DISSERTATION

IVORY POACHING, SOCIALITY, AND THE ROLE OF BEHAVIOR IN CONSERVATION

Submitted by

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ABSTRACT

IVORY POACHING, SOCIALITY, AND THE ROLE OF BEHAVIOR IN CONSERVATION

The potential of animal behavior to contribute to conservation biology has been

acknowledged for decades, but empirical work to realize this potential has been surprisingly slow

(Sutherland 1998; Caro 2007; Angeloni et al. 2008; Berger-Tal et al. 2015). Behavior that

reliably conveys the response of populations to human threats may be particularly useful in

assessing population status and recovery potential as it can be measured over relatively short

time periods. African elephants (*Loxodonta africana*) rely heavily on behavioral decisions and

are highly dependent on complex social processes that revolve around older animals (Douglas-

Hamilton 1972; Moss 1988; Wittemyer et al. 2005b). Within the last decade poaching of

elephants for their ivory has increased to meet rising demand on international markets (Maisels

et al. 2013; Wittemyer et al. 2014), which has disproportionately been targeted toward older

elephants for their larger tusks (Wittemyer et al. 2013; Chiyo et al. 2015). In this dissertation I

analyze behavior in the context of a well-studied population of African elephants in northern

Kenya under illegal killing pressure, with emphasis on social behavior. I describe baseline levels

of sociality among adult male elephants prior to the intensification of poaching, compare

hierarchical social network structure of female elephants before and during poaching, investigate

fine-scale social strategies among young females following family mortalities, assess the utility

of a flight metric as a behavioral indicator of harvest pressure, and examine the overlap in area

use of two adjacent subpopulations. This work contributes to the growing literature on

conservation behavioral methods and advances understanding of sociality in this threatened

species.

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Chapter 1: Introduction

Behavioral responses of wildlife to anthropogenic pressures may affect fitness and associated demographic trends, and may provide managers with proxies for population health (Sutherland 1998; Angeloni et al. 2008; Berger-Tal & Saltz 2016). In social species, interactions with conspecifics may be an important component of such responses. This dissertation addresses questions founded in animal behavior to understand the indirect effects of unsustainable harvest on a threatened species, highlighting the ways in which sociality studies may be useful for conservation and advancing theory on cooperation in a complex society. It encompasses analyses on the behavior of a population of African elephants (*Loxodonta africana*) in Samburu, northern Kenya that has been intensively monitored since 1997 (Wittemyer 2001). The population experienced a surge in ivory poaching in 2009 that continued at a high intensity through 2013 (Wittemyer et al. 2014). Much of the following work reflects elephant behavior in the context of illegal harvest.

Chapter 2 characterizes bonds among male African elephants. Male elephants undergo discrete periods of sexual activity and inactivity, the seasonal timing of which varies from bull to bull. As a result of their mismatched sexual periods and changing motivations for conspecific association between periods, social bonds among male elephants have been challenging to quantify and remain poorly understood. We control for this aspect of bull biology by quantifying social association indices among pairs of bulls (only considering pairs to be available to associate if they were in the same motivational state—sexually active or inactive—on the date of the observation). We show that social preference is much stronger than was previously thought and that when sexually inactive bulls tend to associate with age-mates. This chapter provides

important baseline information for the species and demonstrates the utility of controlling for motivational states in animals.

Chapter 3 compares social structure in adult female elephants over a sixteen-year period during which the population experienced intensifying illegal harvest. Harvest disproportionately targeted older females for their larger tusks (Wittemyer et al. 2013), mirroring the targeted removal of highly connected nodes in theoretical networks (Albert et al. 2000). We use social associations to construct clustering trees and social networks. Significantly distinguishable structural change points on cluster trees indicated that the nested hierarchical structure of female elephant society present in undisrupted periods is maintained despite high mortality. Daughters in the disrupted period replicate their mothers' social environments, which is the mechanism by which complex structure is resilient to perturbation. Females from highly disrupted groups that could not replicate their mothers' social patterns because of severe family mortality strengthened bonds within their mothers' more distant contact networks, regardless of relatedness. By bridging theoretical networks with an empirical system this chapter presents rare evidence for evolved mechanisms of network resilience and provides novel information on how this highly social species responds to harvest pressure.

The context of novel bond formation defined in Chapter 3 is used to investigate female elephant social strategies following family mortality at a finer scale in Chapter 4. We use the types and directions of behavioral interactions collected while following individuals to understand the bonding choices elephants make. Our results suggest that there are measureable social costs to lost bonds, but that behavioral flexibility allows individuals to improve their social environment following family mortality. Orphans experienced less affiliation and more aggression than their non-orphan counterparts. Alloparenting (directing parenting behavior

toward calves that are not their own) and acting submissive were negatively related to the time

an elephant was orphaned and whether they belonged to their natal group, indicating that

elephants alter their behavior as they integrate into new groups. This chapter provides insight

into the evolution of social behavior in elephants and the implications of age-selective poaching

for remaining young females in a matriarchal society. Our results suggest that the fission-fusion

nature of this society allows elephants to compensate for their lost bonding partners over an

extended period of social integration, and that the persistence of older individuals in the

population may be critical to this process.

Chapter 5 tests the utility of anti-predator flight metrics as proxies for anthropogenic

pressure. Rapid behavioral assessment has been suggested as an inexpensive and easily

implemented method to gauge human pressure on wildlife (Caro 2005). However, if flight

metrics are related to non-human variables they could be misleading for management efforts. We

use mixed-effects models predicting reaction of elephants to observer vehicle approaches in

which we treat individuals as random effects and include ecological, anthropogenic, spatial,

social, and demographic predictor variables. We show that elephant response is better predicted

by non-human variables than it is by harvest pressure. We discuss the implications of our results

for population monitoring and behavioral assays conducted *in situ*. This chapter provides a

unique perspective on a problem that has long been identified in wildlife management but is

rarely dealt with.

Finally, Chapter 6 investigates spatial segregation between elephant sub-populations. We

compare the photographic identification records of two long-term elephant monitoring projects

(Samburu/Buffalo Springs National Reserves and Mpala Ranch) that are located close to one

another relative to an elephant's ranging ability (approximately 75 km). Despite the proximity of

the two study areas, we find no overlap among photographic records but use radio-collar tracking data to show that there is evidence of infrequent shared space use. We highlight the importance of projects like these for wildlife corridor planning and ongoing national development, and emphasize the value of combining tracking data with observational methods.

<u>Chapter 2: Controlling for behavioral state reveals social dynamics among male African</u>

<u>elephants, *Loxodonta africana*</u>[1]

Introduction:

In social systems with contest polygyny, males attempt to monopolize receptive females, and male-male relationships are often competitive (East & Hofer 1993; van Hooff & van Schaik 1994). Despite this expectation of competitive relationships, preferential association has been demonstrated among males in polygynous taxa (e.g. ibex: (Villaret & Bon 1998); chimpanzees: (Langergraber et al. 2007)). Empirical work has linked companion preference among males to reproductive success when coalitions or coordinated displays facilitate copulations (Connor et al. 2001; Ryder et al. 2009; Schülke et al. 2010). In societies in which reproductive benefits of association are not apparent, reports of preferential associations among males are rare (Fischhoff et al. 2009).

Motivational state is highly relevant to the structure of social relationships. Male interactions often vary in relation to the reproductive status and distribution of females (Emlen & Oring 1977). During mating periods, competitive or coalition-based interactions likely dominate whereas the influence of reproductive competition may be less apparent during periods of sexual inactivity. Social interactions while sexually inactive may provide benefits including information exchange (e.g. (McComb et al. 2001; Sonerud et al. 2001), predator defense (e.g. (Hamilton 1971), foraging facilitation (e.g. (Baird et al. 1991)), or resolution of dominance hierarchies (Beacham 2003; de Villiers et al. 2003; Evans & Harris 2008). Understanding one's status in a

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[1] Adapted from: Goldenberg, S. Z., de Silva, S., Rasmussen, H. B., Douglas-Hamilton, I., and Wittemyer, G. 2014. Controlling for behavioural state reveals social dynamics among male African elephants, *Loxodonta africana*. *Animal Behaviour* 95:111-119.

hierarchy can prevent future contest among competitors, which is especially beneficial for species with weaponry (Rowell 1974). Investigation of social preference is potentially confounded by such shifts in behavioral states (sexually active to inactive). Few studies of sociality assess differences in structure across behavioral states, despite the potential difference in cost/benefit ratios (but see (Lusseau 2007; Fischhoff et al. 2009; Patriquin et al. 2010)).

African savannah elephants engage in contest polygyny, with females coming into estrus for 4-6 days once every 4 years (Moss & Poole 1983). Mature males have distinct periods of sexual activity and inactivity throughout the year (Poole 1987). Because females can come into estrus at any time of year (Poole 1989a), mature male elephants undergo sexually active periods asynchronously (Hall-Martin 1987; Poole 1987; Rasmussen 2005). Grouping behavior reflects these periods, as males often are found among all-male groups when sexually inactive and found among mixed groups when sexually active (Poole & Moss 1981), suggesting that motivation to associate with conspecifics changes between states (Fischhoff et al. 2009).

Quantifying relationships among males necessitates a framework that accounts for this marked difference in motivational state. Dyadic association indices incorporate observations when one individual is seen without the other as rejected opportunities to associate (Cairns & Schwager 1987; Ginsberg & Young 1992). Previous studies using association indices have found weak or random relationships among male African elephants (Croze 1974; Moss & Poole 1983; Chiyo et al. 2011), but have not accounted for the dynamic and individual-based schedules of sexual activity that may drive association. Collapsing multiple states into one category potentially distorts values by including males as potential associates when they may be predisposed towards avoidance (i.e. one is seeking female associates while the other is seeking male associates), limiting understanding of what may be driving social behavior. Here, we

control for mixed motivational states by conducting state-based calculations of association indices in a population of free-ranging elephants in Samburu, northern Kenya. We investigate male-male associations and the social network metrics that arise from those associations to gain insight into the strength of bonding and the drivers of male sociality.

Assuming the distribution of females is the primary driver of male conspecific association during sexually active periods (Emlen & Oring 1977), but that it plays a limited role during sexually inactive periods, we expect associations among male elephants to be structurally different in relation to their reproductive state. Males may use sexually inactive periods to assess competitors (of close stature/age) and resolve rank to mitigate potentially costly contests (Beacham 2003), or male-male bonding may be driven by other non-contest-related benefits such as information exchange across male age classes (Evans & Harris 2008; Chiyo et al. 2011) or predator defense (McComb et al. 2011). If males use sexually inactive periods to foster bonds that confer benefits like shared knowledge similar to those found among females in the species (McComb et al. 2001; Wittemyer et al. 2005b), we expect evidence of preferred companionship. The structure of preferred companionship may provide insight into the benefits of such affiliations. To assess the importance of incorporating state in social analyses, we compare elements of social structure (association index values and social network metrics): (1) disregarding behavioral states and (2) differentiating state-based social properties. We present individual-based comparisons of state-dependent differences in social metrics. We investigate relationships among age, association and social network structure across states to provide insight regarding possible drivers of observed social patterns. Finally, we relate our findings to previous work on male elephant society (Evans & Harris 2008; Chiyo et al. 2011).

Methods:

Study Population

      This study is a part of an ongoing long-term monitoring project that has maintained individual-based records of the elephant subpopulation that uses the unfenced Samburu and Buffalo Springs National Reserves in northern Kenya (0.3-0.8˚N, 37-38˚E) since 1997 (Wittemyer 2001; Wittemyer et al. 2013). The reserves are located along the Ewaso N'giro River, the only permanent water source in this semiarid savannah ecosystem and thus a focal area for wildlife. Because of the sparse, semiarid vegetation, good visibility at the study site enables researchers to detect groups and solitary individuals easily. The elephants that use these reserves are habituated to vehicles, allowing detailed behavioral observation, but move in and out of the reserves regularly; they are a part of a larger population that ranges within the Laikipia/Samburu ecosystem (Wittemyer et al. 2005a).

Data Collection

      Between August 1999 and November 2003, observations of elephants were collected while performing established transects on a daily basis within Samburu and Buffalo Springs National Reserves that resulted in complete coverage of the parks at least once per week (see further description in (Wittemyer et al. 2005b)). Observations were also collected opportunistically outside of the reserves where few roads exist, making systematic surveys impossible; elephants were located during opportunistic surveys through the use of radiotracking collars (Rasmussen 2005). When elephants were encountered the identities of all individuals over 18 years old in the group (younger males were often difficult to distinguish and therefore noted by age rather than identity), the GPS location, date, time and group activity were recorded

(Wittemyer et al. 2013). Individuals were identified using unique ear patterns and tusk shape (Douglas-Hamilton 1972; Moss 2001). Bulls were considered a part of a group if they were spatially clustered (within a 500 m radius of an observationally estimated center) and coordinated in movement and activity (Wittemyer et al. 2005b; Chiyo et al. 2011). The presence of musth signaling (i.e. temporal gland secretion and urine dribbling) was recorded (Poole 1987) and used to verify model accuracy in defining states of sexual activity and inactivity (see *Delineating States* below). For days when a bull was observed more than once, only the first observation of the day was included in analyses (Rasmussen 2005; Wittemyer et al. 2005b). Bull ages were estimated using established criteria, including shoulder height, tusk girth and head shape (Moss 1996), the accuracy of which was established using molar dentition from dead or immobilized individuals (Rasmussen et al. 2005).

There were 154 bulls identified over the course of the study. It is common to use the most frequently observed individuals in analyses to minimize effects driven by poor sampling (Whitehead 2008). We defined our focal bulls (N = 32) as those seen at least 20 times in the sexually inactive state because we anticipated social interactions to be strongest during the sexually inactive state, when mate competition would not structure interactions. The number of observations in the sexually active and inactive states of these focal bulls was similar (median: inactive = 42; active = 45). There were 3473 observations of focal bulls in known states in 2018 distinct aggregations over the 4-year study. Focal bulls were estimated to be between 21 and 41 years old at the midpoint of the study. To analyze the relationship between age and strength of association, we divided pairs of individuals (dyads) into four categories in which 'age-mates' were defined as individuals born 5 or fewer years apart. Age classification was determined by the youngest member of the dyad, for which 'old' bulls were at least 30 years old and 'young' bulls

were younger than 30 years old. The 30-year cutoff criterion was based on the age of musth

onset in the study population (Rasmussen et al. 2008). Therefore, our four categories were 'age

mates (old)', 'non-age-mates (old)', 'age-mates (young)' and 'non-age-mates (young)'.

Delineating States

When sexually active, mature males overtly musth-signal whereas younger males

typically do not overtly signal their state (Ganswindt et al. 2005). Therefore, we applied a hidden

Markov model (HMM) (Rabiner 1989) to characterize individual males' sexual state to allow

state delineation based on behavioral traits other than overt musth signaling. In this model, the

frequency of association type (mixed-sex group, bull group, lone bull) served as the observable

signal with state-specific probabilities, and sexual state served as the unobservable (hidden) state

(Rasmussen 2005). Sequences of these observable group contexts (i.e. association type) were

used to infer underlying sexual state (Rasmussen 2005; Ganswindt et al. 2005; Rasmussen et al.

2008). Models relied on three sets of parameters: (1) the probability of starting in a given state,

(2) the probability of switching to another state given the current state and (3) the probability of

producing a particular observable signal given the current state. Models with differing numbers

of states were tested and parameters were determined using maximum likelihood. Model

parameters (i.e. state transition and observable signal probabilities) were optimized on temporal

sequences from multiple bulls simultaneously to avoid model overfitting that might arise from

individual-based model optimization. Because males associate with other males when both

sexually active and inactive, the HMM state assignment does not predict the strength of

relationships among males in either state. Rather, differences in costs and benefits of male-male

association between sexual states may lead to differences in social metrics. For example, if bulls

form coalitions while sexually active (when they are frequently found in mixed-sex groups) but do not benefit from relationships with particular individuals while sexually inactive, we might expect to see higher dyadic association index values among sexually active males than among sexually inactive males. In contrast, if benefits from association with particular males are higher when sexually inactive, we might expect the opposite trend.

Bulls included in the HMM procedure were those seen at least 30 times/year (N = 38). To verify that sexual state corresponds to associational preference and that association shifts with underlying state, models were first applied to a subset of older bulls (>35 years; N = 12) with regularly occurring musth periods and concurrent visual signals to determine whether model-defined sexually active periods based on association type accurately distinguished these periods of heightened reproductive activity (Poole 1987) (see (Rasmussen 2005) for details of verification). When this cross-validation procedure confirmed HMM assignments, the same modelling steps were applied to temporal sequences of younger bulls without regularly occurring musth periods. Finally, a combined model was optimized for all bulls. Although varying numbers of states were tested, the best combined model included two states, assigning bulls to state 1 (sexually inactive, in which the probability of association with females was low) or state 2 (sexually active, comprising musth and sexually active nonmusth, in which the probability of association with females was high). The combined model preserved most of the state designations from the age-specific models (91-99%). Models were fitted using Mathematica (Wolfram Research 2004). For further details on model definition and results, see (Rasmussen 2005) and (Rasmussen et al. 2008).

States were assigned for each day on which a focal bull was seen for all but 61 occasions over the 4-year study. A bull seen consecutively in the same state less than 28 days apart was

assumed to be in that state for the days between sightings. If two consecutive sightings of a bull were within 28 days but he was in different states on those days, the interim period was split evenly between the two states. If two consecutive sightings of a bull were more than 28 days apart, his state during that period was considered unknown, during which the individual was excluded from state-based calculations (see below).

Calculating Association Indices

Association indices measure the strength of association between two individuals (Cairns & Schwager 1987). Because bulls in our study system were as likely to be identified when apart as they were when together and because all individuals within a group were registered, we used the simple ratio index (hereafter 'AI') to determine the strength of dyadic bonds: $AI = N_{AB}/(N_{AB} + N_A + N_B)$, in which N_{AB} is the number of times that individuals A and B were seen together, and N_A and N_B are the number of times that individual A or B was seen without the other, respectively (Cairns & Schwager 1987). AI was only calculated for dyads that comprised focal bulls. The number of observations per dyad ranged from 0 to 211 for sexually inactive dyads (median = 28) and from 0 to 146 for sexually active dyads (median = 22).

To evaluate the effect of including motivational state, we calculated AI using three approaches: (1) using all observations of focal bulls regardless of group type or sexual state (the 'all-data sample', $median_{obs} = 95$), (2) using only observations of bulls in all-male groups (the 'all-male sample', cf. (Chiyo et al. 2011), $median_{obs} = 38$) and (3) using only data for which the members of the dyad were both categorized with identical sexual states (i.e. observations on dates when the members of a dyad were in different states or when one member was in an unknown state were not included in calculations). AI values for dyads were calculated

independently for both the sexually active (median$_{obs}$ = 45) and inactive states (median$_{obs}$ = 42).

Association index data were non-normal even after arcsine transformation. As a result,

nonparametric statistical approaches were used to compare the distributions of AI values derived

from sexually active and inactive data. We also tested for any association between the AI value

of a dyad and their absolute age difference using the Mantel test (Mantel 1967) implemented in

the package 'ade4' for R (Thioulouse et al. 1997). All analyses and associated statistical tests

were performed in R v.2.15.1.

Permuted Data Sets to Test for Random Association

Permuted data sets can be used to provide a distribution of random association against

which to compare observed data (Manly 1995). We used the swap method described in (Bejder

et al. 1998) to generate random associations from our observation data, in which the number of

times a bull was seen and the group structure in terms of number and sizes of observed groups

were maintained (i.e. the column and row totals). We additionally excluded all observed groups

that were composed entirely of nonfocal individuals before permutation in order to increase the

statistical power of the permutation tests while maintaining biological validity. This approach,

which we will henceforth refer to as Permutation I, effectively retains the observed data structure

and controls for variation among bull sightings (Bejder et al. 1998; Whitehead et al. 2005). Two

individuals from two distinct groups, for which each individual was only present in one of the

groups, were randomly selected and swapped. Our modification accounting for different

motivational states was to swap two bulls only if they were in the same sexual state on both dates

on which the groups were observed (state 1 for sexually inactive random matrices and state 2 for

sexually active random matrices), thereby keeping the state-specific social attributes the same

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(Croft et al. 2011). As such, randomly chosen bulls that were in different states were not available for swaps. This contrasts with the all-male and all-data approaches, in which bulls could be swapped despite being in different states. Although AI was only calculated for dyads composed of focal bulls, swaps could occur among all known bulls in the population, distributed among 2018 observations of distinct groups. Observed dyadic association strengths higher than those derived from permutations suggest the existence of social preferences.

Two thousand permutations of 1000 swaps each (two million total swaps from the original data set) were completed and dyadic AI calculated for every permutation for each of the four samples (all-data, all-male, sexually active or sexually inactive). The distributions of observed and random AI values were therefore derived from the same data set, regardless of subsampling structure. This large number of swaps served to decrease autocorrelation among AI values between permutations. After each 1000 swaps, the AI and sample size (i.e. the sum of the observations of bulls A and B: $N_S = N_A + N_B + 2N_{AB}$) of each dyad were calculated. After 2000 permutations were completed, all AI values corresponding to a given sample size were grouped and the 95th quantile was determined (Table 2.1). Observed AI values were considered significant when greater than or equal to the 95th quantile of the sample size-specific distribution of randomly generated AI values. We controlled for sample size in this way to avoid bias potentially introduced by subsampling by state and consequent reductions in sample sizes. Because there were few randomized values corresponding to the highest and lowest sample sizes, a function for the sample size and corresponding 95th quantile value was fitted using nonlinear least squares (the nls() nonlinear regression function in R) and used to predict the significance cutoff value for the highest and lowest sample size distributions that had too few values for empirical estimation. We chose a one-tailed distribution because we were interested in preferred

companions. These procedures were implemented in R v.2.14.0 (R Development Core Team 2010).

Table 2.1: This example table demonstrates how AI values were grouped by sample size. The 95th quantile value for this sample size was 0.416; AI values higher than 0.416 were considered significant in this sample size class.

Dyad	AI	Sample size	Permutation
1	0.021	29	5
1	0.135	29	6
2	0.160	29	2
2	0.074	29	4
2	0.510	29	6
3	0	29	3
3	0.110	29	5
52	0.051	29	23
74	0.108	29	200
405	0.275	29	1050

Modular Structure

To determine whether bull social networks were modular (i.e. whether bulls associate more closely with a subset of individuals), we constructed undirected weighted networks in which nodes representing individuals were linked by edges whose thicknesses were proportional to AI values. We then analyzed these networks using established techniques (Newman 2006) to identify structural components that may relate to the drivers of male-male associations. We examined structure using the Walktrap community detection algorithm in iGraph v.0.6.5 for R (Pons & Latapy 2005), which accounts for weighted edges. This approach uses a short random walk to identify nodes that are henceforth referred to as 'modules'. We tried 3, 4 and 5 steps for each state-based network, choosing the partition that maximized modularity (Newman 2006). To determine whether the observed partition was likely to occur by chance for each state, we compared the observed maximum modularity to the distribution of modularity maxima obtained

for the 2000 permuted data sets obtained via Permutation I, described in the previous section. Departure from what would be expected at random suggests the existence of modules in the population.

Network Metrics

We compared nodal metrics from ego-networks (graphs consisting of the immediate neighbors of each focal individual, in which neighbors share an $AI > 0$ with the focal individual) for each bull across states to assess how individual bulls differ from one another socially. We created ego-networks using the 'statnet' package for R. Three primary network metrics were examined for each individual and compared across the sexually active and inactive states as a means to infer differences in their social drivers: (1) 'ego-network size' (also known as degree centrality, the number of direct connections to the individual), which directly measures the number of companions an individual has had, (2) 'ego-network density' (sometimes referred to as clustering coefficient, the proportion of an individual's companions that are also connected to one another), which is a measure of community integrity defined as the propensity of a subject's companions to associate with one another and (3) 'betweenness centrality' (the number of shortest paths in the entire network that pass through an individual), which indicates how centrally embedded the subject is within the full network (Wasserman & Faust 1997). Individuals with higher betweenness are structurally important to the integrity of networks since they tend to bridge different social groups (Lusseau & Newman 2004) and can be biologically relevant by facilitating information exchange or maintaining social cohesion (Williams & Lusseau 2006; Chiyo et al. 2011). We also computed a related measure for a subset of analyses,

'eigenvector centrality', which is also influenced by the centrality of an individual's contacts themselves.

To test the null hypothesis that network measures do not depend on sexual state, we generated 10,000 permutations samples of the sexually active and sexually inactive data sets, respectively. This procedure, henceforth referred to as Permutation II, preserved associations among individuals on any given day, the sizes of aggregations in which they were observed and the total number of observations per individual, but it randomly assigned their sexual state. The mean values of the three network metrics and differences between the two states for the permuted data sets were computed.

Ethical Note

Observations were conducted in a noninvasive manner (ACUC R217B) and with permission of the Kenya Wildlife Service (wildlife authority in Kenya), the Samburu and Isiolo County Councils (local managers of the protected areas) and the University of Oxford and Save the Elephants (host institutions).

Results:

Comparing Association Index Values across Sampling Approaches, Sexual States and Age Classes

AI values were significantly greater among sexually inactive bulls than among active bulls (Wilcoxon signed-ranks test: $W = 131465.5$, $N = 414$, $P < 0.001$). Because data were nested across the other treatments (all-male or state-based treatments were a subsample of the all-data treatment), statistical comparisons were not appropriate, although it was clear that AI means

were higher with state-based treatments. This shift in means was not related to differences in sample sizes across the treatments, as the all-data and all-male treatments showed similar AI distributions, but had markedly different sample sizes. Similarly, the all-male, sexually active and sexually inactive treatments had similar sample sizes, but showed differences in the distributions of means.

Identification of significant dyads varied depending on data treatment (Fig. 2.1). Dyadic AI was significantly greater than expected by chance for 12.8% of potential dyads in the sexually inactive state (mean AI ± SD = 0.334 ± 0.118, N = 62) and 6.8% of potential dyads in the sexually active state (mean AI ± SD = 0.310 ± 0.251, N =29). In contrast, 16.1% in the all-data sample (mean AI ± SD = 0.079 ± 0.025, N = 80) and 15.9% in the all-male sample (mean AI ± SD = 0.117 ± 0.043, N = 79) were significantly greater than expected by chance when disregarding state. Mixing states by randomizing individuals into groups that could not occur biologically deflated the randomized AI distribution relative to when biological constraints were imposed in the randomization procedure. As a result, the threshold above which AI values were considered significant was deflated in the all-data and all-male samples, resulting in more significant dyads.
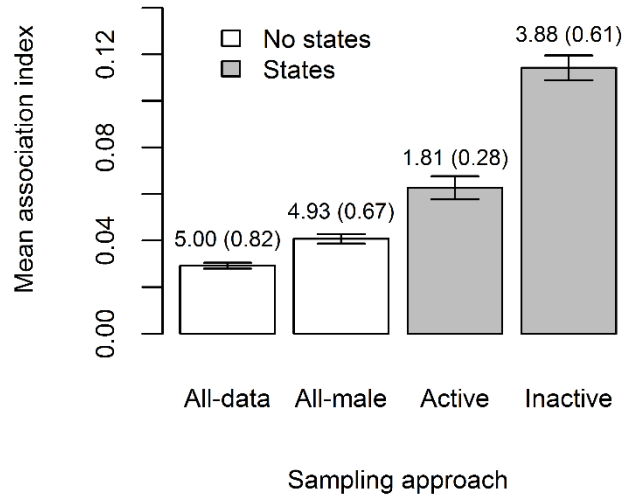
Figure 2.1: Mean dyadic association index ± SE among male African elephants based on sampling approach (all-data, all-male, state specific: active, inactive). Numbers above bars indicate the mean ± SE number of significant affiliates per bull. Standard errors were determined empirically.

The average AI for the inactive state and the number of significant dyads per individual when inactive were positively correlated with their age (Spearman rank correlation: AI: r_S = 0.422, N =32, P < 0.05; significant dyads: r_S = 0.472, N =32, P < 0.05). However, these relationships were not found among sexually active bulls (AI: r_S = -0.014, N = 32, P = 0.938; significant dyads: r_S = 0.028, N = 32, P = 0.879; Fig. 2.2). Across both states, significant dyads included age-mates and non-age-mates. The proportion of significant dyads differed by dyadic age category in the inactive state (chi-square test: χ_3^2 = 31.575, P < 0.001) but not in the active state (χ_3^2 = 2.157, P = 0.541; Fig. 2.3). Age differences among significant dyads tended to be smaller among inactive dyads (median: inactive: 5; active: 10), with 54.8% and 34.4% of significant dyads composed of age-mates in the inactive and active states, respectively. Of the

significant inactive age-mates, 82.4% were older dyads. However, there was no significant

relationship between the absolute within-dyad age difference and its AI value in either state

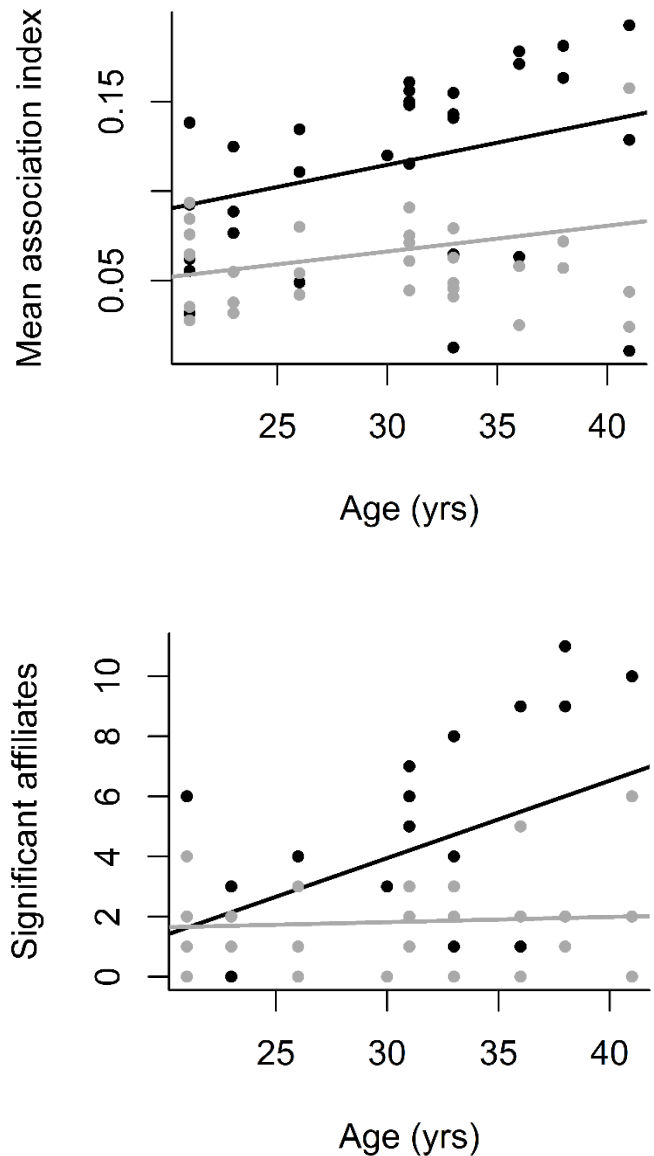(Mantel test: inactive: r = -0.1073, P = 0.96; active: r = 0.0633, P = 0.10).

Figure 2.2: Mean (top) association index and (bottom) number of significant associates for individual African elephant bulls ordered by bull age. Black dots: sexually inactive; gray dots: sexually active. See text for details. Lines show linear fits.
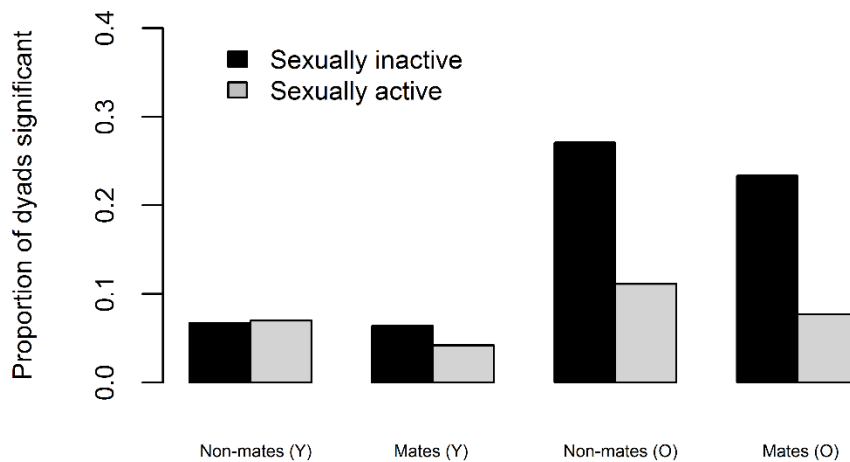
Figure 2.3: Proportion of significant dyads to available dyads among dyadic age categories of male African elephants. Assignment of 'old' or 'young' was determined by the age of the youngest member of the dyad (old: ≥30 years; young: <30 years). Age-mates were separated by 5 or fewer years.

There was a positive correlation in the AI between sexually inactive and sexually active states among dyads for which both could be calculated (Spearman rank correlation: $r_S = 0.214$, N = 414, P < 0.001). Among dyads for which AI was significant in both states (N = 7), 85.7% were composed of bulls over 30 years old at the midpoint of the study. The median age difference among these dyads was 7 years.

Module Detection and Network Statistics

Greater modularity (q_{max}) than expected under the null model of chance association was found in both the sexually inactive and active states, with the q_{max} in the active state higher than that in the inactive state (Permutation I: P < 0.0005; Fig. 2.4). However, observed values

(inactive: $q_{max} = 0.082$; active: $q_{max} = 0.21$) were below the 0.3 threshold taken to indicate

meaningful structure (Whitehead 2008). The composition of modules differed across states. On

average, sexually inactive bulls had larger and denser ego-networks but lower betweenness

relative to when active (Permutation II: $P < 0.0001$). The ego-network sizes and densities

observed in either state, as well as betweenness in the inactive state, were unlikely to have arisen

through chance association ($P < 0.0005$). Only betweenness in the active state was not different

from random (Fig. 2.5). The relative values of network measures under each treatment are

provided in Fig. 2.6.
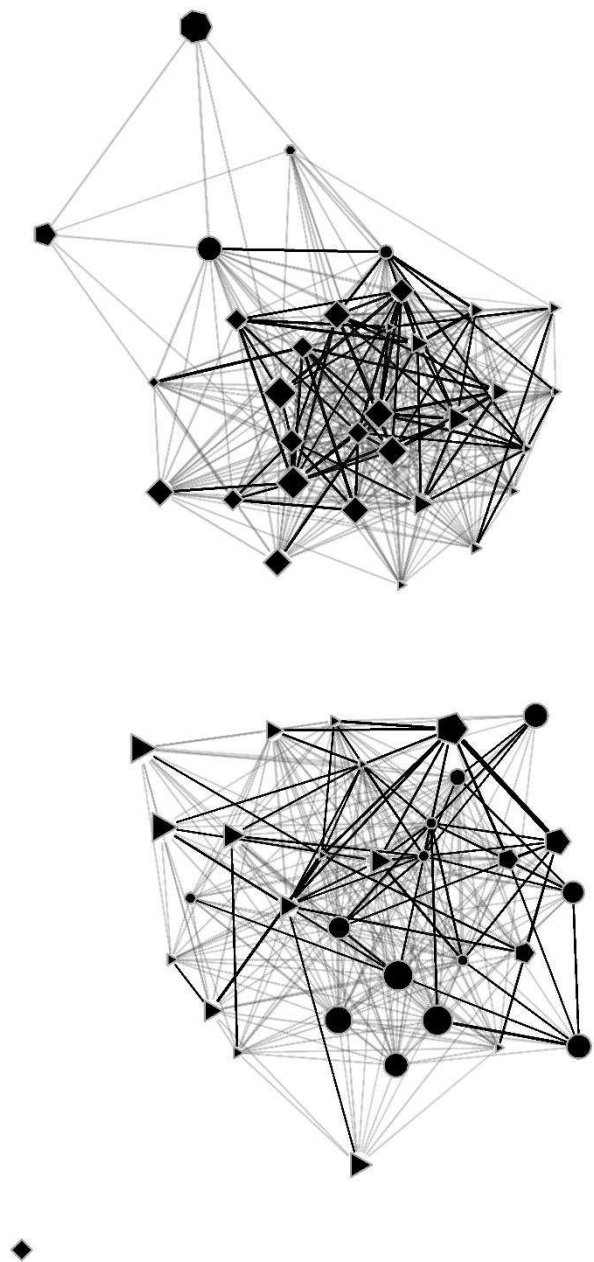
Figure 2.4: social networks of male African elephants when (top) sexually inactive and (bottom) sexually active, constructed using Fruchterman and Reingold's force-directed placement algorithm. Nodes represent individual bulls, with node size corresponding to age at the midpoint of study, and shape representing module assignment. Edge weight corresponds to dyadic association index value. Edge color denotes whether the association index value was found to be significant (gray: nonsignificant; black: significant).
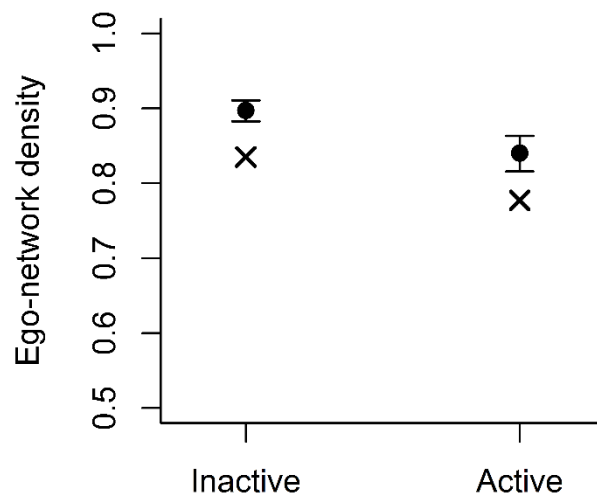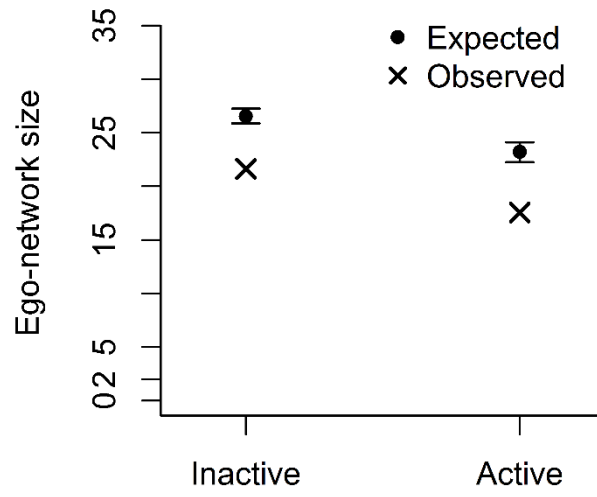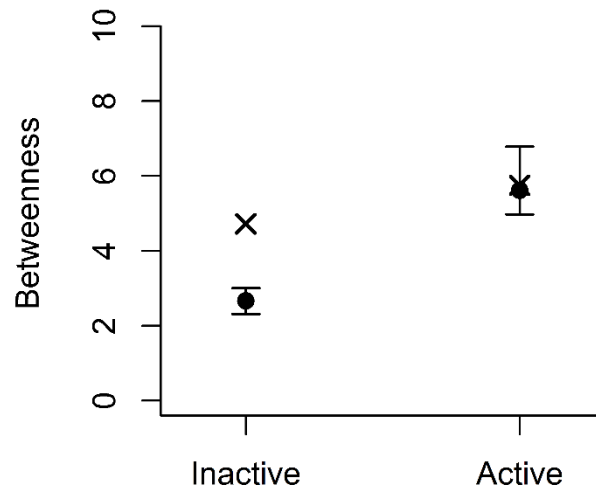
Figure 2.5: (top) Ego-network size, (middle) density and (bottom) betweenness metrics derived from elephants in the inactive and active sexual states relative to the corresponding permuted values. Expected metrics present the average and confidence interval of the permuted data set averages (mean ± 95% CI, N = 2000 data sets). Observed metrics present the state-specific averages of the 32 focal bulls (confidence intervals were not computed because there was only one observed data set).
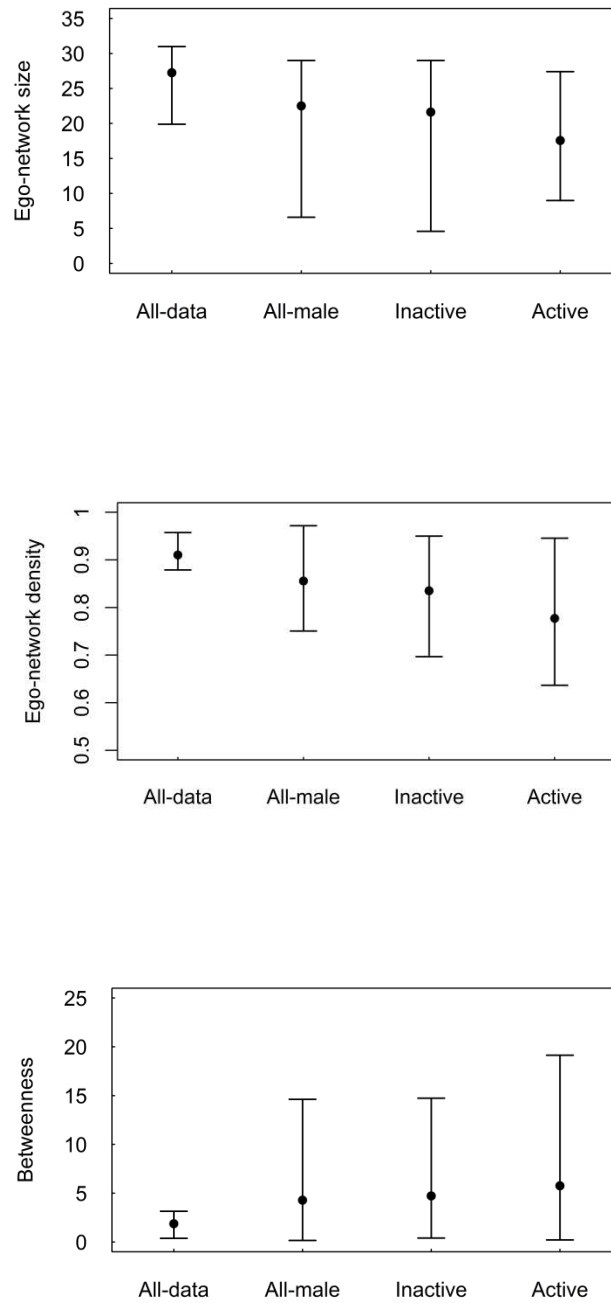
Figure 2.6: Mean ± 95th quantile for ego-network size, density and betweenness, respectively, for male African elephant bulls ($N = 32$) in all analytical approaches: all-data, all-male, sexually inactive and sexually active.

The relationship between network measures and age varied with sexual state. In the sexually inactive network, density was negatively correlated with age (Spearman rank correlation: $r_S = -0.49$, N = 32, P < 0.01), but no other measures exhibited a significant relationship. In the sexually active network the reverse was true: density showed a significant positive correlation with age ($r_S = 0.42$, N = 32, P < 0.05), while size and betweenness showed negative correlations with age (size: $r_S = -0.46$, N = 32, P < 0.01; betweenness: $r_S = -0.43$, N = 32, P < 0.05). There was no correlation between age and eigenvector centrality in the sexually inactive state ($r_S = 0.29$, N = 32, P = 0.1129), but there was a significant negative correlation in the sexually active state ($r_S = -0.44$, N = 32, P < 0.05).

Discussion:

Variation in social interaction among animals may arise from segregation due to reproductive states (as shown here), dynamic environments (Gill & Wolf 1975), shifts between life history tactics (Bon et al. 2001; Fischhoff et al. 2009), or changes in life state (Patriquin et al. 2010), among other processes. The behavioral state-based analytical approach implemented here on male African elephants provides an effective way to partition and quantify relationships related to different contexts. By accounting for motivational states in our study system, we were able to assess more precisely the social complexity of male African elephants, an animal previously assumed to be relatively asocial. Our results demonstrate that associations among pairs of bulls are much stronger than previously reported in studies in which sexual state was not controlled for (thereby diluting associations by considering behaviorally restricted periods as missed opportunities to associate; (Chiyo et al. 2011)). However, while association indices were stronger in our state-based treatment compared to standard approaches, we used a more

conservative definition of what constitutes significant dyadic affiliation. This is because partitioning data sets for the state-based analyses reduced the denominator of the AI, which can itself result in higher AI values. To account for this, we defined significant affiliates (i.e. those with AI values greater than random) not with respect to the average of the population at large, but relative to dyads that had the same total number of samples (N_S) in permutations. We then compared the number of significant dyads relative to those derived from permutations that allowed biologically unfeasible associations (all-data and all-male). Lack of adherence to the assumption that all individuals are equally likely to associate is an acknowledged problem in approaches to social data, often discussed with respect to unrecognized spatial and temporal constraints (Whitehead et al. 2005). This study provides an explicit example of how such problems driven by behavioral state can bias inference.

Significant Affiliates, Age and Sexual State

A surprising result of these analyses was the presence of significant affiliates across behavioral states. In particular, we expected males to be highly individualistic in their sexually active state due to the high levels of mate competition typical of polygynous species. Most of the observations of sexually active males occurred in mixed-sex groups and it is possible these results reflect attraction to the same resource (i.e. estrus females) among males with overlapping sexually active periods, and consequently may not reflect male-male companion preference (Lee et al. 2011). Active periods become more consistent as bulls age, and those males that come into musth show a high degree of temporal fidelity in the timing of their musth periods across years (Poole 1987; Rasmussen 2005), possibly enhancing the effect of overlapping resource attraction, although such a hypothesis is less applicable to younger, nonmusth individuals.

If male interactions are used to assess the ability of possible competitors (Beacham 2003; de Villiers et al. 2003; Evans & Harris 2008) or coalition partners (Connor et al. 2001), persistent relationships among age-mates may be beneficial by facilitating contest resolution based on previous knowledge rather than potentially dangerous conflict (Rowell 1974). Such a hypothesis has less relevance to non-age-mates, in which substantial size asymmetries presumably reduce the probability of conflict. The observed difference in median age difference among significant sexually active dyads relative to inactive dyads may be a function of young males shadowing older, more experienced males during sexually active states to gain experience (the information exchange hypothesis of (Evans & Harris 2008)) or to access mating opportunities as noncompetitive sneakers (Perrill et al. 1978). The drivers of significant sexually active affiliates were not definitive, and further work documenting directions and types of male interactions may provide insight to this question.

The greater proportion of significant affiliates that were age-mates among inactive dyads may indicate that competitor assessment plays a role during inactive periods, possibly by reaffirming dominance hierarchies or renegotiating relations based on dynamic variables like body condition (i.e. repeated assessment of the physical state of competitors). The majority of these were among older dyads (82.4%), potentially in relation to higher benefits of resolved rank among bigger bulls that come into musth during their active periods. However, the tight and extended nature of bonds between males (recorded in GPS radiotracking data reported in (Rasmussen 2005)), and the tendency for the proportion of significant dyads to be among older bulls regardless of their being age-mates suggest that other mechanisms besides simple competitor assessment also play a role in male relationships. Disproportionate bonding with age-mates may arise from cooperative benefits as has been documented in other taxa (Langergraber

et al. 2007). Vigilance enhancement of antipredator benefits (Hamilton 1971) are probably important benefits in the study ecosystem where human predation is relatively high (Wittemyer et al. 2013), and foraging facilitation has been observed among male groups, whereby multiple individuals feed on a resource that was made accessible by joint activity or by a member of the group (Wittemyer pers. obs.). Such cooperative relationships may occur more frequently among relatives (Chiyo et al. 2011). In addition, males grow up in highly social female-structured societies before dispersing (Lee et al. 2011). It is possible that the extended significant relationships recorded are not costly and are simply a manifestation of the species' social propensity. Determining the motivations giving rise to these social relationships, which appeared to be manifested over multiple years and were stable despite dynamics in the study system, was beyond the scope of this study.

A positive association between dyadic age difference and AI value was found in a study of all-male groups in Amboseli National Park, Kenya (Chiyo et al. 2011). Sexually inactive males in our study did not show such a trend. This disparity could reflect behaviors that manifest from differences in the age structure of the two populations (Wittemyer et al. 2013). The Amboseli population had a greater spread of age differences in the sample analyzed (up to 40 years) than that in our system (up to 20 years). Alternatively, differences may reflect incompatibility across our different analytical approaches, supported by the fact that trends derived from the all-male sample (as conducted by (Chiyo et al. 2011)) differed from those derived from either the sexually active or the sexually inactive samples. Specifically, older bulls in the present study and in Amboseli were more often observed in all-male groups than were younger bulls (Chiyo et al. 2011); as such, metrics derived from all-male groups alone may exaggerate the role of older bulls within networks.

State-specific Network Structure

We found weak (but higher than expected by chance) modular structure in networks for both states. However, the 32 focal individuals were partitioned differently in each state and the sexually active social network was more clearly divided into modules. Age-related homophily does not appear to account for the observed modules as each module included bulls in different age groups (Fig. 2.4). Modularity may be partially due to the use of geographically distinct 'bull areas' (Croze 1974) during the inactive state (manifested in the study system as an 'east' versus 'west' distinction), when individuals focus on foraging rather than mate searching. Such spatial segregation probably facilitates repeated encounters and the emergence of conspecific preferences, although, by and large, our sample of focal males inhabited the western bull area. In the Samburu system, mature males focused their sexually active states on one of the three time periods coinciding with female receptivity (Rasmussen 2005; Wittemyer et al. 2007a). This temporal segregation in sexual activity with attraction to the same resource, estrus females, also may serve to structure social contacts of males using the same areas. This is consistent with the observation that modularity tends to be higher in the sexually active state. Although modularity values were unlikely to have arisen by chance, they were nevertheless very weak relative to those found in female African or Asian elephants, *Elephas maximus* (de Silva & Wittemyer 2012), perhaps a manifestation of the lower level of sociality in males (Lee et al. 2011; Chiyo et al. 2011). The weakness of the modularity and the lack of obvious drivers of the structure make inference difficult.

All ego-network metrics, except betweenness in the sexually active state, were significantly different from expectations based on randomizations of association (Permutation I). Individuals formed larger and better connected networks when sexually inactive relative to when

active, an outcome that was the opposite of expectations based on randomization by state

(Permutation II). Networks are likely to be structured by the different levels of competition and

motivations for aggregating across sexually active and inactive periods (discussed above).

Although we did not investigate the costs and benefits of grouping among males between sexual

states, our finding that most observed ego-network values were unlikely to have arisen by chance

indicates that further work targeting such shifting cost/benefit ratios may be fruitful.

Network centrality metrics measure the extent to which an individual is a social hub, and

they can potentially be used to discern individuals that are important for the structural integrity

of networks. Chiyo et al. (2011) found that network centrality (measured as eigenvector

centrality) was positively correlated with age in their study of male sociality in Amboseli

National Park, Kenya, suggesting a possible function of older individuals in maintaining social

cohesion. In contrast to the Amboseli study, we found a significant negative correlation between

age and eigenvector and betweenness centrality measures when bulls were sexually active and

found no significant relationship when sexually inactive. The significant negative correlation

between age and eigenvector (as well as betweenness) centrality when bulls were sexually active

could be due to increasing temporal asynchrony in sexual activity with age that is inherently

driven by avoidance of overlap with older, sexually active bulls (whose sexually active periods

are more synonymous with aggressive musth).

Future Directions

The duration of sexually active periods in male elephants decreases with age as these

periods become more synonymous with musth and therefore more energy intensive (Rasmussen

2005). In addition, younger bulls in the Samburu system that did not experience musth tended to

have two sexually active periods annually whereas older bulls had one (Rasmussen 2005). This

suggests that the duration of overlap in motivational state between two bulls will be dynamic

over the course of their lives and, therefore, their potential and motivation to associate may vary

over time. State-specific analyses as conducted here are essential to identify and understand such

dynamics, and more broadly to parse out the potential drivers of complex behaviors in dynamic

social systems. Our analyses suggest that not controlling for inherent structure that influences the

ability of individuals to associate can strongly affect the results and interpretation of social

dynamics.

Time-ordered network analyses and approaches like the exponential-family random

graph model (ERGM) or the multiple regression quadratic assignment procedure (MRQAP) may

be particularly helpful for understanding state-dependent networks (Blonder & Dornhaus 2011;

Pinter-Wollman et al. 2013), but such approaches require large volumes of data (beyond that

available here). The present study represents a 4-year time window, which is a snapshot

considering elephants can live up to 6 decades in the wild (Moss 1988). More detailed behavioral

observations and longitudinal data are needed to address temporal changes in association within

a state-based framework and to test alternative hypotheses about their social function.

Unfortunately, the Samburu population continues to experience high rates of human-caused

mortality that have strongly altered the sex and age class structure, particularly among males

(Wittemyer et al. 2011, 2013). As a result, the majority of the individuals in this study are dead,

precluding further research into the drivers and structure of long-term bonding among these

males. The differences in social properties among age classes documented here and elsewhere

(e.g. (Chiyo et al. 2011)) suggest that such age-selective harvest will impact the social structure

of a population. Further work addressing whether and how bulls compensate for the loss of age-

mates as they mature may help to elucidate the driving costs and benefits of association among males.

Chapter 3: Vertical transmission of social roles drives resilience to poaching in elephant networks[2]

Introduction:

Network topology determines process direction and strength, from information flow on the internet and electrical transmission on power grids (Watts & Strogatz 1998) to eco-evolutionary processes like sexual selection (Oh & Badyaev 2010), disease transmission (Naug 2009), and cultural exchange (Allen et al. 2013). Network perturbations threaten connective integrity, with implications for functionality and the benefits that individual components derive from structure (Fewell 2003; Phan & Airoldi 2015). Targeted removal of nodes may lead to destabilization, a shift in structure reflective of shifting optima, or regeneration of original structure (O'Donnell 1998; Flack et al. 2006; Naug 2009; Barrett et al. 2012). While theoretical work has demonstrated that redundancy in complex networks (Albert et al. 2000) and redirection of ties following removal of highly connected nodes can lead to structural resilience (O'Donnell 1998; Santos et al. 2006; Zhong et al. 2011), whether these or alternative processes occur in evolved systems requires investigation. There is evidence for functional collapse after the removal of key social hubs in the few animal studies on perturbation in complex social networks (O'Donnell 1998; Flack et al. 2006). However, these studies of natural networks are often short term or conducted in captive systems. *In situ* and longer term studies will illuminate how natural networks respond to perturbation.

Elephant populations have experienced a resurgence in ivory poaching over the last decade, which has targeted older cohorts for their larger tusks (Wittemyer et al. 2013, 2014). The importance of older elephants is well recognized, raising concerns about the impacts of age-selective poaching on population function (McComb et al. 2001). Elephants maintain complex societies, characterized by clearly detectable social tiers (strongly cohesive core groups nested within moderately cohesive bond groups, which in turn are nested within less cohesive clan groups) (Wittemyer et al. 2005b) and heterogeneously distributed social ties, with older females serving as connectivity hubs (McComb et al. 2001). Older elephant removal is analogous to the targeted knockouts of highly connected nodes in other networks (Albert et al. 2000; Flack et al. 2006). Disproportionate removal of old individuals may therefore reduce the potential benefits of grouping, resulting in disintegration of structure organized around matriarchs. However, novel bonding after increased mortality has been recorded in elephants (Charif et al. 2005; Wittemyer et al. 2009), and may be a mechanism for social resilience congruent with compensatory behavior following uncontrolled knockouts in other species (Engh et al. 2006; Barrett et al. 2012), but the emergent patterns of these relationships in the context of changing harvest conditions are not understood.

Using the context created by this selective harvest, we investigated emergent grouping patterns among individually identified adult female elephants in northern Kenya's Samburu and Buffalo Springs National Reserves (0.3-0.8° N, 37-38° E) over a sixteen year period (Wittemyer et al. 2013, 2014). We quantified different social metrics (ego-network properties and hierarchical grouping structure) to elucidate if and how elephants, like individual agents in theoretical models, reconstruct their social ties following disruption and to characterize the impact of their behavioral responses on broader network structure. We investigate the interaction

between past and present social circumstance using longitudinal demographic and association data to assess: 1) the degree to which elephant social structure is robust to endogenous perturbations, and 2) the mechanisms by which social robustness occurs. With its salient baseline social features, long-term dataset, and current ivory poaching crisis, this study system provides a rare opportunity to test theoretical models on the resilience and drivers of complex social networks, as well as provides empirical insight into how elephant behavior is affected by illegal killing.

Methods:

Data Collection

The unfenced study system is semiarid savannah receiving approximately 350 mm of rain annually in two wet seasons (Barkham & Rainy 1976). When elephants were encountered along four established reserve transects, the date, time, GPS coordinates, group size, individuals present, and observation accuracy were recorded. Elephants were considered to be associating when behaviorally coordinated and spatially cohesive within 500 m of an observer-estimated center (Wittemyer et al. 2005b). Focal interaction data were collected for 30-minutes or less in a sampling day, during which all interactions with conspecifics were recorded (Archie et al. 2006). Data were collected across all seasons. Observations were conducted noninvasively (IACUC 12-3414A) and with permission of the Kenya Wildlife Service, the Samburu and Isiolo County Councils, Colorado State University, and Save the Elephants.

Data Analysis

We investigated network properties in our study population across three sampling periods representing different ecological and harvest conditions: the moderate productivity, low poaching period T1 (June 1998 – May 2001), the high productivity, low poaching period T2 (June 2001 – August 2004), and the moderate productivity, high poaching period T3 (June 2012 – July 2014). A severe drought in 2009 was an additional source of disruption prior to T3 (Wittemyer et al. 2013).

To ensure observation consistency and quality, we only included observations for which all breeding females present were identified and only used observations conducted by three primary observers. We limited analysis to parous females, where females were considered parous starting in the month in which they had their first calf. We compared age distributions of females across periods using Kruskal-Wallis chi-square tests. We used the simple ratio index as an association index (AI) to measure strength of association between pairs of females: $AI = \frac{N_{AB}}{N_A + N_B + N_{AB}}$, where N_{AB} is the number of observations for which both individuals were in the same group, and N_A and N_B are the number of observations when A was without B and B without A, respectively (Ginsberg & Young 1992). A modified approach was applied where AI values were calculated only during periods when dyad members were parous and alive on the date of the observation, thereby controlling for demographic changes over time (Whitehead et al. 2005; Goldenberg et al. 2014). We calculated AI separately for each of the three sampling periods.

To limit bias introduced by small sample size, we only included females observed 10 times or more within a sampling period ($N_{T1} = 97$, $N_{T2} = 130$, $N_{T3} = 120$) (Whitehead 2008). We used AI values to examine structure at the individual and population scales using ego-networks and cluster analyses, respectively. We constructed distance matrices (distance = 1 – AI) and

clustered individuals using Ward's linkage rule (Romesburg 1984; Wittemyer et al. 2005b). We plotted the cumulative number of bifurcations for each 0.05 increment in cluster tree height to locate points of structural change, where significant slope changes on the cumulative bifurcation plot (using Mann-Whitney U tests) were identified as points at which clustering patterns change (Wittemyer et al. 2005b; de Silva & Wittemyer 2012). All individuals represented on a unique, contiguous branch below the identified knot value were considered a group.

We first performed this procedure with all females in each sample to determine core group structure. We then determined the oldest female (matriarch) of each core group and conducted a separate cluster analysis using matriarchs as representatives of core groups to more clearly delineate higher order structure that may be dampened by the strong associations within core groups when all individuals are included (Wittemyer et al. 2005b). Because bond and clan groups are most apparent during the wet season (Wittemyer et al. 2005b), we recalculated AI between matriarchs using observations during the wet season, where wet season was defined for the study system using threshold normalized difference vegetation index values (Wittemyer et al. 2007a). As with previous AI calculations, we excluded matriarchs seen fewer than 10 times (N_{T1} = 39, N_{T2} = 49 N_{T3} = 39).

We constructed networks from AI values, where nodes represent females and ties between nodes represent AI strength (Krause et al. 2009), visualizing networks using Gephi (v.0.8.2) (Bastian et al. 2009). We then calculated ego-network metrics using the *statnet* package for R (Handcock et al. 2003). Because elephants are long-lived and age is associated with increased group survival (McComb et al. 2001), we used Pearson correlations to compare metrics to age, where age at the midpoint of each sampling period was used. *P*-values were

Bonferroni-adjusted where multiple comparisons were used. Statistical analyses were done in R

(v.3.0.3) (R Core Team 2013).

Identification of Mechanisms Driving Structure

We used Mantel tests to compare matrices of AI values to understand whether behavior is

consistent within individuals and within mother-daughter and other pairs. We conducted four

sets of comparisons: 1) AI among individuals present in two adjacent sampling periods, 2) AI

among mothers and AI among their daughters within the same period, 3) AI among mothers in

one period and AI among their daughters in the following period, and 4) AI among daughters in

T3 and among oldest bond group members outside daughters' core groups in T2. The third

category was subdivided for the T2-T3 test using mother-daughter pairs for which the mother

was dead in T3 and for which the mother was alive in T3 to illuminate whether association

indices are correlated with a history of family mortality. For all generational tests, the order of

daughters in matrix rows and columns corresponded to the ordering of the older generation

matrix, so that corresponding cells in the two matrices represented relevant matched pairs. We

ran one thousand permutations for each Mantel test.

To address the mechanisms related to node-level metrics, we implemented generalized

linear models (GLMs) predicting a female's degree, betweenness, and clustering coefficient

using Poisson, gamma and beta regressions, respectively, on a subset of females from T3 for

which mothers were known to be alive in T2 and covariates were available (N = 67). We used a

quasi-GLM to correct for overdispersion in the Poisson model, adjusting coefficient standard

errors by the overdispersion parameter (Zuur et al. 2009). Explanatory variables included age in

T3, mother's age in T2, core group size in T2, core group size in T3, bond group size in T2, bond

group size in T3, number of calves in T3, mother's degree in T2, mother's betweenness in T2, mother's clustering coefficient in T2, and whether the mother was alive in T3.

To further investigate behavioral mechanisms we used focal follow data of affiliative behaviors directed toward conspecifics in T3. For each female observed for at least one hour while feeding, we combined all follow data and calculated the rate at which she directed affiliative behaviors (e.g. body rubbing, trunk touching, greeting) toward non-core group members. We conducted a Spearman correlation of affiliation rate with birth year to elucidate whether age structures social initiative.

Results and Discussion:

Despite the population changes over time (Fig. 3.1), agglomerative clustering of elephant pairs (dyads) revealed hierarchically structured social organization across the study, with distinguishable core and bond groups with similar group size AI values (Fig. 3.2; Table 3.1) (Wittemyer et al. 2005b). Structure was conserved despite ~70% turnover in the population's adult females and a significant decline in average age between T1 and T3 (Age $_{T1}$-Age $_{T3}$: χ^2 = 6.47, df = 1, p-value < 0.05). The matrilineal composition of core and bond groups, however, changed over the study, particularly where previously distinct matrilines fused after groups were affected by mortality (Fig. 3.3). Eight of nine females that fused into a different core group in T3 had lost their mothers, and seven of nine core groups that fused into different bond groups in T3 lost their matriarchs (defined here as the oldest member of the group) between T2 and T3.
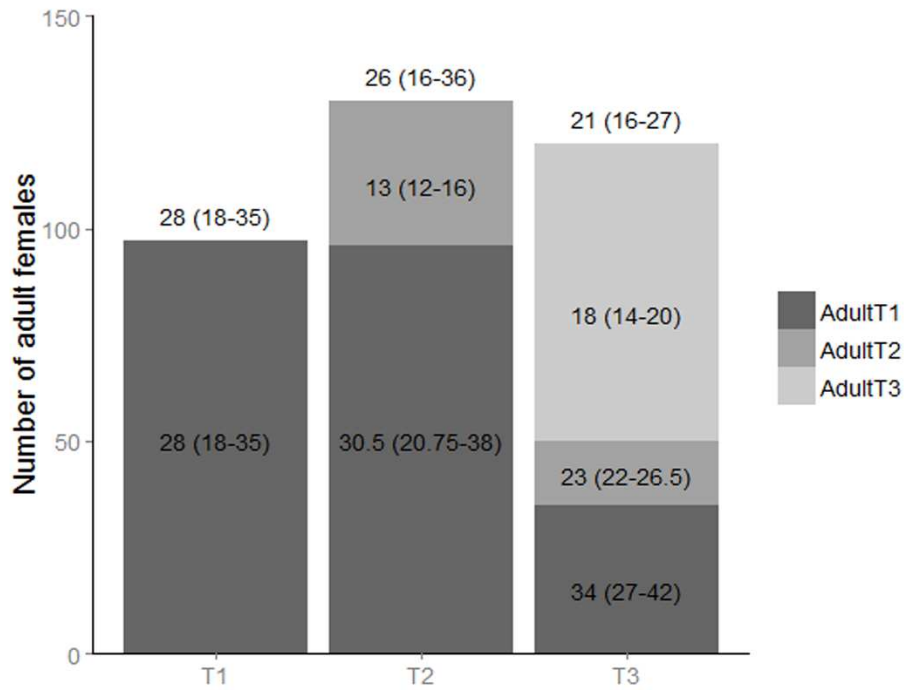
Figure 3.1: Study females changed with time due to maturation and mortality, with a 70% turnover in the population's adult females over the study and a resulting downward shift in age. Cohorts of females are shaded based on when an individual was first present in the analysis. Median ages (with interquartile ranges) for cohorts (within bars) and overall (above bars) are presented.
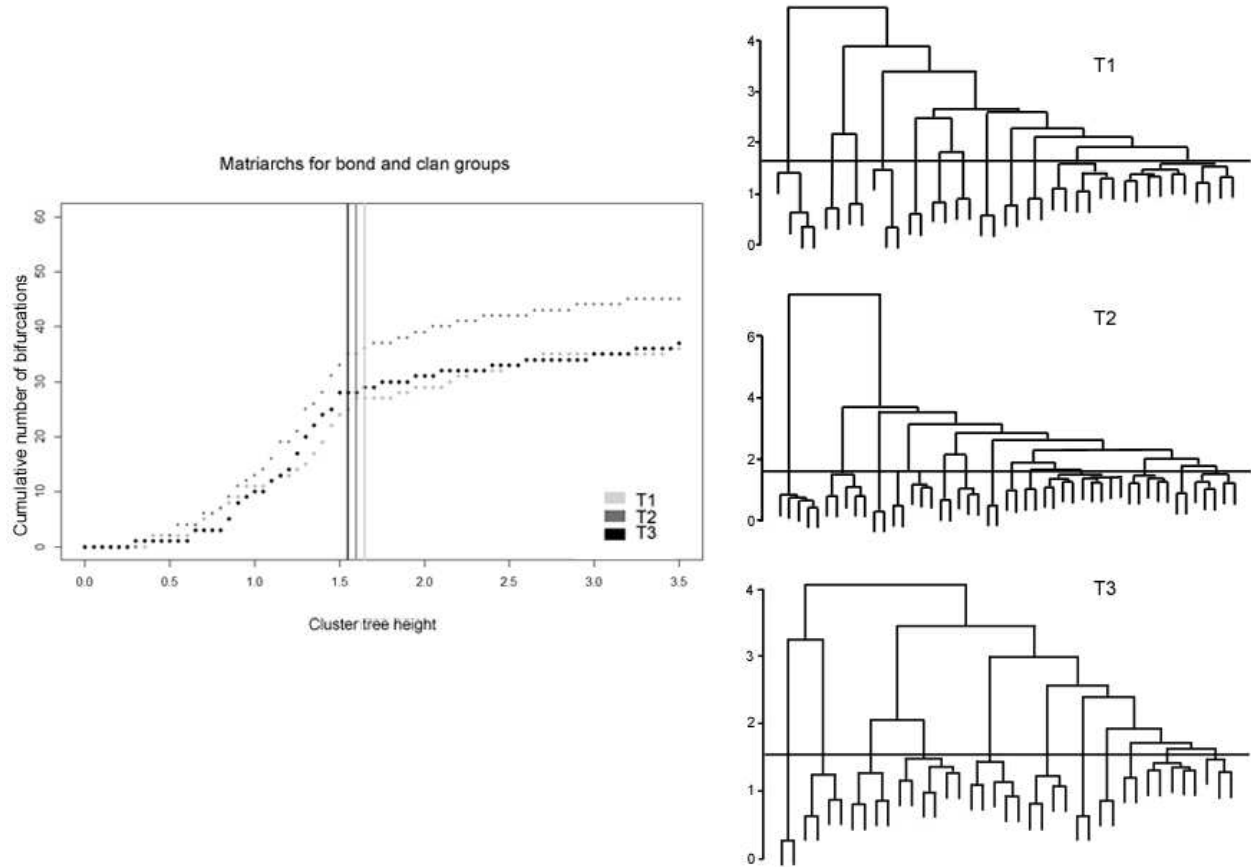
All females for core groups
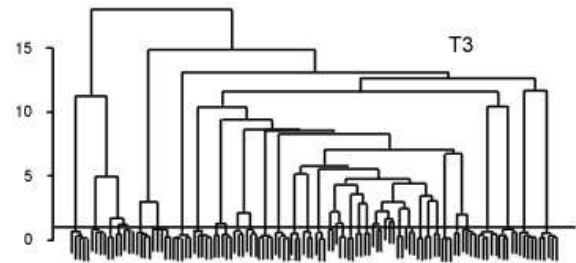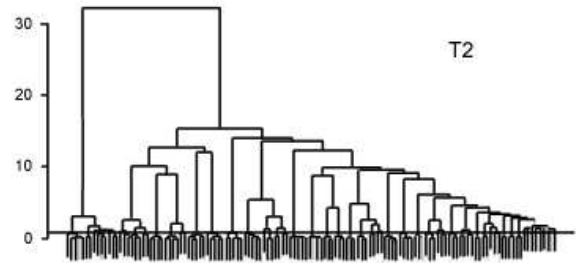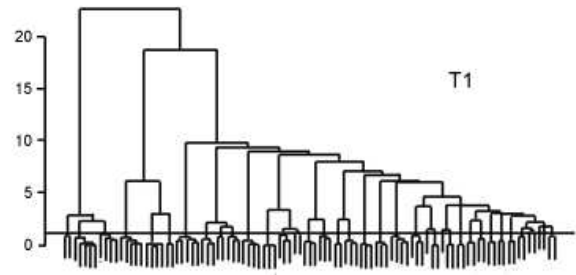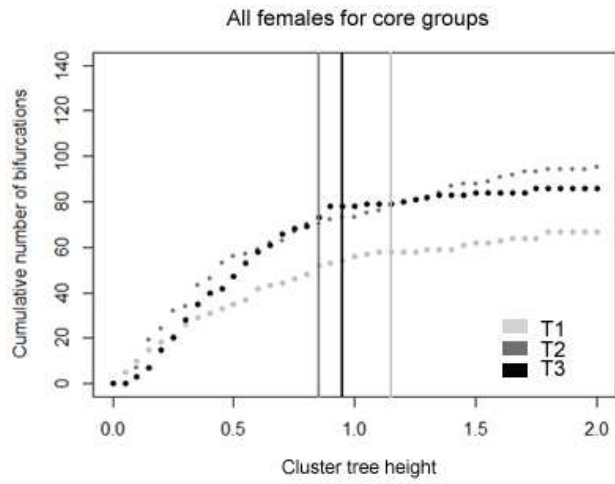
Figure 3.2: Cumulative number of bifurcations from Ward's clustering trees for every 0.05 increment in cluster tree height. Results are shown for the analysis using all females (top) and core group matriarchs only (bottom). Cutoff lines on cluster trees (horizontal) and cumulative bifurcation diagrams (vertical) indicate structural change points demarcating core groups (top) and bond groups (bottom).

Table 3.1: Cluster tree height values used as cutoffs to define structural tiers (knots), and the compositional characteristics of delineated groups.

| Tier	T1				T2				T3			
	Knot value	Number of groups	Median (IQR) group size	Median (IQR) AI	Knot value	Number of groups	Median (IQR) group size	Median (IQR) AI	Knot value	Number of groups	Median (IQR) group size	Median (IQR) AI
Core	1.15	39	7.5 (4.75-10.5)	0.76 (0.58-0.92)	0.85	59	6.5 (3.5-9.75)	0.83 (0.73-0.89)	0.95	42	7 (5-11.25)	0.77 (0.72-0.87)
Bond	1.65	12	21 (12.13-29.13)	0.46 (0.38-0.54)	1.6	14	17.75 (14-34.63)	0.33 (0.21-0.53)	1.55	11	25.5 (19-37.25)	0.30 (0.16-0.40)
Clan	2.75	4	33.5 (28.75-80.25)	0.44 (0.32-0.47)	2.4	7	32 (23.5-38)	0.27 (0.23-0.47)	------	------	------	------
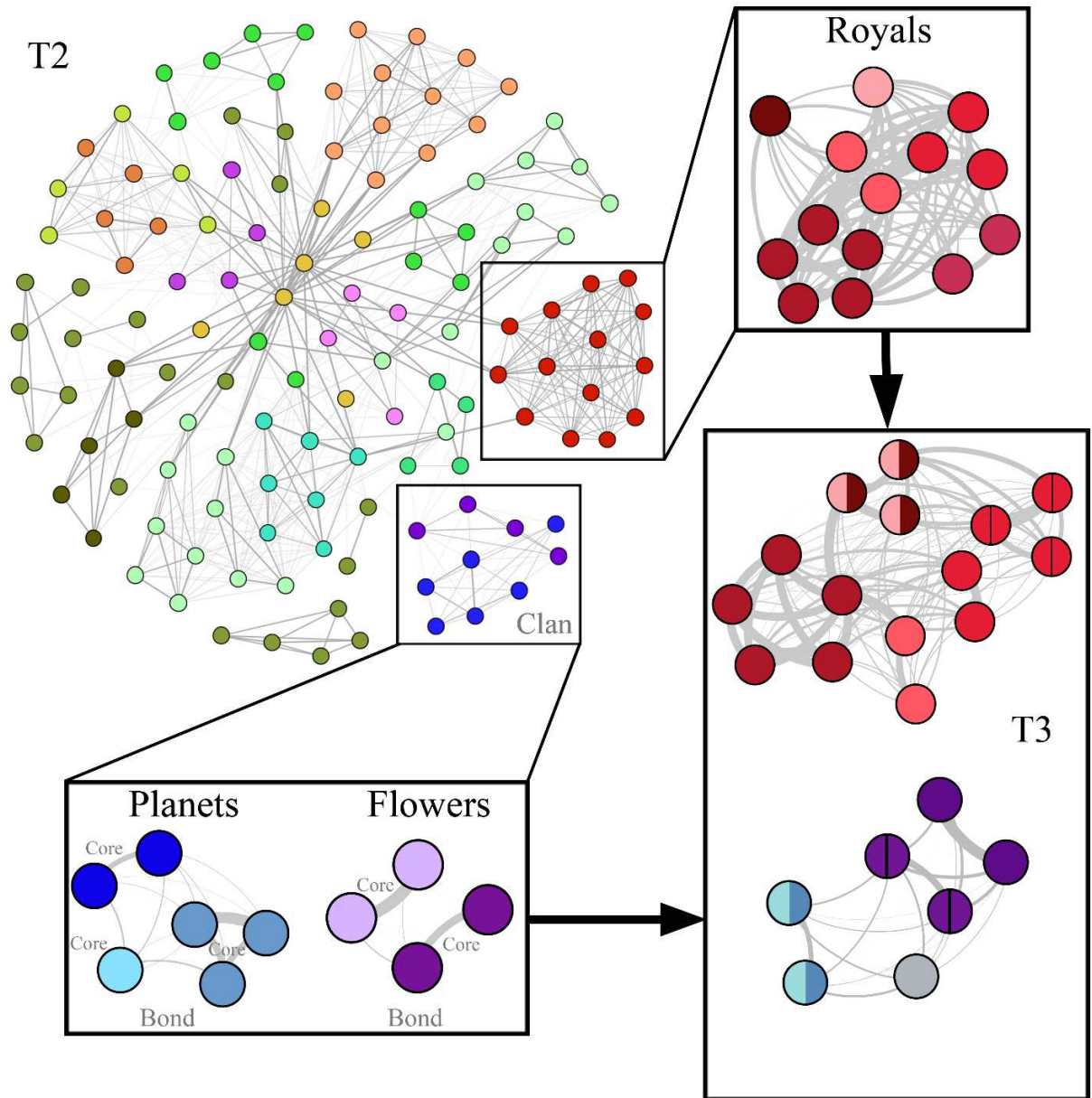
Figure 3.3: Despite changes in matriline composition over time, core and bond group structure are maintained in elephant society. Nodes in the T2 population network (top left) represent individual female elephants, width of edges between nodes represents association index strength, and colors differentiate bond groups. Insets of three of these bond groups (the Royals, a group that experienced low adult mortality, and the Flowers and Planets, groups that experienced high adult mortality) are shown. Matching nodes represent distinct core groups, where hybridized nodes represent fusion of matrilines and black lines through nodes represent core groups that fissioned after T2. The Flowers and Planets merged into one bond group by T3. Gray words distinguish the nested tiers of female elephant society.

In contrast to core and bond groups, the inability to detect clans in T3 may suggest that this structure was not beneficial during the disrupted period or that clans are a manifestation of lost links among older age cohorts. It has been suggested that as young females reach breeding age, resource competition within groups becomes more intense and older females lead permanent fissions of core groups into discrete core groups that together comprise a bond group (or fissions in bond groups into discrete units that comprise a clan group) (Wittemyer et al. 2005b). The altered age structure after poaching reduced the number of connected multi-generational lineages, potentially severing the foundational connections necessary for clans to emerge.

In this population, the relationship between age and network position appears to be relative: the oldest individuals available have higher degree and betweenness centrality. Degree, the number of contacts per individual, was significantly positively correlated with age in all sampling periods (T1: $r = 0.308$, $p < 0.01$; T2: $r = 0.335$, $p < 0.01$; T3: $r = 0.281$, $p < 0.01$). Betweenness, the number of shortest paths that go through an individual within the larger network, was significantly correlated with age in T2 and T3 (T1: $r = 0.137$, $p = 0.180$; T2: $r = 0.212$, $p < 0.05$; T3: $r = 0.221$, $p < 0.05$). Thus, the oldest individuals in the population tended to serve as social bridges (higher betweenness) and hubs (higher degree). In extreme cases, we witnessed this clustering even within highly disrupted families, where surviving relatives coalesced around the oldest female in the group even if she was a juvenile. These findings indicate that the overall structure of female elephant society is resilient regardless of age composition.

To investigate the role that older individuals play in structuring social environments, we examined the relationship between the social positions of daughters and their mothers (Wittemyer et al. 2009) or their bond group matriarchs using Mantel tests of dyadic AI. We first

tested associations among individuals present in more than one period to determine whether

elephants are socially consistent over time. Second, we tested whether mothers' associations with

each other were correlated with their daughters' relationships. AI of individuals over time and in

mother-daughter pairs both within and between sampling periods were all significantly

correlated (Table 3.2), indicating that individual contact patterns were consistent over time and

that closely associated mothers have daughters that are also closely associated. This correlation

held even after a mother died. To assess the possibility of the alternative hypothesis that

daughters' social positions are more a function of their broader social environment than that of

their mothers', we also compared the social associations of these daughters with those of their

oldest bond group member outside of their core group. While significant, the correlation was

considerably lower than that between mother-daughter pairs (Table 3.2).

Table 3.2: Mantel test correlations comparing association indices within individuals across time
and between generations within and across time periods.

	r	p-value
Within individuals across periods	0.94 (T1-T2)	< 0.01 (T1-T2)
	0.89 (T2-T3)	< 0.01 (T2-T3)
Between mother-daughter generations within periods	0.94 (T1)	< 0.01 (T1)
	0.95 (T2)	< 0.01 (T2)
	0.88 (T3)	< 0.01 (T3)
Between mother-daughter generations T1-T2	0.90	< 0.01
Between mother-daughter generations T2-T3, mother alive in T3	0.84	< 0.01
Between mother-daughter generations T2-T3, mother dead in T3	0.89	< 0.01
Between non-mother-daughter generations within bond groups	0.64	< 0.01

Similar to Mantel tests, GLMs showed that mother betweenness in T2 was the strongest

predictor (significantly positive) of daughter betweenness in T3 (Table 3.3). Network position

was unrelated to mother death. Age was positively correlated with social position, but was not as important in predicting daughters' positions. While age was significantly correlated with social position in our univariate analysis at the population level, the GLM was a multivariate analysis focused on a narrower age distribution (11-27 year olds rather than 9-58 year olds). Collectively, these results suggest that the conserved structure in elephant social networks was a function of individuals maintaining their social positions over time and daughters replicating the contact patterns of their mothers.

Table 3.3: Standardized coefficient values for GLMs predicting degree, betweenness, and clustering coefficient for a subset of females in T3 for which mothers in T2 were known and covariates were available (N = 67). Significant coefficients (p-value < 0.05) are demarcated in bold.

	Degree	Betweenness	Clustering coefficient
Age T3	0.02450	0.07286	0.03655
Core group size T2	0.02992	0.15657	-0.07387
Core group size T3	-0.03377	-0.07788	-0.01919
Bond group size T2	0.04818	0.12688	-0.06959
Bond group size T3	-0.01597	-0.05627	**0.10363**
Calves T3	-0.01728	-0.00050	-0.06568
Mother alive in T3	-0.02223	0.03032	-0.06620
Mother age T2	0.02905	0.06079	-0.07852
Mother degree T2	0.05437	0.11820	-0.04866
Mother betweenness T2	0.04434	**0.44652**	-0.11417
Mother clustering coefficient T2	0.05688	0.29848	-0.06525

While lineage-replicated behavior was a key component in network resilience, active contact building revealed the extent to which this replication is learned. Birth year was positively correlated with initiation of affiliative behaviors toward non-core group members ($\rho = 0.45$, $p <$

0.01; Fig. 3.4), indicating that social exploration was primarily conducted by younger elephants. Juveniles actively built their contacts within the context created by their mothers, which is likely the means by which daughters replicated the network positions of their mothers. This mechanism allows individuals whose mothers' close contacts are gone to strengthen bonds, conserving the general network properties that they experienced before disruption. Fusions of previously distinct matrilines occurred in groups where removal of most adult elephants meant daughters could not replicate the social networks of their mothers (Fig. 3.3). This active contact building often involved strengthening bonds with elephants that were distant contacts in their mothers' networks.
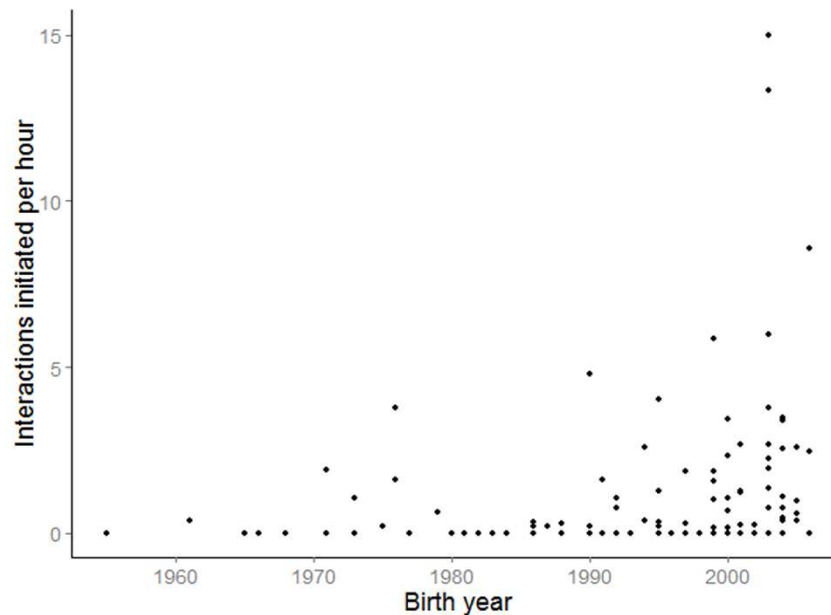
Figure 3.4: Younger elephants initiate affiliative interactions toward non-core group members at a higher rate than older elephants.

The remarkable stability in elephant population structure across periods of demographic change was attributable to the ability of young elephants to emulate the contact patterns of their

mothers within a hierarchically clustered context. The social arena set by the grouping decisions of matriarchs may buffer network collapse by providing maturing females with social opportunities from which they can build their own contact structure. Our finding that younger females are more interactive with individuals outside of their immediate core group underscores the active role that they take in shaping their own contacts and suggests this emergent property is more a function of learning than of classic inheritance (McDonald 2007). Thus, the apparent inheritance of social position appears to be an interaction between the tiered sociality defined by older relatives and the active maintenance and generation of social ties by younger females (Silk et al. 2004). We did not explicitly assess the role of primary productivity here, but ecological dynamics are likely important in structuring networks, as elephant associations are known to reflect seasonal changes (Wittemyer et al. 2005b). Further analysis of the relationship between productivity and network structure merits investigation. Although this study demonstrates structural resilience in elephant society regardless of age composition in the population, further study is needed to understand the fitness repercussions of family mortality and loss of matriarchs. Our work highlights the potential that empirical systems offer for understanding of social network evolution and function and demonstrates the mechanism by which network integrity is maintained in this social species.

Chapter 4: The social costs of being an orphan in elephant society

Introduction:

Social bonds formed early in life may define fitness trajectories in long-lived, social species (McDonald 2007; Stanton & Mann 2012). As the loss of social partners can be a challenge in such societies, the ability of young animals to buffer against perturbations to their social environment by engaging in compensatory behavior may be essential in order to survive into adulthood and successfully reproduce (Engh et al. 2006; Nunez et al. 2015). A growing body of literature is documenting the importance of established social bonds for later challenges (Silk et al. 2003; McDonald 2007; Nunez et al. 2015; Goldenberg et al. 2016), but the processes by which animals establish and maintain bonds in dynamic contexts remains poorly resolved. Fission-fusion dynamics, in which animals vary the size and composition of their social groups, allow animals to adjust to changing competitive and cooperative scenarios (Aureli et al. 2008). Understanding how animals generate the social environments that may benefit them in the long-term and how they are received by potential partners can advance understanding of the form and function of fission-fusion sociality.

Bond strength and relatedness are highly correlated for many social animals (Silk 2007), but cooperative bonds among nonrelatives in several species have served to identify a range of social strategies (Griffin & West 2002; Cameron et al. 2009; Clutton-Brock 2009). For example, vampire bats regurgitate for unrelated roost mates to expand their future meal donor network (Carter & Wilkinson 2015), and hyenas choose social partners based on dominance rank to maximize feeding opportunities (Smith et al. 2007). Social expansion beyond kin has also been recorded in more reactive circumstances. For instance, army ants that lose their queen fuse with

neighboring colonies despite low relatedness to improve reproductive success (Kronauer et al. 2010), and elephants (Wittemyer et al. 2009; Goldenberg et al. 2016) and humans (Goldenberg 2009) strengthen bonds with non-kin in response to severe societal disruption. Reactive responses like these are especially illuminating of network formation and partner selection processes.

By changing the availability of bonding partners, selective removal experiments with known individuals are a powerful way to characterize animal response to an altered social context. Previous experimental work in captive colonies of wasps (O'Donnell 1998) and pigtailed macaques (Flack et al. 2005) has demonstrated the role of individual actors in maintaining or failing to maintain normative population structure. Similarly, simulation studies have pointed to individual behavioral rules as determinants of social patterns following knockouts (Santos et al. 2006). Such removal approaches may be informative in contextualizing the ecology and evolution of social behavior in non-captive systems but are challenging to implement *in situ*.

Female African elephants (*Loxodonta africana*) provide a rare evolved system in which to investigate the mechanisms of bonding following selective removals because they are highly social (Douglas-Hamilton 1972; Moss 1988; Wittemyer et al. 2005b), their sociality is thought to be closely tied to fitness (McComb et al. 2001; Wittemyer et al. 2007b; Lee et al. 2016), and recent mortality is altering social environments (Wittemyer et al. 2013; Goldenberg et al. 2016). Elephant populations have been experiencing increased ivory poaching over recent years, typically targeting older elephants for their larger tusks (Wittemyer et al. 2013, 2014; Chiyo et al. 2015). Older female elephants are important members of family units that act as knowledge repositories (McComb et al. 2001), affect the calving success of family members (Lahdenperä et

al. 2016; Lee et al. 2016), and provide access to preferred resources through their dominance status and ecological knowledge (Wittemyer et al. 2007b; Foley et al. 2008). Loss of old females therefore presents a serious challenge for the elephants bonded to them, but fission-fusion dynamics may facilitate compensatory bonding to overcome these challenges (Farine et al. 2015). Though this particular harvest pressure is recent, elephant evolutionary history has been punctuated by die-offs from hunting and drought (Foley et al. 2008; Yravedra et al. 2012); social challenges like these are therefore not evolutionarily novel.

The elephant population that uses the Samburu and Buffalo Springs National Reserves in northern Kenya has been studied continuously since 1997 through a project that maintains individual-based records of births, deaths, and social associations (Wittemyer 2001). A period of high mortality in older age cohorts began in 2009 in this population, initially with a severe drought followed by a rise in ivory poaching. The mortality affected families differently, creating a natural removal experiment characterized by heterogeneous age structures among families (Wittemyer et al. 2013). Previous work in the population has revealed that social restructuring occurs following deaths (Wittemyer et al. 2009; Goldenberg et al. 2016), but the behavioral processes that facilitate integration and novel bond formation remain unclear.

We recorded the social interaction behavior of females of diverse ages, developmental stages, and histories of family mortality to elucidate the processes by which individuals restructure their social networks after disruption. We treated the behavior of non-orphans belonging to their natal groups as a control. We tested the following hypotheses: 1) to compensate for the potentially greater cost they experience after losing mature social partners, young orphans in non-natal groups will initiate affiliative interactions more than will older elephants, non-orphans, or orphans in their natal groups; 2) disruption and social integration will

be associated with greater social costs, but orphans in non-natal groups will adjust their behavior to minimize social costs and maximize social benefits more so than non-orphans or orphans in natal groups; 3) because matriarchs confer the greatest advantages to their associates in elephant society, we tested whether orphans direct interactions toward matriarchs relative to alternative entry points to social integration. We discuss the implications of results for social bond formation and resilience to disturbance.

Methods:

Data Collection

We collected data in the Samburu and Buffalo Springs National Reserves in northern Kenya (0.3-0.8°N, 37-38°E) between May 2012 and April 2015. When we encountered groups of elephants along established transects we recorded the date, time, activity, GPS coordinates, identity of individuals present, and accuracy of the observation according to protocol (100% identified, breeding females identified, or incomplete identification; Wittemyer et al. 2005b), where groups were considered aggregations of elephants that were behaviorally coordinated and spatially cohesive within 500 m of an observer-estimated center (Wittemyer et al. 2005b). We registered new calves as they were encountered, and assigned ages to older elephants using established estimation methods (Moss 1996). We recorded missing individuals and considered them dead when absent from their core social groups on consecutive sightings or when identified from a carcass (Wittemyer et al. 2013).

We conducted focal sampling ('focal follows') during feeding and resting activities ($N_{follows\_feeding} = 1568$, $N_{follows\_resting} = 278$; $N_{hours\_feeding} = 435.75$, $N_{hours\_resting} = 79.93$) on a subset of females chosen to represent a range of disruption ($N_{orphan} = 61$, $N_{non-orphan} = 39$), age (6 to 34

years), and development (preparous through multiparous). We divided follows into feeding and resting categories to control for activity-driven differences in interaction frequency. During focal follows we observed individuals and recorded all interactions with other elephants and their directions (Altmann 1974), defining interactions from the literature (Archie et al. 2006; Poole & Granli 2011) (Table 4.1). Focal follows continued until one of the following occurred: 1) the animal went out of sight, 2) the animal switched activity, or 3) the follow reached 30 minutes. We completed no more than one follow in each activity on a given animal in a given sampling day to control for behavioral autocorrelation, such that a maximum of 60 minutes was collected on each animal per day (i.e., 30 minutes feeding, 30 minutes resting). The median lengths of feeding and resting focal follows were 14.75 and 15 minutes, respectively. We collected observation and interaction data across both wet and dry seasons and only collected interaction data when elephants appeared to be unperturbed by the presence of the research vehicle (i.e., did not direct attention or behaviors towards the research vehicle).

Table 4.1: Ethogram of elephant interactions

	Interaction	Description
Affiliative	Body rub	*A* rubs *B* with her body
	Ear brush	*A* brushes her ear on *B*
	Greeting	*A* rumbles when *A* and *B* meet
	Head rub	*A* rubs *B* with head
	Herd	*A* rubs *B* resulting in their coordinated movement
	Playful fight	*A* and *B* intertwine heads and spar with no escalation
	Playful head rest	*A* rests head on *B*'s body
	Test mouth	*A* holds trunk to *B*'s mouth
	Trunk grasp	*A* grabs *B*'s trunk
	Trunk touch	*A* touches *B* with trunk
	Tusk rub	*A* rubs *B* with tusk
Aggressive	Displacement	*A* approaches *B*, *B* leaves
	Forward trunk swing	*A* swings trunk in direction of *B*
	Kick back	*A* kicks *B* with back foot
	Pursuit	*A* chases *B*
	Push	*A* pushes *B*
	Stand tall	*A* faces *B* with head held above shoulders
	Supplant	*A* approaches *B*, *A* takes *B*'s place
	Tusk	*A* hits/pokes *B* with tusks
Exploratory	Trunk reach to smell	*A* holds her trunk in the direction of *B*
Submissive	Back toward	*A* moves toward *B* rear first
Alloparental	Allosuckling	*A* attempts to breastfeed from *B*
	Other	*A* protects/comforts *B* (a calf that is not her own; associated with calf crying or environmental stimulus)

Data Analysis

We used hierarchical Bayesian negative binomial regression models with uninformative priors to predict interactions in order to account for overdispersion, the large number of zeros in our count data, and individual heterogeneity (Kery & Royle 2016). To test our hypotheses related to the general social environment of orphans and the paths to social integration, we conducted two different sets of models structured on predictions of: 1) interactions for a given focal follow, and 2) interactions with a given social partner. Response variables explored in models were counts of affiliative, aggressive, submissive, exploratory, and alloparental interactions (see Table 4.1 for ethogram of interactions).

The counts of affiliative interactions per individual were combined for analyses, as were aggressive interactions (Table 4.1). Separate models were used to analyze counts of reception and initiation events to distinguish between the actions and acceptance of orphans. Because young calves were largely inactive while families rested, we did not assess alloparenting while resting. The recipients of backing toward and trunk reaching interactions were difficult to discern while animals were clumped together, precluding analyses of these interaction classes for resting elephants.

We fit models using Markov-Chain Monte Carlo (MCMC) by running three parallel chains of 100,000-500,000 iterations each depending on convergence time, which was assessed using trace plots and the Gelman diagnostic. The first 10% of iterations were discarded as burn-in after assessments. We ran models using JAGS (Plummer 2003) combined with the *rjags* package in R (R Development Core Team 2010; Plummer 2016).

In focal follow interaction models, the log length of the follow was included as an offset to control for observation time. In partner interaction models, we included the log length of the

sampling time during which both the focal animal and the social partner were alive to control for the potential for two individuals to interact. We standardized continuous predictor variables $\left(\frac{x_i - \mu}{\sigma}\right)$, where x_i represents variable x at observation i, and μ and σ represent the variable mean and standard deviation, respectively, prior to running models for ease of convergence and interpretation and varied the intercept by elephant to control for individual heterogeneity. The process model for the probability of an interaction was defined as:

$$\ln(\lambda_{i,j}) = \alpha_j + \boldsymbol{\beta} \boldsymbol{x}_{i,j} + \ln(\gamma_{i,j}),$$

where $\lambda_{i,j}$ is the expected interaction count for elephant j during focal follow i (for the set of models predicting interactions in a follow) or with social partner i (for the set of interactions predicting interactions with a partner), α_j is the random intercept for elephant j, $\boldsymbol{\beta}$ represents the vector of fixed effects coefficients associated with covariates $\boldsymbol{x}$, and $\ln(\gamma_{i,j})$ is an offset controlling for sampling effort. The conditional probability was defined as:

$$\left(y_{i,j} \mid \boldsymbol{\beta}, \alpha_j, \mu_\alpha, \tau_\alpha, r\right) \sim negbinom\left(r, p_{i,j}\right) \times$$

$$\boldsymbol{\beta} \sim normal(0, 0.1) \times$$

$$\alpha_j \sim normal(\mu_\alpha, \tau_\alpha) \times$$

$$\mu_\alpha \sim normal(0, 0.1) \times$$

$$\tau_\alpha \sim uniform(0.001, 100) \times$$

$$r \sim uniform(0, 100),$$

where μ_α and τ_α are the mean and precision of α_j, respectively, r is the dispersion parameter, and $p_{i,j}$ is the probability that an interaction occurs.

Predictor variables $\boldsymbol{x}$ spanned family history, group composition, demography, and ecological conditions. To define social context, we included covariates characterizing the aggregation of elephants during the focal observation (as defined in *Data Collection*) as well as

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the core group of the focal female. We assigned core group membership from which these latter

covariates were derived using structural change points on clustering trees (described at length

elsewhere: Romesburg 1984; Wittemyer et al. 2005b; Goldenberg et al. 2016), built using the

simple ratio index as a measure of association strength (AI: Cairns & Schwager 1987; Ginsberg

& Young 1992). Analysis was conducted on all females recorded in a completely identified

aggregation of individuals (N_{obs} = 1182; observation frequency among included individuals:

median$_{obs\ counts}$ = 35, inter-quartile range$_{obs\ counts}$ = 20.5-48.25). We defined a core group's

matriarch as its oldest member (Archie et al. 2006; Wittemyer & Getz 2007).

For the set of models predicting interactions during a focal follow, covariates included in

models were a binary variable delineating if a female's core group was her natal group (*natal*)

(Wittemyer et al. 2009; Goldenberg et al. 2016), a binary variable delineating if the focal

female's mother was dead on the day of the focal follow (*orphan*), matriarch age (*matriarch

age*), AI with matriarch (*matriarch AI*), mean AI within the core group (*mean AI*), number of

dispersal-aged males in the core group (*dispersing males*), core group adult to juvenile ratio

(*adult:juvenile*), core group size (*core size*), number of calves six-months old or younger in the

core group (*group young*), size of the aggregation (*aggregation size*), number of mature bulls (30

years or older or a bull of any age that was in musth) present in the aggregation (*mature bulls*),

focal female age (*age*), a binary variable delineating if the focal female was parous (*mother*), a

binary variable delineating if the focal female had a calf three-months old or younger (*own

young*), ecosystem average normalized difference vegetation index at the time of observation

(*NDVI*), and the time of day that the focal follow began (*time*). We assessed correlations among

covariates, and removed individual covariates where correlations exceeded |r|=0.6. Age and

whether a female was a mother were highly correlated (r=0.74-0.75), as were AI with matriarch

and mean AI within the core group (r=0.79-0.81). Whether the female was a mother and mean

AI within the core group were therefore not included in models, as the continuous predictor *age*

was more informative than *mother* and *matriarch AI* more directly addressed our hypotheses

than did *mean AI*. Several covariates controlled for behavioral variability without directly testing

hypotheses (i.e., *NDVI*, *time*, *aggregation size*, *core size*, *mature bulls*, *own young*,

adult:juvenile), and are not emphasized as we focus on reporting results directly related to our

hypotheses with relevance to elephant social strategies.

If models predicting interactions in focal follows showed differences between orphans

and non-orphans or between elephants in their natal group or non-natal group, we re-ran models

on a subset of data including orphans only ($N_{follows\_feeding}$ = 998, $N_{follows\_resting}$ = 186; $N_{hours\_feeding}$ =

280.38, $N_{hours\_resting}$ = 53.61), replacing the binary variable delineating orphans from non-orphans

with a continuous variable distinguishing the time (in days) the focal animal was orphaned (*time*

orphaned). This separate set of analyses allowed us to disentangle the temporal aspects of social

disruption and integration among orphans that may explain differences in social environments, as

well as differences between natal and non-natal orphans.

For the set of models predicting interactions with a particular individual throughout the

study, covariates were the absolute age difference between the focal animal and the social

partner (*age diff*), a binary variable delineating if the partner was a matriarch (*matriarch*), a

binary variable delineating if the partner was a young calf (defined as less than two years old for

more than half of the sampling period; *calf*), a binary variable delineating if the partner was the

focal animal's calf (*own calf*), a binary variable delineating if the partner was male (*sex*), a

binary variable delineating if the partner was from the focal animal's natal group (*natal*), a

binary variable delineating if the partner was not from the focal animal's natal group but was

from its current core group (*core*), and a binary variable delineating if the partner was a mother (females were considered mothers if they had at least one calf for more than half of the sampling period; *mom*). *Own calf* and *mom* were included to control for mother-calf interactions so that the patterns of interactions with other elephants could be distinguished. As with the set of models predicting interactions per focal follow, directions of interactions were also treated separately in this set of analyses (i.e., initiated vs. received). A similar process was used as with the first set of models whereby explanatory variables were examined for correlations > 0.6. *Mom* and *sex* were strongly correlated for models in which the focal animal was the recipient of aggressive interactions (r = -0.76-0.89). *Mom* was also correlated with *age diff* for the feeding recipient aggressive model (r = -0.60) and with *matriarch* for the resting recipient aggressive model (r = 0.61). *Mom* was therefore removed from these models. Interaction partners that directed aggressive behaviors to focal animals were never young calves or the calves of focal animals; these variables were therefore removed from relevant models. *Calf* was removed from the resting model in which focal animals were aggressive actors, as no aggressive interactions directed towards a young calf while resting were observed. Submissive and alloparenting interactions were not examined in predicting interactions per partner due to sample size limitations.

Results:

Orphan Affiliation Patterns

Contrary to Hypothesis 1, being an orphan did not clearly predict initiated affiliation, nor did age (Fig. A.1; Table 4.2). The received affiliation environment was clearly different between orphans and non-orphans in that non-orphans were more likely to receive affiliative interactions (Fig. 4.1), consistent with Hypothesis 2 that family disruption would be associated with greater

social cost. Further, in the orphan only subset, natal group membership was predictive of received affiliation in both activities (feeding and resting), supporting Hypothesis 2 (Fig. A.2; Table 4.3). The amount of time an elephant was orphaned was unrelated to the affiliation she received (Fig. A.2; Table 4.3).

Table 4.2: Coefficient estimates for models including orphans and non-orphans. Standard deviations are in parentheses. Models are listed in the top row and coefficients are listed in the first column.

	Initiating affiliative (feeding)	Initiating affiliative (resting)	Receiving affiliative (feeding)	Receiving affiliative (resting)	Initiating aggressive (feeding)	Initiating aggressive (resting)	Receiving aggressive (feeding)	Receiving aggressive (resting)	Initiating submissive (feeding)	Receiving submissive (feeding)	Initiating exploratory (feeding)	Receiving exploratory (feeding)	Initiating alloparenting (feeding)
Age	0.042	-0.048	0.270	0.027	0.642	0.498	-0.344	-0.216	-1.319	1.312	-0.094	0.209	-1.529
	(0.079)	(0.100)	(0.085)	(0.092)	(0.146)	(0.647)	(0.121)	(0.184)	(0.838)	(2.418)	(0.131)	(0.133)	(0.579)
Time	0.033	0.040	0.022	0.004	0.200	-1.432	0.159	0.034	0.472	0.994	-0.107	0.090	0.549
	(0.048)	(0.099)	(0.045)	(0.085)	(0.130)	(0.862)	(0.092)	(0.173)	(0.667)	(2.639)	(0.121)	(0.115)	(0.254)
Orphan	0.036	-0.127	-0.235	-0.402	-0.079	-2.052	-0.008	0.479	-1.074	-1.055	-0.239	0.284	-0.788
	(0.177)	(0.246)	(0.187)	(0.218)	(0.343)	(1.427)	(0.235)	(0.449)	(1.193)	(2.767)	(0.300)	(0.312)	(0.770)
Matriarch age	-0.026	0.124	-0.062	0.097	0.109	-0.147	0.010	0.013	-0.044	0.869	0.090	0.127	-1.002
	(0.095)	(0.118)	(0.101)	(0.101)	(0.185)	(0.750)	(0.118)	(0.221)	(0.769)	(2.590)	(0.156)	(0.150)	(0.478)
Matriarch AI	0.044	-0.070	-0.010	-0.087	-0.029	0.420	0.068	-0.385	1.707	0.398	0.340	0.201	0.379
	(0.094)	(0.122)	(0.102)	(0.106)	(0.167)	(0.938)	(0.119)	(0.176)	(1.127)	(2.650)	(0.173)	(0.144)	(0.468)
Dispersed males	0.024	0.004	0.029	-0.008	0.424	-0.176	0.102	0.405	0.054	-0.093	0.066	-0.108	0.816
	(0.100)	(0.147)	(0.102)	(0.134)	(0.198)	(0.873)	(0.131)	(0.229)	(0.953)	(2.633)	(0.179)	(0.175)	(0.480)
Adult:juvenile	0.157	-0.006	0.180	-0.008	0.251	0.732	0.152	0.137	0.243	-0.670	0.152	0.037	0.193
	(0.087)	(0.120)	(0.086)	(0.114)	(0.176)	(0.850)	(0.111)	(0.179)	(0.912)	(2.703)	(0.160)	(0.152)	(0.428)
Core size	-0.017	0.046	0.045	0.047	-0.346	1.276	-0.116	-0.241	1.125	-0.032	0.199	-0.358	-0.024
	(0.102)	(0.132)	(0.109)	(0.122)	(0.190)	(0.973)	(0.131)	(0.236)	(0.866)	(2.730)	(0.169)	(0.186)	(0.408)
Natal	0.111	0.193	0.112	0.201	-0.051	-0.374	-0.451	0.458	-1.982	-1.684	-0.200	-0.330	-0.462
	(0.203)	(0.251)	(0.222)	(0.231)	(0.369)	(1.467)	(0.250)	(0.452)	(1.531)	(2.855)	(0.371)	(0.320)	(0.930)
Own calf	0.994	-0.719	0.929	-1.589	-3.350	-0.665	0.129	-2.571	-0.730	0.620	1.012	-1.398	-1.789
	(0.389)	(0.816)	(0.357)	(0.768)	(1.945)	(2.947)	(0.799)	(2.066)	(2.859)	(3.060)	(0.951)	(1.175)	(2.510)
Group young	0.031	0.008	0.128	-0.043	0.115	0.069	-0.088	-0.184	-0.231	-0.305	-0.204	0.208	0.887
	(0.055)	(0.093)	(0.050)	(0.090)	(0.138)	(0.694)	(0.110)	(0.200)	(0.595)	(2.661)	(0.146)	(0.126)	(0.308)
NDVI	-0.110	0.063	-0.058	0.038	0.037	-1.292	-0.253	0.324	0.225	1.269	-0.157	-0.189	-0.109
	(0.052)	(0.106)	(0.048)	(0.089)	(0.134)	(1.140)	(0.106)	(0.142)	(0.599)	(2.306)	(0.139)	(0.143)	(0.371)
Aggregation size	0.058	0.089	0.030	0.052	0.097	0.904	0.329	0.127	0.808	-0.198	0.354	0.130	-0.719
	(0.053)	(0.101)	(0.048)	(0.089)	(0.135)	(0.757)	(0.091)	(0.146)	(0.662)	(2.491)	(0.132)	(0.125)	(0.517)
Mature bulls	0.037	-0.023	0.050	0.005	0.118	1.101	0.114	-0.032	-2.215	-0.619	-0.054	0.165	-1.958
	(0.048)	(0.098)	(0.044)	(0.086)	(0.122)	(0.766)	(0.080)	(0.159)	(1.590)	(2.821)	(0.131)	(0.107)	(1.459)

Table 4.3: Orphan subset model coefficient estimates. Standard deviations are in parentheses. Models are listed in the top row and coefficients are listed in the first column.

	Receiving affiliative (feeding)	Receiving affiliative (resting)	Initiating aggressive (resting)	Receiving aggressive (resting)	Initiating submissive (feeding)	Receiving exploratory (feeding)	Initiating alloparenting (feeding)
Age	0.298 (0.109)	0.078 (0.139)	1.389 (1.603)	-0.135 (0.242)	-0.495 (2.073)	0.311 (0.163)	-1.730 (0.961)
Time	0.020 (0.056)	0.060 (0.114)	-0.207 (1.787)	0.153 (0.208)	1.687 (1.911)	-0.003 (0.148)	1.322 (0.379)
Time orphaned	0.063 (0.112)	-0.011 (0.150)	-1.651 (2.004)	-0.243 (0.247)	-1.608 (2.277)	-0.118 (0.195)	-1.739 (1.043)
Matriarch age	0.018 (0.124)	0.068 (0.141)	0.340 (1.933)	0.234 (0.257)	0.324 (1.890)	0.143 (0.195)	-1.773 (0.698)
Matriarch AI	-0.077 (0.123)	-0.212 (0.140)	-0.095 (1.892)	-0.598 (0.212)	1.429 (2.153)	0.238 (0.181)	1.726 (0.794)
Dispersed males	0.011 (0.124)	-0.158 (0.171)	-0.429 (1.870)	0.602 (0.311)	0.327 (2.076)	-0.008 (0.211)	0.210 (0.619)
Adult:juvenile	0.243 (0.106)	-0.099 (0.150)	1.696 (1.862)	0.180 (0.232)	-0.547 (2.082)	0.062 (0.194)	0.198 (0.537)
Core size	-0.114 (0.141)	0.147 (0.196)	2.340 (1.948)	-0.429 (0.360)	0.486 (1.964)	-0.351 (0.240)	0.635 (0.673)
Natal	0.230 (0.250)	0.324 (0.307)	-1.686 (2.232)	1.069 (0.602)	-3.388 (2.533)	-0.525 (0.380)	-1.874 (1.197)
Own calf	1.062 (0.441)	-1.804 (0.836)	-0.497 (3.099)	-2.952 (1.998)	-0.178 (3.124)	-0.907 (1.245)	-1.140 (2.667)
Group young	0.156 (0.064)	-0.090 (0.120)	0.281 (1.585)	-0.147 (0.240)	-0.430 (2.116)	0.254 (0.156)	1.261 (0.459)
NDVI	-0.036 (0.063)	0.063 (0.118)	-0.347 (2.013)	0.450 (0.157)	0.533 (1.928)	-0.154 (0.184)	-0.098 (0.457)
Aggregation size	0.007 (0.060)	-0.007 (0.115)	1.276 (1.673)	0.168 (0.175)	0.682 (1.886)	0.017 (0.164)	-0.375 (0.619)
Mature bulls	0.046 (0.058)	-0.005 (0.121)	1.111 (1.595)	-0.102 (0.196)	-1.235 (2.349)	0.150 (0.143)	-2.078 (1.508)

Feeding
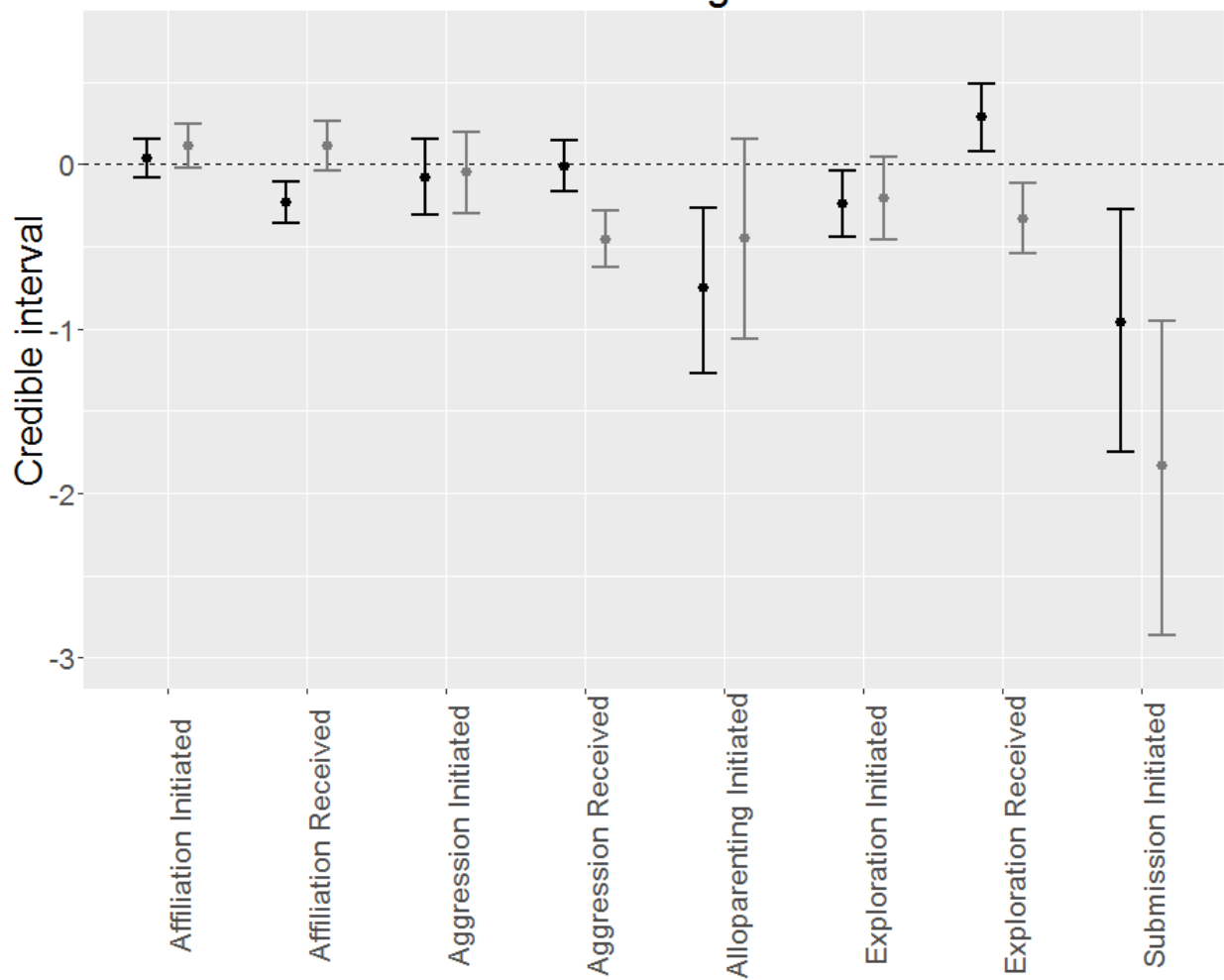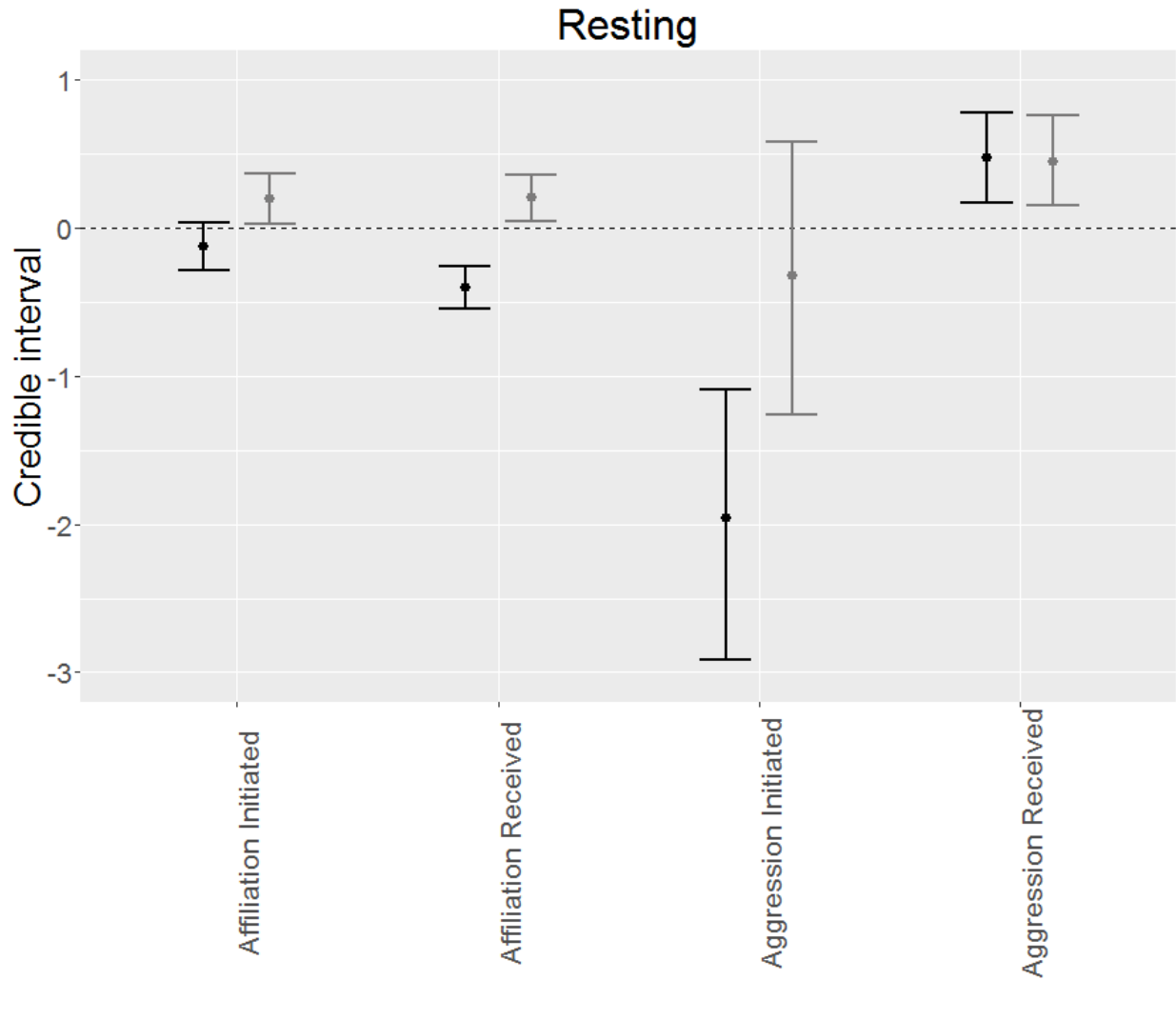
Figure 4.1: Credible interval estimates for *orphan* (black; non-orphan = 0, orphan = 1) and *natal* (gray; non-natal = 0, natal = 1) covariates in models including both orphans and non-orphans, where points represent median values and upper and lower bars represent 75% and 25% range, respectively. Natal group membership was independent of orphan status. Values above zero represent positive relationships with being an orphan or belonging to a natal group.

Costs and Benefits Among Orphans

Consistent with Hypothesis 2, resting orphans received more aggression than resting non-orphans (Figs. 4.1 & A.1; Table 4.2); However, resting non-natal orphans received less aggression than resting natal orphans (Fig. A.2; Table 4.3). This trend was reversed while

animals fed, with non-natal orphans receiving more aggression than natal orphans. Orphans received more aggression the more recently they were orphaned (Figs. 4.2 & A.2; Table 4.3).
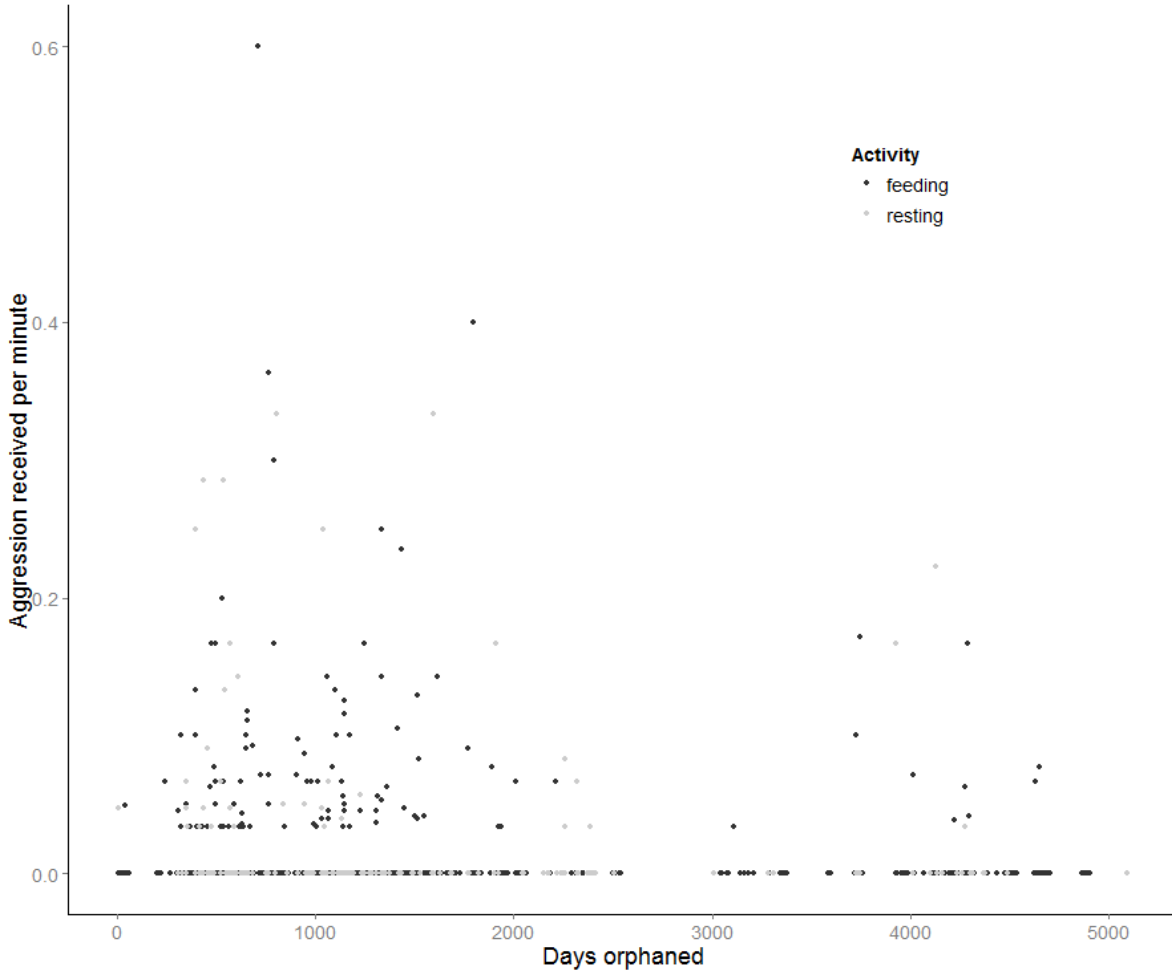
Figure 4.2: Aggression directed toward orphans was negatively related to time orphaned.

Contrary to Hypothesis 2, non-orphans were more likely to exhibit the submissive "backing toward" behavior than orphans (Figs. 4.1 & A.1; Table 4.2). Natal group membership was negatively related to initiated submission in the orphan only model, though this estimate was associated with a large amount of uncertainty (Fig. A.2; Table 4.3). This behavior trended negative with time orphaned (Fig. 4.3).
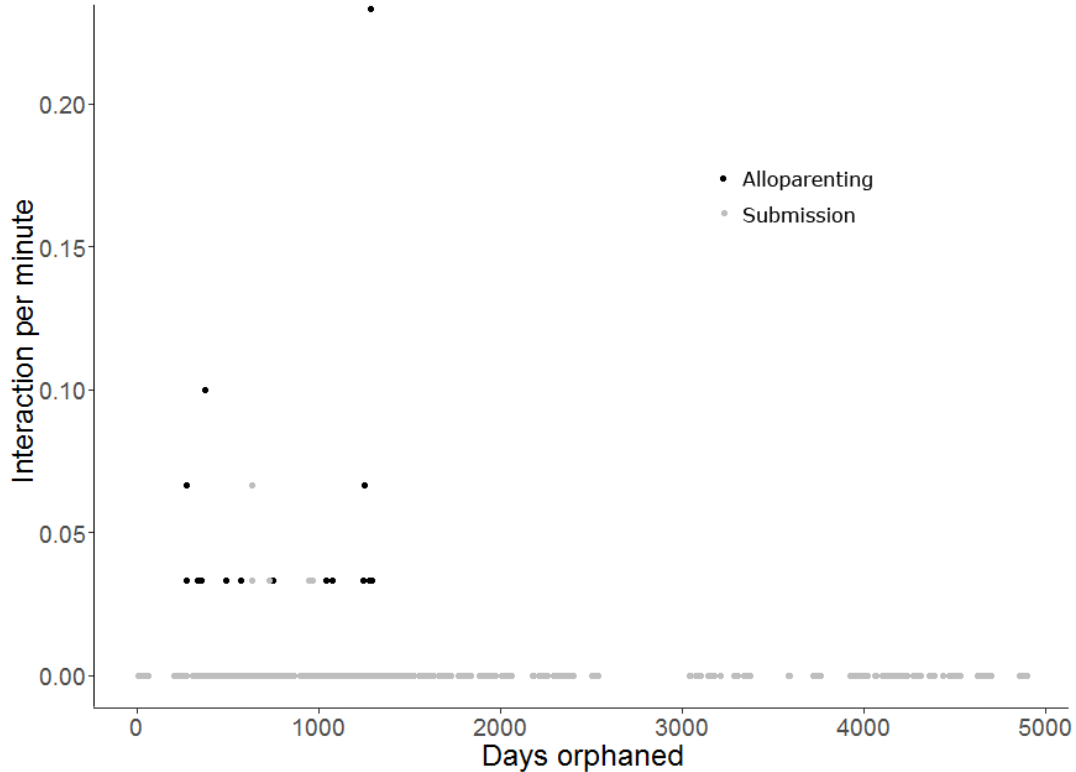
Figure 4.3: Submission and alloparenting initiated by orphans were negatively related to time orphaned.

In models including both orphans and non-orphans, orphans were less likely to alloparent than their non-orphan counterparts (Figs. 4.1 & A.1; Table 4.2), opposite to the relationship predicted by Hypothesis 2. In the subset model of orphans only, however, non-natal orphans were more likely to alloparent than natal orphans as predicted by Hypothesis 2 (Fig. A.2; Table 4.3). There was a strong negative relationship between alloparenting and the time a focal animal was orphaned (Figs. 4.3 & A.2; Table 4.3), suggesting that orphaned elephants were more likely to alloparent the more recently they became orphans. Additionally, strong bonds with matriarchs were predictive of alloparenting among orphans (Fig. A.2; Table 4.3). Both orphans and non-

orphans were more likely to alloparent if their groups had younger matriarchs (Fig. A.1; Table 4.2).

Orphan Bonding Targets

In contrast to Hypothesis 3, whether a focal animal's bonding partner was a matriarch did not structure the affiliation she initiated, nor did the age difference between focal animals and their social partners (Fig. A.3; Table 4.4). Alternative hypotheses for indirect social integration through age mates or young bulls were not supported, but whether social partners were young calves was a strong predictor of the affiliative interactions that focal elephants (orphans and non-orphans) initiated while feeding (Fig. A.3; Table 4.4).

Regardless of whether orphans targeted matriarchs directly as bonding partners, matriarchs structured the social environment. Focal elephants received less aggression and exhibited more submission if they had stronger associations with their matriarchs. Elephants received more exploratory trunk reaches if they were associated with groups led by older matriarchs and if they had stronger bonds with their matriarchs (Fig. A.1; Table 4.2).

Table 4.4: Coefficient estimates for models predicting interactions with specific partners. Standard deviations are in parentheses. Models are listed in the top row and coefficients are listed in the first column. Blank cells represent covariates that were removed because of strong correlations with other covariates or because they lacked variation for relevant datasets.

	Affiliative actor (feeding)	Affiliative actor (resting)	Affiliative recipient (feeding)	Affiliative recipient (resting)	Aggressive actor (feeding)	Aggressive actor (resting)	Aggressive recipient (feeding)	Aggressive recipient (resting)	Exploratory actor (feeding)	Exploratory recipient (feeding)
Age difference	-0.039 (0.049)	-0.085 (0.075)	0.013 (0.051)	-0.156 (0.079)	0.024 (0.090)	-0.132 (0.225)	0.040 (0.063)	0.016 (0.114)	0.051 (0.083)	-0.007 (0.098)
Partner mother	-0.021 (0.118)	-0.080 (0.168)	-0.063 (0.126)	-0.098 (0.176)	0.206 (0.253)	-0.254 (0.593)	-------	-------	-0.078 (0.207)	0.062 (0.245)
Partner matriarch	-0.067 (0.105)	-0.261 (0.241)	0.172 (0.169)	0.318 (0.252)	-0.152 (0.274)	0.548 (0.700)	-0.045 (0.150)	-0.094 (0.300)	0.161 (0.299)	-0.085 (0.360)
Partner young calf	1.033 (0.083)	-0.351 (0.158)	1.309 (0.082)	-0.157 (0.149)	-0.461 (0.557)	-------	-------	-------	0.237 (0.254)	0.144 (0.215)
Partner own calf	1.402 (0.114)	1.024 (0.186)	2.148 (0.120)	1.396 (0.186)	0.116 (0.321)	-0.515 (0.638)	-------	-------	-0.315 (0.393)	0.238 (0.350)
Partner male	0.058 (0.078)	-0.060 (0.139)	0.308 (0.078)	-0.131 (0.138)	-0.032 (0.181)	-0.310 (0.497)	-0.176 (0.149)	0.100 (0.272)	-0.004 (0.067)	-0.080 (0.190)
Partner core-non-natal	0.667 (0.171)	0.479 (0.265)	0.458 (0.191)	0.362 (0.274)	0.212 (0.301)	0.612 (0.925)	0.275 (0.226)	-0.255 (0.576)	0.070 (0.414)	0.486 (0.389)
Partner natal	0.587 (0.087)	0.649 (0.154)	0.602 (0.087)	0.437 (0.151)	0.049 (0.203)	0.135 (0.530)	0.033 (0.157)	0.020 (0.294)	-0.010 (0.198)	-0.149 (0.234)
Focal mother	-0.004 (0.125)	-0.425 (0.177)	-0.105 (0.122)	-0.312 (0.167)	0.003 (0.202)	-0.007 (0.550)	0.209 (0.132)	0.040 (0.235)	0.263 (0.168)	0.228 (0.197)

Discussion:

Indirect effects of mortality events, like altered social relationships, can destabilize populations (Milner et al. 2007). Among highly social species, deaths of key individuals can affect dominance and association networks for remaining animals (Williams & Lusseau 2006). Due to high levels of illegal killing for ivory, such removals are common in most African elephant populations (Wittemyer et al. 2014). Previous work in our study system has shown that elephants that experience disruption may become members of core groups that are different from those they were born into, presumably to improve their altered social context (Wittemyer et al. 2009; Goldenberg et al. 2016). This study addresses an unanswered and critical piece to this process: how do orphaned elephants integrate into society without their older relatives and do they experience greater costs as a result of social marginalization? Our results point to an elongated and complex process of social integration for orphaned animals in this society, but also highlight the advantage that a fission-fusion social system confers on animals that must compensate for lost bonding partners (Farine et al. 2015). This study contributes to a larger understanding of social bonding in dynamic environments and provides specific insight to the response of a threatened species to ongoing disruption.

Social Costs and Acceptance of Orphans

Social environments of orphans and non-orphans clearly differed: non-orphans received more friendly behaviors from other elephants than did orphans, and orphans were on the receiving end of aggression more frequently. Further, remaining tightly associated with natal groups was tied to more affiliation generally and less aggression while feeding (Figs. 4.1 & A.1; Table 4.2). These results support Hypothesis 2, which predicted that family disruption and social

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integration would be associated with social cost. While decreased received affiliation as a result

of being orphaned or leaving a natal group may not in itself be a social cost, it may reflect

peripheral positions of orphans that may be tied to disadvantage in this highly social species.

These results call into question the decision to leave one's natal group, and suggest that it may be

the best option only after the natal group has been substantially degraded. The elephants we have

observed to join new groups (Wittemyer et al. 2009; Goldenberg et al. 2016) are usually from

families that have been dramatically reduced in size, though this is not always the case.

Interestingly, our finding of lower received affiliation did not change for orphans with

time but received aggression seemed to wane (Fig. 4.2), suggesting that elephants may not fully

integrate with new groups but may experience greater tolerance over time. Consistent with

Hypothesis 2 that orphans would adjust their behavior to minimize costs to bonding targets,

integrating orphans may facilitate tolerance by acting subordinate more if they are in their non-

natal groups and when they are more recently orphaned (Fig. 4.3); this is likely manifested as

relinquishing resources. These results highlight the subtlety to the long-term impacts of being an

orphan. We previously demonstrated that elephants reconstruct association patterns and

emergent population social structure to resemble that found prior to poaching (Goldenberg et al.

2016); the present finer-scale results indicate that reconstruction is not synonymous with total

recovery for disrupted elephants.

Orphan Behavior and Social Integration

We did not find support for Hypothesis 1 that young orphans belonging to non-natal

groups would initiate more friendly behaviors than older elephants, non-orphans, or orphans

within their natal groups to compensate for their lost bonds. Initiated affiliation did not differ by

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orphan status or age, and exhibited the opposite trend as expected with natal group membership (natal group membership was positively related to initiated affiliation; Fig. 4.1). These results were likely related to the fact that orphans integrating into non-natal groups often remain spatially peripheral, at least initially, whereas orphans that remain with their natal groups are less peripheral. Despite the affiliation limitations for peripheral animals, orphans seemed to actively improve their social positions in less direct ways. This was apparent in the negative relationships between submission and time orphaned, alloparenting and time orphaned, and alloparenting and natal group membership (Fig. 4.3), which suggest that as elephants navigate their new social contexts they alter their behavior to reduce costs and increase benefits to bonding targets (consistent with Hypothesis 2).

Elephant life history strategy favors strong investment in calves (Lee 1986; Lee & Moss 2011). Alloparenting is thought to benefit mothers by lending more eyes to vulnerable calves and to benefit young allomothers by enabling parenting practice in this and other species (Lee 1987; Pillay & Rymer 2015). In our study, alloparenting was more common in groups with younger matriarchs and more commonly conducted by natal members of their groups, possibly reflecting the greater access that more integrated non-orphans may have to young calves. However, the negative relationship between the time an elephant was orphaned and alloparenting in the orphan only model (controlling for age) indicates that this behavior may facilitate integration in non-natal groups. Years prior to the intensification of ivory poaching in the population, we observed an orphaned subadult integrate into an unrelated family by alloparenting the recently born matriarch's calf (Wittemyer pers. obs.). She remained with that group when she gave birth to her own calf and is a part of their core group approximately fifteen years later (Goldenberg et al.

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2016). As such, alloparenting can serve as a bridge to social integration, but it is likely not the only bridge used by orphans.

Social Partners

Hypothesis 3 related to the particular bonding partners targeted by focal elephants. While directing affiliation toward matriarchs, who confer the greatest advantages to their associates (McComb et al. 2001; Foley et al. 2008), would be a direct path for orphans (Hypothesis 3), affiliating with age-mates, dispersing bulls, or young calves may still allow orphans to benefit from matriarch proximity and knowledge without interacting with dominant matriarchs directly. We did not find evidence that orphans affiliate directly with matriarchs more so than they do with other elephants, but our results showed that all sampled elephants direct attention to groups with older matriarchs and to matriarchs generally (manifested as more exploratory trunk reaches directed toward those in groups with old matriarchs and toward those with strong bonds with matriarchs). In contrast to the subtle relationships among the interactions of orphans with matriarchs, interactions with young calves were clear. For non-orphans and orphans alike, affiliation was strongly positively predicted by whether social partners were young calves (Fig. A.3; Table 4.4). This result is consistent with the alloparenting trends discussed above.

Matriarch Influence on Social Environments

The ability of matriarchs to structure the social environments and resource access of other animals (McComb et al. 2001; Wittemyer et al. 2007b; Foley et al. 2008) persists in this population that has lost so many older females (Wittemyer et al. 2013; Goldenberg et al. 2016). Focal animals exhibited more submissive behavior if they had stronger bonds with their

matriarchs (likely reflective of greater proximity and therefore opportunity for backing toward matriarchs), and received more aggression if they had weaker bonds with matriarchs. Despite the non-nepotistic (Archie et al. 2006) or weakly nepotistic (Wittemyer & Getz 2007) hierarchies described within elephant families, our results indicate that the aggression an animal receives is still influenced by their relationship with their matriarch. Access to matriarchs through the indirect routes of alloparenting and submission may place elephants in better social positions.

Conservation Implications of Orphan Behavior

African elephants face considerable pressure from poaching throughout their range linked to the rise in international demand for ivory (Wittemyer et al. 2014; Turkalo et al. 2016). Demographic parameters are often the focus of studies on overexploited populations (e.g., (Servanty et al. 2011; Bragina et al. 2015)), but indirect effects like altered social relationships should be considered in population monitoring of threatened and endangered species dependent on social processes (Milner et al. 2007). Social behavioral metrics derived from studies like these may provide indicators of the resilience of populations to harvest. For example, high proportions of orphans from disrupted families integrating into new groups may buffer against downstream mortalities resulting from the loss of mothers and matriarchs. Linking social environments experienced by orphans to calving parameters (e.g., orphans that receive more aggression are less likely to raise calves to weaning age) will provide further insight to the potential of behavioral data to inform conservation objectives.

Importantly, throughout our study we observed several unaffiliated young females over brief periods that subsequently disappeared. The fate of these animals is unknown, but we suspect they did not survive. While not definitive, it is notable that the orphans we observed for

longer periods tended to integrate into social groups within the study period and subsequently survived. This appears to indicate a diversity of experiences (possibly strategies) among elephant orphans, with differential fitness. Future work should illuminate the bonding decision-making process in young female elephants that may vary substantially with elephant context and personality. Whether different social decisions are associated with different fitness outcomes is of direct relevance to conservation goals.

Poaching affected families in the Samburu system differently, such that some families survived relatively intact whereas others lost all of their adult females (Wittemyer et al. 2013). It is notable that age and the presence of older individuals structured many of the interactions that we investigated, and suggests that the survival of at least some older elephants may be critical to this process of social integration. The mortality experienced by the Samburu population, while disruptive, was lower than that in other populations (Maisels et al. 2013; Wittemyer et al. 2014). The behavioral processes toward social integration documented here may be absent in heavily poached populations that experience greater loss of old females. The downstream demographic effects of younger and reconstituted families, and the prevalence of social behavioral flexibility across populations experiencing different levels of pressure have yet to be studied, but will likely play important roles in the recovery of elephant populations.

Chapter 5: Challenges of using behavior to monitor anthropogenic impacts on wildlife: a case study on illegal killing of African elephants[3]

Introduction:

Animals modify their behavior to avoid predation while attempting to minimize related fitness costs (Lima & Dill, 1990). Anti-predator responses (e.g., proactive responses like grouping patterns or reactive responses like increased vigilance) have been used to monitor populations and as a proxy for mortality impacts (Caro 2005; Creel et al. 2014). In particular, anti-predator behaviors have been measured as indicators of human activities in harvested or otherwise disturbed populations (Benhaiem et al. 2008; Reimers et al. 2009; Magige et al. 2009; Kiffner et al. 2014; Tarakini & Crosmary 2014). Anti-predator behavior in wildlife may not only serve as a useful metric of threat, but can directly influence fitness via energetic trade-offs (Anthony & Blumstein 2000; Frid & Dill 2002; Lone et al. 2015). Flight from suitable habitat and heightened vigilance may reduce access to resources and increase energy expenditure, which in turn contributes to poor body condition and decreased reproductive rates (Frid & Dill, 2002). Thus, wildlife behavior may serve as a proxy for population status or health, where direct fitness metrics are not possible or practical to collect (Bejder et al. 2009).

Flightiness (quantified as flight initiation distance, time to flight, or distance of flight) is the most common response recorded by researchers because of its apparent connection to predator stimuli and the relative ease with which it can be measured (Stankowich & Blumstein 2005; Setsaas et al. 2007; Benhaiem et al. 2008). However, these metrics should be tailored to

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[3] Adapted from: Goldenberg, S.Z., Douglas-Hamilton, I., Daballen, D., and Wittemyer, G. 2016. Challenges of using behavior to monitor anthropogenic impacts on wildlife: a case study on illegal killing of African elephants. *Animal Conservation*.

systems of interest; whether flightiness is effective as an anti-predator metric across evolutionarily disparate taxa should be tested. Additionally, relevant variables influencing flightiness may be unavailable or unknown and therefore excluded from analyses (Gill et al. 2001; Griffin et al. 2007). For instance, an anti-predator response may result from variables unrelated to the anthropogenic threat of interest like the social nature of the activity, population density, habitat quality relative to alternative sites, or the presence of vulnerable young (Cooper 2009; Moller et al. 2013; Semeniuk et al. 2014). While these potential pitfalls have been recognized (Gill et al. 2001), few studies using behavior to understand human impacts have also assessed the extent to which non-anthropogenic variables account for anti-predator behaviors or have assessed the applicability of such a general metric.

Despite the complications of interpreting flightiness, it may be of considerable value to wildlife managers. Poaching of wildlife is a pervasive problem (Muth 1998; Dinerstein et al. 2007; Magige et al. 2009; Wittemyer et al. 2011), and direct information about such illegal activity is often difficult to obtain (Knapp et al. 2010; Liberg et al. 2012) Measuring flightiness is markedly easier and less expensive than directly measuring illegal harvest (Caro 2005). Such behavioral indicators can advance the design and implementation of monitoring programs, enhance security operations (Anthony & Blumstein, 2000), and provide timely warning for wildlife managers (Donadio & Buskirk 2006; Wildermuth et al. 2013).

The African savannah elephants (*Loxodonta africana*) of the Laikipia/Samburu ecosystem of northern Kenya—a region divided into a variety of land use patches (Kahindi et al. 2010)—comprise the second largest Kenyan elephant population and one of the largest on the continent to range primarily outside of protected areas (Omondi et al. 2002). The population has been intensively studied since 1997 in a project that records social, movement, and demographic

parameters of individual elephants in a relatively small protected area within the ecosystem (Wittemyer 2001). Ivory poaching is a considerable risk to these elephants (Wittemyer et al. 2011, 2013, 2014) and the population range was designated as one of the sites for the Monitoring of Illegal Killing of Elephants (MIKE) programme of the Convention on International Trade in Endangered Species (CITES). It has been intensively monitored for illegal killing since 2002 (Kahindi et al. 2010). This coupling of behavioral and demographic data provides an opportunity to investigate the relationship between behavioral monitoring and high effort, demographic-based measures of human impact, and to assess the utility of flight metrics in elephants.

While some studies have examined correlations between flight behavior and demographic parameters (Müllner et al. 2004; Griffin et al. 2007), rigorous analyses exploring potential confounding variables that may explain flight behavior are rare (Donadio & Buskirk 2006; Kiffner et al. 2014). Elephants have been shown to discriminate among threats that are associated with different levels of risk, like between garments belonging to people from different ethnic groups (Bates et al. 2007) and voices belonging to people of different ages and genders (McComb et al. 2014). This sophisticated ability to differentiate threats may extend to elephants' keen spatial understanding (Polansky et al. 2015; Wittemyer et al. 2016); understanding risk inherent to area use may influence anti-predator behavior. These characteristics specific to elephants may complicate the employment of widely used flight metrics. Nonetheless, if flight behavior reliably reflects poaching levels such metrics would provide a valuable management tool to assess pressures on this wide ranging species, particularly where monitoring ability is spatially limited relative to the population's range as in this study system. In this study, social, ecological, demographic, spatial, and anthropogenic variables are related to elephant response to the approach of humans in vehicles in protected areas (where elephants are accessible for study).

This behavioral metric was designed to provide an index of human threat exposure that the wide-ranging study individuals encountered in inaccessible, poorly monitored regions. We test the hypothesis that this behavioral metric collected within a protected area could serve as an index for human pressure in the greater ecosystem by assessing the relationship between elephant reactivity and illegal killing levels, collected independently. We identify the variables offering the greatest predictive insight on behavioral response of elephants to research vehicle approach and discuss the implications for wildlife management.

Methods:

Data Collection

Research teams led by one of three primary observers collected data in Samburu and Buffalo Springs National Reserves, northern Kenya (Fig. 5.1) between 2000 and 2014. The reserves are unfenced, border the Ewaso Ngiro River (the only permanent water source in the region), and are situated within a complex human land use mosaic throughout which elephants range (Omondi et al. 2002). The reserves represent less than 10% of the monitored elephants' range (Wittemyer et al. 2005a). Elephants are individually identified by ear and tusk idiosyncrasies (Douglas-Hamilton 1972; Moss 1996) as a part of an ongoing individual-based monitoring project (Wittemyer 2001). Elephant ages are known from observed births or estimated using established methods (Moss 1996). New calves are registered as they occur and individuals are considered dead when their carcasses are found or when repeatedly missing from their group (Wittemyer et al. 2013). Rates and locations of poached carcasses are available from the CITES MIKE programme (Kahindi et al. 2010; Wittemyer et al. 2014). Global positioning system (GPS) locations were available for a subset of tracked females ($n = 12$) at 1-3 hour

intervals with 5-20 m spatial accuracy, allowing accurate determination of the time each collared individual spent within or outside protected areas. Collared elephants in this study ranged from an estimated 23 to 48 years old and were associated with core groups ranging in size from 5 to 22 individuals. Observations of tracked families ranged from 5 to 87 (median = 18.5, sd = 26.5).

We recorded the behavioral responses of known elephants to the research vehicle, termed *reaction index* (RI), when we approached an elephant group within 20 m consistent with research protocol. The measure is a relative ranking from 1-4, where behavior is ranked as 1 = calm with activity uninterrupted, 2 = initially skittish but calm within 10 minutes, 3 = actively avoiding vehicle, and 4 = running from the vehicle. RI is considered a group-level metric, as all group members generally behave similarly in the presence of a research vehicle. In addition to RI, we recorded the date, time, GPS coordinates, aggregation size (an aggregation was defined as a spatially cohesive and behaviorally coordinated group of elephants within a 500 m radius of an observer-estimated center) (Wittemyer et al. 2005b), individuals present, and presence of bulls in musth.
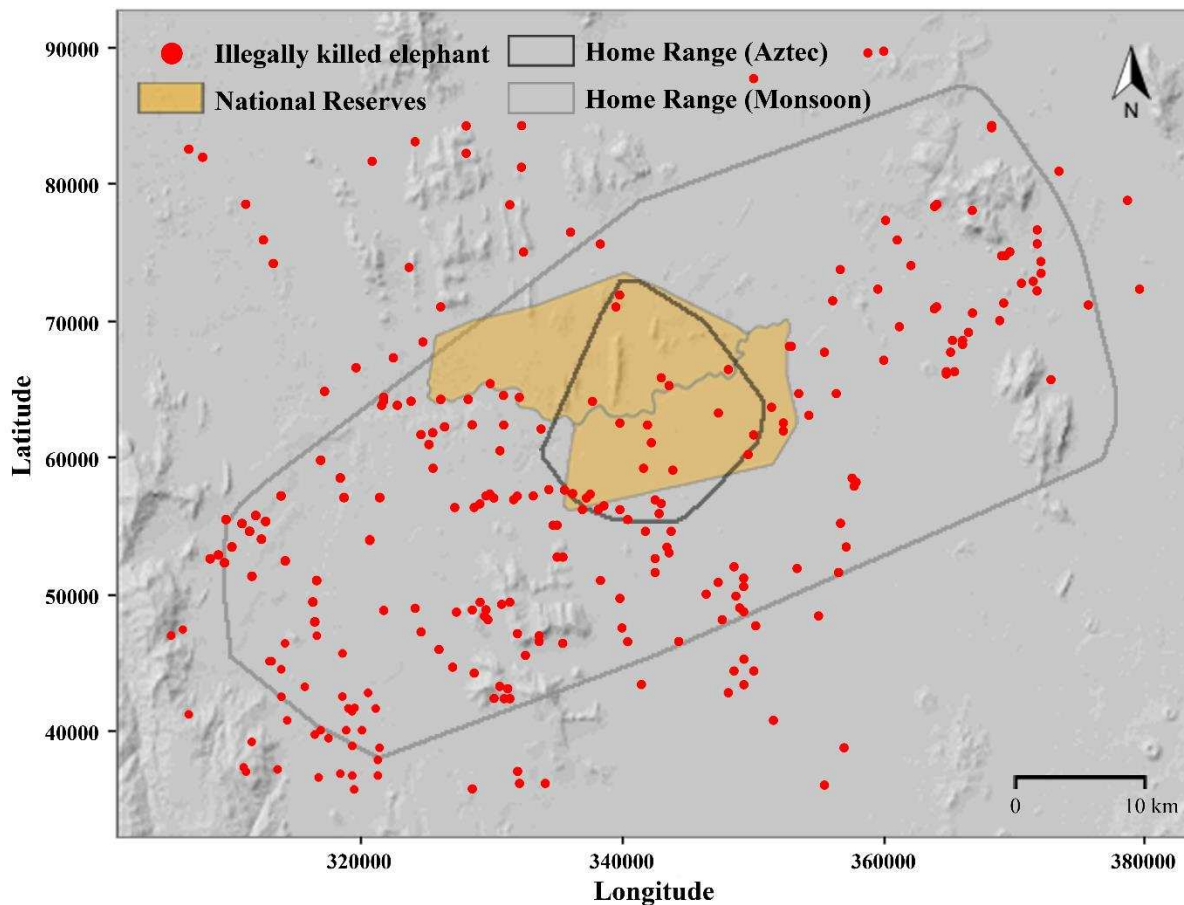
Figure 5.1: Poaching levels varied by elephant home range. The 95% minimum convex polygon home ranges are presented here for two radio-collared females with different space use strategies that exposed them to different levels of poaching (red dots represent poached elephant locations between 2000 and 2014).

Data Analysis

Due to very few observations of RI = 3 or 4, we consolidated RI values = 2, 3, and 4 into a single category representing reactive behavior. Similar to other systems (Kiffner et al. 2014), for the purpose of analysis we binned these behaviors as RI = 0 (did not react) and RI = 1 (did react). To examine the factors influencing RI, we fitted a set of candidate regression models with RI as the response variable. We conducted analyses on two subsets of the data: 1) from observations including radio-collared females only, and 2) from all available observations for

which all breeding females present were recorded (population level). The former allowed us to analyze the effects of time since entering protected areas and home range, which we expected might influence elephant responses to human beings. Therefore, we collated information for the subset of individuals for which radio-tracking data were available, where each female represented a distinct core group (the closest level of bonding in elephant society) (Wittemyer et al. 2005b).

For this radio-tracked subset, we ran generalized linear mixed-effects models with a logit link function in which core group identities were incorporated as random effects. Intercepts were allowed to vary by core group identity, thereby partitioning variance due to independent variables from inherent baseline reactivity levels of core groups and controlling for repeated measures within groups. Population-level models did not incorporate a random effect. Within the regression models, we investigated aggregation specific covariates including aggregation size (*size*); presence/absence or number of calves present ≤ 3 months of age (based on a developmental threshold (Lee 1986; Owen-Smith 1988), present/absent: *calf*, count: *calves*); ratio of mature females to juveniles in the core group (*adult:juvenile*); presence or absence of a bull in musth (defined by urine dribbling, *musth*) (Poole 1989b); number of core group members that died or were wounded within one year prior to the date of the observation (*mortality*); age of matriarch (*age*); time since entering the protected area (where we considered the adjacent Samburu and Buffalo Springs National Reserves a single protected area block, *time*), and proportion of months in the year that we saw the group in the protected area (*months*).

Model covariates explored on study area conditions at the time of the observation were ecosystem primary productivity measured as 10-day composite Normalized Difference Vegetation Index (*NDVI*) for a region comprising the core range use of the study population (960

km^2), as described in (Wittemyer et al. 2007a); the proportion of illegally killed carcasses in the Laikipia/Samburu ecosystem for the year of the observation (*PIKE*), with higher PIKE values occurring in the latter years of the study (Kahindi et al. 2010; Wittemyer et al. 2014); and the PIKE value ascertained for each radio-collared female for the year of the observation within the 95% minimum convex polygon area of her home range, constructed from radio-tracking data (Median$_{points}$: 22,281, Range$_{points}$: 6,891-53,066; *mcp PIKE*) (Fig. 5.1). We also considered the year of the observation (*year*). We assessed correlations between explanatory variables using Pearson correlations, considering two variables to be strongly correlated when r > 0.6. Only *year and PIKE* met this criterion. We therefore excluded *year* from the models because we were especially interested in the effects of poaching pressure on elephant response. All relevant covariates were available for 354 observations for the subset comprised of radio-collared elephants. For the population level dataset that did not consider core groups independently, 3,356 observations of elephant aggregations were available.

We ran models predicting the probability of a reactive response to a research vehicle in R using the *glmmADMB* and the *stats* packages (R Core Team 2013; Skaug et al. 2014). We standardized covariates prior to running models to aid in model convergence and for ease of interpretation. For each of the two datasets, we determined a set of candidate models including a global model with all uncorrelated independent variables and interactions hypothesized to be of importance (social-seasonal interactions as well as the interaction between matriarch age and young calves) (Moss 1988; McComb et al. 2011), subsets of the global model, and a varying-intercept-only null model for the radio-collar subset (Table 5.1). We compared models using a model selection approach, and used Akaike's Information Criterion corrected for small samples

(AICc) as the metric for comparison with the *bbmle* package for R (Burnham & Anderson 2002; Bolker & Team 2014). We present and interpret results from the top ranked model.

Table 5.1: List of candidate models for all observations and the radio-collared subset

Radio-collar observations	varying intercept only
	size+calf+adult:juvenile+musth+mortality+months+age+time+NDVI+PIKE+
	mcp PIKE+NDVI*size+NDVI*calf+NDVI*musth+NDVI*adult:juvenile+calf*age
	size+calf+musth+age+adult:juvenile+calf*age
	size
	calf
	musth
	age
	adult:juvenile
	calf*age
	mortality
	NDVI
	NDVI+NDVI*size+NDVI*calf+NDVI*musth+NDVI*adult:juvenile
	months+time+PIKE+mcp PIKE
All observations	size+calves+musth+NDVI+PIKE+NDVI*size+NDVI*calves+NDVI*musth
	size+calves+musth
	size
	calves
	musth
	NDVI
	NDVI+NDVI*size+NDVI*calves+NDVI*musth
	PIKE

Statement on Animal Subjects

We collected data with permission from the Kenya Wildlife Service, Colorado State University, the Samburu and Isiolo County Councils, and Save the Elephants (IACUC 12-3414A).

Results

Radio-collared Dataset

The top model for the radio-collared female cohort (global model; Table 5.2) indicated *NDVI* was a strong positive predictor of elephant reactivity. RI during the wet season was

heightened in the presence of a bull in musth and diminished with the presence of a young calf

and increasing group size (Fig. 5.2), however only the coefficients for *NDVI* and *NDVI*musth*

were significant (i.e., coefficient 95% confidence intervals did not overlap 0). The proportion of

months in the year that a core group spent in the protected areas was significantly negatively

related to RI (Fig. 5.2). Contrary to our expectations, neither mortality data nor time since

entering the protected reserves was correlated with RI. *PIKE* was in fact negatively related to RI,

though this result was not significant in the radio-collar dataset. The standard deviation of

random intercepts (3.03e-8) was large relative to the mean (1.48e-14), indicating that inherent

differences between groups were important in this system (Table 5.3).

Table 5.2: Ecological, social, demographic, anthropogenic, and spatial variables were related to reaction of African elephants to researchers in Samburu and Buffalo Springs National Reserves, Kenya. The models accounting for ~95% of AICc weight in both the radio-tracked and population level datasets are presented.[4]

Radio-collar observations (N$_{observations}$ = 354)

Model	AICc	ΔAICc	*ωi*
size+calf+adult:juvenile+musth+mortality+months+age+time+NDVI+ PIKE+mcp PIKE+NDVI*size+NDVI*calf+NDVI*musth+ NDVI*adult:juvenile+calf*age	259.40	0	0.57
NDVI+NDVI*size+NDVI*calf+NDVI*musth+NDVI*adult:juvenile	260.94	1.5	0.26
NDVI	262.36	3.0	0.13

All observations (N$_{observations}$ = 3356)

Model	AICc	ΔAICc	*ωi*
size+calves+musth+NDVI+PIKE+ NDVI*size+NDVI*calves+ NDVI*musth	1756.13	0	1.00

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[4] Δ*AICc* represents the difference in AICc value between the model and the top-ranked model, and *ωi* represents Akaike weight (totaling one across all considered models), where lower AICc values and higher weight correspond to models with greater explanatory power.

Effect size
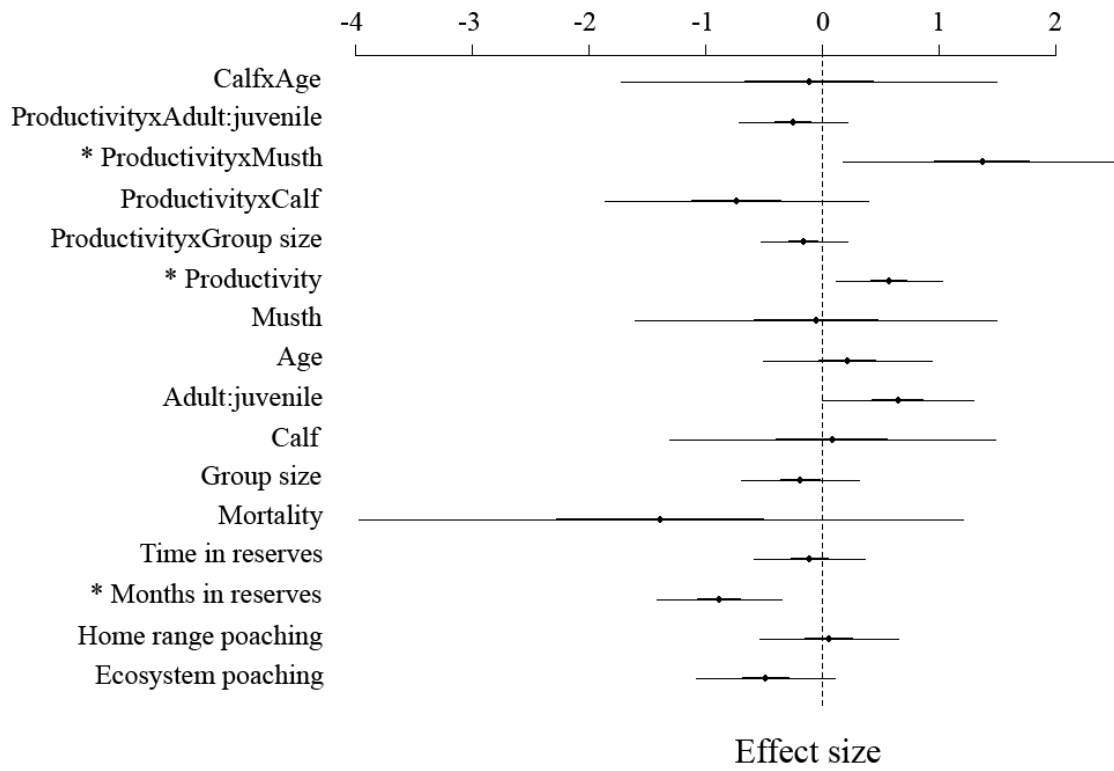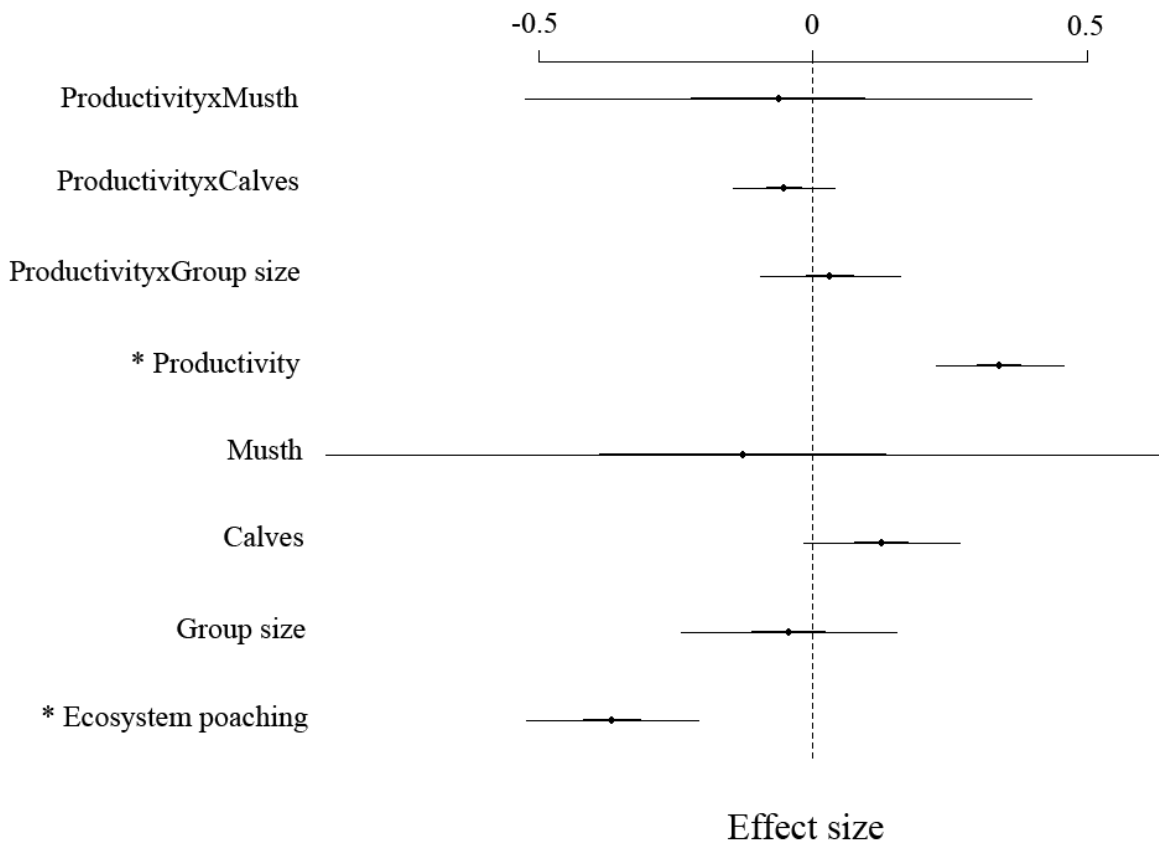
Figure 5.2: Standardized coefficient values from the top model for radio-collared females (top) and the population level (bottom). Asterisks denote significant coefficients. Thick and thin lines around estimates represent 50% and 95% confidence intervals, respectively.

Table 5.3: Intercept values in mixed-effect models predicting reactive behavior for radio-collared females represent differences among core groups in baseline reactivity levels, where higher intercept values represent elephant groups that were more likely to respond when controlling for explanatory variables.

Radio-collared elephant	Intercept value
Aztec	-4.68e-8
Rosemary	-4.42e-8
Resilience	-2.22e-8
Mercury	-1.53e-8
Jerusalem	-1.44e-8
Wendy	-2.81e-10
Annabelle	-2.16e-10
Maua	1.12e-8
Goya	1.61e-8
Bonsai	3.29e-8
Amina	3.56e-8
Monsoon	4.75e-8

Population Level Dataset

Results from the top model assessing predictors of RI for the population level dataset, again, did not support our hypothesis that an increase in illegal killing rates predicted reactivity (Table 5.2). Rather, *PIKE* was significantly negatively correlated with RI in the top model, and *NDVI* was significantly positively associated with a reaction (Figs. 5.2-5.3). In addition, the number of young calves present was positively correlated with RI (Fig. 5.2).
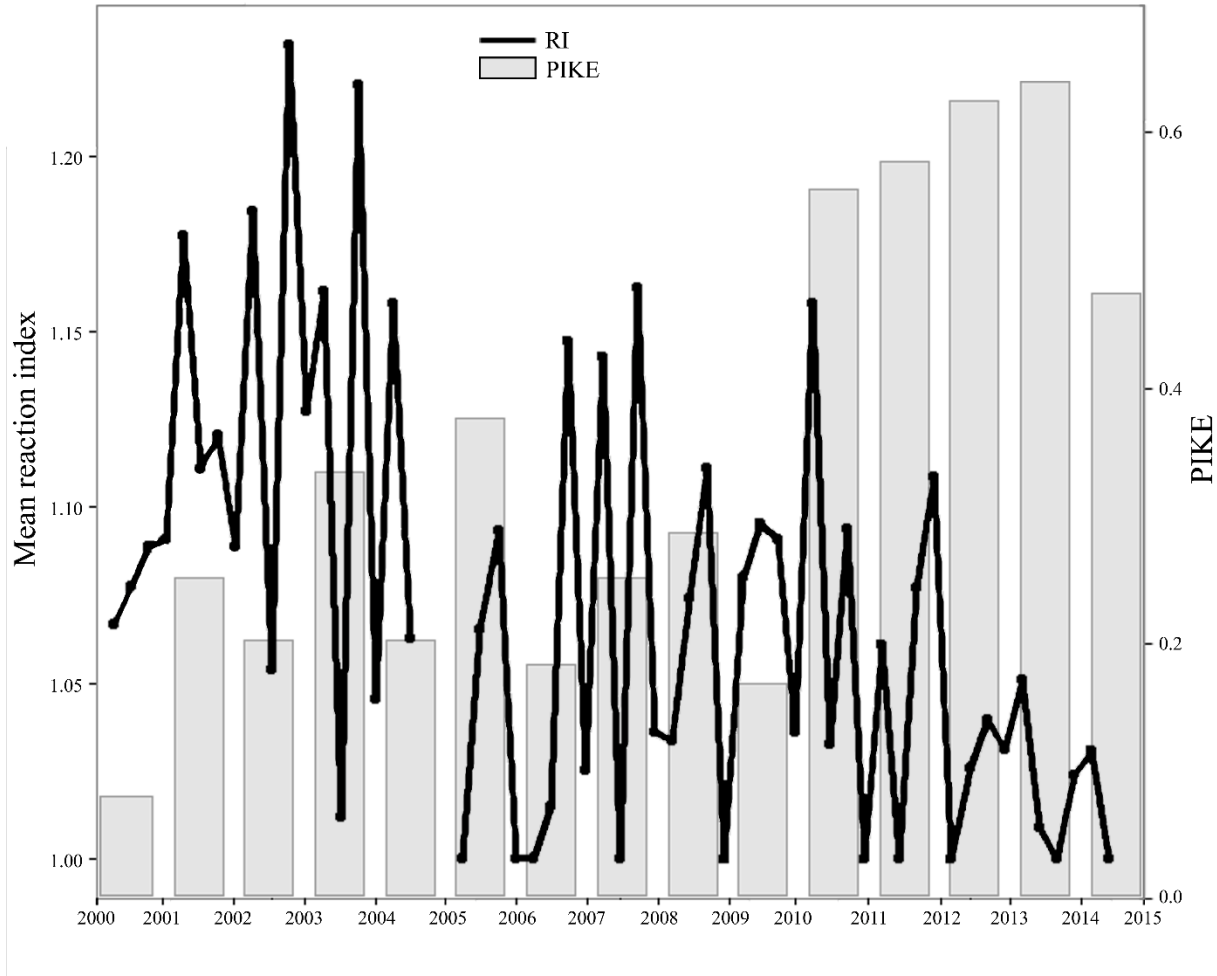
Figure 5.3: Mean RI (reaction index) and PIKE (Proportion of Illegally Killed Elephants). For this figure the mean of raw RI values was calculated at quarterly intervals. Annual PIKE values are plotted at the midpoint of each year.

Discussion

Reaction Indices and Illegal Killing

Behavioral assessment can be a valuable and low cost approach to monitor threats to populations; however, behavior can be influenced by multiple factors, complicating simple interpretation of its meaning (Gill et al. 2001). Our results demonstrated that a high level of poaching did not increase reactivity as recorded for the study population inside the reserve. Contrary to our expectation, PIKE was negatively correlated with RI, significantly so in the

population level dataset. In the subset model for which spatial use was controlled, there was no relationship between reactivity and the PIKE specific to an elephant's home range. These results may be a function of the highly nuanced reactions that elephants demonstrate towards humans. Elephant defensive responses to visual, olfactory, and auditory human cues recorded in a different Kenyan population captured fine-scale discrimination between ethnic groups and genders associated with different degrees of risk (Bates et al. 2007; McComb et al. 2014). It is likely that the elephants in this study did not perceive research vehicles as a threat connected to the poaching experienced outside the protected area, given that poaching in our study area is primarily conducted on foot and tourist presence (within vehicles) has been consistently high in the protected area for decades. Elephant experiences with vehicles in the reserves likely range from positive to negative, but are rarely fatal (vehicle collisions have occurred). Consistent lack of association with mortality risk may lead to tolerance of vehicles by elephants, which may be especially heightened in periods when risk from humans on foot is high.

Furthermore, levels of poaching pressure are low inside the protected areas relative to the outlying, unprotected areas (Wittemyer et al. 2013). Elephants' keen spatial knowledge (Polansky et al. 2015) likely structured results in our study. Elephants have been shown to move more quickly through high-risk areas and spend more daylight hours in low-risk areas (Graham et al. 2009) as well as to adjust resting patterns and circadian activity patterns relative to risk (Wittemyer et al. 2014, 2016). They react strongly to a person on foot within the reserves. However, such mismatches between threats to wildlife (e.g., person on foot) and the behavioral monitoring stimulus (e.g., vehicle approach) are common, especially in areas where walking on foot is prohibited and dangerous (Frid & Dill 2002; Caro 2005; Donadio & Buskirk 2006; Kiffner et al. 2014). Assessing whether generalized behavioral monitoring stimuli are

appropriate proxies for threat is critical; employing such proxies offers a simple and inexpensive monitoring approach, much sought if effective. In particular, monitoring of elephant populations often occurs in spatially restricted areas (e.g., bais in Central African forests) (Turkalo et al. 2013), where broader ecosystem monitoring is prohibitively difficult to perform.

Differences in reactivity were related to differences in spatial use across groups. Among collared groups, those that spent a greater proportion of the year within the protected areas were calmer. Repeated exposure to vehicles (tourist and researcher) likely allows elephants to more readily recognize that people in vehicles are not a threat and therefore minimize unnecessary flight responses. In contrast, time since entering the reserves by collared individuals had no effect on elephant RI. Taken together these results suggest that longer-term spatial patterns are more predictive of behavior toward human approach in the reserves and that more recent experience is less important. A trend towards lower reactivity during increased poaching could indicate an association between vehicle presence and safety, though active avoidance of vehicles was not uncommon. Our unexpected findings related to elephant behavior and human activity underscore the importance of testing the assumptions of behavioral assessment prior to interpretation of such data (Gill et al. 2001; Bejder et al. 2009). Complexity in the degree to which elephants adjust behavior to exploitation pressure has been observed in other systems as well (Caro 2005; Kiffner et al. 2014).

Environmental Stimuli and Inherent Group Traits

Despite reactivity not being an effective indication of poaching pressure, a number of interesting insights were gleaned through this analysis. For example, elephants were more reactive when NDVI was high in both datasets. Elephants undergo dramatic changes in body

condition between the wet and dry seasons (Foley et al. 2001; Wittemyer et al. 2007a; Rasmussen et al. 2007), and greater tolerance of potential threats during the dry season may reflect a physiological state of energy conservation rather than risk assessment (Gill et al. 2001). The study elephants expand their range and travel more during the wet season (Wittemyer et al. 2007b), and reactivity may therefore also relate to changing movement patterns and associated risks on the landscape, though the fine-scale spatial variables did not emerge as important in analyses. In addition, increased forage availability (and related increased physiological condition) during the wet season corresponds to a period of greater social activity, with the largest aggregation sizes (Wittemyer 2001) and the majority of mating and birthing events (Wittemyer et al. 2007a) occurring during that time. The positive interaction found between NDVI and the presence of a musth bull supports the idea that reproductive events heighten excitement in elephants which in turn influences response to human observers.

While primary productivity and group composition strongly predicted elephant response, model intercepts varied considerably among core groups, indicating that baseline differences in the temperament across groups existed. Social animals may gauge their anti-predator responses by the responses of those around them, which may be especially relevant where more experienced, dominant, or bolder individuals are present in the group. In elephant society matriarchs may have disproportionate effects on group behavior (McComb et al. 2001; Foley et al. 2008); observed differences among groups may therefore relate to inherent differences among matriarchs, though the collection of RI as a group metric limited such inference here. Inherent matriarch effects may also interact with environmental covariates. For example, differences in social dominance among individuals are correlated with differential use of the protected areas (Wittemyer et al. 2007b), which itself was a predictor of group behavior. Lower reactivity could

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therefore relate to individual traits like dominance, potentially complicating the ability to characterize level of threat within the ecosystem based on individual responses unless their social context is determined.

Implications for Personality Research

While aspects of this study are specific to elephant behavior, our findings hold implications for the use of behavior to assess human impact in wild populations and extend to other disciplines like personalities (Dall et al. 2004). Reaction to a human observer is often employed as a measure of shyness-boldness (Réale et al. 2007). While such metrics may represent inter-individual differences along the shyness-boldness personality continuum, it is also possible that they are more reflective of the subject's recent experiences, reproductive state or ecological conditions. In our case, environmental context was a strong driver of our behavioral metric. Mixed-effects models allow investigation of such behavioral metrics by partitioning the variance due to differences among individuals while controlling for the effects of environmental variables (Dingemanse & Dochtermann 2013). Individual intercepts can thereby be interpreted as metrics of personality, after controlling for external stimuli that influence the behavioral metric. In this particular study, the behavioral measure was a group level metric and therefore not easily used for personality measures. However, matriarchs are known to disproportionately affect group behavior, which may be true for group responses to predator stimuli. As such, the variation among core group intercepts reported here potentially reflected personality differences among matriarchs. In this case, elephants with higher intercepts might be considered less bold or more reactive than the rest of the individuals in the sample.

Ensuring the Utility of Flight Response Monitoring

In addition to demonstrating the complexities of behavioral assessment, our study highlights the need to extend such research beyond conventionally adopted flight metrics and tailor metrics for greater relevance to the system of interest (Gill et al. 2001; Kiffner et al. 2014). Elephants assess threat using olfactory, auditory, and visual cues (Bates et al. 2007; McComb et al. 2014), and cues of researchers are different from those of the specific humans that might present risk to elephants in this system. Behavioral studies should be carefully designed to address potential mismatches between threats to wildlife and anti-predator stimuli. Efforts should also be made to measure other variables that may affect the study species, like availability of alternative habitat, seasonal constraints on activities like breeding or socializing, and presence of vulnerable young. Further, behavioral manifestations unrelated to human stimuli may also be informative. For example, we have observed instances in which elephants known to have experienced poaching events responded calmly to research vehicles in the days following the event but were generally skittish toward other stimuli unrelated to humans. Recognition of such nuances in study systems will be critical for the effective use of behavioral indicators (increasingly being advocated for use in the conservation of species that are difficult to monitor) (Berger-Tal & Saltz 2016) to characterize population threats and trends. Finally, it is essential for researchers to account for confounding proximate variables that may explain wildlife behavior in studies measuring personality traits or effects of human disturbance. The mixed-effects approach implemented here provides a promising avenue for future work in both fields, where inherent differences among individuals may be separated from environmental variables (Dingemanse & Dochtermann 2013).

Chapter 6: Evidence of strong spatial segregation between elephant subpopulations in the contiguous Laikipia-Samburu ecosystem in Kenya[5]

Introduction:

Connectivity within populations affects important ecological and evolutionary processes like gene flow, disease dynamics, and cultural exchange (Noad et al. 2000; McCallum & Dobson 2002; Epps et al. 2005). Understanding connectivity is especially relevant in the context of conservation as landscape-level changes may alter wildlife movement. Such changes disproportionately affect wide-ranging species (Seidler et al. 2015) and those whose movement corridors are not protected (Didier et al. 2011). However, assessing connectivity across and within populations is difficult given the ephemeral and often cryptic nature of dispersal. Comparative, long-term datasets of known individuals can provide critical information and insights for wildlife managers and policy makers to determine whether and how subpopulations are connected.

The Laikipia-Samburu elephant (*Loxodonta africana* Blumenbach) population is the second largest in Kenya with approximately 7415 individuals, primarily relying on range outside of governmentally protected areas (Poole et al. 1992; Litoroh et al. 2010). The 34,000 km^2 Laikipia-Samburu ecosystem is a complex land use mosaic comprised of private, government, and community lands (Thouless 1995), which represent varying levels of risk to the region's elephants (Ihwagi et al. 2015). The region is undergoing large-scale development projects (*LAPSSET Corridor Development Authority*, 2015), with unknown consequences for elephants

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[5] Adapted from: Goldenberg, S.Z., Oduor, S., Kinnaird, M. F., Daballen, D., Douglas-Hamilton, I., and Wittemyer, G. 2016. Evidence of strong spatial segregation between elephant subpopulations in the contiguous Laikipia-Samburu ecosystem in Kenya. *African Journal of Ecology* 54:261-264.

and other wide-ranging animals. Social interactions drive spatial segregation between elephant groups at the local scale (Wittemyer et al. 2007b). Social segregation may also occur at larger scales, but few opportunities to test this hypothesis exist. Understanding current levels of connectivity among elephants of the Laikipia-Samburu landscape can provide deeper insight to spatial segregation in this species as well as provide fundamental information for planners and researchers. Here, we elucidate the degree of overlap between individuals using two intensively studied areas within the spatially contiguous study ecosystem.

Methods:

Photographic records of individual elephants using the 220 km^2 Samburu and Buffalo Springs National Reserves (SBSNR) (compiled through a monitoring project started in 1997), were compared with records collected on the 200 km^2 Mpala Ranch (compiled through a monitoring project started in 2009). The two study areas are separated by approximately 75 kilometers (Fig. 6.1). SBSNR are protected areas in the lowlands of the ecosystem, surrounded by community conservancies and permanent settlements. In contrast, Mpala is embedded in a mosaic of smallholder farms and large private ranches on the Laikipia plateau. Both projects use ear and tusk idiosyncrasies to identify individuals (Wittemyer 2001), facilitating comparison. Our comparative search included breeding females ($N_{SBSNR} = 356$, $N_{Mpala} = 573$) and dispersed males ($N_{SBSNR} = 239$, $N_{Mpala} = 139$) (Wittemyer 2001).
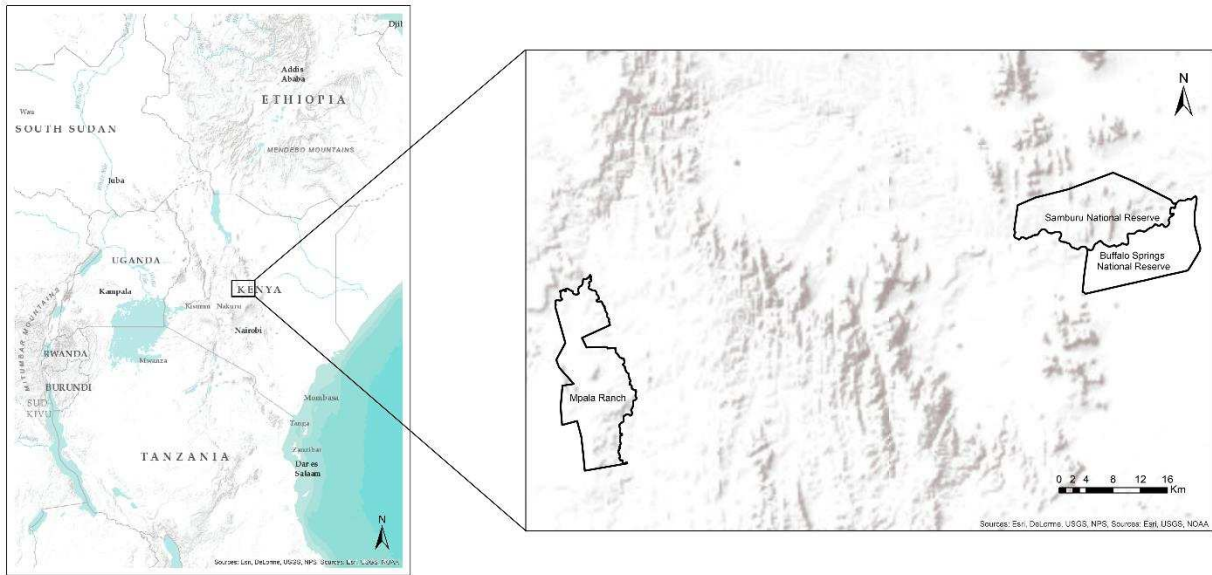
Figure 6.1: The study areas Mpala Ranch and Samburu and Buffalo Springs National Reserves are located in north central Kenya and are separated by approximately 75 km.

Results and Discussion:

No overlap was identified among the photographically documented elephants using Mpala and SBSNR. This was unexpected given radio-tracking evidence of connectivity between the two areas (Fig. 6.2), and the short distance between the two study areas relative to the tens of kilometers elephants can travel in a day and the thousands of square kilometers that can be encompassed in an elephant's home range (Wittemyer et al. 2007b; Wall et al. 2013). Radio-tracking evidence revealed that one male (30-35 years old) and one female (20-25 years old) traveled between SBSNR and Mpala between 2012 and 2015. Given the social structure of elephant society (Douglas-Hamilton 1972; Moss 1988), the female was likely traveling with her family group (approximately 20 individuals), whereas it is unclear whether the male was alone or

in a herd. Both elephants were collared in Samburu National Reserve (along with approximately

two dozen elephants tracked at the same time).
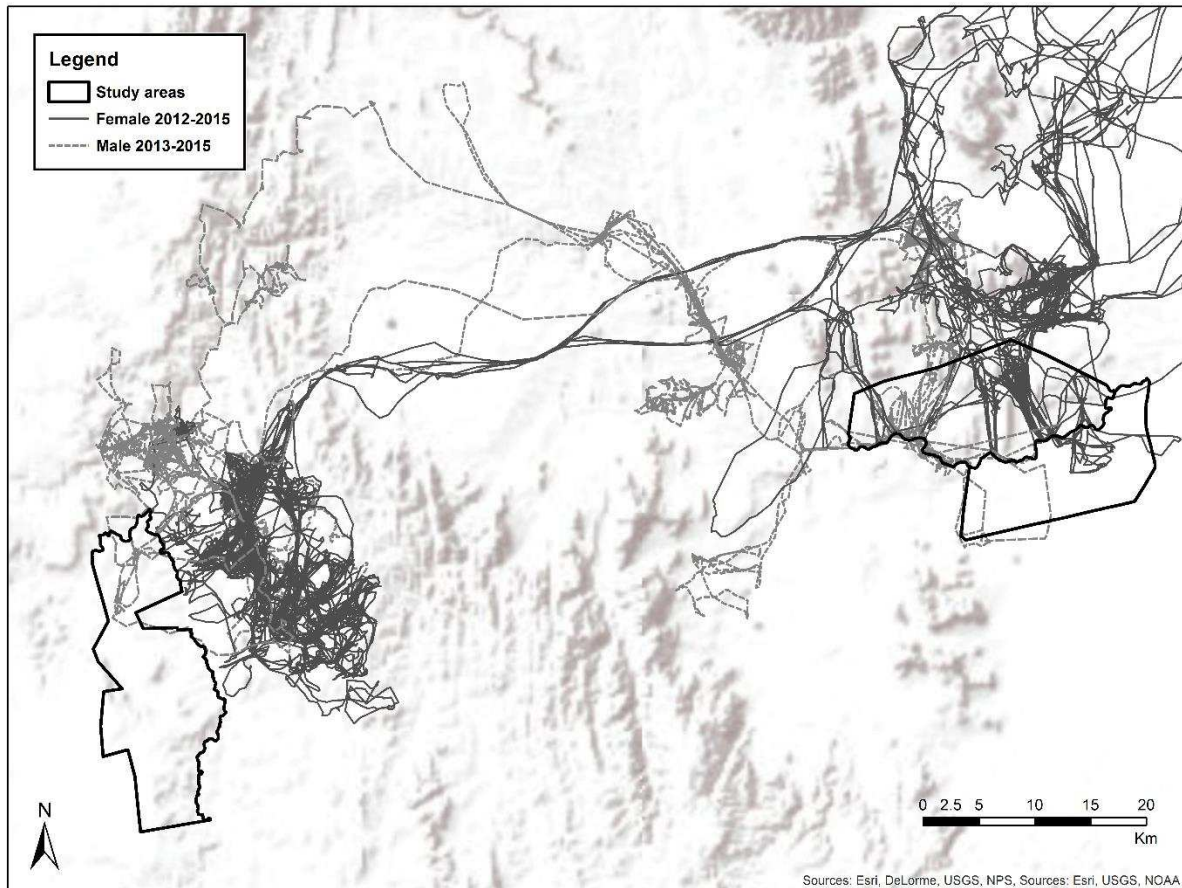
Figure 6.2: The paths of two radio-tracked elephants between 2012 and 2015 demonstrate connectivity between Mpala Ranch on the Laikipia plateau and Samburu and Buffalo Springs National Reserves in the lowlands despite zero overlap among the more than 1300 adult elephants identified in the two areas.

The duration between elephant re-sightings from the long-term Samburu study varies

among family groups, but in the extreme can span ten years (i.e. the longest recorded time

between two consecutive sightings of a family). The six year duration of the Mpala study could

limit the ability to capture SBSNR elephants that (very) infrequently use Mpala. It is also

possible that elephants using the two study areas were not detected while in the reserves. Radio-tracked elephants have entered the northern part of Mpala without detection. In Samburu, unidentified elephants from outside the subpopulation were observed using areas just outside the boundaries of the park (Wittemyer pers. obs.). Irrespective of incomplete sampling, it is clear strong intra-population structuring limits the interaction of the known elephants across the Laikipia-Samburu ecosystem.

Thouless (1995) suggested that the elephant use of the Laikipia plateau is relatively recent, with more elephants gradually moving into the area from the lowlands in response to increased poaching pressure and changing land management practices in the 1970s and 1980s. Thus, range use in this population may be changing continuously, with elephant knowledge of alternative habitats becoming increasingly crucial as development and ivory poaching continue in the region (Wittemyer et al. 2014; *LAPSSET Corridor Development Authority Request for Proposals* 2015).

Long-term datasets on known individuals are rare, but provide invaluable information on population processes (Clutton-Brock & Sheldon 2010). Such datasets may be even more powerful when there is the potential for comparison within species or populations. In this instance, comparable datasets revealed the surprising result that despite being separated by a short distance relative to an elephant's ranging ability (Wall et al. 2013), these two subpopulations demonstrate strong spatial segregation. While radio-tracking data identified ephemeral connectivity between the two populations, it is notable that the use of Mpala by the tracked individuals was brief (a matter of hours for the male). This study demonstrates the value of both individual-based monitoring and tracking data sets to understand connectivity and segregation, where the combined data provides stronger inference than either dataset alone.

Range overlap outside Mpala and SBSNR among some individuals remains a possibility and rare connectivity events, as evident from radio-tracking data, suggest that genetic exchange may still occur despite the strong degree of segregation. Conservation efforts targeted at maintaining movement corridors can facilitate such exchange, which can be critical to sub-population persistence (Keller & Waller 2002; Okello et al. 2008).

Older elephants are known to hold more information than younger elephants (McComb et al. 2001; Polansky et al. 2015); the selective harvest of older elephants for their larger tusks in this population in recent years (Wittemyer et al. 2013) may thus threaten connectivity with the loss of corridor knowledge. Targeted movement studies addressing generational changes in movement may shed light on the long-term effects of ivory harvest for subpopulation connectivity. Our findings demonstrate the utility of GPS technology in identifying rare events that may have implications for population dynamics.

Chapter 7: Conclusion and future directions

Addressing conservation challenges requires diverse skill sets and creative approaches. As an older field, animal behavior encompasses a rich theoretical foundation that may be of value in navigating wildlife conservation problems. In this dissertation, I explored research questions rooted in animal behavior (predator responses, socio-ecology, and reproductive tactics) in the context of a population of African elephants that experienced a sudden rise in age-selective overharvest. I investigated long- and short-term responses as behavioral indices, as well as baseline behavior, illuminating how such data may provide insight to what the population was experiencing.

The downstream demographic effects of overharvest in species with slow life histories are well documented (Stockwell et al. 2003), and the potential for behavioral repercussions has also been noted (Williams & Lusseau 2006). However, the relationship between the two is poorly understood. Elucidating the interaction between demography and behavioral patterns is certain to lead to fresh insights that will be beneficial to wildlife managers and conservation practitioners. For example, in this work we demonstrated a degree of social resilience to continuous poaching among female elephants. If such measures of social resilience are related to demographic parameters (e.g., integrated orphans have greater calving success than peripheral orphans or social integration breaks down when many matriarchs die), social metrics can be used to refine estimates of recovery from overharvest or as proxies for population health where longer term demographic studies are impossible or impractical. Planned work in this population will integrate the data presented in this dissertation on social strategies with calving histories of individual females to develop this line of inquiry.

In addition to the implications for demographic trajectories, social strategies during disruption may affect emergent population trends in landscape use. Elephants are ecosystem engineers (Campos-Arceiz & Blake 2011; Haynes 2012); where and how they move impacts ecological communities. Additionally, risk (e.g., poaching and human-elephant conflict) is distributed heterogeneously across the landscape (Ihwagi et al. 2015), and understanding how landscape use reflects risk-taking is important to assessments of population recovery (Wittemyer et al. 2016). Because female elephants move in groups, their social patterns should be reflected in their movement decisions. However, the link between social relationships and landscape use is poorly understood. Future work will use the social bonds investigated in this dissertation to clarify this emergent property of sociality.

The work here sheds new light on the behavioral flexibility and social complexity of this threatened species. Though still not widely implemented, behavioral metrics offer promise for conservation goals, and these chapters provide insight into the utility of such metrics for wildlife studies while laying the foundation for future research.

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Appendix I: Chapter 4 model results

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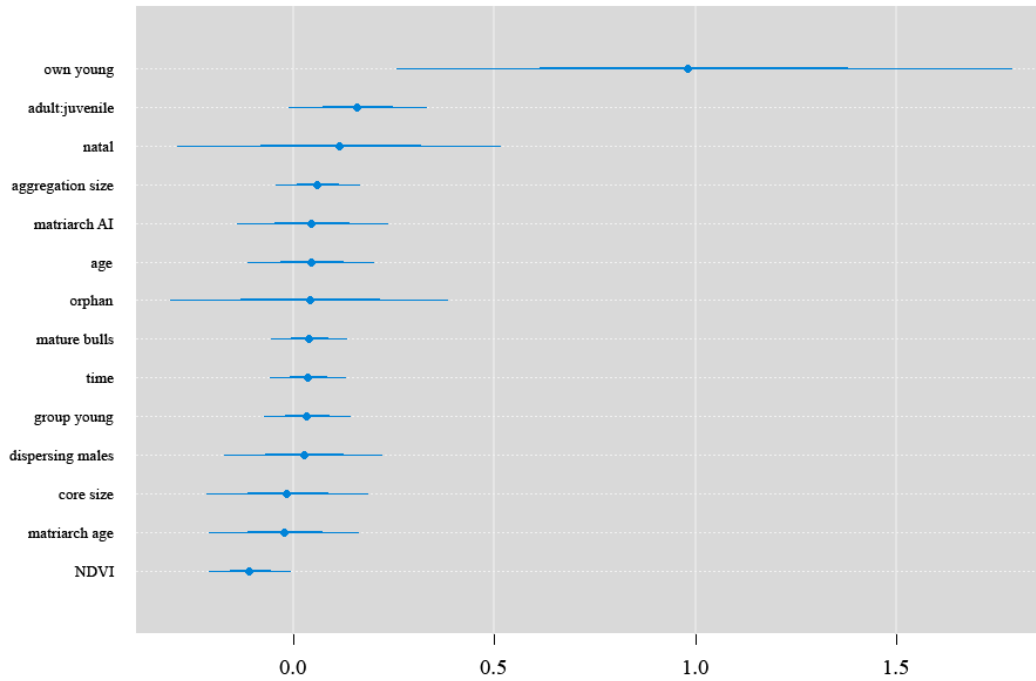
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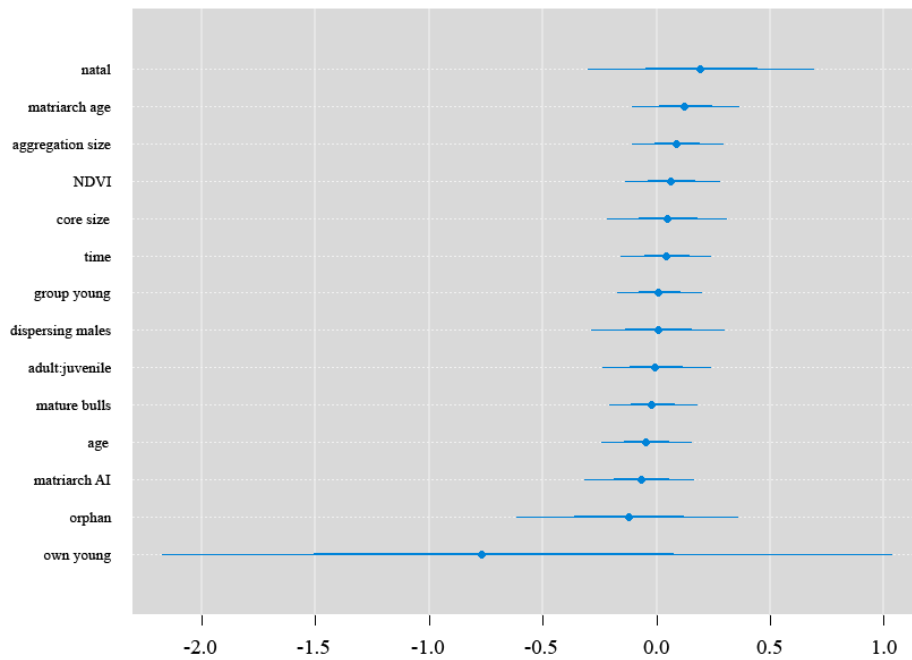
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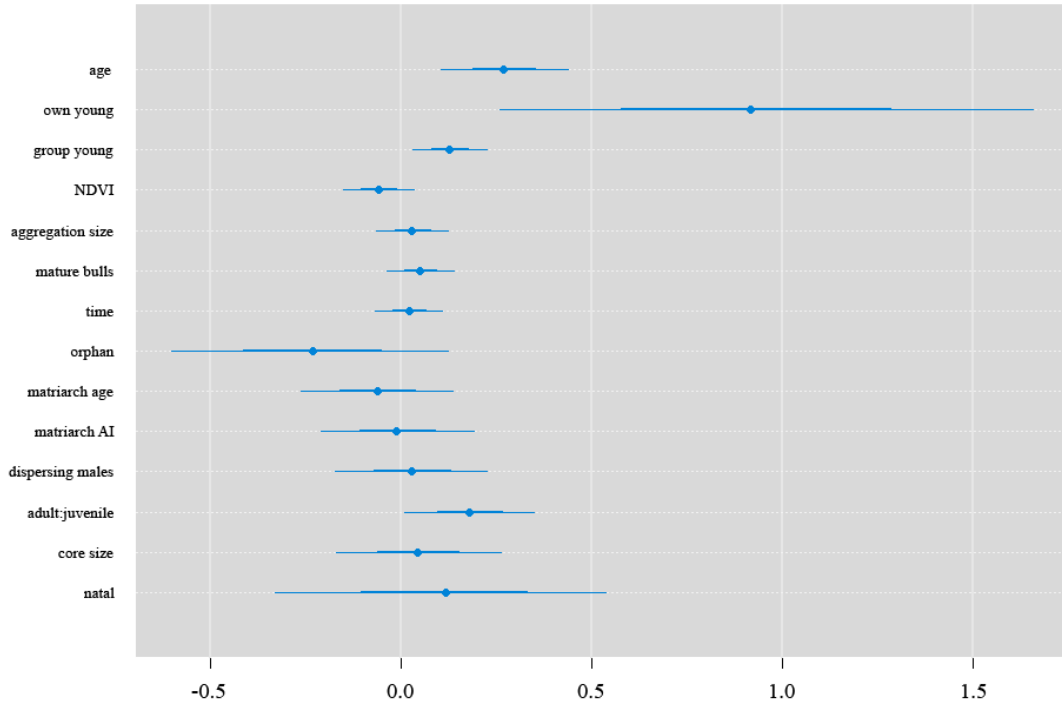
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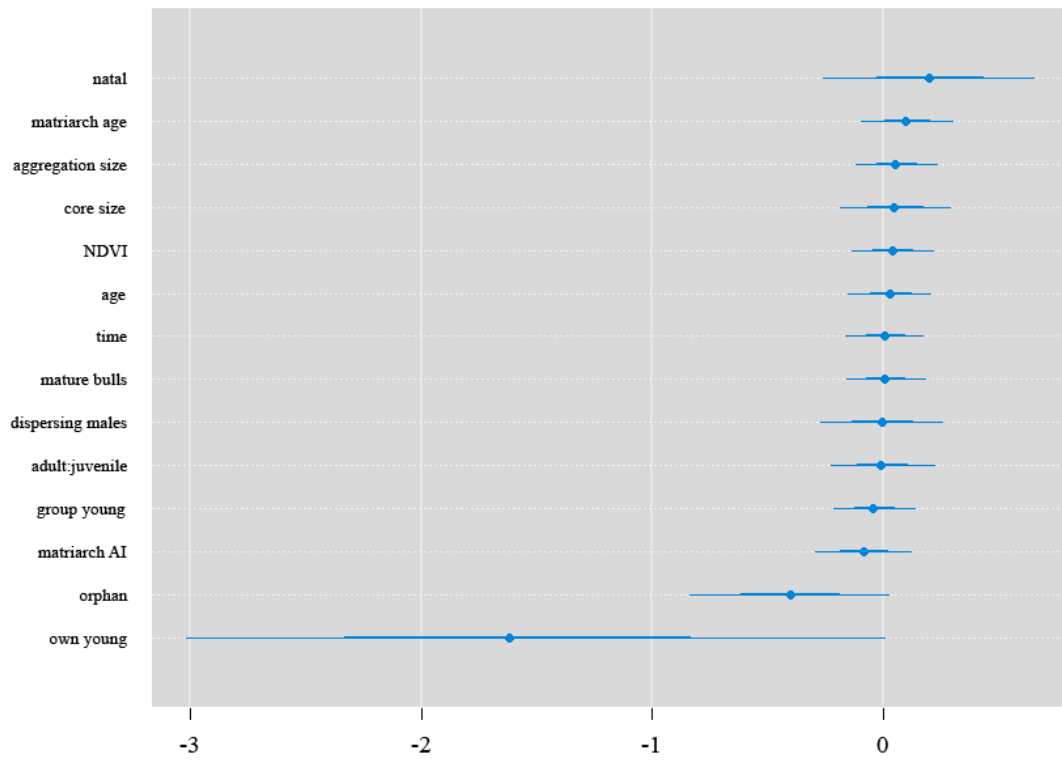
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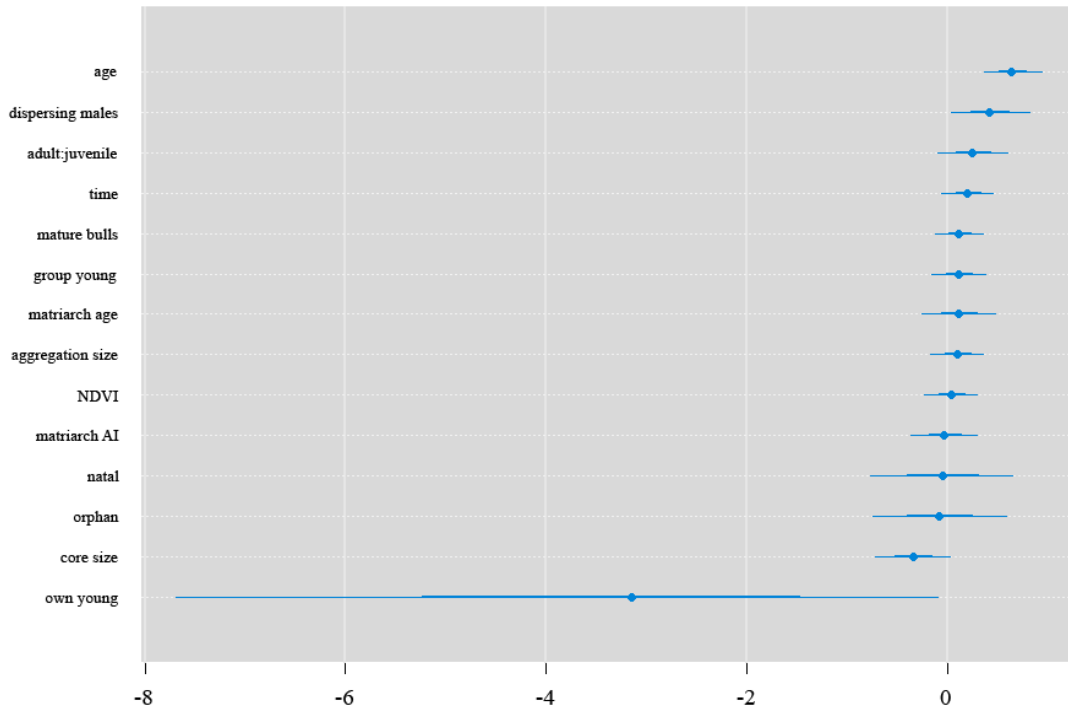
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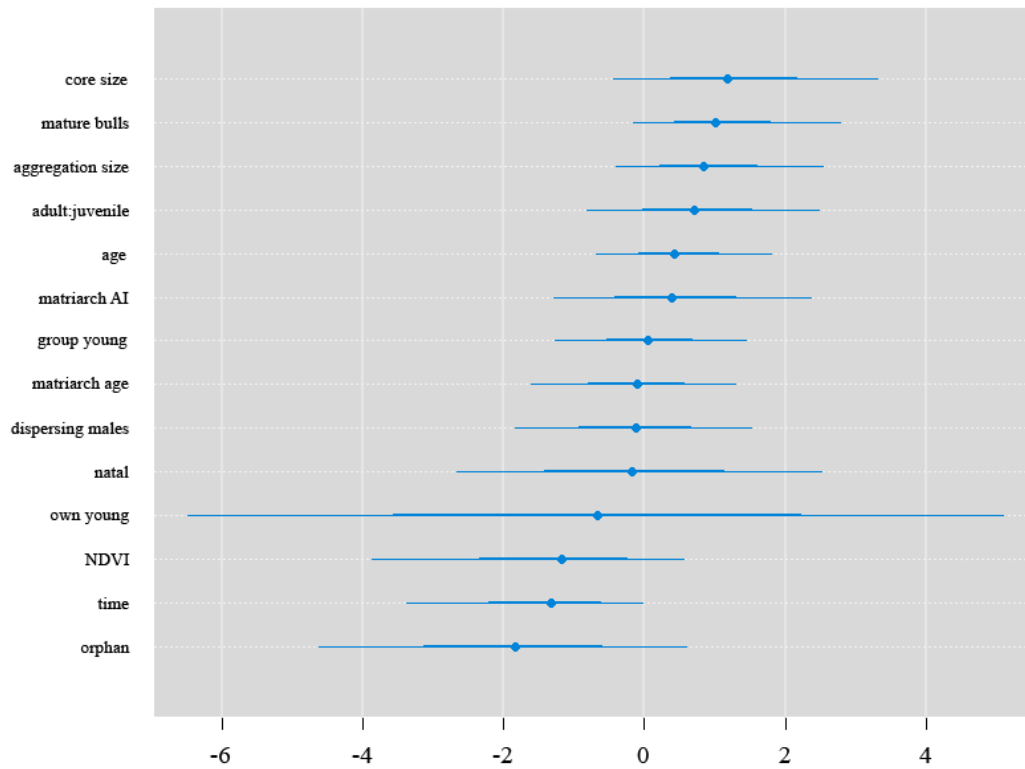
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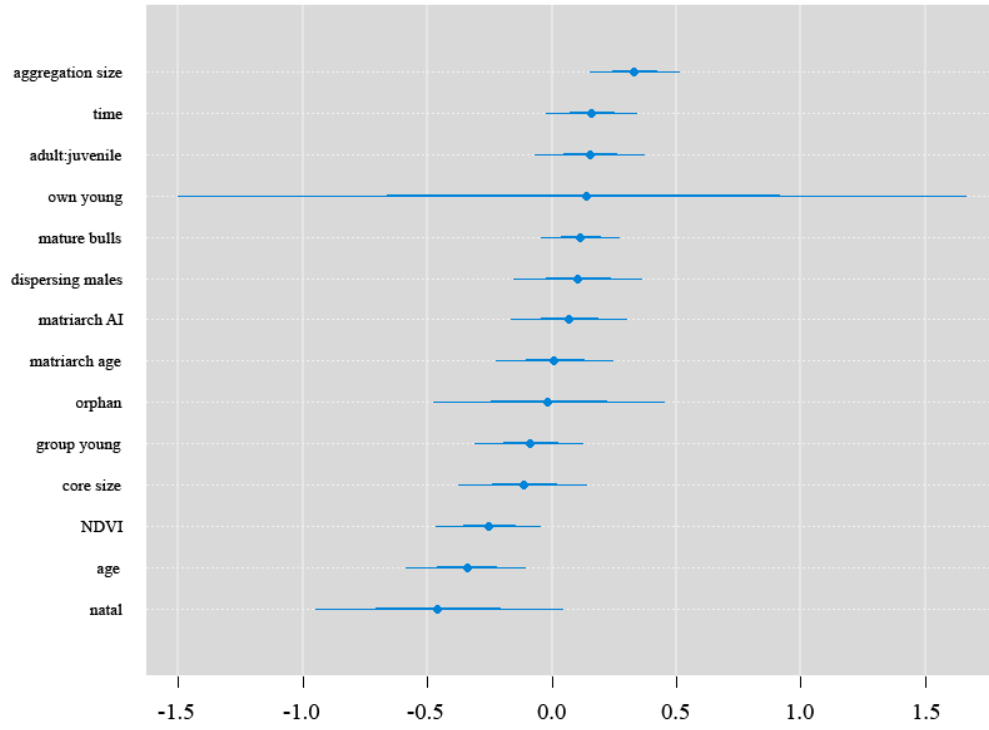
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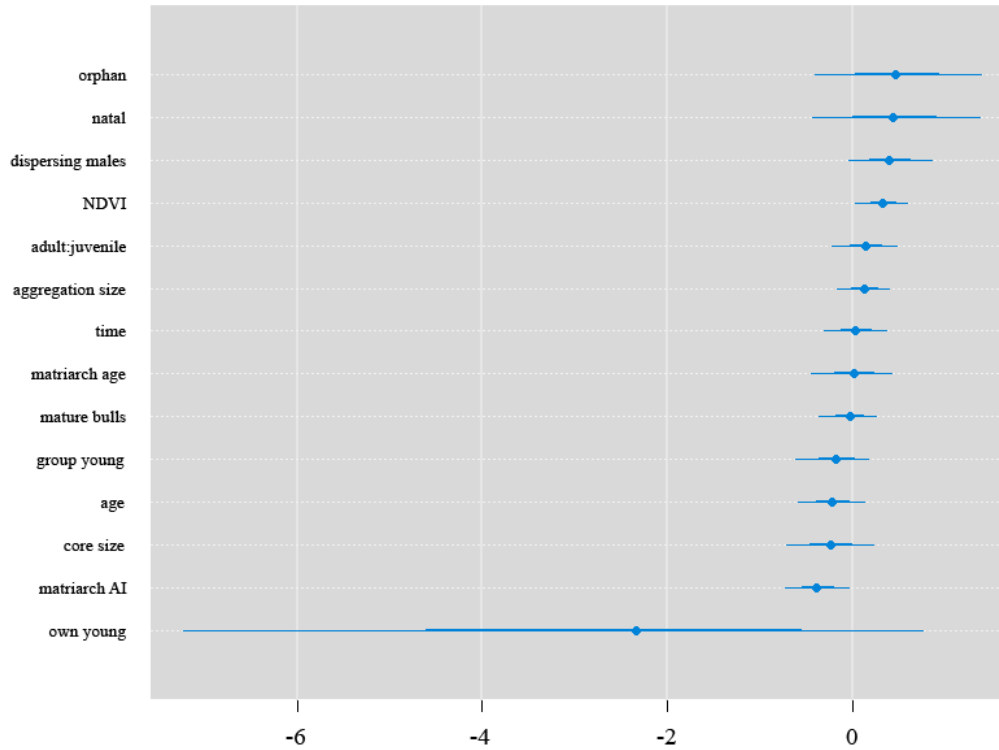
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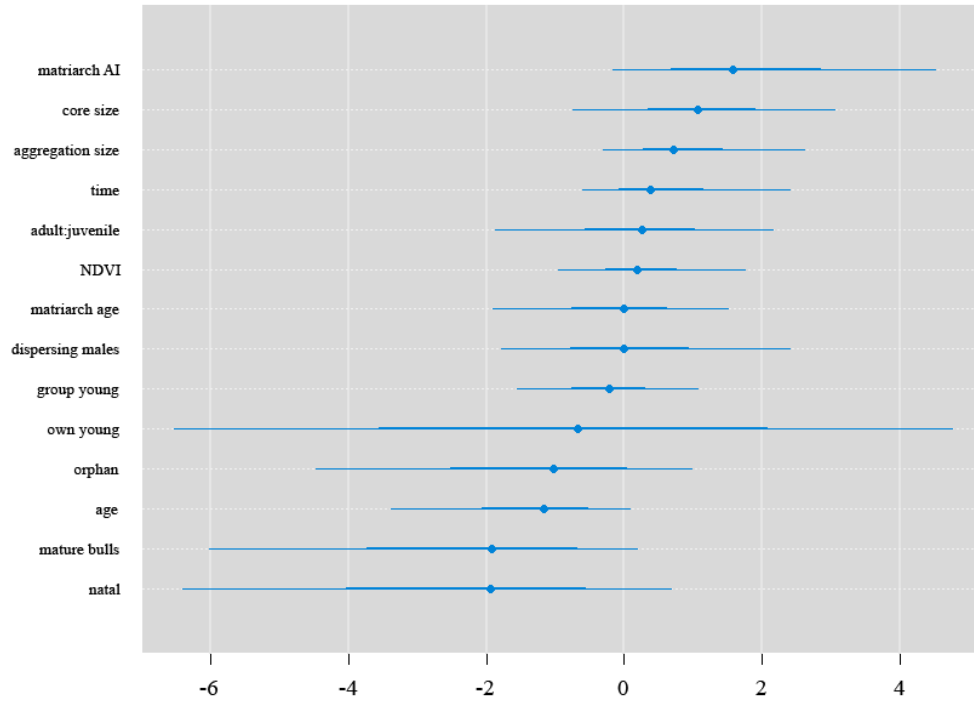
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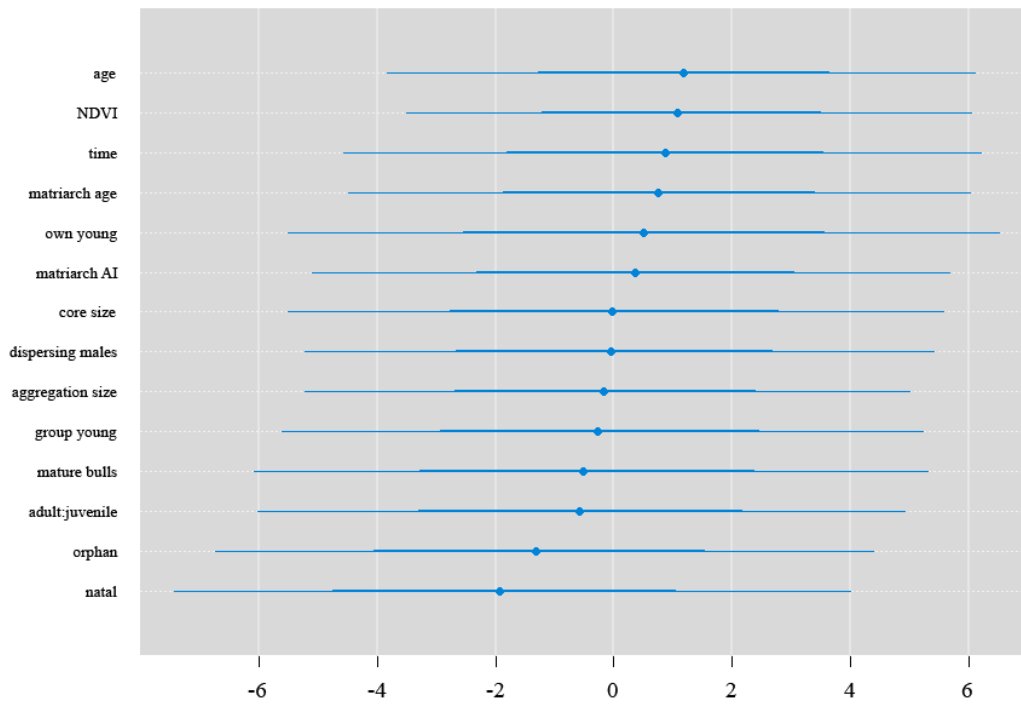
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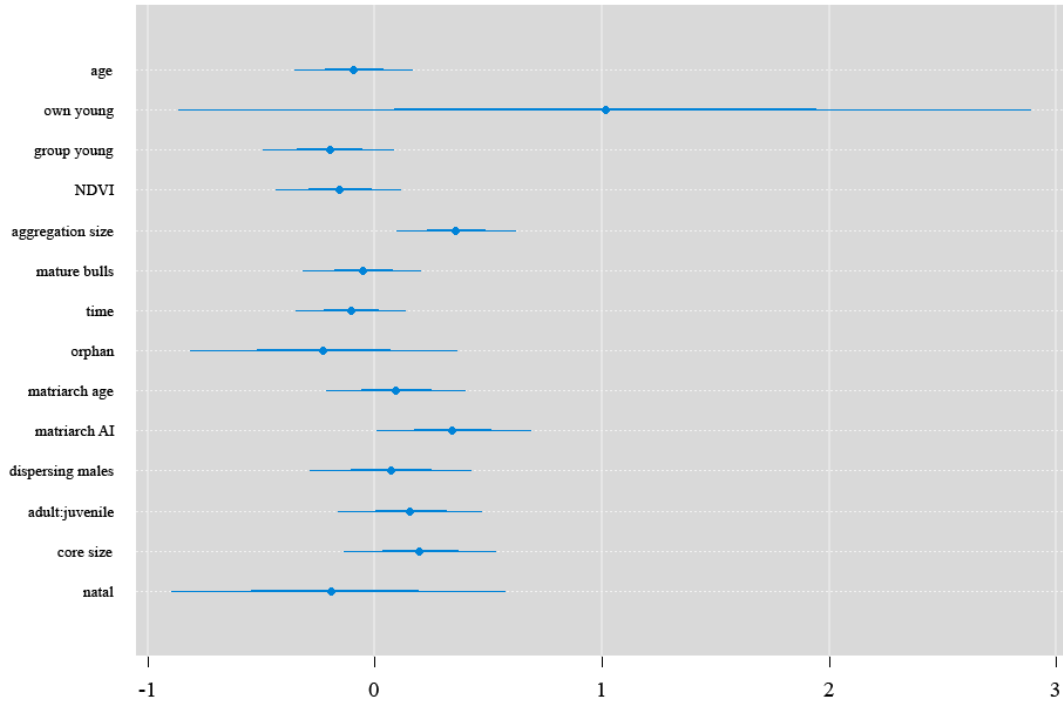
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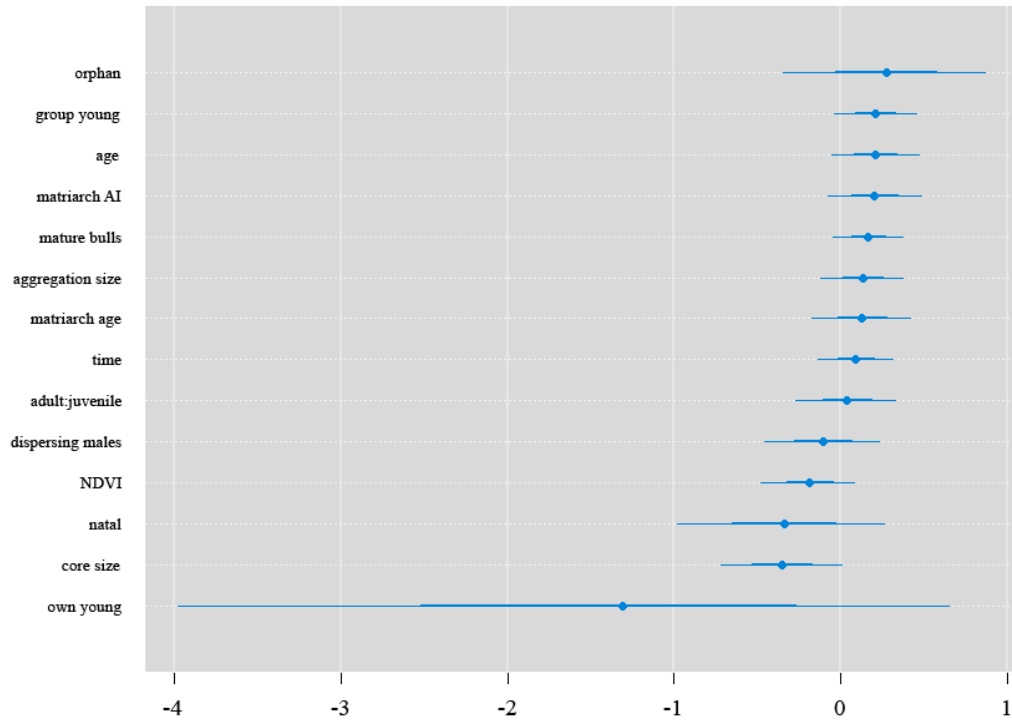
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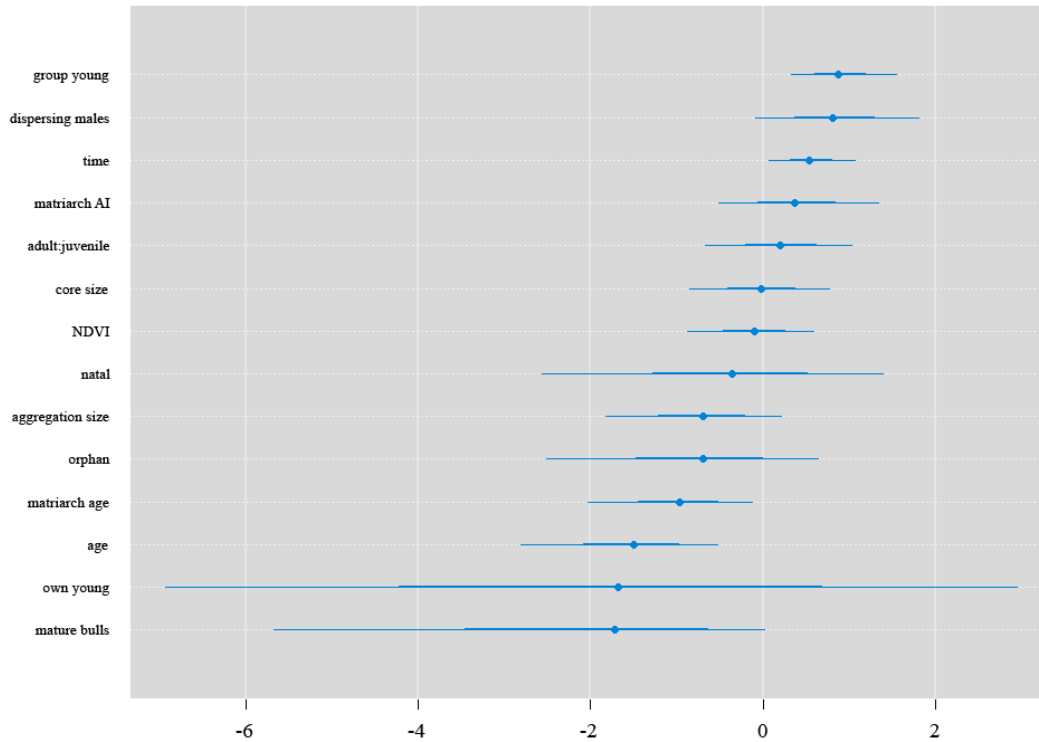
Figure A.1: Estimates of standardized coefficients for Bayesian models predicting interactions per focal follow, where thick lines represent 68% credible intervals and thin lines represent 95% credible intervals.

Receiving affiliative interactions (feeding)
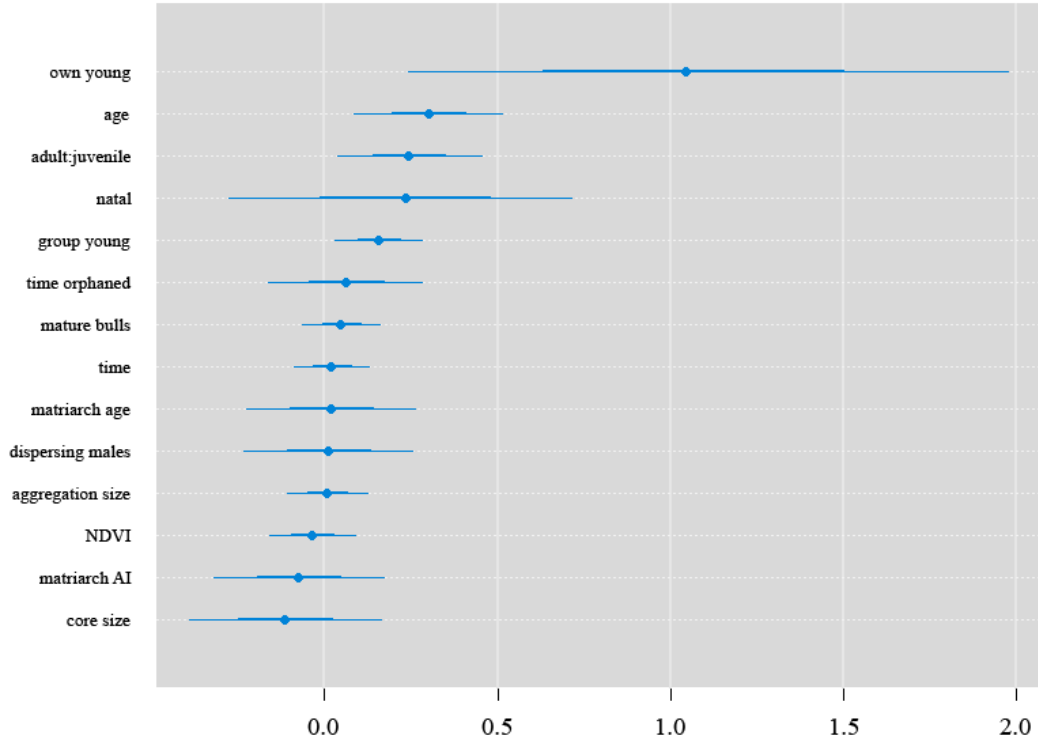
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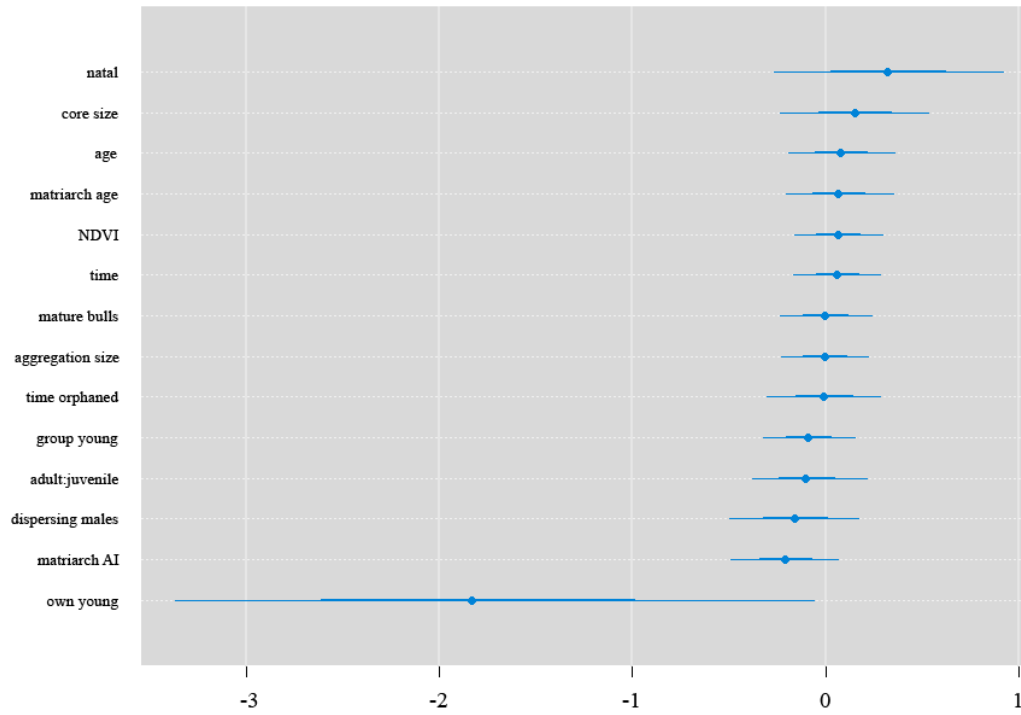
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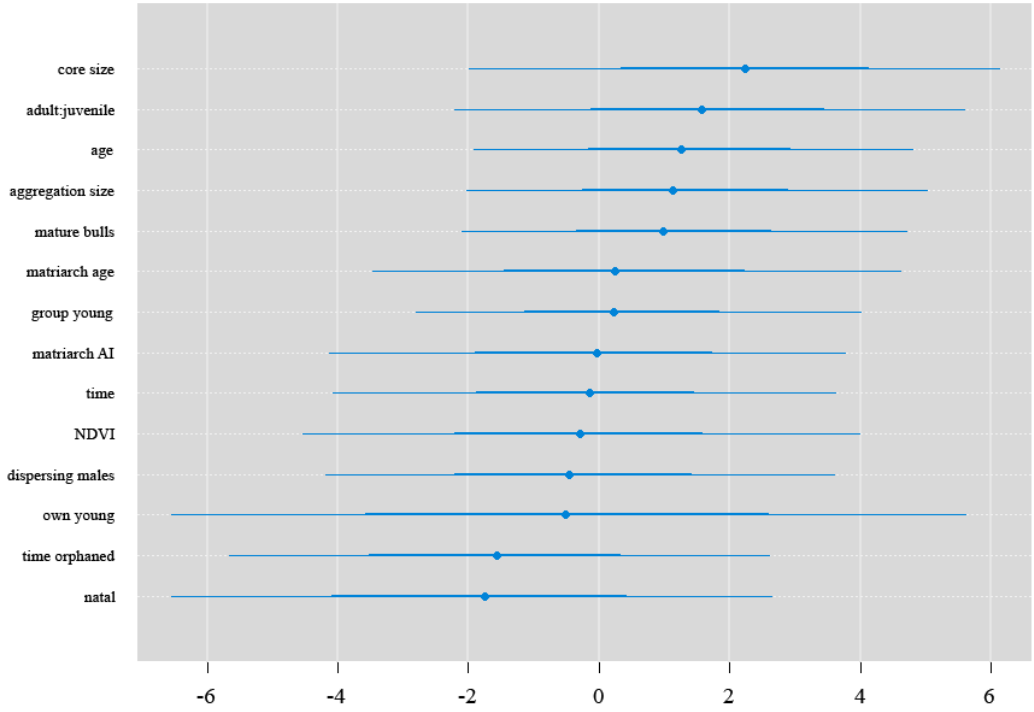
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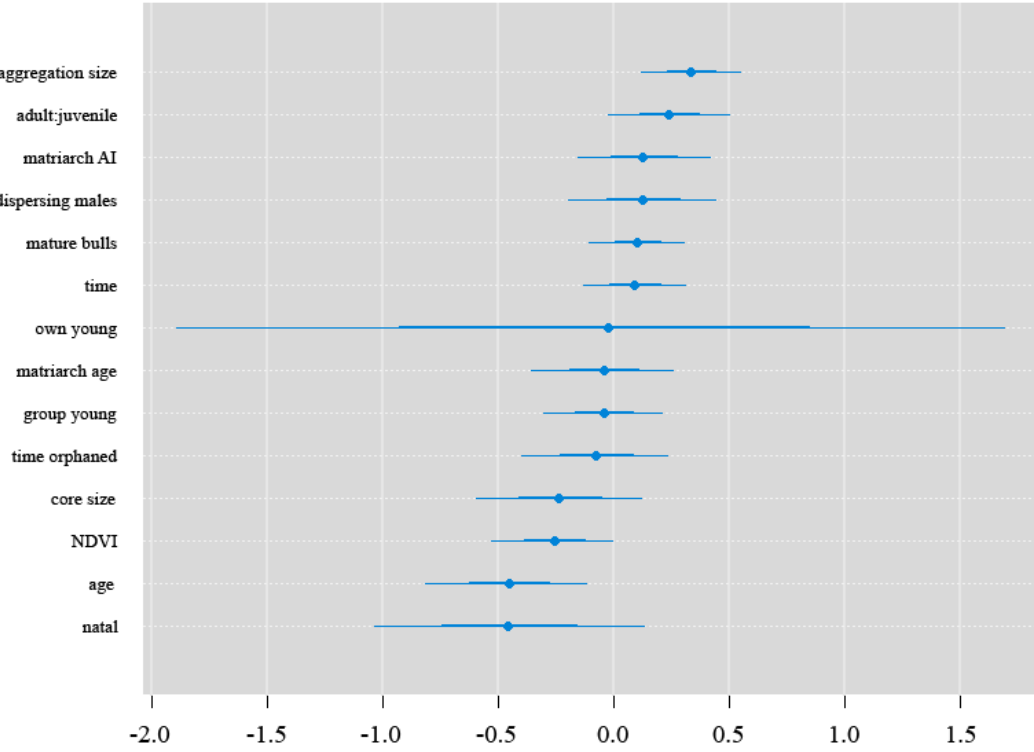
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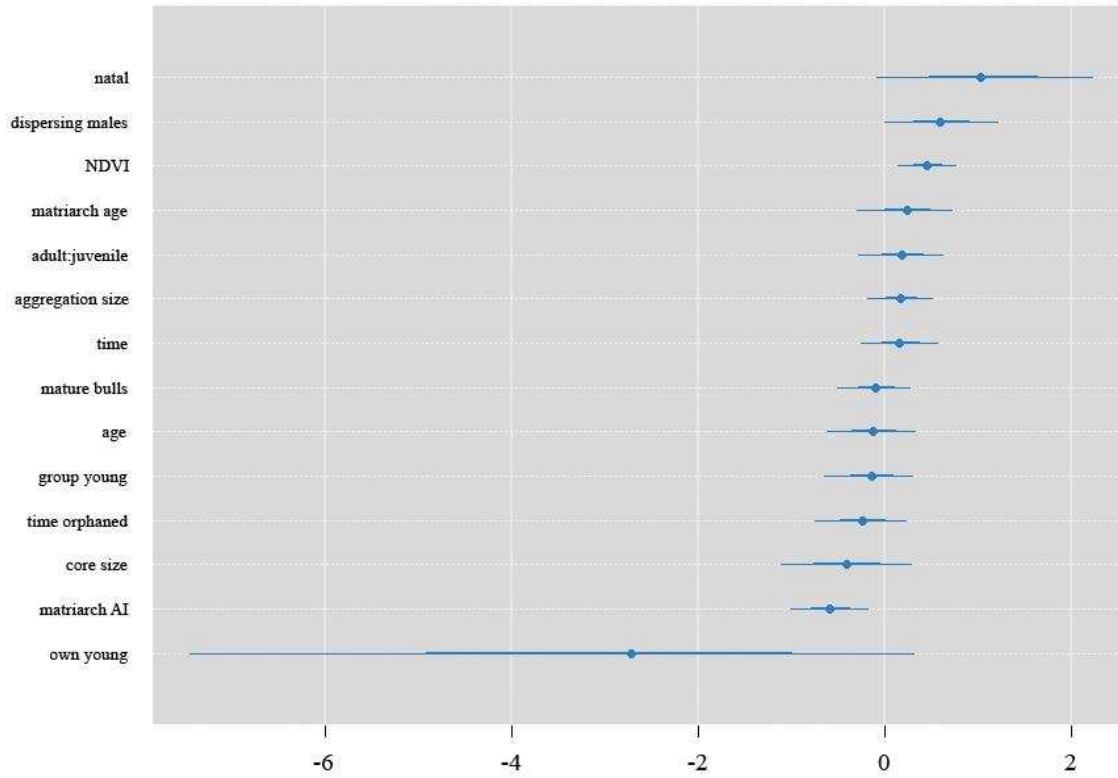
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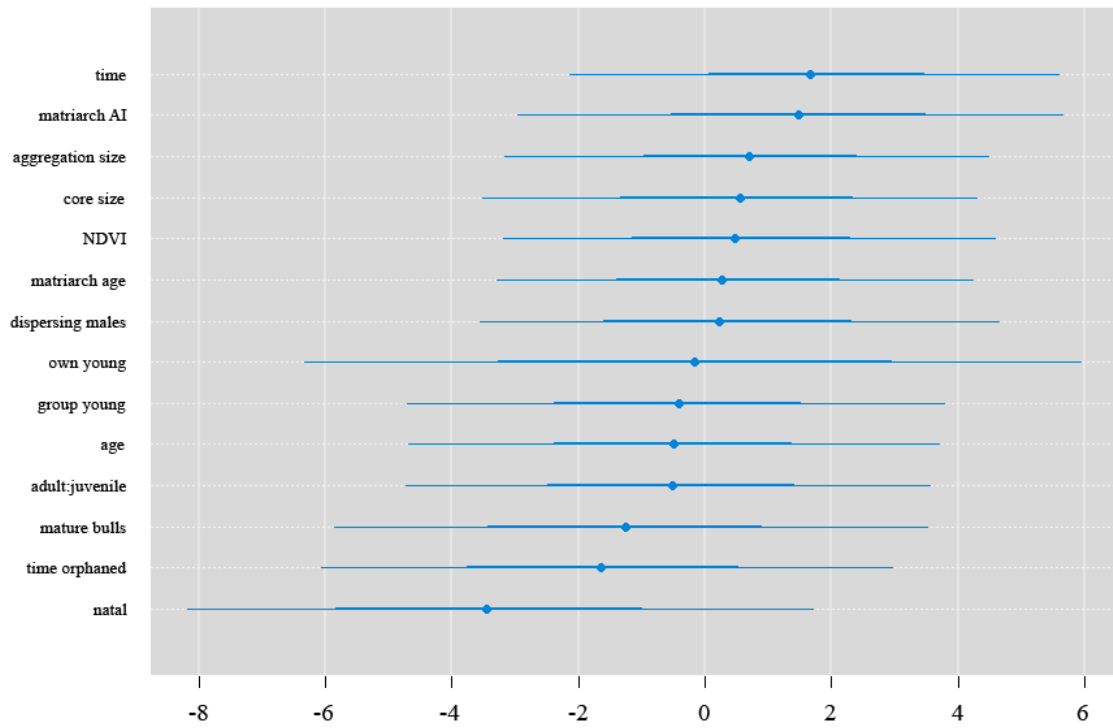
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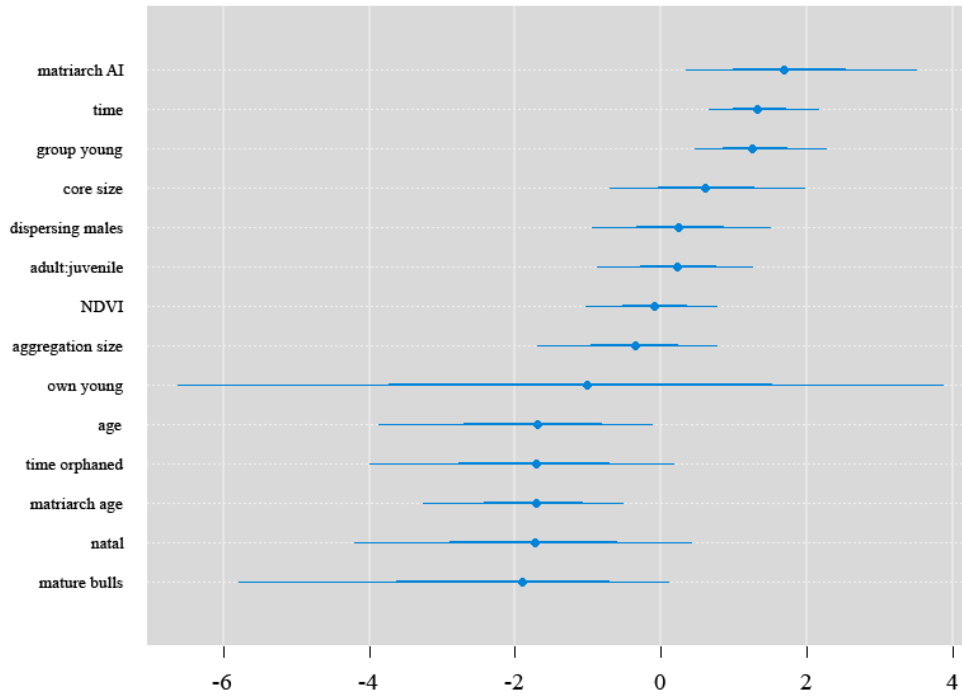
Figure A.2: Estimates of standardized coefficients for Bayesian models predicting interactions per focal follow in the orphan subset, where thick lines represent 68% credible intervals and thin lines represent 95% credible intervals.

Focal is affiliative actor (feeding)
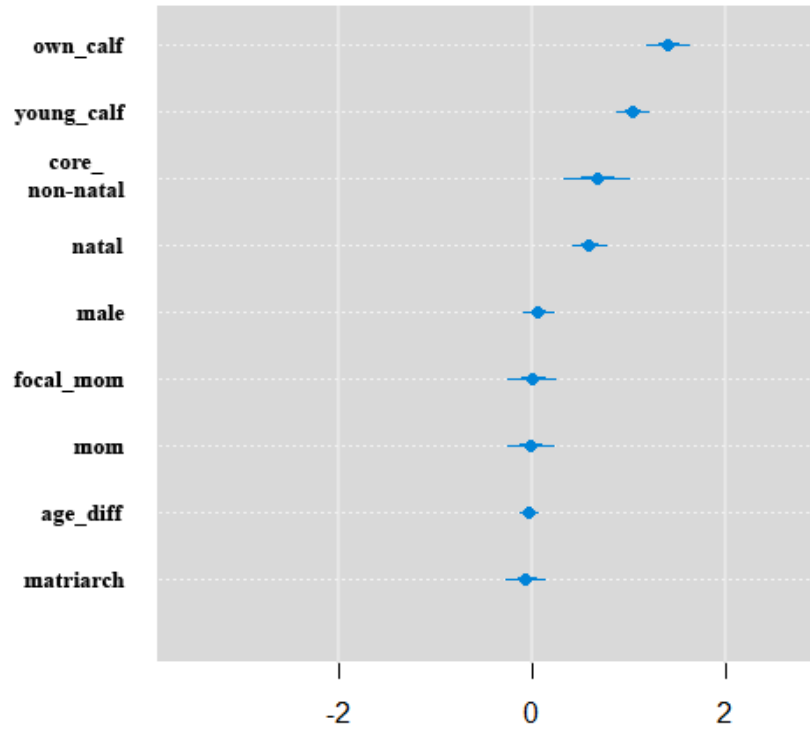
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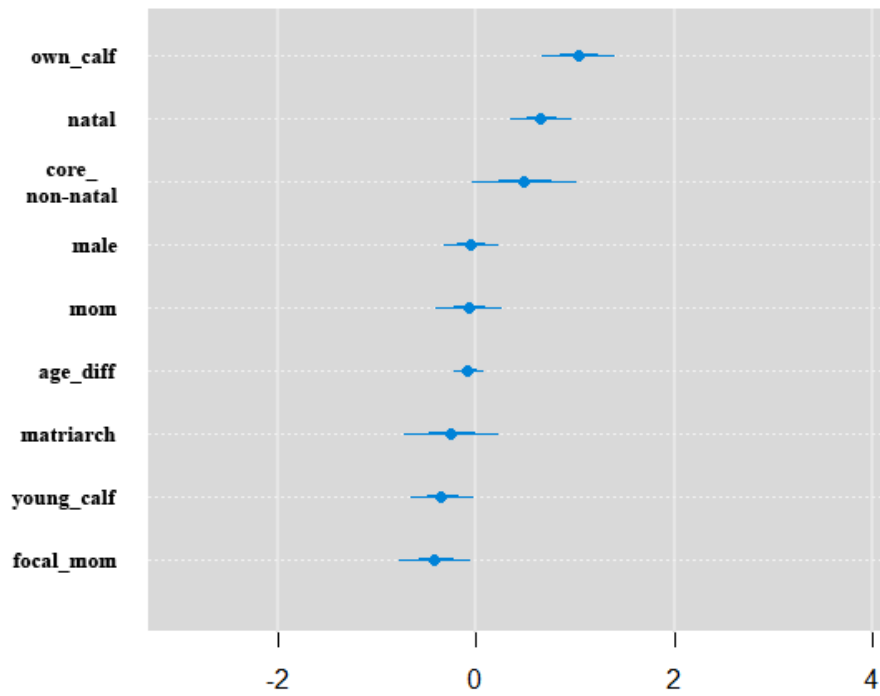
Focal is affiliative recipient (feeding)
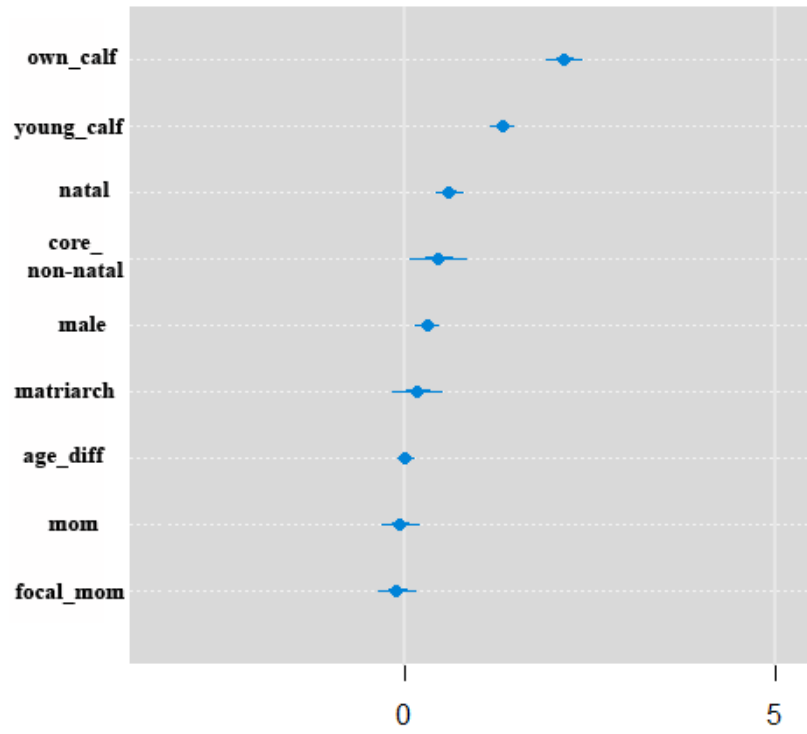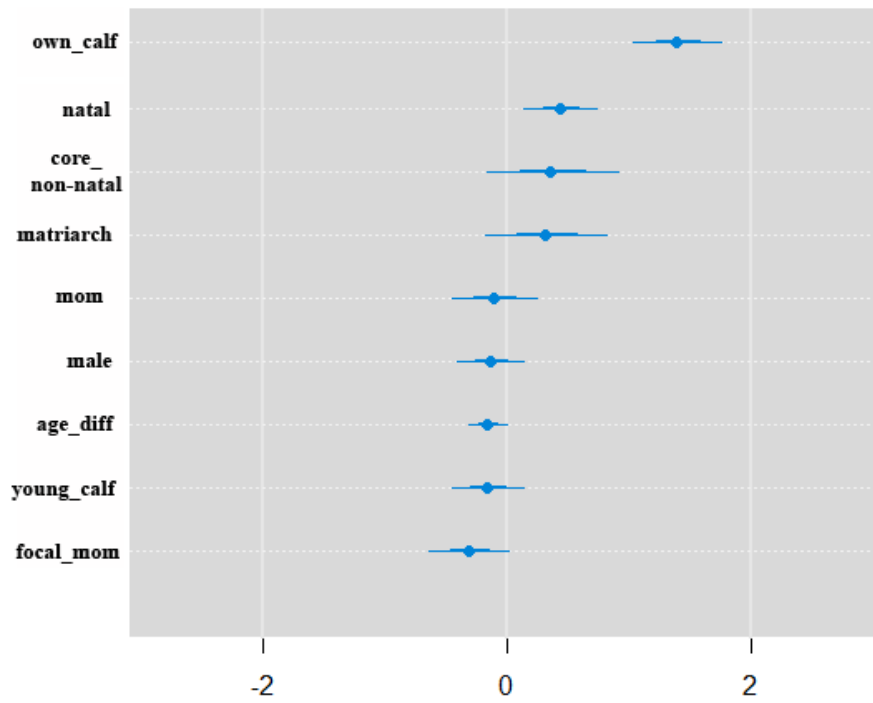
Focal is affiliative recipient (resting)

Focal is aggressive actor (feeding)

Focal is aggressive actor (resting)

Focal is aggressive recipient (feeding)
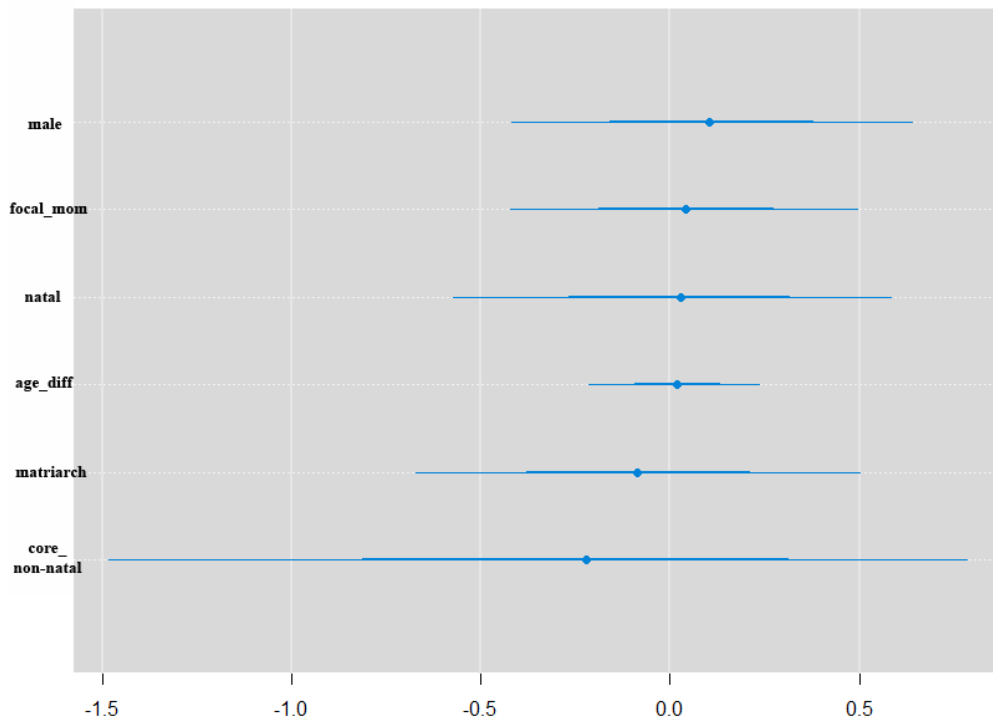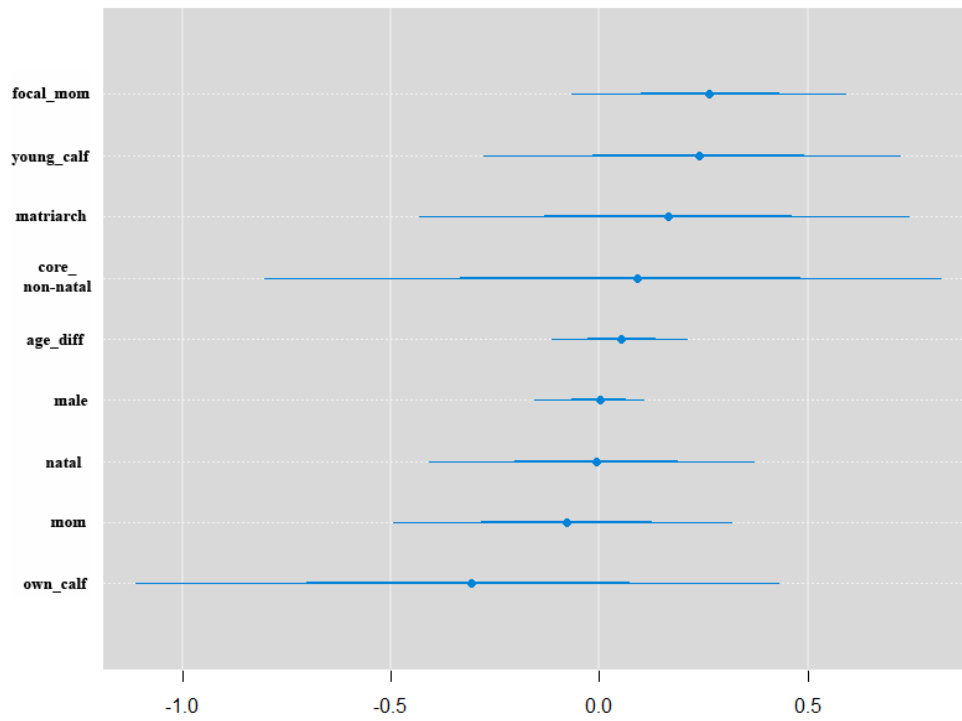
Focal is aggressive recipient (resting)
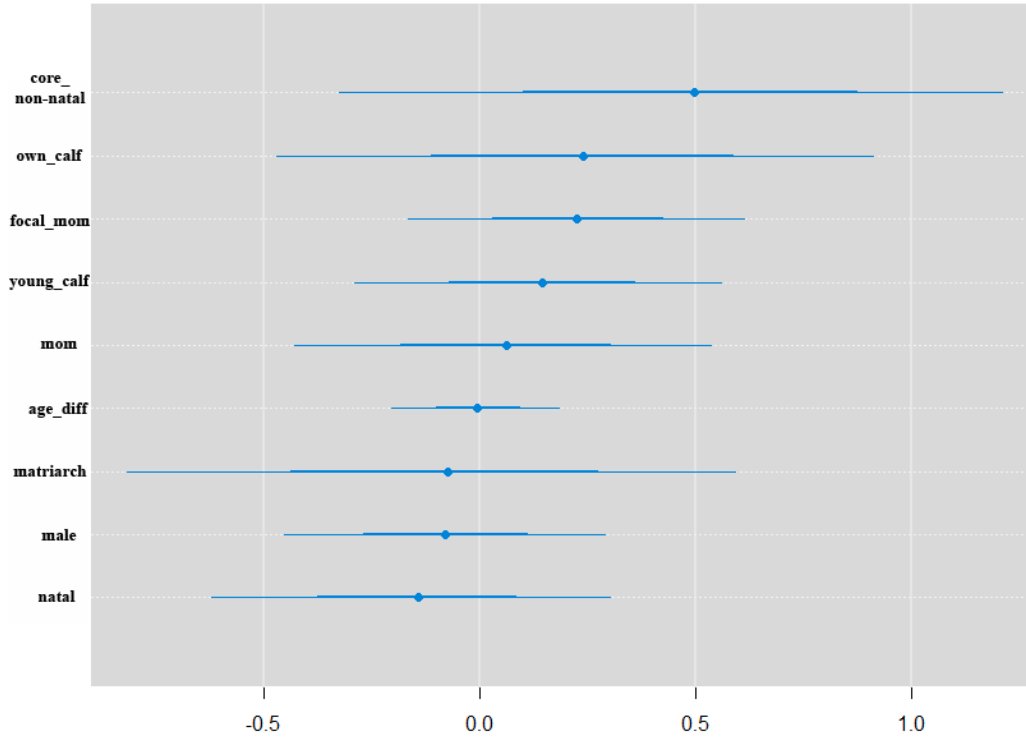
Figure A.3: Estimates of standardized coefficients for Bayesian models predicting interactions per partner, where thick lines represent 68% credible intervals and thin lines represent 95% credible intervals.

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