitating very intensive coverage of different sites (for example, Young *et al.* 2009, Marshal *et al.* 2010, Rood *et al.* 2010, Tsalyuk *et al.* 2019) with little or no field effort (see Pettorelli *et al.* 2005, 2011), my analyses based on field vegetation surveys and satellite-derived NDVI data showed that NDVI was not useful in mapping the spatial distribution of forage abundance for elephants in tropical forests. The primary reason for this limitation was that canopy cover and abundant non-food vegetation undermined the ability of NDVI to detect relevant food plant abundance variables in the lower vegetation strata, where most large herbivores feed. This problem was further aggravated by high plant diversity in tropical forests, which makes food plant species a small subset of the total species richness in such habitats. Further, graminoids, which form a large part of the elephant diet (Baskaran *et al.* 2010), are present at the ground level and their abundance was negatively related to vegetation variables, primarily shrubs and tree canopy, which contributed to primary productivity measured by NDVI. Since elephants have a higher dietary breadth than other herbivores, this problem is expected to be even worse for other herbivores. Previous assessments of NDVI in other habitats (Borowik *et al.* 2013, Willems *et al.* 2009) had also found similar limitations, but NDVI as a measure of forage availability for large herbivores in a tropical forest had not been examined previously. Therefore, until alternate methods are developed to map forage abundance for herbivores in forest habitats, the use of such remotely sensed indices as indirect measures of forage abundance, as has been done before (for example, Rood *et al.* 2010, Srinivasaiah *et al.* 2012, Lakshminarayanan *et al.* 2015, Pokharel *et al.* 2019), should be avoided, and field sampling should be the preferred method in studies related to the foraging ecology of elephants and other herbivores in habitats with substantial tree canopy. It might be worth exploring three-dimensional mapping technologies such as LiDAR in the future (see Pisek 2018).

Socioecology and female elephant societies: food distribution, within-group and between-group agonism, dominance relationships and their foraging consequences

In the second part of my thesis, I carried out the first empirical investigation of the link between ecological variations and agonistic behaviour within and between groups, and a study of dominance relationships and their foraging consequences in female Asian elephant societies. These chapters shed light on how the socioecological model performs in female Asian elephants in a small resource-rich grassland habitat, furthering the existing understanding of proximate mechanisms shaping social relationships in elephants.

The gross feeding ecology (grass dominated diet, Baskaran *et al.* 2010), abundance of grass and water, and the seemingly continuous rather than discrete nature of grass distribution in the grassland habitat of Kabini were not expected to elicit contest competition, according to general expectations of socioecological models (Wrangham 1980, van Schaik 1989). However, we found frequent agonistic contests at the individual level as well as at clan level, indicating strong feeding competition, as agonism results in the loss of time and feeding opportunities and time (for example, Janson 1985, Vogel 2005). Such strong contest would seem to contradict socioecological theory if viewed based on diet types, presenting a graminivore paradox (see Snaith and Chapman 2007 for a review of the "folivore paradox"). Contest competition has been observed in African savannah elephants also (Archie *et al.* 2006), although about half the contests were over specific high-value point resources and not grass (Wittemyer and Getz 2007). However, the usefulness of diet type in the interpretation of food abundance and distribution has been questioned before (Snaith and Chapman 2007, Koenig *et al.* 2013, Wheeler *et al.* 2013). In my study, the quantification of grass resources showing higher grass abundance in the Kabini grassland than its neighbouring forests explained frequent clan-level agonistic encounters as well as more frequent individual-level agonism during between-clan encounters, in keeping with expectation from socioecological theory. However, even though we found frequent within-clan agonism also, it was not related to local variability in grass abundance, in contradiction to socioecological theory (see below).

I found that within-group contest increased with group size, as expected from simple models of competition (see van Schaik *et al.* 1983, Koenig and Borries 2006, Wheeler *et al.* 2013). This effect of group size may not seem to be in total agreement with functional explanations of fission-fusion that is said to reduce within-group conflict (Aureli *et al.* 2008, see also de Silva *et al.* 2017 for elephants). However, in the light of the strong between-clan contest regime in Kabini, and the advantage of larger group size in between-clan contests (Nandini 2016, Gautam and Vidya 2019), fission-fusion may be balancing the forces of within-group and between-group competition which work in opposite directions to govern group size in this resource-rich small habitat. Between-clan contests demand larger group size and cooperative action to win (Nandini 2016, Gautam and Vidya *unpublished*), but also come with stronger within-clan contest that constrains group size (Gautam and Vidya 2019, see also Sterck *et al.* 1997). A previous study of female associations in this population also found constraints on group size, and suggested that fission-fusion helped in maintaining extended associations within the constraint (Nandini *et al.* 2017). Simultaneous operation of between-group contest, within-group scramble and contest, and fission-fusion processes, in a novel feeding competition regime (strong BGC and strong WGC in the grassland habitat) created by an anthropogenic intervention presents an interesting, but also challenging, system for any future attempts to quantify the foraging, energetic, physiological or reproductive costs and benefits associated with variations in group size (*sensu* Markham *et al.* 2015, Grueter *et al.* 2018). These competition-based explanations could also be simultaneously compared or combined with the suggested cooperation- or affiliation-based explanations to understand variations in group size and other aspects of sociality (Silk *et al.* 2007, Sussman *et al.* 2005, Koenig *et al.* 2006, Majolo *et al.* 2016, Willems and van Schaik 2015) in elephants.

My examination of the influence of food distribution on within-group contest yielded the puzzling lack of an effect of grass dispersion or abundance on within-clan agonism. Based on existing understanding, I propose two alternate explanations for this finding, which could be explored in the future. The first explanation stems from the peculiar resource distribution seen in the larger spatial context- the man-made reservoir on Kabini has created the small grassland habitat which is rich in resources (water and green grass) and is surrounded by vast forests with poorer resource availability in the dry season. This small, resource-rich habitat in the lean season incentivises even the subordinate females in groups with weakly expressed dominance hierarchies to engage in contest competition. Thus, a Red Queen effect type of competition to maximise feeding intake might be in operation - a rare possibility in Koenig and Borries (2009)'s fusion of the socioecological framework with game theory models (see below). This could also be said of between-clan contest. Between-clan contest was very frequent in the Kabini grassland, in contrast to very rare observations of between-clan agonistic interactions (Baskaran 1998) or largely non-agonistic co-occurrence of different groups (de Silva *et al.* 2017) in previous studies. Although large differences in grass abundance were found across focal zones in the grassland and across plot-clusters within zones, they did not explain the rates of between-clan contest. However, this remains a speculative solution to the puzzle of frequent agonism until more comparisons are made with quantitative dominance data from other habitats and populations, which do not seem to exist currently. The second explanation concerns the relevant scale at which within-group competition operates in elephants and whether the random placement of quadrats in my study captured that scale. Future studies could consider variables such as inter-individual distances and group spread. Grass abundance in plot-clusters positively influenced the duration of between-clan agonistic encounters, suggesting monopolisability/usurpability by groups at that local scale rather than the large stretches of grassland (focal zones).

Since group size is advantageous to win between-clan contests and since between-clan contests commonly result in exclusion of the losing groups from foraging areas (Nandini 2016, Gautam and Vidya unpublished), future studies could attempt to quantify feeding rates, group spread and inter-individual distances between adult females in groups of different sizes. This should be done by continuous follows of foraging behaviour in a single group during their stay in the focal zones. Data on such variables will not only help understand the costs and benefits of larger groups in a strong between-group and within-group feeding competition regime (see Sterck *et al.* 1997, Markham *et al.* 2015, Grueter *et al.* 2018), but also the flexibility in foraging behaviour when within-group competition is high.

From my work on dominance structure in female Asian elephants, I found an age-based individualistic dominance structure showing non-significant linearity and weak directional consistency, indicating a weakly expressed dominance structure. These findings in my study demonstrate the replicability of dominance patterns in this population (see Nandini 2016). In addition, although the directional consistency index of dominance was low overall (average DCI~74%), it was variable, which demonstrates the continuous nature of expression of dominance, in a society that falls towards the egalitarian side of the egalitarian-despotic continuum. Consistent with the canonical expectations of socioecological theory (Koenig and Borries 2009, Wikberg *et al.* 2013, Koenig *et al.* 2013), I found that clans showed a positive relationship between frequency of agonism and despotism (measured by directional consistency), although the slope was statistically not significant due to small number of clans for which we had sufficient data. Based on Koenig and Borries (2009)'s framework of socioecological and game theory variables, the low agonism and low despotism seen among female Asian elephants in the tall-grassland habitat at Uda Walawe (Sri Lanka) was not surprising, more so due to fission-fusion processes that are expected to dampen within-group competition (de Silva *et al.* 2017). In contrast, the weak expression of dominance and absence of rank-related skew in foraging benefits (see below) despite frequent agonism in the Kabini population contradicts the socioecological model, but seems to fit into the Red Queen effect type of feeding competition, under which individuals would intensively compete for food and subordinates show substantial reversals in a habitat that supports high resource incentives in the lean season (see Koenig and Borries 2009). Stronger expression of dominance seen in African savannah elephants despite lower agonism seems to contradict socioecological models, but can be explained by game theoretic explanations in a species with explicit weaponry (tusks, Archie *et al.* 2006). More quantitative studies of agonism and despotism from different populations and species, as well as simulation-based testing of socioecological and game theory predictions, can further our understanding of sociality and dominance in the extant populations/species of Proboscideans, where fission-fusion adds another layer of complexity to the verbal models of socioecological theory.

In my assessment of foraging consequences of dominance relationships, I found little or no rank-related skew in occupancy of better feeding sites. Given that within-clan relationships are not linear and show low consistency in dominance relationships, strong effects of priority of access to the dominants is not expected in the socioecological framework. Rank-related skew is also not expected since fission-fusion provides flexibility in decisions related to group membership to avoid within-group contest and since grass is a low-quality resource, although weak rank-related skew does not seem to fit with high agonism observed among clan-members. I suggest that future studies measure the relationship between dominance and foraging success by also quantifying other indicators of foraging and energetic success, such as feeding rate, search effort, and food-site-residence time. Such methods have been successfully used to investigate rank-related skew in species with despotic as well as egalitarian social systems (for example, Janson 1985, Vogel 2005, Grueter *et al.* 2016).

Lastly, it is important to remember that this study was conducted in a novel competition regime around the Kabini backwaters, which was formed as a consequence of a recently (in terms of elephant generations) constructed reservoir on the river. While this is an interesting system of study, it is likely that the strong competition seen in Kabini may not be observed in more natural habitats (forests/savannah woodlands) of Asian elephants. It would be important to follow radiocollared groups in order to quantification aspects of agonism, dominance structure, and its consequences in forest habitats.

Conclusion

In conclusion, the first part of my thesis underlines the limitations of a remotely sensed measure of forage abundance, highlighting the inevitability of the need to measure abundance of food plants in the field to study the foraging ecology of elephants in habitats with abundant non-food vegetation and tree canopy. The second part of my thesis has explored aspects of female Asian elephant socioecology that were not studied previously or for which quantitative assessment was lacking, and in addition, also demonstrates replicability of a few aspects of dominance structure. The results from my field investigations, especially the direct quantification of food distribution, agonistic contests, and competitor density, provide only partial support for the socioecological model of female sociality in Asian elephants. My synthesis of the relationship between feeding competition and social structure using my own results and existing literature, while being limited by paucity of existing information in other populations, lays the groundwork for other researchers to further investigate the contribution of ecology to variations in female sociality in different populations of the three extant species of elephants. These results and inferences have important implications to the study of social behaviour and ecology of Asian elephants and will, I hope, be useful to researchers working on other species also.

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