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The interplay of the physical landscape and social dynamics in shaping movement of African savanna elephants (loxodonta africana)

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ABSTRACT

THE INTERPLAY OF THE PHYSICAL LANDSCAPE AND SOCIAL DYNAMICS IN SHAPING MOVEMENT OF AFRICAN SAVANNA ELEPHANTS (*LOXODONTA AFRICANA*)

by
Maggie Wiśniewska

Free ranging African savanna elephants (*Loxodonta africana*) are increasingly impacted by human-induced habitat loss and poaching for ivory. Because elephants live in tightly knit groups, this combination of threats not only reduces the size of their populations but also degrades their social interactions. Long-term relationships with socially competent individuals, such as experienced seniors, benefit the ability of other group members to access limiting resources and avoid danger. Understanding how anthropogenic pressure may affect persistence of elephant populations is important, because elephants are an economically important keystone species. This dissertation characterizes how individual elephants influence the movement of their social partners, and how the social network properties of elephant groups related to information sharing may change when socially competent members are killed by poachers. To that end, two techniques commonly used to study movement of individuals in their habitat, and one used to study the consequences of repeated social interactions, are modified and extended to incorporate a number of the social processes typically found in groups of elephants. First, an established, choice-based statistical framework for movement analysis is modified and validated using synthetic and empirical data. It allows for simultaneous modeling of the effects of the habitat quality and social interactions on individual movement choices. Next, this new model is applied to a unique set of remotely sensed tracks from five male elephants navigating across the same habitat in southern Africa. A key result is that known dominance relationships observed at water points and other gathering places are determined to persist even when elephants are ranging more widely across the landscape. Lastly, an existing ‘social network and poaching’ simulation model is parameterized with data from wild elephants. It reveals debilitating effects of poaching on various network metrics thought to correlate with group communication efficiency. The modeling and simulation tools developed over the course of this doctoral research may be generalized to include the influence of ‘dynamic points’ other than social conspecifics, such as predators or poachers, on long-term movement patterns, and thus may provide a tool to both understand and mitigate human-wildlife conflict. In addition, they may aid hypothesis testing about disturbance of social dynamics in animal systems subject to exploitation by humans or lethal management.

THE INTERPLAY OF THE PHYSICAL LANDSCAPE AND SOCIAL DYNAMICS IN SHAPING MOVEMENT OF AFRICAN SAVANNA ELEPHANTS (*LOXODONTA AFRICANA*)

by
Maggie Wiśniewska

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APPROVAL PAGE

THE INTERPLAY OF THE PHYSICAL LANDSCAPE AND SOCIAL DYNAMICS IN SHAPING MOVEMENT OF AFRICAN SAVANNA ELEPHANTS (*LOXODONTA AFRICANA*)

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“My mother was my first country, the first place I ever lived.”

-Nayyirah Waheed

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CHAPTER 1

INTRODUCTION

1.1 Background

1.1.1 Movement ecology of free-ranging animal collectives

The ability to move is necessary for free-ranging animals to persist in their habitat (*1*). Movement allows for acquisition of resources and avoidance of danger which in turn affect individual survival and reproductive success (*2*–*5*). In group-living species, such as the great desert skinks (*Liopholis kintorei*) or the king penguins (*Aptenodytes patagonicus*), the movement behavior of individuals can impact resource use by conspecifics and the stability of entire populations, for instance by efficient discovery or development of foraging skills (*6*–*9*). For example, movement decisions by experienced pod members in killer whales (*Orcinus orca*) benefit resource acquisition and fitness of their kin especially when resources are scarce (*10*). Finally, movement of animal groups often impacts entire ecosystems (*11*–*13*). This phenomenon is well manifested in the effect of swarming locusts (order Orthoptera; family Acrididae) or migrating blue wildebeest (*Connochaetes taurinus*) on nutrient cycling, plant growth and species richness across areas spanning hundreds of kilometers (*14*, *15*).

The blue wildebeest and other relatively large-bodied and long-lived species moving in groups, such as wolves (*Canis lupus*) or the eastern gray kangaroo (*Macropus giganteus*), are particularly impactful as ecosystem engineers (*16*). Given their relatively large datary and space use requirements, fulfilled through wide-ranging movement, large-bodied keystone species are increasingly more vulnerable to human encroachment (*17*, *18*). The pervasiveness of anthropogenic activities (e.g., buildout of infrastructure supporting the global economy from agriculture to mining activities), climatic changes and biodiversity loss alter natural movement patterns of animal groups through creation of barriers, displacement or inadvertent setting of ecological and perceptual traps (*19*–*24*). The consequences of perturbing movement by animal groups include extirpation, emergence of novel pathogens, loss of ecological services or human-wildlife conflict (*25*–*27*). For instance, white storks (*Ciconia ciconia*)—a useful ecological indicator species, foraging in landfills in southern Europe, exhibit partial migration and higher reproductive rates than fully migratory, wetland populations at higher latitudes (*28*–*30*). Planned closures of these facilities, in compliance with the European Union Landfill Regulations, may severely reduce this population through direct mortality, collapse of colonial breeding and loss of experienced migrators (*31*). Understanding space use patterns in this population in the context of changing physical landscape and interactions with conspecifics in breeding colonies may offer insights about how comparable conditions would affect at-risk species with important ecological functions, such as the greater noctule bat (*Nyctalus lasiopterus*) — a key insectivore of agriculture pest, or the European bison (*Bison bonasus*) shaping Europe's remaining primeval forests (*32*–*35*). This perspective is increasingly important because many group-living species, to persist in human altered habitat, already depend on some degree of conservation, management or policy interventions (*36*–*38*).

1.1.2 African savanna elephants as a model system

In this dissertation, I evaluate the interplay of physical and social dynamics in shaping movement behavior of free-ranging African savanna elephants (*Loxodonta africana*), from now referred to as ‘elephants’. Elephants are a prominent example of a widely ranging keystone species with complex sociality and subject to increasing anthropogenic pressure, introduced in the Section 1.1.1 (*39*–*43*).

As the largest terrestrial herbivores, elephants shape many of the continent’s ecosystems, for instance by limiting the encroachment of woody vegetation and intensive fire onto the African savanna (*44*, *45*). Due to ongoing habitat loss, for instance driven by agriculture, logging or armed conflict in traditional wilderness zones, some elephant populations seek resources outside of protected areas often trespassing on private property. Resulting damage to agricultural crops or property antagonizes local stakeholders and prioritizes research on conflict mitigation initiatives focused on exclusion of elephants from human-dominated areas—many of which are locally or temporally effective, anthropocentric and thus unsustainable (*46*–*49*). Presence of exclusion barriers, such as electric or range fences limits the ability of many populations to admix, reducing genetic diversity, and access resources critical for survival (*46*, *50*, *51*).

At the same time, elephants are increasingly threatened by poaching for ivory. During the last two poaching phases (ca. 1970-80 and 2007-2016) the continental elephant population decreased from approximately one million to 400,000 individuals (*52–55*). The ecological consequences of this decline range from altered nutrient cycling to changes in community structure (*56*, *57*). For instance, extirpation of African forest elephants (*L. cyclotis*)[1], along with elimination of their seed dispersal has already led to a drastic decline in recruitment of many fruiting plants which are important resource for a variety of animals in in the Equatorial Afrotropic—the second largest carbon-sequestering rainforest complex on Earth (*62*). Furthermore, release from browsing and trampling pressure by elephants will likely result in denser tree stands, low recruitment of large tree species and an overall decrease in species heterogeneity and carbon stock (*56*, *63*).

Together, habitat degradation and poaching impede movement and contribute to a rapid decline of elephant populations across their range. In fact, the International Union for Conservation of Nature Red List of Endangered Species recently changed the status of elephants from vulnerable to endangered (*61*). Fortunately, another recent study determined potentially suitable habitats across Africa and indicated that elephants as a genus occupy merely 17 percent of that area (*64*). Judicious integration of suitable yet still unoccupied habitats into conservation planning may prevent, or at least slow down, further population

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[1] In the past, despite genetic evidence indicating that there may exist two species of the African elephant (*Loxodonta spp. Lin.*), namely the forest (*L. cyclotis*) and the savanna elephant (*L. africana)*, the International Union for Conservation of Nature (IUCN) cautioned against premature split of the *Loxodonta* genus into two species. The organization was concerned about the uncertainty of the protection status of populations inhabiting potential hybrid zones (e.g., Southern Chad). However, in face of growing evidence, the genus was split into two species (*58–60*). More recently, IUCN's Red List of Endangered Species, with input of the African Elephant Specialist Group under its auspices, has changed the conservation status of both species from vulnerable and endangered to endangered and critically endangered, respectively (*61*) to more appropriately reflect the threat to African elephants.

loss and extirpation of elephants from the wild. This kind of effort will require a transboundary approach focused on enrichment and expansion of the existing protected areas and ensuring increased coexistence with humans across unprotected areas which must serve as connectors between protected fragments.

I argue that the success of such efforts will depend on a comprehensive and socially contextual perspective about the movement ecology of elephant groups. Their multilevel social structure functions as a fluid aggregate of closely knit groups—each made of related individuals bound by long-term relationships, is fundamental to understanding how male elephants and female herds use their habitat, and thus an important factor in their conservation and management. Yet, the interplay of physical and social processes that affects elephant movement is still poorly understood.

1.1.3 Movement ecology of elephants

Extensive research on elephant movement focused on individual behaviors has helped answer important questions about space use, conflict with humans and conservation of elephants (*65*, *66*). For instance, real-time tracking of elephant movements has shown that measuring basic properties of a trajectory, such as speed, can help rangers locate and treat injured individuals or deter crop-raiders (*67–69*). Linking high-resolution animal tracking with increasingly available data on Earth's surface and atmosphere has already offered a more holistic perspective on the feedback between the causes and consequences of animal movements (*5*, *70*). Elephants, for example, avoid mountains, prefer to raid crops at night and form spatially explicit memories about key resources and relatives (*2*, *43*, *70*–*72*).

Consideration of simultaneous movement by multiple individuals in the context of the physical environment, still rare in most group-living species, including elephants, should be a natural extension of progress in movement ecology and its application to conservation (*73*, *74*). Asking how different elephants respond to their environment and conspecifics may clarify meaningful differences in motivations or mechanisms driving individuals with diverse traits; and how their motivation is shaped by pursuit or avoidance of physical versus social resources (*8*, *75*). For instance, evaluating movement decisions by non-crop-raiding male elephants may inform management of their crop-raiding conspecifics across wildlife corridors or transitional zones (Table 1.1). Specifically, characterizing forage species preferred by non-crop raiding individuals may inform 1) selection of similar future habitats and rehabilitation of existing habitat to reflect the preferred forage composition; and 2) designing translocation of trespassing males which if paired with conspecifics that could set a good foraging example learn to rely on resources outside of buffer and transitional zones and human settlements (Table 1.1) (*76*–*79*). In addition, this perspective may contribute to development of more informative models of group movement (*77*, *80*, *81*)

Table 1.1 Definitions of Different Areas used by Elephants and Example Conservation Goals

Area type	Purpose	Proposed management goals
core habitat	for use by and conservation of wildlife	prioritize research into/maintenance of high-quality resources; landscape rehabilitation
wildlife corridors	for maintenance of vital connections for wildlife transfer/dispersal between core habitats	prioritize research into/maintenance of quality resources; landscape rehabilitation; methods encouraging directional moment (e.g., olfactory stimuli)
buffer zones	for protection of wildlife from damaging external impact	prioritize research into/maintenance of quality resources at the internal edge and sustainable deterrents encourage rare use on the external edge
transitional zones	for human use to prevent encroachment by wildlife	prioritize research into/maintenance of sustainable deterrents (e.g., unpalatable crops gradients; beehives); encourage/develop avenues for stewardship/ownership by local stakeholders

Sources: (*82*, *83*)

1.1.4 Limitation to studying group movement by elephants

Limited knowledge about group movement in elephants is in large parts due to 1) the scarcity of multi-individual tracking in wild populations and 2) the constraints of still developing tools for simultaneous assessment of the physical and social predictors of multi-individual movement (*84–86*).

The multi-individual tracking of free-ranging animals, which until recently was prohibitively expensive for most research projects, is becoming more affordable and capable of transmitting relatively accurate positional data at moderately high-resolution for extended periods of time (*87–91*). Deployment of most tracking devices, on the other hand, is still a big barrier, because it usually requires anesthesia (*92*). Sedating multiple individuals in a social unit, as part of a group tagging effort, is logistically daunting but also dangerous for the subjects (through potentially exposing them and their young to predation). Unless remote deployment methods become available for commercial use, multi-individual tracking of elephants in the wild will remain a challenge and a rarity. Instead, tracking of arbitrarily selected individuals in a group is assumed to be sufficient in capturing the behavioral repertoire of the entire group. Justification for this practice stems from past evidence that females spend much of their time in proximity to other herd members and engage in similar activities (*93*, *94*). More recent analysis of resource preference in closely associating female elephants suggests that this view may be an oversimplification (*74*). In addition, this justification is not easily applicable to movement of male elephants which, depending on their age, reproductive status and availability of resources, frequently transition between solitaire and group movement modes (*95*, *96*).

Analysis of multiple trajectories, although a growing effort in studies of group-living species, is still challenging, particularly in free-ranging animals (*86*, *97–99*). In elephants, and other widely ranging species, the resolution of movement data (e.g., typically ranging from daily to quarter-hourly records), although constantly improving, is still too coarse for techniques developed using nearly continuous, highly synchronized movement by large groups with well-defined centroids and relatively simple landscapes (e.g., schools of fish or synthetic particles) (*100–102*). Evolution of these methods has led to many sophisticated approaches based on maximum-likelihood estimation or Bayesian inference. They generally differ in the types of questions they are suited for (i.e., exploratory, explanatory or predictive); the degree of expert knowledge-based parameterization required for model development; and the ease of output interpretation (*103*). For instance, behavioral change point or state-space models aim to explore different modes of movement by one or multiple individuals (*104–107*). In contrast, resource selection (RSF) or related step selection function approaches seek to explain how the habitat features affect the pattern of individual space use or movement characteristics (*108–110*).

Compared to other perspectives, the RSF family of models involves relatively little expert knowledge for model parameterization. This is desirable in animal systems with limited (e.g., given possible space and time scales of collection, or emphasis on contrasts instead of gradient of biological process) or potentially erroneous empirical record (e.g., due to instrument or human error). Such data may, for example, obscure 1) the process of asking relevant question or 2) stochastic events associate with the process of interest and result in biased model parameters as well as misleading estimates (*11*, *103*, *111*). Instead, the RSF family of models rely on generally confirmable natural phenomena and established ecological principals, such as forage quality preferences in herbivores. The interpretability of the outputs from these models is relatively user-friendly and benefits non-statisticians tackling basic or applied questions about multi-individual movement (*80*, *112*) .

Finally, regardless of the analytical method used, integration of multi-individual movement and landscape data, remains a fundamental challenge. The decisions about spatiotemporal resolution prior to collection of such data, usually made by different entities, arise from equipment limitations and disparate research priorities between academics, practitioners and governmental organizations (*113*–*115*). For instance, a small non-governmental organization, such as Elephants For Africa (using tracking equipment with lithium batteries and manual data retrieval) is likely more judicious about its choice of data resolution compared to the decisions that pioneers in the field of anima tracking at Max Planck Institute of Animal Behavior are able to afford (*116*, *117*). Resulting disparities require ensuring that the scale of an animal's choice is compatible with available environmental data (*11*, *118*). For instance, the 250 meters per pixel resolution of the Normalized Difference Vegetation Index (NDVI) — a proxy for vegetation productivity, produced by Moderate Resolution Imaging Spectroradiometer (MODIS) instruments aboard the National Aeronautics and Space Administration’s (NASA’s) Terra satellite, is too coarse to assess interactions occurring at the level of a mother-calf unit (typically a few meters only) near a point resource. Fortunately, it is still useful for parsing social dynamics during moderate- to long-distance movement-related behaviors.

1.1.5 The role of disturbed social network as a potential factor motivating movement behavior in elephant groups

As most behaviors in elephant herds, their movement is a social process where core units — the smallest functional units consisting of one or several adults with their immature offspring, form temporary associations most often with other units within their matriline2 (*119*, *121*). This process, known as fission-fusion

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[2] Social structure in elephant herds ranges from matrilinear associations of closely related females and their immature offspring core groups or families, to bonded groups consisting of several related core groups, to even larger aggregates referred to as clans consisting of multiple bonded groups. Elephant from different clans interact with each other but less frequently. These interactions are often initiated by either the most mature females, or the most gregarious juveniles exhibiting indiscriminate play behavior (*39*, *119*, *120*).

dynamics, is thought to mitigate the costs of group-living (e.g., competition over resources) (*4*, *122*). It seems to be facilitated by long-term interactions among mature females and serves as an opportunity for younger conspecifics to learn about and engage in their social landscape (*123–125*). The benefits of social interaction in elephants have been extensively studied and range from increased fitness to antipredator defense (*126*, *127*). In comparison, social dynamics in male elephants are less well understood, but existing evidence indicates that their sociality ranges from solitary to gregarious. Males exhibiting gregarious tendencies often form preferred affiliations, at first with multiple males of varying ages in aggregates commonly referred to as bachelor groups, and later in life with similarly aged conspecifics in more stable bonded groups (*128–130*). Their social interactions play an important part in the development of leadership structure during collective movement and the development of crop-raiding behavior (*48*, *78*, *131*, *132*).

Poaching for ivory, and to lesser extent trophy hunting, target the largest and oldest elephants with the most prominent tusks (*125*, *129*, *133*, *134*). Elimination of the oldest and presumably most socioecologically experienced females has been correlated with changes in movement by their surviving kin (*135*). In addition, reports on habitat use and movement in poached populations indicate a shift in group foraging towards lesser quality resources, potentially away from danger (*135*, *136*). Analysis of movement speed during periods of high poaching activities revealed that herds and male elephants move faster suggesting that they detect and attempt to avoid risk (*137*). Analysis of the social network — an emergent property of repeated interactions among social partners, in heavily poached herds indicated that the composition and association patterns were conserved among close but not distant surviving kin (*125*). Whether removal of the older individuals and the associated change in the network structure at the population-level relate to group functionality is an outstanding question in elephants—because simultaneous time series data on behavioral, demographic and poaching-induced mortality, necessary to detect patterns between associations, individual fitness and group performance, are collected mostly opportunistically, with little to no spatial replication, and are rarely shared due to the species' conservation status or concerns over intellectual property.

As for male elephant associations, behavioral record in populations subject to culling indicates that some juvenile elephants maturing without seniors entered musth — a period of heightened sexual activity, prematurely and exhibited aberrant levels of aggression which ceased after reintroduction of mature males (*130*, *132*). Direct evidence on the effect of poaching on the structure of their social network is missing.

I believe that the disturbance to elephant social networks in survivors, whether members of herds or male elephant groups, may impact the way they navigate the landscape. This impact may occur through removing portions of spatially explicit memories about resource distribution and phenology or increased levels of agonsim between fragmented social units. Because this idea is difficult to test directly for reasons explained above, simulating poaching to determine its effect on network features (which in many simulated and a few empirical systems have been associated with group cohesion and transfer of valuable information) may be an early useful step. Tying changes to the characteristics of social networks and to movement behavior may inform our understanding of the mechanistic causes of movement behavior - a perspective that is rarely undertaken by movement ecologists and animal behaviorists (*11*). This kind of assessment can add to the holistic perspective on movement ecology, which considers movement to be a product of intrinsic motivation (e.g., gestation), motion capacity (e.g., incapability of running), navigational capacity (e.g., spatially explicit memory), extrinsic triggers (e.g., distance to quality resource) and consequences of movement (ability to remain in protected habitat). In addition, it may improve our perspective on actions useful for mitigation of human-elephant conflict, for instance by translocating socially functional units instead of single individuals - which so far has proven to be problematic (*78*, *129*, *138*) and conserve this economically important but endangered, keystone species (*139*, *140*).

1.2 Aims

Given data and tool limitations in research on movement-related behaviors in elephants, I decided to study how elephants integrate information about landscape structure and social dynamics in their movement; and whether poaching disturbance to social dynamics relates to group performance - a potential mechanism underpinning movement decisions. My work is, therefore, divided into two aims detailed in the following Sections 1.2.1 and 1.2.2.

1.2.1 First aim

My first aim has two objectives: to develop a statistical model for analyzing how group-living animals integrate sociophysical information in their movement; and to estimate if behavioral tendencies by a group of five male elephants, measured with behavioral sampling at a local scale, can be recovered from long-term movement patterns use with this statistical model.

To achieve my first objective, presented in Chapter 2, I developed a spatially explicit, statistical model for analyzing simultaneously the effects of the landscape structure and social dynamics on the movement of group-living animals. This tool is modified from an established research selection framework (RSF) used to study habitat preference in animals (*118*, *141*, *142*). Unlike the traditional approach, this modified 'social resource selection function' (SRSF) takes into account the social impact by treating distances between group members as time-varying physical influences. I validated the SRSF model by fitting it to simulated group movement with predictable characteristics and empirical movement from a herd of domestic goats (Capra aegagrus hircus) (*143*, *144*). I found that the estimated patterns of movement resembled the observed patterns in the simulated and real-world testing scenarios. More importantly, I also found that consideration of the physical environment without the social landscape, or vice versa, produced less parsimonious explanations of the individual movements than considering both pieces of information in tandem.

To carry out the second objective, which I detail in Chapter 3 and Appendix A, I fit the SRSF model to high frequency movement data that are very regular across five male elephants residing in the same region of the Etosha National Park in Namibia. Prior to this study, the dominance hierarchy in this group had been inferred from long-term traditional behavioral sampling at several high visibility points (*145*). I tested if this dominance hierarchy could be recovered from movement patterns (*95*). The results indicated that estimated habitat preferences (i.e., tendency to movement towards water sources) made sense in the context of elephant biology, and that observed dominance relationships could be indeed recovered directly from movement patterns. In conclusion, my work showed that a modification of the SRSF output allows for the assessment of social affinities between animals analogous to that of a social network approach.

In general, the SRSF model is useful for research on movement behavior in group-living animals as a function of the impact of social information on resource preferences. Its application in other systems may inform outstanding theoretical questions about behavioral processes underlying the distribution of individuals within their social units, inside entire populations, and in relation to heterospecifics across space and time (*146*). In addition, the added perspective on the structure of social interactions in mobile anima, analogous to a social network perspective, from multi-individual movement alone (without the need for direct observation) may be valuable to research on animal social networks in species with that are challenging to observe directly (e.g., cryptic or nocturnal animals) (*147*).

1.2.2 Second aim

My second aim has one objective: using animal social network analysis, I and my collaborators characterized if poaching disturbance of social dynamics relates to a decrease in four network features associated with efficient group performance. Although we did not test this link explicitly, we assumed that the social dynamics depicted using social network analogy underpin complex behaviors such as group movement in search of resources. This effort is described in in Chapter 4 and Appendix B.

To that end, we modified an existing social network simulator by parameterizing it with association data from free-ranging elephants inhabiting the Amboseli National Park in Kenya. Next, we simulated a series of social networks and nonrandom poaching events, targeting most mature or gregarious network members (*148*). Finally, we quantified four network features generally correlated with social cohesion and the efficiency of transferring socially valuable information. Unlike elimination of the most mature individuals, targeted poaching of the sociable conspecifics was detrimental. It degraded three out of four network features considered in my analysis as correlates of group communication efficiency (*149*). These findings suggest that further inquiry into the relationship between resilience to poaching and group performance in free-ranging elephants is warranted (*125*). The simulator we developed through this research can be modified for hypothesis testing in other systems, wild or captive, subject to human disturbance or lethal management.

After submitting this work as a research manuscript to journal *PLOS Computational Biology* (*PLOS CB*), we received feedback form the journal's two reviewers. The first main point raised by the reviewers pertains to the formula used to calculate the association index (*AI*) (i.e., an index expressing the rate of association between two individuals based on the number of times they were observed associating out of the total number of times their social group was observed). The criticism offered by the reviewers appears to be correct, and we will most likely incorporate this suggestion during the revision process. To do so will require repeating the simulation experiments in the empirically based portion of this study. This process, however, will likely not require a major changes to the existing simulation and analysis process.

The second main criticism offered by the reviewers is in regard fact that we treat each AIs between two individuals as independent, when in fact they may not be (e.g., AI between individuals A and B is correlated with AI between individuals A and C). The reviewers graciously suggested a potential approach to resolving this issue. In the coming days, we plan to discuss this criticism as well as the suggested resolution and chart our way forward. Although both issues raised will require reassessing our data, and potentially our conclusion, we are grateful for, and excited about, the overall positive feedback. In the words of one of the reviewers, "This is clearly a vitally important topic from a conservation perspective, and is additionally theoretically interesting. I generally found the paper to be interesting, well written, and of great scientific merit."

In Chapter 4, we presented this research as it was submitted to *PLOS CB*. Upon addressing the reviewers' concerns, we will resubmit this work for further consideration at *PLOS CB*.

CHAPTER 2

MODELING THE PHYSICAL AND SOCIAL IMPACTS ON INDIVIDUAL MOVEMENT IN GROUP-LIVING SPECIES

2.1 Abstract

Two key, extrinsic factors that shape the movement of group-living species are the physical environment, for instance, proximity to consumable resources, and social dynamics, such as interactions with conspecifics. However, much remains unknown about how individuals engaged in group movement integrate complex information about their physical and social landscapes. In this research, a spatially explicit, statistical model was developed based on the established ‘resource selection function’ to simultaneously test for, and separate, the impact of physical and social influences on an individual’s movement. Unlike the traditional approach, this modified ‘social resource selection function’ (SRSF) takes into account social impact by treating distances between group members as a spatial type of time-varying physical influences. As a proof of concept, validation of this approach is carried out by fitting it to multi-individual movement and physical landscape data simulated in a process resembling the three-zone model of animal aggregation. The SRSF model proved capable of recovering all key characteristics of the simulations. The key characteristics of this simulation representing an individual’s choice of a habitat with particular physical and social resources are reflected in the estimates from the SRSF model. To evaluate how it performs when applied to empirical data, the SRSF model was fit to remotely

sensed movement of a free-ranging herd of domesticated goats and high-resolution, aerial imagery of the study site. The estimates of individual preference for movement towards locations occupied by conspecifics and at the edge of vegetation are consistent with our expectations about foraging behavior in goats. This work provides and validates a new tool for examining movement behavior in group-living animals as a function of the impact of social information on resource preferences. Application of this framework may inform outstanding theoretical questions about behavioral processes underlying the distribution of individuals within their social units, inside entire populations, and in relationship to heterospecifics across space and time.

2.2 Introduction

Physical and social environments shape animal movement decisions and affect their fitness and their ecological niche (*150*, *151*). The physical environment includes persistent resources, such as food or shelter, which an animal may seek out (*2*, *152*). It can also include less tangible and more dynamic features, such as areas associated with higher predation risk or other dangers, which an animal may avoid (*153*–*156*). Some features, like waterholes, can simultaneously serve as both a vital resource and a serious risk (*157*), in which case, an animal's behavior may depend on its physiological needs and assessment of risk (*158*). The social environment can include information about the movement of conspecifics who provide experience or leadership (*10*, *127*), those with whom it may be desirable or necessary to coordinate movements (*8*, *159*, *160*), and those whom it may be desirable to avoid (*161*). The physical and social factors can operate at various scales, often simultaneously (*118*, *162*), and interact in complex ways (*163–165*). For instance, African savanna elephants (Loxodonta africana) traveling with dominant matriarchs, or the most mature close kin, accessed better quality resources and spent more time in protected habitats than individuals moving with subordinate matriarchs (*94*). As another example, compared to historically migrating herds with presumably continual learning about ecological conditions from experienced elders, populations of free-ranging bighorn sheep (*Ovis canadensis*) reintroduced to novel habitats failed to migrate for several decades when subject to spatiotemporal shifts in vegetation (*166*). Together, these results indicate that considering the combined effects of the physical and social factors on animal movement may better inform our ideas about their behavior and ecology (*167*, *168*), and guide wildlife conservation efforts (*65*, *169–171*) and management outcomes (*67*, *114*, *172*).

Simultaneous analysis of physical and social stimuli in free-ranging animals depends on access to individual movement data and data on the physical and social contexts of individual movement (*173*). In the past, habitat-dependent movement analyses were limited due to coarse spatiotemporal resolution of physical and movement data, as well as lack of scale correspondence between them (*174*, *175*). In addition, due to logistical constraints of studying animal populations in the wild, many earlier studies of movement in social species focused on a few, key individuals with conspicuous characteristics (*39*, *176*). Advances in remote sensing and wearable tracking devices have improved the acquisition of high-resolution physical and movement data (*177–179*). The ongoing miniaturization and improved reliability of tracking devices (*168*) make it increasingly possible to acquire multi-individual data and draw inferences about collective movement patterns (*180*). Analysis of multi-individual movement, although still limited to a few species (*8*, *151*, *179*), has already offered novel insights into group movement patterns (*181*), leadership structure (*98*), as well as context-dependent landscape use (*182*, *183*). For example, Strandburg-Peshkin and her research team (*97*) reported that individual movement decisions in a troop of olive baboons (*Papio anubis*) were strongly influenced by the number of conspecifics that had recently visited an area of interest, and, secondarily, by several landscape features, such as the density of vegetation and distance to human-made roads. In addition, while moving away from dense vegetation was not apparent at coarse scales, this behavior was common at a fine scale, implying that proximity to dense vegetation may impede individual baboons from tracking others. This study demonstrated how coupled, multi-scale analysis of physical and social variables allows for a biologically relevant interpretation of group movement behavior.

Recent methodological developments enabling simultaneous analysis of multi-scale preferences for the physical and social environment (*118*, *162*, *184*) have presented exciting possibilities for research in animal movement (*11*, *81*, *168*). For instance, several mathematical approaches (*185*), such as agent-based (*186–189*), state-space (*73*, *80*, *105*) and resource-selection models (*118*, *190–192*), have facilitated multi-scale analyses of individual movement in relation to the physical environment (*91*, *168*, *193*, *194*). Application of these techniques to understand multi-individual movement in animal groups, at multiple spatiotemporal scales, is beginning to be implemented in the field of movement ecology (*97*, *98*, *166*). However, many studies that assess the physical and social influences on collective movement use empirical data to conduct parameter estimation and validate pertinent model predictions. To our knowledge, it is still rare for published models assessing the simultaneous effect of the physical and social landscape on individual movement to validate their approaches using data with well-understood characteristics (*195*). Given their potential for repeated empirical application, the development and validation of new movement models in social species will benefit from using data with known structure allowing for a high degree of confidence about the model behavior and its predictive properties (*196*–*198*).

Here, I present a novel statistical model of collective movement in a heterogenous physical landscape. Our model is a spatially explicit, statistical tool designed to explore the interplay between landscape structure and complex social dynamics in shaping individual movement choices in group-living species. We developed this model by extending the established ‘resource selection function’ framework (RSF) based on a conditional logistic regression (CLR) (*118*, *141*, *142*). As does the traditional approach, our model operates on movement data and the imagery of the physical landscape. In our model, however, I account for the social landscape by converting the positions of all nonfocal individuals into a time-varying, neighbor distance map. This approach allows for the simultaneous treatment of the map of neighbor distances with maps of the physical environment. Thus, I named our model a ‘social resource selection function’ (SRSF). I validated the SRSF model by fitting it to group movement data simulated with movement rules inspired by the three-zone model of animal aggregation (*143*). This is a self-propelled particle model in the context of three interdependent zones representing repulsion from, orientation with, and attraction towards others. To test its usefulness as a statistical tool with real-world application, I fit the SRSF model to remotely sensed movement data on a herd of domestic goats (*Capra aegagrus hircus*) and the aerial imagery of the research site (*179*).

I predicted that the key aspects of the group movement simulation would be reflected in the SRSF model estimates of 1) the nearest neighbor distance and 2) resource density preference functions. I also predicted that fitting the SRSF model to empirical data would produce estimates consistent with known foraging behaviors of domestic goats (*144*, *179*, *199*). I discuss our results in the context of our modeling process and the underlying assumptions. I also offer our insight about collection and processing of remotely sensed movement data, in a patch-corridor landscape. Finally, I consider real-life applications of the SRSF model and the importance of using multi-individual movement in a range of biological fields from conservation biology to wildlife management.

2.3 Methods

2.3.1 The SRSF model

The SRSF model is an extension of the existing RSF approach (*109*, *118*, *141*, *191*). Mechanistically, the RSF approach treats an individual's location at any moment in time as a choice made out of a 'sample' set of alternative locations (*141*). This set of locations is bounded spatially, usually by a consideration of how far the individual in question could plausibly have moved from its previous location in the time available. The relative probability of ending up at different destinations is modeled using a CLR as a function of various environmental parameters that differ between locations. Some of these, for example '*resource density*,' may be measurements of local conditions. Others, such as 'distance to water' or 'distance to human settlements' may be values related to more distant features, but which the individual might reasonably perceive or know about. One such measurement, '*distance to previous location*,' is a proxy for the effort required to move to the new location. As long as individuals are optimizing benefit-cost ratios in their movements, such as when foraging, I would expect this particular variable to almost always be important, and indeed previous work shows that it is (*200*, *201*).

The SRSF model adds to the RSF framework by considering the locations of other individuals in a moving group as time-varying point features of the landscape. One individual (the focal individual) is modeled, and the locations of the others are incorporated as a single '*distance to nearest neighbor'* value that can be calculated for any location on the landscape (Figure 2.1). I could treat each nonfocal individual as a separate predictor, which would be appropriate if, for example, individuals respond differently to different group members. In this project, however, I assume for simplicity that all group members are identical in how their proximity influences the focal individual.

To fit the SRSF model, some decisions have to be made at the outset. For a location to be a choice, the landscape must be made up of discrete areas, and because local measurements are often derived from remote imagery the usual practice is to make it a grid. Choosing the grid cell (or pixel) size requires a balancing of various interrelated factors, such as the spatial scale of the landscape features under consideration and the length of the typical movement distance between locations. In cases of high-resolution movement data, in which locations are close together in time, a second choice is required: whether to subsample every nth location (creating larger movements) (*202*). There are no rules of thumb for these choices yet, and full consideration of all possibly relevant factors is outside the scope of this paper. Here, I will simply explain the choices I made for the purpose of the validation I carried out.

For any given movement *m*, the 'choice' is a binary response where a potential location i is either the endpoint at which the individual was recorded (*yi* = 1) or one of the sampled alternatives (*yi* = 0). For convenience I will label the chosen location with the subscript j ($j \in i$). The probability of a movement is modeled as a CLR:

$$p_m = \frac{e^{X_j \beta}}{\sum_i e^{X_j \beta}}$$

where X is a matrix of k predictor variables derived from the landscape data and β is a k by 1 vector of parameters to be estimated. Thus, p_m is the predicted 'preference value' for the location the individual is found in divided by (and therefore conditional on) the sum of the preference values for the random sample of possible locations. In practice, depending on the grid size of the landscape and the boundary of possible distances reached, the denominator could include hundreds or even thousands of pixels. This can make computation of the expression, which is repeated for every movement in a dataset, time consuming — a challenge that then translates into model fitting. It is thus a standard practice to randomly select a fixed number (e.g., 20–100; considered as a fair representation of a unbiased sample) of non-chosen alternative locations, on the assumption that they will comprise a representative sample of the landscape variation available to the individual (Figure 2.1) (*203*).

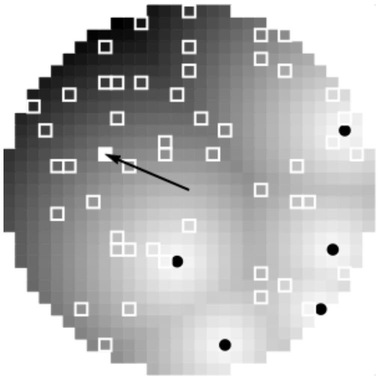


Figure 2.1 The sociophysical landscape in the social resource selection model (SRSF model).

Notes: Physical and social landscapes around the focal individual between time *t* and *t + 1*, in a radially bounded, heterogeneous, 2-D grid. The center of the grid is the location of the focal individual at time t. Empty white squares are a 'sample' set of 30 locations available at time *t + 1*. Filled white square represents the location chosen by the focal individual at time *t +1*. Black arrow shows the movement between time t and time *t +1*. Black circles indicate the locations of all neighbors at time *t +1*.
Source: (*203*)

I fit the CLR model by maximizing the log-likelihood of the entire set of n movements m, denoted as

$$L = \sum_{m=1}^{n} p_m$$

using quasi-Newton nonlinear maximization.

2.3.2 SRSF model interpretation

I performed variable selection by first fitting models with all possible subsets of ‘physical’ and ‘social’ landscape variables, and with each included variable in either linear or quadratic forms. The sole exception was the ‘distance from previous location’ variable, which was always included in a linear form to represent cost of movement (see SRSF model in Section 2.3.1). I then ranked models using Akaike’s Information Criterion (AIC) (*204*) and calculated importance scores for each variable as the cumulative Akaike weight of the models in which it appeared (*156*, *205*).

Interpretation of SRSF model output depends on the functional shape of the model for each variable over the range of values of that variable. In particular, quadratic functions have a single maximum or minimum but that may or may not occur within the range of the variable. Thus, I divide fitted functional forms into four categories: monotonically increasing; or decreasing (each of which might arise from a linear or quadratic expression), indicating a preference for larger or smaller values respectively of the variable in question; convex with the maximum within the data range (a preference for intermediate values), or concave with the minimum within the data range (*118*).

2.3.3 Multi-individual movement and physical landscape data for model validation and testing

I validated the SRSF model in two ways. I first fit it to simulated group movements in a heterogeneous landscape and compared the estimated parameters to those of the simulation. I then fit the SRSF model to the movements of a semi free-ranging herd of domestic goats in an arid landscape to test if the model recovers the most obvious and well-documented physical and social drivers of their movements (goats move together while browsing vegetation) (*144*, *179*, *199*).

2.3.4 Simulated movements

I simulated group movements on a heterogenous, two-dimensional grid. Group movement rules were modified from the three-zone, agent-based flocking model (*206*) in which two social forces (repulsion-attraction and orientation) operate at different separation distances within the interval {0, +∞} (Figure 2.2a). The model returns a social force vector acting on each individual which combines the repulsion, attraction and orientation forces from all (or a subset) of neighbors, and to which the focal individual responds by turning. The repulsion becomes important when the focal individual is too close to a neighbor, risking collision. The attraction starts affecting the focal individual when it moves too far from all of its neighbors and risks separation. The orientation acts upon the focal individual at an intermediate distance to all of its neighbors, thereby maintaining a relatively low risk of both collision and separation. Our version of the model also includes limited perception; individuals only respond to neighbors within a specified angular range around the direction they are facing (*206*, *207*) (Figure 2.2b).

A simulation landscape with multiscale heterogeneity was created by generating an image of 1000 by 1000 random grayscale pixels and iteratively adding a blurred version back to the developing landscape, using successively larger radii for the blurring kernel. The final image was binarized to create a physical environment with two habitat types (i.e., pixels having a value of 0 or 1), and then blurred one more time with a radius of 20 pixels to soften the ’edges’ between the habitats (i.e., creating 0-1 gradients across the edges) (Figure 2.2c). Most ecosystem transitions are not sharp, but in this case the edge blurring is done to allow simulated organisms to locate themselves with respect to a habitat edge, which has intermediate values. It also generates an edge effect whereby, for example, an individual that strongly prefers habitat ‘1’ will not only tend to stay within patches of ‘1’ pixels, but even avoid the edge where values begin to drop off. The smoothing method, of course, raises the question of what kernel radius to use when fitting, and methods for choosing an optimal radius (which might be different for different environmental variables) have been published by our research group elsewhere (*118*)).

To add the physical environment to the group movement model, I simply applied a quality function to the landscape array (indicating what values the individual prefers), and then for each individual I calculate the net attraction force of every pixel within a given perception radius and angle. These forces were weighted by a declining function of distance. This net environmental force vector was added to the net social force vector with a parameter that scaled their relative weights (Figure 2.2b).

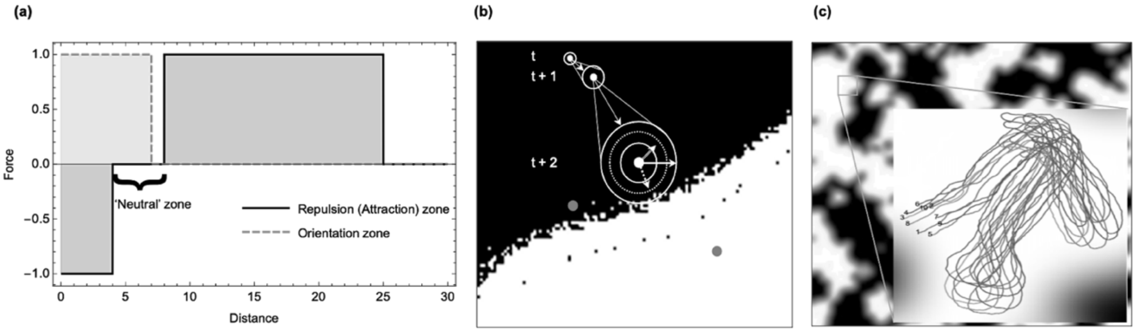


Figure 2.2 Modification of the three-zone movement model and group movement simulation

Notes: (a) A discontinuous version of the three-zone model; it requires two step functions detailing three zones of constant value for optimal social spacing 1) to prevent collisions with or separation from neighbors and 2) to facilitate directional orientation. The first function with parameters r and a defines repulsion and attraction strength (solid lines); repulsion occurs at relatively shorter between-neighbor distance (e.g., $y = -1$ for $0 < x \leq 4$), whereas attraction at relatively long distance (e.g., $y = 1$ for $8 \leq x < 25$). Beyond the maximum a value an individual loses track of its neighbors. The second function with parameter o defines orientation strength (dashed line). Orientation occurs at relative short to medium between-neighbor distance (e.g., $y = 1$ for $0 < x \leq 7$). At a medium distance (e.g., $y = 1$ for $4 < x \leq 7$) there is no repulsion or attraction affecting the individual. (b) Example diagram representing the forces acting on the focal individual (white dot) at the end of the third consecutive movement (*t + 2*), with previous two movements (*t, t + 1*) shown to depict the path. The net distance force (dashed, white arrow) and the net angle force (double-line, white arrow) are exerted by the surrounding environment and neighbors (grey dots). The net force (single-line, white arrow) is an aggregate of the net distance and angle force. Repulsion and attraction forces are represented by the inner and outer solid, white circles around the focal individual, whereas the orientation force is represented by the dashed white circle around the focal individual. The angle of perception is represented by the cone surrounding the net force between the three movements. (c) Simulated tracks of 10 individuals in an example, 1000 x 1000 pixelated landscape consisting of two-pixel types with values of 0 or 1. Smoothing of this landscape using a circular kernel with 20-pixel radius created 0-1 gradient. Pixels with values approximately equal to 0.5 (shades of gray) represent the edge between two habitat types, whereas pixels with values above 0.5 (shades of white) represent resource-rich habitat.

To simulate group movement on a heterogenous grid, a number of parameters, detailed in Table 2.1, have to be set first. Setting meaningful values for these parameters depends on understanding how they may be impacted by the spatial resolution of the underlying, physical landscape. For instance, the value preset as the length of a movement only makes sense if considered in the context of both pixel size and the characteristics of the preferred habitat (e.g., homogenous versus mosaic). To exclude occasions where any individual became permanently separated from the group, I evaluated only the set of locations where the focal individual and at least one of its neighbors were within a distance smaller than three times the group's median diameter. Using this cutoff process, I managed to preserve a majority of simulated, group movement data.

Table 2.1 Summary of the Parameters Required to Carry Out the Group Movement Simulation

Model parameters	**Parameter values**	**Parameter details**
Repulsion-Attraction force	near *r* = 0 – 4 pixels near *a* = 8 – 25 far *r* = 0 – 10 far *a* = 14 – 25	Repulsion-attraction strength is a discontinuous movement function with parameters r and a; it defines two zones of constant values at different social separation distances within the interval {0+∞} setting the preferred distance between the focal individual and its neighbors (Figure 2.2a).
Orientation force	near *o* = 0 – 7pixels far *o* = 0 – 13	Orientation strength is a discontinuous step function with parameter o; it sets the strength of positioning oneself in the same direction as the neighbors. The interval between r and a parameter is a neutral zone (Figure 2.2a).
Social force	0.95	Fraction weighing the total strength of all the forces exerted by other individuals, compared to those exerted by the environment (Figure 2.2b)
Habitat type	edge *v* = 0.5 intensity in-patch *v* = 1	Habitat type v expresses the density of two-pixel types on a 0-1 gradient in a mosaic of high ('in-patch') and intermediate ('edge') resource density patches (Figure 2.2c).

2.3.5 Predictions about simulated movements

I predicted that the functional forms of the SRSF model estimates would be simultaneously consistent with both the neighbor distance and resource density functions in the group movement simulation. For instance, when the simulation parameters specified a 'preference' for high resource density, so should the fitted SRSF model function. Although the fitted functions, built using generic polynomial equations, could not replicate the exact shape of the simulation functions, I decided that a notable parallel between them would be the grounds for validation of the SRSF model. To test our predictions, I performed four experiments manipulating four different aspects of the group movement simulation. In each experiment, each model analyzed the movement of one individual in the context of the remaining group members. Data simulation and fitting the SRSF model using simulated data were performed by two members of our group. The person responsible for the fitting process was not aware of the parameters used in the respective simulations.

In the first experiment (E1), I evaluated the performance of the SRSF model using simulated movement data subsampled at an increasingly large interval in a group of 10 individuals. At each sampling interval, I selected the first location of each individual's trajectory followed by every nth location. I predicted that the SRSF model estimates would most accurately recover the preferred social distance and resource density at some intermediate sampling interval because it would be most suitable for a simultaneous assessment of the physical and social landscapes occurring at different scales. I planned to use the most appropriate sampling interval as a parameter in the following experiments.

In experiment two (E2), I tested the accuracy of the SRSF model in capturing the preference for a specific neighbor distance and resource density. Figure 2.3 exemplifies our predictions for this experiment regarding the direction and the magnitude of a difference in both parameters.

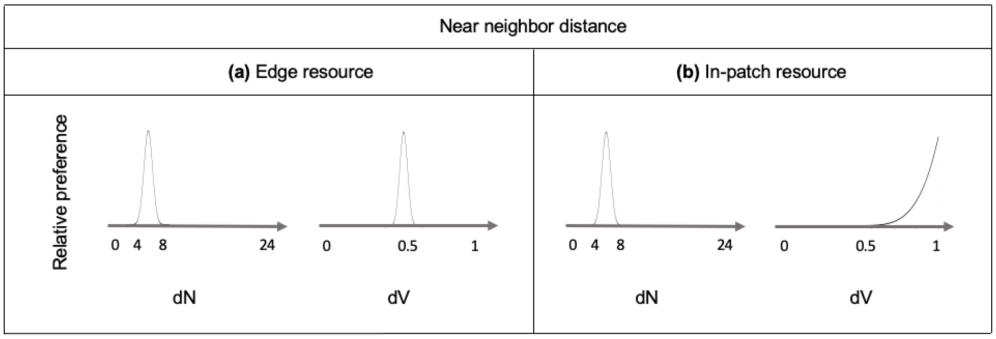


Figure 2.3 Example predicted functional forms of the SRSF model.

Notes: Fits of the SRSF model to simulated group movement data used the following preference: (a) near neighbor distance (dN) (*r* = 0 – 4, *a* = 8 – 25, *o* = 0 – 7) and the edge of resource (dV) (*v* = 0.5) or (b) near dN and in-patch dV (*v* = 1). The SRSF model estimates are expressed in terms of relative preference of a given location as a function of dN and dV. I evaluated the movement preferences of each individual in the context of others and the surrounding landscape (N =10).

In the third experiment (E3), I assessed the sensitivity of the SRSF model to varying amounts of social signal available to the focal individual by simulating groups of two, six and 10 individuals respectively. The parameters for social distance and resource density were kept constant across all group size simulations. I predicted that as the number of individuals in a group increased, the average spacing between individuals would decrease below the optimal spacing specified in the simulations, due to 'crowding' in a pixelated landscape. As for resource density, I predicted that the fitted functions would reflect the simulated parameter regardless of the group size.

Finally, in experiment four (E4), I evaluated the ability of the SRSF model to simultaneously discover physical and social drivers of movement with incomplete social data. After simulating the movements of a group of 10 individuals, I created random subsets of 10, 9, 8, … …2 tracks, simulating a situation in which only some individuals in a group were tracked. I predicted that incomplete social information in smaller subsets would yield poorer estimates of the sociophysical preference, because group members would be responding to ‘unseen’ social forces, effectively adding ‘noise’ to their movements.

2.3.6 Empirical movements

To assess how the SRSF model performs when fitted to empirical data, I used a subset of herd movement data on a semi-free-ranging group of 16 adult, domesticated goats inhabiting Tsaobis Nature Park, Namibia (15° 45’E 22° 23’S) (*179*). In September 2015, each animal was equipped with a wearable tracking device which included a GPS logger programmed to collect longitude and latitude data every second. The herd browsed freely within the park, between the hours of 6:30 a.m. and 2:30 p.m. for a total of 10 days, except for occasional active herding events to prevent trespassing on neighboring properties. Because a detailed assessment of the species’ socioecology is beyond the scope of this publication, I evaluated subset of data from one day characterized by 1) prolonged absence of active herding events, 2) a nearly complete, continuous coverage of GPS data and 3) the abundance of biologically relevant and easily classifiable physical landscape attributes (i.e., vegetation).

Although the data presented in this study were characterized by a near-complete coverage of GPS points, occasional tracking device failure, unique to each device, led to desynchronization in the recording of consecutive locations across all devices. To proceed, I selected only the locations with timestamps present in trajectories of all goats and applied the cutoff process described in the Section 2.3.4. This synchronized subset of movement data consisted of approximately four and a half hours of group movement equivalent to 8049 movements per animal. Finally, to set movement in the context of the underlying landscape and to express them in real-world units (i.e., meters), I projected the synchronized trajectories in the Universal Transverse Mercator coordinate system (UTM) (*208*).

Goats are generalist browsers, tracking the edges of bushes and larger vegetation patches, and most of the daily activity of the Tsaobis goats was this behavior (Figure 2.4a). I therefore used vegetation as our physical landscape data layer. The layer was derived from an orthorectified, composite RGB color image obtained by aerial survey. The original image's 3 cm^2 resolution was down sampled to 30 cm^2 pixels, making it more computationally tractable while maintaining resolution on par with the width of a goat, and therefore with minimum social distances. The pixels were classified into vegetation and a few other categories using a supervised maximum likelihood technique (Figure 2.4b). For this analysis, however, I generated a simple binary vegetation/non-vegetation array and smoothed it using a 10-pixel (30 cm^2) radius kernel allowing for more realistic interpretation of the behavior around the edge (as an alternative to a preference or avoidance of one habitat type within a binary landscape) (Figure 2.4c). Values around 0.5 represent the edge; other values between 0 and 1 represent areas just outside or inside the patch.

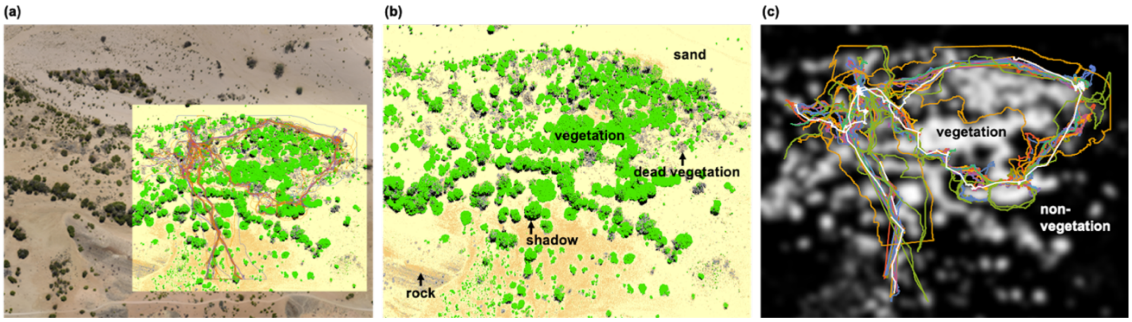


Figure 2.4 Goat movement and the physical landscape.

Notes: (a) An overview of the 'core movement range' measuring approximately 430 x 368 meters with juxtaposed goat trajectories shown in context of a high-resolution, color aerial image (i.e., 30 cm^2 pixels), (b) land-type classified (using the supervised maximum likelihood classification tool) (ESRI 2015)) featuring five habitat types (i.e., dead and live vegetation, rock, sand and shadow). (c) An overview of a binarized, gray-scale map featured in (b) to enhance the contrast between vegetation and non-vegetation features and blurred by averaging each pixel around the center of each vegetation patch with the neighboring pixels using 10-pixel radius. The gray region represents the edge of the vegetation ($v = 0.5$), the white region represents the inside of a dense vegetation patch ($v > 0.5$) and the black region represents little to no vegetation ($v < 0.5$).

2.3.7 Predictions about empirical movements

Since our intention has been to develop a tool for analysis of movement behavior by real animals, which are unlikely to recognize strict zones in their landscape, I fit the SRSF model to the previously described goat movement as a function of neighbor distance and vegetation density. To determine the most appropriate resolution for simultaneous analysis of the sociophysical landscape, in experiment five (E5) I fit the SRSF model to movement data subsampled at an increasingly large interval. I then use the most appropriate sampling interval as a parameter in experiment six (E6) detailing the closeness of the SRSF model estimates to observed data. And lastly, to explore if fitting the SRFS model to goat movement in the context of each landscape alone versus a coupled landscape would produce different conclusions about goat behavior, I parsed the results from E6. I predicted that fitting the SRFS model to movement of goats at intermediate sampling intervals would most reliably estimate species-specific behaviors of interest. Because domestic goats typically browse as a group (*144*, *199*), I predicted that the SRSF model estimates would reflect a preference for movement towards other goats but avoid running into nearby group members (i.e., a monotonic function peaking at relatively near social distance and decreasing at distances approaching less than one body length to reflect the avoidance of collision). I also predicted that the SRSF model estimates would reflect the movement towards the edge of vegetation (i.e., a convex quadratic function with a peak at an intermediate density of vegetation). Finally, I anticipated that simultaneous analysis of the physical and social landscapes would in general reflect the patterns seen after fitting the SRSF model to either landscape separately.

2.3.8 Software used

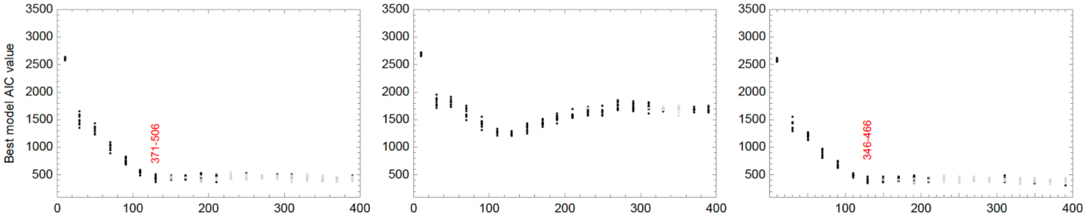
Data processing and statistical analyses were carried out in Mathematica 12.1.0.0 (Wolfram Research, Inc. 2019) and RStudio 1.0.136 programming languages (R Core Team 2017), as well as ArcGIS 10.4.1 mapping software (ESRI 2016).

2.4 Results

2.4.1 Outcomes of fitting the SRSF model to simulated data

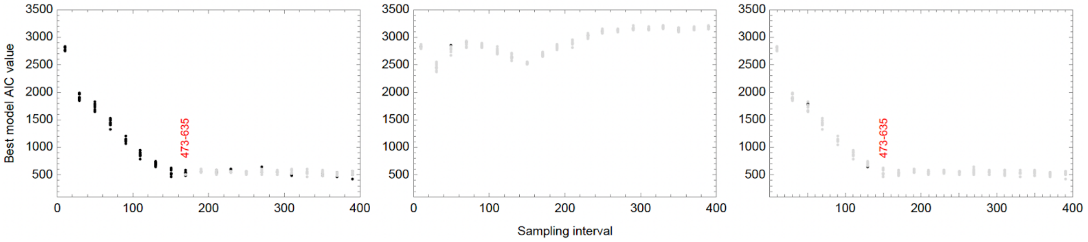
As I predicted, the SRSF model estimates indicate that social distance and resource density are predictors of movement preferences among simulated individuals.

In E1, where I tested the SRSF model on group movement subsampled at increasingly large intervals in the context of two landscape types, an intermediate sampling interval produced the most parsimonious results (lowest AIC values) regardless of the habitat type. In addition, considering the physical and social contexts separately and then jointly revealed that these cues impact individual movement choices simultaneously, although not always uniformly. In the case of the edge of the vegetation as a preferred resource, the sociophysical landscape resulted in more parsimonious estimates than either landscape alone (Figures 2.5a, 2.5b and 2.5c). In contrast, when the in-patch habitat was the context for group movement, models considering only social dynamics as well as sociophysical dynamics produced equally parsimonious results (Figures 2.5d, 2.5e and 2.5f).


(a) Social landscape

(b) Physical landscape (edge)

(c) Sociophysical landscape (edge)


(d) Social landscape

(e) Physical landscape (in–patch)

(f) Sociophysical landscape (in–patch)

Figure 2.5 Results from experiment 1 – subsampling simulated movement.

Notes: Comparison of the best SRSF model AIC values in E1 characterizing trajectories of 10 simulated individuals, subsampled at a number of intervals within the interval 10 – 390 in increments of 20. The black dots represent best full models (i.e., y = x + x^2), whereas gray dots represent best reduced models (i.e., y = x). The top panels detail results of fitting the SRSF to movement data in the context of edge as the preferred, physical resource density (dV) (*v* = 0.5) and the (a) the social, (b) physical or (c) the sociophysical landscape. The bottom panels (d, e, and f) detail results of fitting the SRSF to the same landscape contexts as described in (a, b and c) while in the context of in-patch dV (*v* = 1). AIC ranges in figures (a), (c), (d) and (f) are inserted on the figures for easier interpretation. To generate an equal amount of data points, I selected 623 random movements per each sampling interval limited by the coarsest subsampling. The preferred social separation (dN) across all sampling intervals was set to near social distance (*r* = 0 – 4 pixels, *a* = 8 – 25, *o* = 0 – 7). For each sampling interval, the radius was set to twice the average pixel distance moved during that interval and fell within the range 40 – 60 pixels.

In E2, I evaluated the SRSF model's accuracy in capturing the difference in preference for social distance and resource density in a group of 10 individuals. The estimates of neighbor distance across the four scenarios did not reflect the 'optimal separation' specified in the simulation models, but they did reflect the actual distances maintained by the simulated individuals, which were generally much smaller than the simulation model optimum, especially for the edge-foraging simulations. Nevertheless, the simulations using the model with larger optimal spacing did generate larger actual spacings and larger estimates of that optimal spacing compared to the model with small optimal spacing

(Figures 2.6a and 2.6c). By contrast, the resource density estimates closely matched the simulation parameters and the observed choices in all experimental scenarios (Figures 2.6b and 2.6d).

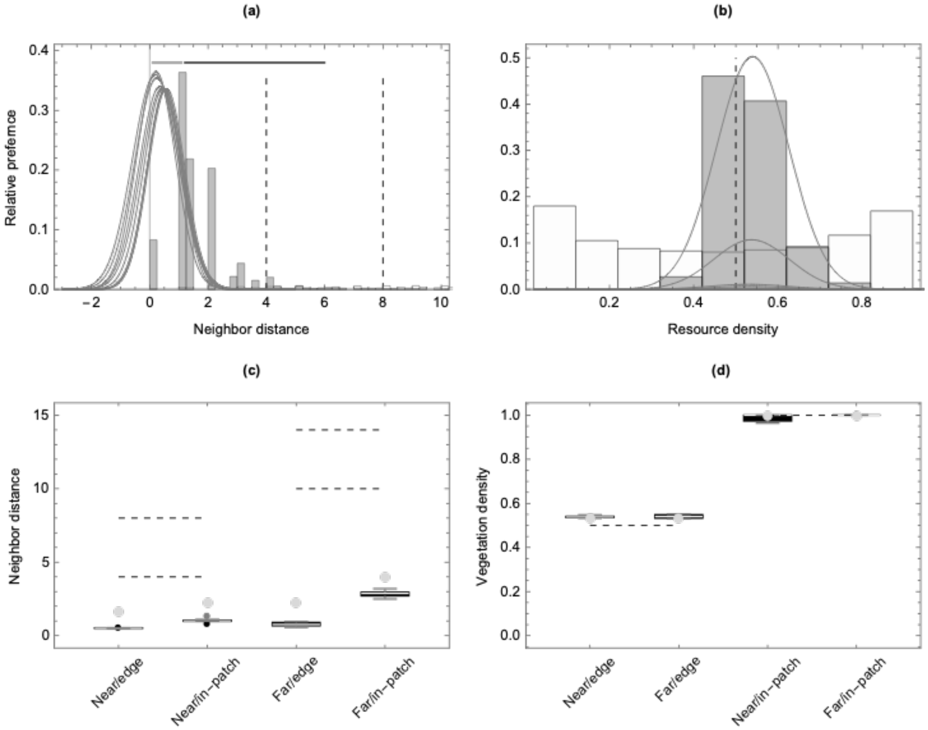


Figure 2.6 Results from experiment 2 – accuracy of the SRSF model fit to simulated movement.

Notes: Top panels represent the comparison of simulated group movement data (histograms) and associated best SRSF model estimates (parabolas) in E2 characterizing location choices by 10 focal individuals across four scenarios with disparate preferences for neighbor distance (dN) and resource density (dV). The histograms represent the distribution of selected (gray bars) and available (white bars) locations in one scenario with the following parameters (dashed vertical lines): (a) near dN (*r* = 0 -4 pixels, *a* = 8 - 25, *o* = 0 - 7) and (b) edge dV (*v* = 0.5). Overlaying the simulated distributions are corresponding functional forms of the best SRSF model estimates expressed in terms of the relative preference for movement towards the preferred value pixels. The scales of the simulated and estimated distributions have been standardized for presentation. Bottom panels represent the averages of the best SRSF model maxima in (c) and (d) featuring four scenarios with some combination of simulated parameters (horizontal dashed lines) defined as follows: 1) near dN and edge dV subsampled at every 130 th location and the radius set to 50 pixels (or twice the mean distance moved in one movement); 2) far dN (*r* = 0 -10, *a* = 14 - 25, *o* = 0 - 13) and edge dV subsampled at every 70th location and the radius set to 30 pixels; 3) near dN and in-patch dV (*v* = 1) subsampled at every 150th location and the radius set to 60 pixels; and 4) far dN and in-patch dV subsampled at every 150th location and the radius set to 55 pixels. The gray dots represent the averages for the chosen dN and dV values; they were different from the simulation model optima due to unexpected simulation dynamics (see Section 2.5 for an explanation). The gray horizontal line (sampling bias) and black horizontal line (crowding bias) in (a) are potential explanations for imperfect estimates of dN and are detailed in Section 2.5.

Next in E3, where I applied the SRSF model to simulated data with different group sizes (i.e., two, six or ten) and constant parameters for both predictors, the estimated optimal neighbor distances were always lower than the model optima (as in E2 above), but the error was smaller for groups of six compared to ten, and much smaller for groups of two (Figure 2.7a). Again, these estimated optima closely matched the observed neighbor distances. For all group sizes, the physical model accurately estimated the preferred vegetation density of 0.5 (Figure 2.7b).

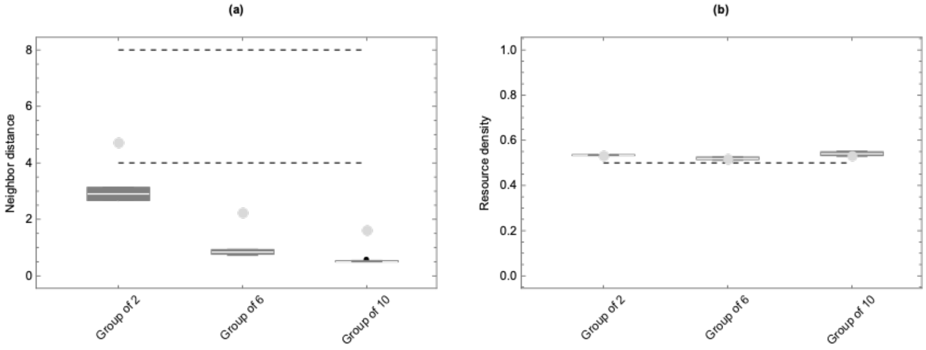


Figure 2.7 Results of experiment 3 - different group sizes.

Notes: Ranges of the best SRSF model maxima in E3 characterizing location choices in a simulated group of 2, 6 or 10 focal individuals as a function of (a) neighbor distance (dN) and (b) resource density (dV). The parameter values (horizontal dashed lines) were the following: near dN (*r* = 0 - 4 pixels, *a* = 8 - 25, *o* = 0 - 7) and edge dV (*v* = 0.5) subsampled at every 130th location and the radius set to 50 pixels (or twice the mean distance moved in one movement). The gray dots represent the averages for the chosen dN and dV values; they were different from the simulation model optima due to unexpected simulation dynamics (see Section 2.5 for an explanation). To generate an equal amount of data points, I selected 623 random movements per individual, per group size.

In E4, where I evaluated the SRSF model using different numbers of tracked individuals sampled from a simulation of 10 individuals, with constant preference values for both predictors, the resulting estimates were more parsimonious in relatively large groups compared to small group regardless of the habitat type (Figure 2.8a and 2.8b).

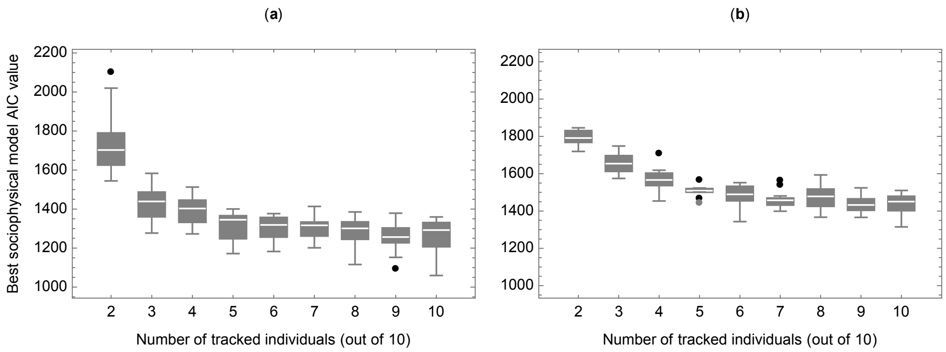


Figure 2.8 Results of experiment 4 - different numbers of tracked individuals.

Notes: Ranges of the best model AIC values in E4 across nine group sizes with a number of tracked individuals ranging from two to 10, sampled from a simulation containing tracks of 10 individuals in the context of a preference for (a) edge resource density (dV) (*v* = 0.5) and (b) in-patch dV (*v* = 1). To generate equal amount of data points across the nine group size categories, I varied the number of iterations per each group size (N2 = 5 groups of 2 individuals, N3 = 4, N4 = 3, N5 = 2, N6 = 2, N7= 2, N8 = 2, N9 = 2, N10 = 1). Across all group sizes, the social preference was set to near neighbor distance (*r* = 0 - 4 pixels, *a* = 8 - 25, *o* = 0 - 7). The tracks in (a) were subsampled at every 130th location and the radius was set to 50 pixels (or twice the mean distance moved in one movement), whereas in (b) the tracks were subsampled at every 150th location and the radius was set to 60 pixels.

2.4.2 Outcomes of fitting the SRSF model to empirical data

The SRSF model estimates of preferred distance to other goats and vegetation density in E5 suggest that although both parameters informed individual movement decisions, the social distance was a stronger signal. This result became evident when I evaluated each trajectory at an increasingly large sampling interval in E5 (Figure 2.9). In the SRSF model fits where only the social landscape was considered, the best model AIC values slightly improved (became smaller) at larger sampling intervals (Figure 9a). When only the physical landscape was included, the best model AIC values got slightly worse (increased) as a function of the sampling interval (Figure 2.9b). Fitting the combined, sociophysical SRSF model to movement data subsampled at large intervals produced more parsimonious results (Figure 2.9c). Given that there was not one best sampling interval, I selected an intermediate sampling interval equal to 50 as an example.

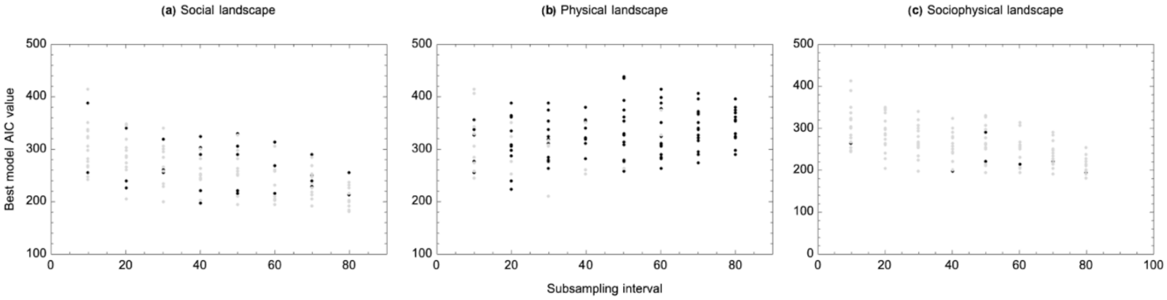


Figure 2.9 Results of experiment 5 - subsampling empirical movement.

Notes: Comparison of the best SRSF model AIC values in E5 characterizing trajectories of 16 goats, each subsampled at eight sampling intervals within the location interval {10, 80} in increments of 10. The black dots represent best full models (i.e., y = x + x^2), whereas gray dots represent best reduced models (i.e., y = x). The three panels detail the results of fitting the SRSF to (a) movement data in the context of the social versus (b) the physical or (c) the sociophysical landscape. To generate an equal amount of data points, I selected 98 random movements per sampling interval limited by the coarsest subsampling. The built-in preferences across all sampling intervals were for near social distance with some repulsion at very near distance and edge resource density. For each sampling interval, the radius was set to twice the average pixel distance moved during that interval and fell within the range 7 – 53 pixels (3 – 25 meters).

The SRSF model estimates of the neighbor distance function in E6 show an overall preference for staying close to other group members, but not the repulsion at short distances that group movement models generally assume (Figure 2.10a). The estimated function for smoothed vegetation density is convex with a maximum around 0.5, indicating the overall preference for the edges of vegetation patches (Figure 2.10b).

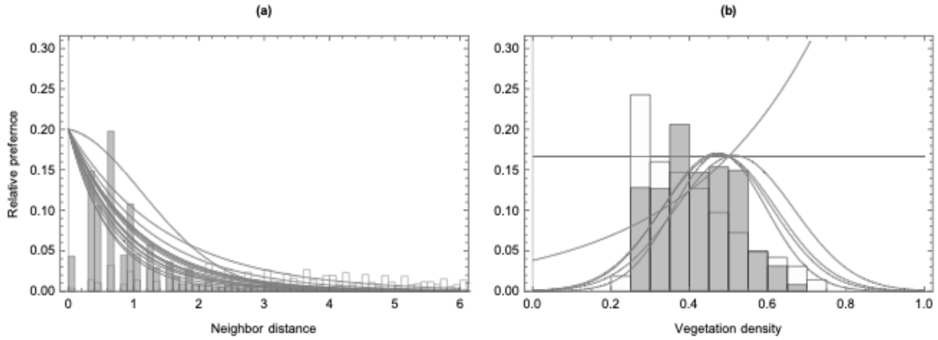


Figure 2.10 Results of experiment 6 – accuracy of the SRSF model fit to empirical movement.

Notes: Comparison of empirical group movement data (histogram) and associated best SRSF model estimates (parabolas) characterizing location choices by 16 goats with an expected ‘preference’ for (a) relatively near neighbor distance and (b) intermediate vegetation density (dV). The trajectories were subsampled at every 50th location. The histograms represent the observed distribution of selected (gray bars) and available (white bars) locations. Overlaying the simulated distributions are functional forms of the best SRSF model estimates expressed in terms of the relative preference for movement towards pixels with the preferred value ranging from 0 (i.e., outside of -vegetation-patch) to 1 (i.e., in-patch) with 0.5 indicating the edge habitat. The scales of the simulated and estimated distributions have been standardized for presentation.

Finally, by parsing the results from E5, I found that simultaneous analysis of the sociophysical landscapes revealed trends about the importance of the social landscape that were not apparent in fitting the SRSF model to goat movement in the context of the social or physical landscape alone (Tables 2.2 and 2.3). While making their movement decisions, the goats did not always prioritize the same information. For instance, goat 10, while navigating in a complex sociophysical landscape, appeared to have considered information about vegetation density and its neighbors as important; goat 12 seemed to prioritized information about the distribution of its neighbors as more important than cues from the physical landscape; while goat 15 did not seem to consider information about vegetation as important, but it did consider social information as important. These results suggest that besides estimating animal resource preferences, the SRSF model may offer insights about unique behavioral tendencies (e.g., independent foraging or leadership versus followership).

Table 2.2 Evidence of Social Stratification – Comparison of the Social and Sociophysical Models

Goat	**Sampling interval**							
	10	20	30	40	50	60	70	80
1	R	R	C	R	R	R	R	R
2	N	R	R	R	R	R	R	R
3	R	R	R	R	R	R	R	R
4	R	R	R	R	R	R	R	R
5	R	R	R	R	R	R	R	R
6	R	R	R	R	R	R	R	R
7	R	R	R	R	R	R	R	R
8	R	R	R	R	R	R	R	R
9	R	R	R	R	R	R	R	R
10	R	R	C	R	R	R	R	R
11	R	R	R	R	R	R	R	R
12	R	R	R	R	R	R	R	R
13	C	R	R	R	R	R	R	R
14	R	R	R	R	R	R	R	R
15	N	R	R	R	R	R	R	R
16	R	R	R	R	R	R	R	R

Notes: Assessment of a change in the SRSF estimates of social parameters between the best social versus sociophysical models as a function of sampling interval ranging from 10 to 80 in increments of 10. The letters used in this table have the following meaning: ‘N’ = no signal, indicating that the social predictor was not important in the best social model and the best sociophysical model; ‘L’ = lost signal, indicating that the social predictor was important in the best social model but not the best sociophysical model; ‘G’ = gained of signal, indicating that the social predictor was not important in the best social model but became important in the best sociophysical model; ‘R’ = retained signal, indicates that the social predictor was important in the best social model and remained so in the best sociophysical model; ‘C’ = change of signal, indicates that the social predictor was important in the best social model and remained so in the best sociophysical model but it changed from a linear form to a quadratic one, or vice versa.

Table 2.3 Evidence Of Social Stratification – Comparison Of The Physical And Sociophysical Models

Goat	Sampling interval							
	10	20	30	40	50	60	70	80
1	N	L	R	G	L	L	L	L
2	N	L	R	C	L	R	R	R
3	N	R	N	R	L	R	L	R
4	N	N	N	L	L	N	L	L
5	R	R	C	L	L	L	C	L
6	N	N	C	C	R	C	R	C
7	N	N	N	G	N	R	R	L
8	N	C	N	L	L	N	L	L
9	R	N	R	L	R	R	R	L
10	N	C	R	R	R	R	R	R
11	N	C	L	C	C	L	L	R
12	N	L	G	L	L	L	L	L
13	R	L	L	L	N	L	R	L
14	L	L	L	N	L	N	L	R
15	N	N	N	N	N	N	N	L
16	N	R	C	L	R	C	L	R

Notes: Assessment of a change in the SRSF estimates of social parameters between the best physical versus sociophysical models as a function of sampling interval ranging from 10 to 80 in increments of 10. The letters used in this table have the following meaning: 'N' = no signal, indicating that the social predictor was not important in the best physical model and the best sociophysical model; 'L' = lost signal, indicating that the social predictor was important in the best physical model but not the best sociophysical model; 'G' = gained of signal, indicating that the social predictor was not important in the best physical model but became important in the best sociophysical model; 'R' = retained signal, indicates that the social predictor was important in the best physical model and remained so in the best sociophysical model; 'C' = change of signal, indicates that the social predictor was important in the best physical model and remained so in the best sociophysical model but it changed from a linear form to a quadratic one, or vice versa.

2.5 Discussion

I present the SRSF model as a spatially explicit, statistical tool for the analysis of social dynamics interacting with the physical structure of the environment and the role this complexity plays in the ability of animal groups to navigate that landscape. This model is based on the RSF framework. Its novelty lies in the treatment of the social context as a time-varying, physical landscape. I validated this approach using simulated group movement data with predictable characteristics, as well as remotely sensed movement and landscape data from a readily herding species. In Sections 2.5.1 and 2.5.2, I discuss the agreement and inconsistencies between my predictions and results, their potential reasons, and their real-life relevance.

2.5.1 Conclusions from validation using simulated data

In general, fitting the SRFS social model (which tested the distance to a nearest neighbor, or the social landscape, as a predictor of individual resource preference) to simulated group movement was more parsimonious at longer location sampling intervals. In contrast, the fit of the physical model (which tested the density of vegetation, or the physical landscape, as a predictor) did not vary systematically with sampling intervals. This difference is likely related to the fact that these processes operate at different spatial scales. In other words, (per the simulation model used to generate group movement data), focal individuals in groups moving across a heterogeneous habitat, have two types of goal: 1) to remain in a group and 2) to arrive at a preferred resource patch. Their movement was likely restricted more by the time-varying distribution of autonomous partners (who had similar but unique goals) than the distribution of resources which in the case of the simulation model was static (but in theory could change, likely on a longer time scale). It is reasonable to expect that considering both landscapes simultaneously may lead to better overall decision, and indeed, fitting the sociophysical model (which considered the social and physical predictors simultaneously) was at least as parsimonious or more so than the outcomes of the other two models considered separately.

The fact that fitting the SRSF model to simulated movement subsampled at intermediate or longer intervals was generally better than fitting it to data subsampled at finer scale intervals indicates that extremely high frequency positional data may not always contain useful information about the question of interest. It also shows that systematic subsampling alone, even when location and landscape data are available at moderately different scales, may reveal sufficient scale compatibility (with an increase in signal-to-noise ratio) and result in meaningful analysis across disparate contexts.

The estimated cumulative effect of the physical environment and social dynamics on individual resource preference changed with the type of physical context. For individuals navigating within the in-patch habitat, which in the real world may be thought of as a vast and homogeneous landscape feature, the ubiquitous physical signal had less weight as a predictor compared to information about social partners. In contrast, the edge of vegetation — a rare and linear feature, potentially difficult to sample properly, was a predictor together with the signal about social spacing. This outcome when considered in light of a real-life example, for instance when an animal is moving along a wildlife corridor in a fragmented landscape, illustrates the importance of biologically meaningful interpretation, and the impact as well as the challenge that sampling regime may have on the SRSF model estimates.

Excluding simulated tracks of some group members diminished the impact of the sociophysical landscape as a complex predictor, regardless of the physical contexts. This result shows that forcing the SRFS model fitting process in the context of a partially described social landscape leads to biased estimates.

In terms of the SRSF model accuracy, the estimates of the preferred resource density reflected key features of the simulation across all experimental scenarios. In contrast, the estimates of preferred neighbor distance were always smaller than in the simulations, particularly in large groups simulated using large social separation and the edge of vegetation optima versus near distance and in-patch optima. This pattern likely emerged as a consequence of ‘sampling’ and ‘crowding’ biases where each simulated movement was a trade-off between maintaining social distance and moving towards rare and clustered edge locations. In a large group with a built-in preference for small social spacing, each individual could remain close to its neighbors while still finding nearby edge resources. However, in a large group with far social distance optimum, the theoretical tendency of each individual was to move away from others and perhaps from the preferred resources. This trade-off seemed less impactful when estimating resource preferences in the context of the in-patch habitat because as an abundant resource it was not as strong a cue as the social landscape. Together these results indicate that most of the discrepancy between the SRSF model estimates and the simulation optima (which were larger than the actual or observed preferences) came from the unexpected simulation dynamics, not the model fitting.

Mitigating the sampling bias in a landscape with rare or linear features may require a more sophisticated process that accounts for the proportion of such features in the local habitat in the current simulation model. The crowding bias may be addressed through 1) allowing a wider range of turning angles and momentum to allow for directional and reversal movements likely to occur in a patch -corridor landscape, 2) limiting the fitting process to movement where all group members are in different pixels and 3) weighing the impact of far neighbors more heavily than currently. The last modification may potentially simplify finding a common scale for analysis of movement in the sociophysical landscapes because it would reduce the need to evaluate repulsion at very small social distances.

2.5.2 Conclusions from validation using empirical data

Fits of the SRSF model to predict movement preferences by goats revealed that the social landscape (e.g., moving towards other goats) was more important than the physical landscape (e.g., moving towards the edges of vegetation patches) in explaining individual movement segments. This was an expected outcome because observations of goats in a natural setting often reveals that while browsing some of the time and moving between vegetation areas some of the time, these animals move as a tight group

When estimated at a range of sampling intervals, the social spacing preference in goats was best captured at intermediate intervals, whereas the preference for vegetation density did not differ across the sampling intervals. This outcome suggests that at short distances goats were not responding to their group members, perhaps because there were not enough rapidly occurring or otherwise noticeable changes. In terms of vegetation density, smoothing of a binary landscape feature enabled the SRSF model to recover the known edge-browsing habit of goats and produced meaningful signals regardless of the scale of analysis. As in the findings from the simulated portion of our study, extremely high-resolution in location samples were not necessarily more informative, at least in the context of our questions. However, this pattern may be an outcome of processing a rather detailed level of spatial and temporal information even at relatively coarse scale.

In general, simultaneous analysis of the sociophysical landscape revealed that most goats preferred to move towards locations near other goats and along the edge of the vegetation. Given that these behaviors are expected in a group-living herbivore, having recovered these behaviors the SRSF model may be a useful tool for analysis of movement in other group-living species that exhibit collective movement.

Unlike in the simulated validation, in this dataset, the SRSF model did not recover a social 'repulsion' effect at small distances. A likely explanation is that goats are not afraid to move near one another, often at distances closer than one body length. This behavior is much less likely to occur in limbless species that exhibit predominantly angular movement which requires more space (e.g., fish or reptiles) and which had served as early model organisms in studies of collective animal movement (*101*, *209*).

Lastly, when contrasted with separate analyses of the physical or social contexts, simultaneous analysis revealed that movement decisions by different goats vary in the relative importance they place on neighbor distance and distance from vegetation edge. There is preliminary evidence suggesting a social stratification into 'leaders' and 'followers’ but more detailed investigation is needed to understand what appears to be presence in different roles within a group of herding animals.

The latter result along with the evidence form the simulated data that fitting sociophysical models to social landscape with incomplete information serve as potential argument for collection of multi-individual data, especially when the goals are to characterize or predict aspects of spatial ecology in group living species with compromised conservation status or other social species that are being managed without regard for their social dynamics (*65*).

CHAPTER 3

ENVIRONMENTAL AND SOCIAL DRIVERS OF MOVEMENT IN MALE AFRICAN SAVANNA ELEPHANTS (LOXODONTA AFRICANA)

3.1 Abstract

Despite their popularity and keystone status, little is known about how African savanna elephants (*Loxodonta africana*) integrate information about their physical and social surroundings while navigating their habitat. This is because (1) tracking of multiple members in a group is rare in wild elephants, and (2) the tools to simultaneously quantify physical and social influences on an individual's movement are just beginning to be implemented in movement ecology. Using a novel approach that incorporates the social landscape of the animals into a resource selection function model, this research evaluates highly synchronized, remotely sensed movement from five male elephants inhabiting Etosha National Park in Namibia. The global movement patterns and social dynamic as estimated with this new sociophysical model reflect known behaviors of male elephants. The finding that dominance hierarchy, usually only observable when elephants gather at water points, is maintained throughout the explored landscape is particularly unique. This result adds to the growing body of evidence on the complexity of social interactions in groups of postdispersal male elephants. This approach using remotely sensed data may inform applied research into the interactions of elephant groups with other species acting as competitors or predators, and the management of ensuing conflicts.

3.2 Introduction

African savanna elephants (*Loxodonta africana*) move in response to the physical suitability of their habitat (e.g., mineral content of the soils, presence of certain crop species, elevation changes or precipitation patterns) and social dynamics (e.g., competition for high quality resources or leadership by seniors) (*2*, *46*, *70*, *94*, *127*, *131*, *210–212*).

Unlike in matrilineal herds of female elephants, the relationship between social dynamics and space use in male elephants is much less documented (*39*). Understanding this interdependence is important because besides their keystone role as a species, male elephants stimulate tourism revenue in many range states (e.g., big tuskers) and drive human-wildlife conflict (e.g., crop raiding) (*78*, *140*, *213*, *214*)

As adolescents, male elephants disperse from their natal groups into a social landscape consisting of postdispersal males of varying ages (*128*). Based on remotely sensed movement data and behavioral observations, it is increasingly evident that male elephants transition between solitary and gregarious states depending on several factors. For instance, males in musth—an annual state of heightened aggression and elevated testosterone lasting approximately two months, spend their time alone, pursuing nonkin estrous females or interacting with other courting males (*215–217*). Non-musth males remain in proximity to genetically related or similarly aged male partners, and the strength of their relationships increases with age (*128–130*, *218*).

An established technique to study spatial and social dynamics in elephants involves correlating metrics of dominance and area-based home range estimates (*219*–*221*). Dominance hierarchy is an index derived from expert knowledge about traits such as age category, and traditional behavioral sampling, for instance frequency of agonistic and affiliative interactions between conspecifics of interest (*145*). This index generally indicates that older and larger male elephants, as well as those in musth, are more likely to be dominant than adolescent males. The metrics for deriving dominance rank are often collected near vantage locations such as water points or tourist viewing areas and provide spatially non-explicit information about rank-dependent behaviors at local scale.

Home range estimation, and associated techniques, although useful for detection of general differences in space use between conspecifics with different behavioral tendencies (e.g., discovery of crop raiding individuals which is useful for wildlife managers) has been subject to much criticism as too coarse and lacking biological relevance (*222*, *223*). As an example, knowing that particular elephants move towards human agriculture is not sufficient to consider their behavior as crop raiders. Their preferences may actually be for fertilizer-induced soil minerals, or an outcome of following affiliates that are not tracked.

More recent studies concerning global-level properties of movement in other group-living animals have shown that movement decisions of individual group members about when, where, why, how and with whom to move are impacted by and impact group-level dynamics (*143*, *167*, *224*). For instance, in schooling fish, individuals responding to locally available information about the proximity and heading of their nearest neighbors together generate self-organizing aggregates that appear robust to splitting—an important antipredator strategy. This emergent phenomenon is referred to as collective movement and depends on the integration of information about social and physical processes.

Scientists interested in movement of elephant collectives are developing tools to tackle similar questions, for instance ‘how do elephants integrate information about the environment and interactions with multiple conspecifics during group movement?’ So far studies of correlations between spatially non-explicit movement modes among individuals with different traits (e.g., reproductive state category) and landscape context have shown how different elephants move in specific habitats. Work by (*225*), which considers movement of female and male elephants, indicates that in face of limited resources movement patterns by low ranking individuals are more energetically costly and less predictable than movement by high ranking conspecifics.

Predicting where or for what reason individual elephants may move while interacting with a complex sociophysical landscape remains an outstanding problem. To tackle this problem, one basic requirement is access to time series data on movement of multiple interacting elephants across geographical gradients (*97*, *98*). Recording movement of multiple male elephants inhabiting the same general region is common, albeit rarely in synchronized form. The decisions about which elephants to track are usually based on arbitrary choices (e.g., achieving a ‘representative’ sample of the population in terms of its age or regional distribution) instead of an explicit multi-individual tracking where several individuals in a social unit are monitored over the same period (*179*, *214*). This practice limits the insights that can be gained from existing non spatially explicit techniques and stymies the development of techniques used in other social systems exhibiting group movement (*86*, *97–99*).

Scarcity of high-resolution, synchronous tracking in elephant groups, except for cases where tracked male elephants happen to use the same area, restricts data processing options meant to reduce inherent autocorrelation (e.g., subsampling or interpolation) and may lead to biased estimates (*203*). In addition, many of the techniques used to study how social dynamics and physical environment drive collective movement differ in their requirements for data necessary for model parameterization (*103*). Given a number of challenges in analysis of collective movement, deciding which techniques to build on for greatest benefit remains a tradeoff between generating the most reliable estimates possible, given available priors, and delivering easily interpretable outputs to benefit not only the scientific community but also practitioners interested in actionable results(*112*).

Characterizing movement of male elephant groups may help scientists tackle basic questions about evolution of social complexity and mechanisms of information exchange in these still poorly understood societies, elephants in general and their congeners (*72*, *216*, *226*). For instance, when male elephants leave their family groups, do they carry with them knowledge about the landscape, or inherit ‘foraging rights’? Or, similarly, does poaching of female elephants affect the ability of their male offspring to successfully track resource phenology as individuals or members of male social networks? In addition, information about social interactions in the context of various habitat features may potentially inform conservation of at-risk elephant populations in areas of rapid anthropization (e.g., railway development through Kenya's Tsavo National Park) (*227*, *228*). For example, translocations of immature male elephants with crop raiding tendencies— a set of behaviors which in some populations seems to socially learned, in groups with seniors who do not raid crop may prevent the problem animals from further developing that habit (*78*). Or perhaps, buffering fields of highly palatable maize with nonpalatable crops, such as a mixture of chili peppers and sweet potatoes, may become a part of sustainable deterrence approach while still providing human stakeholders with highly nutritious products (*212*, *228*, *229*).

To explore the sociophysical landscape as an interconnected set of stimuli acting on individual movement, I use highly synchronized movement data from five semi-free-ranging (although in fenced park, able to navigate across vast region spanning at > 900 km^2), male elephants inhabiting Etosha National Park (ENP) in Namibia. Besides a detailed account of their movement, recorded every 15 minutes, I also know the relative dominance rank within this group, based on behavioral and endocrine records spanning multiple field seasons. Although I cannot be certain if the tracked elephants perceive one another as affiliates, I treat them here as a socially functioning group given that they reside predominantly in the northeastern region of ENP and interact frequently (i.e., daily).

To simultaneously test for, and separate, the impact of landscape structure and social dynamics on resource preferences of individuals in this group, I use a recent improvement on the established ‘resource selection function’ framework (RSF) (*110*, *118*, *141*, *142*). Unlike the RSF framework, this framework which I refer to as the ‘social resource selection function’ (SRSF) considers the corresponding locations of nonfocal individuals in a group as time-varying point features on the landscape allowing for coupled treatment with the maps of the physical environment. This model is described in detail in Chapter 2 of this document. I fit the SRSF model to approximately two years of tracking data and the imagery of the physical landscape. These landscape features include a time-varying map of remotely sensed photosynthetic activity, which I refer to as vegetation productivity, and two static maps of perennial water points and auxiliary points. Based on frequent visitation, I suspect that the auxiliary points contain valuable resources (e.g., fruiting trees, mineral deposits or water seeps) (*230*–*232*).

My objective is to test if the social and physical resource preferences as estimated using the SRFS model match my expectations about individual dominance rank assessed locally (*95*). I hypothesize that the estimates of resource preferences by male elephants parallel the observed dominance hierarchy and general foraging tendencies seen in herbivores (e.g., preference for movement towards water sources or high-quality forage). My predictions are that 1) the most influential elephants, acting as strong attractants or repellents towards their conspecifics, are more dominant than less gregarious and less influential elephants; that 2) compared to less influential elephants, more influential individuals prefer to move towards areas containing high quality forage (*94*).

I discuss my findings in the context of elephant ecology and social dynamics. I also consider the applicability of the SRSF model as a tool for evaluation of collective movement in other elephant populations, other species, or between elephants and their heterospecifics, such as predators or poachers (*115*).

3.3 Methods

3.3.1 Study area

ENP (16° 88'E 18° 58'S - location of a research station near Mushara water point where most behavioral and demographic data had been collected) is located in northwestern Namibia. The park is classified as a semi-arid ecosystem. The region where the five male elephants resided during most of the study period, between October 2009 and November 2011, is located in the northeast region of ENP. Over the course of data collection, this area received approximately 97 mm of rain per month in the wet season (between May and October) and 3 mm of rain per month in the dry season (between November and April). This region is bound by a saline pan to the west, and by mopane (*Colophospermum mopane*)-dominated woodland to the east and south (*233*). In the northeast it is bordered by a mosaic of small- and large-scale agricultural operations on commercial or private land (*234*). Multiple perennial waterholes seeding the region are important sources of water for wildlife, especially in the dry season. During the wet season, ephemeral rain puddles and seeps are also available but not explicitly considered in this study (*235*, *236*).

3.3.2 Male elephant population

The five, semi-free-ranging males considered in this study belong to a large subpopulation of ENP's elephants (N males ≈ 225; N herds ≈ 20) ranging predominantly in the northeastern portion of the park. Based on behavioral and demographic data, the collared male elephants were previously classified into several age, reproductive and social categories (Table 3.1) (*95*, *216*, *220*).

Besides socializing with each other, the collared elephants had likely interacted with other herds and males navigating the study region, although I do not know if the collared individuals perceive one another as affiliates. However, given that they reside predominantly in the northeastern region of ENP and have been observed to interact frequently (e.g., near several water points), for the purpose of this research I assume that they are members of a social group.

Table 3.1 Classification of the Five Collared Males into Several Established Age, Reproductive and Social Categories

Collar	Relative age range	Social rank	Reproductive state	Affiliation pattern
AG 264	35-44.9 years	5	in musth in July of 2010/11	bonded
AG 265	25-34.9 years	4	in musth in July of 2010/11	bonded
AG 266	15-24.9 years	3	in musth in July of 2010/11	bonded
AG 267	25-34.9 years	1	not in musth	mostly solitary
AG 268	≥ 50 years	2	not in musth	solitary

Notes: Data on absolute age in the ENP population of postdispersal male elephants are not available; the age structure of this population were determined on the basis of a number of morphological features (Figure A.1.1 in Appendix A.1). The operational age categories are: 1) one quarter (which can be thought of as an early postdispersal male); 2) half (young adult); 3) three quarters (prime adult); 4) full (mature adult); or 5) elder. Dominance hierarchy is represented here as a ranked system, where rank 5 indicates most dominant and rank 1 indicates most submissive individuals. Musth is a rut-like period of hypersexual activity, aggression and elevated testosterone in sexually mature males. Immature males may undergo a premusth period characterized by behavioral displays of aggression without elevated testosterone. In bonded groups, males appear to spend a notable portion of their time with long-term affiliates.
Source: (*128–130*, *234*)

3.3.3 Social landscape

In September 2009, the ENP personnel fitted five male elephants with Global Positioning System (GSP) and satellite Global System for Mobile Communication (GSM) devices. These devices were programmed to record positional data consisting of longitude, latitude, as well as speed and elevation, every 15 minutes. The tracking period started approximately one month after deployment of these devices. To express tracking data in real-world units (i.e., meters) and analyze them in the context of the physical landscape, I used the Universal Transverse Mercator coordinate system (UTM) projection (*208*). The resulting datasets had a median of 70840 movements per individual. Median tracking duration was 24.97 months per individual.

Movement data included in the analysis were characterized by the following set of features: 1) location sample intervals ≤ 15 minutes; 2) movement distance ≤ 300 meters; 3) distance to all nonfocal individuals ≤ 20000 meters. By applying these filters, I aimed to eliminate unreliable location data (e.g., generated due to equipment or human error); and ensure that each focal individual navigated in a landscape where the effect of its conspecifics was possible through a combination of visual, auditory and/or olfactory stimuli.

3.3.4 Physical landscape

To evaluate movement data in the context of the physical landscape, I considered maps of vegetation productivity, permanent water sources and auxiliary points. To construct a map of vegetation productivity, I used data from the 16-day 250m Normalized Difference Vegetation Index (NDVI) (Figure 3.1a) (*237*). I also created a map of the perennial water points by extracting their coordinates from existing geospatial records generated by ENP personnel (Figure 3.1b). These coordinates were manually corrected to represent actual locations of the water points as opposed to adjacent locations (e.g., at the edge of the service roads near the water points) (*235*). Finally, based on the density of large turning angles in frequently visited areas, I compiled a map of auxiliary points other than known water points (Figure 3.1c). All records containing information about the physical attributes of the landscape were projected using the UTM coordinate system.

Given the relatively coarse landscape resolution, I could not determine the type or quality of resources that may be found at the auxiliary points (e.g., fruiting trees, mineral deposits or water seeps). Possible explanations of behaviors occurring at these points that are worth exploring include: directed movement towards and away from specific point resources; meandering while foraging; being lost; or following/chasing a conspecific. Consideration of the auxiliary point map, although predictably important for at least for some elephants, has two potential benefits. First, understanding how various spatially confounded features impact animal movement together or separately may clarify the interpretation of model estimates. For example, if the distribution of the auxiliary points predicts an individual's movement only when it is also impacted by a conspecific, it may indicate a link between social behavior and acquisition of the resources found at auxiliary points. Secondly, given that the auxiliary attractants are estimated fairly accurately , this approach may help in detecting areas of interest to moving animals besides known or easily observable features.

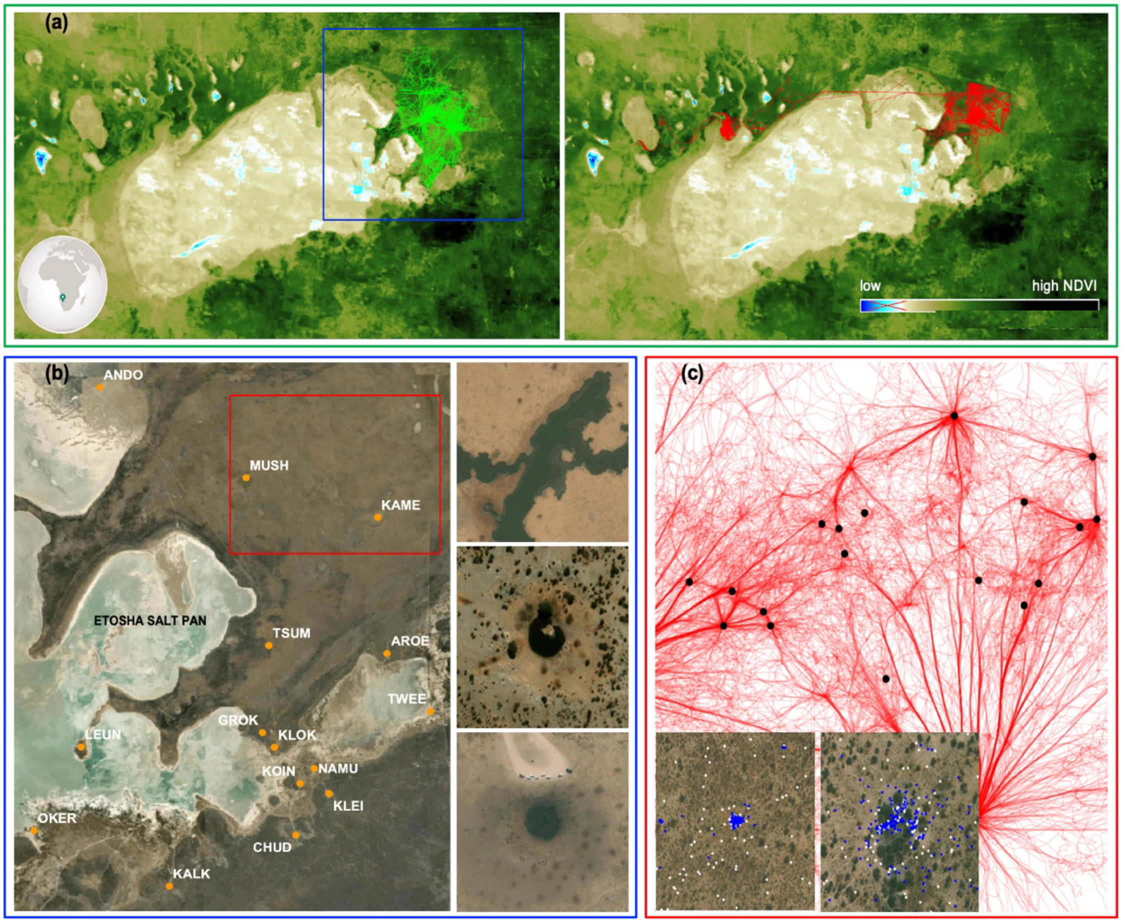


Figure 3.1 Elephant movement and the landscape data.

Notes: (a) An overview exemplifying trajectories of two male elephants AG 267 (green trajectory; top left) and 264 (red trajectory; top right) (for behavioral and demographic detail see Table 3.1). The trajectories are set in the context of an example map of remotely sensed vegetation productivity (NDVI generated every 16 days at 250 meter resolution, for the region encompassing Etosha National Park (ENP). Only NDVI values presumed to represent vegetation were considered. The blue and white value pixels were considered as bare ground, salt pans or otherwise noninformative. The featured tiles span a region of approximately of 200 square kilometers. (b) The distribution of the perennial water points (orange dots) in the northeastern area of ENP (blue square in (a)). (c) An overview of an example set of auxiliary points (black dots) with details of two such points with high turning angle locations These points were diagnosed by searching for frequently visited turning points within the core range of elephant movement (red square in (b)) in ENP.

3.3.5 Application of the SRSF model

The SRSF model is an extension of the established RSF framework with a social landscape components (*109*, *118*). It simultaneously estimates the physical environmental and social influences on an individual's movement across the landscape. The inputs are data on movement of multiple animals (or, if desired, other mobile agents such as rangers or poachers) and 2) physical layers (e.g., imagery of vegetation or poaching hotspots) (*54*, *132*, *135*, *238*). The SRSF model treats the end location of each movement by the focal individual as a choice from a random ‘sample’ set of alternatives bounded within an accessible radius. The relative probability of choosing different locations is modeled using a conditional logistic regression (CLR) as a function of various parameters that differ between available locations (*200*, *201*). Unlike the traditional approach, the SRSF quantifies social impact by using a time-varying map of distances between the focal animal and its conspecifics, which can be thought of as a map of the social environment that changes with every movement. For a given movement *m*, the ‘choice’ is a binary response where a potential location *i* is either the endpoint at which the individual was recorded (*yi* = 1) or one of the alternatives (*yi* = 0). For convenience, I will label the chosen location with the subscript j ($j \in i$). The probability of a movement is modeled as a CLR:

$$p_m = (1 - s)\frac{e^{X_j \beta}}{\sum_i^c e^{X_i \beta}} + s\frac{1}{c}$$

where *X* is a matrix of *k* predictors derived from the landscape data, *β* is a *k* by 1 matrix of parameters to be estimated and *s* is the probability of a ‘stochastic event’: an external stimulus such as a fright that results in a movement in which the endpoint is not ‘chosen’. In that case, all of the *c* possible endpoint locations have the same probability, i.e., 1/*c*. Thus, *pm* is the probability of the animal’s observed location conditional on the qualities of other reachable locations and on the probability of a stochastic, non-choice-type movement. The CLR is fit by maximizing the log-likelihood of the entire set of movements n, denoted as

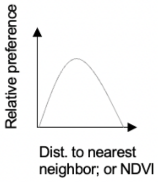
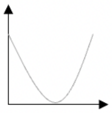
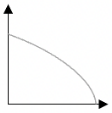
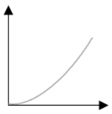
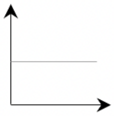
$$L = \sum_{m=1}^{n} p_m$$

using quasi-Newton nonlinear maximization.

I performed variable selection by first fitting models with all possible subsets of ‘physical’ and ‘social’ landscape variables (e.g., distance to a particular point resource, such as water, or a neighbor at any given location) in their quadratic forms. Each fit always included a linear function representing distance to the previous location - an established proxy for the effort required to move to the new location. I ranked the models using Akaike’s Information Criterion (AIC) and calculated importance scores for each variable as the cumulative Akaike weight of the models in which it appeared (*204*, *205*).

Interpretation of the SRSF model outputs depends on the functional form for each variable over the range of its values and the combined importance score for the quadratic expressions for each variable. Because I assumed that the cost of movement, represented by a decreasing linear function, would always be important, I exclude it from further reporting and discussion. The functional forms or the remaining variables can be divided into five categories: monotonically increasing or decreasing in this case arising from quadratic expression (indicating a preference for large or smaller values of the variable in question); convex with the maximum within the data range (a preference for intermediate values); concave with the minimum within the data range (a preference for large and small values indicating a back-and-forth movement between the variable in question and other locations); or constant over the data range (lack of preference for a specific value) (*118*). Table 3.2 details all possible functional forms and proposed behavioral interpretations in the context of example predictors evaluated in this study.

Table 3.2 A Set Of Possible SRSF Model Outputs With Possible Behavioral Interpretations

	SRSF outputs and possible interpretations				
	concave	convex	monotonic decreasing	monotonic increasing	constant
SRSF output in a functional form					
Relative preference for movement towards locations …	intermediately distant from a nearest neighbor; with intermediate NDVI	Near, or far from, a nearest neighbor; with low or high NDVI	near a nearest neighbor; with high NDVI	far from a nearest neighbor; with low NDIV	no effect of the predictors
Potential interpretation of the social context	trail or partly avoid neighbor *x*	encounter and seek neighbor *x*	follow neighbor *x*	avoid or disregard neighbor *x*	no effect of neighbor *x*
Potential interpretation of the physical context (NDVI is a proxy for vegetation greenness)	seek areas with moderate vegetation greenness	move between areas with low and high vegetated greenness	seek areas with high vegetated greenness	seek areas with low vegetated greenness	no effect of vegetation greenness

Notes: The SRSF outputs are expressed as the relative preference for movement towards locations defined by the physical variable (e.g., vegetation productivity) and the social variable (e.g., distance to nearest neighbor)
Source: (*118*)

3.3.6 Predictions about movements in elephant group

To test my predictions, I performed three experiments by fitting the SRSF model to three different subsets of movement data (Figure 3.2). In the first experiment

(E1), I considered movement data occurring in the proximity (i.e., ≤ 2000 meters) of the perennial water points (Figure 3.2a). In experiment two (E2), I evaluated movements recorded in the proximity to the auxiliary points using the same distance cutoffs as in E1 (Figure 3.2b). Finally, in the third experiment (E3), I used the remaining movement data without binning them into distance categories (Figure 3.2c). The choice to filter movement data in this way stems from the fact that social interactions are presumably more likely to occur near the relatively rare water sources, and because combining observations occurring at the landscape scale would likely diffuse the importance of social interactions and generate biased model estimates.

After filtering for reliable locations for all five collars (described above in Section 3.3.3 Social landscape), and for the different regions of interest (E1-E3) different numbers of movements remained. The numbers of movements in the filtered sets ranged from 924 to 3201. For that reason, I chose 900 as a constant sample size for E1-E3, fitting the SRSF model to 900 movement segments selected at random from the available set. To assess the robustness of the results to this random sampling, I repeated it five times for every experiment. It turned out that 900 movements is sufficient to give consistent results even when those are less than one quarter of the available movements, while reducing the computational burden proportionally.

The physical predictors within each fit included vegetation productivity (as defined by NDVI index), as well as distance to the nearest water point and auxiliary points. The social models considered the distance to each of the four nonfocal elephants as the predictors of interest.

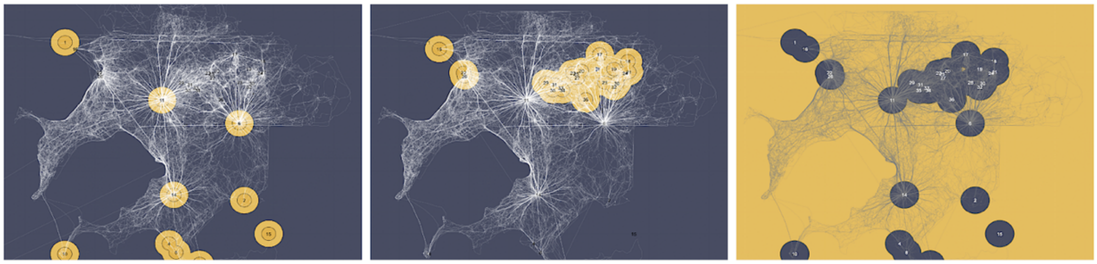

(a) (b) (c)

Figure 3.2 An overview of elephant movement in three unique types.

Notes. (a) In experiment one (E1), I fit the SRSF model to movement occurring near the perennial water sources illustrated as yellow circles with radius from water points ≤ 2000 meters). In this experiment, the subset of movement of the focal individual, consisting of 900 movements, was estimated as a function of the physical (i.e., vegetation productivity and distance to the auxiliary point sources) and social predictors (i.e., distance to each conspecific). The fit per each individual was repeated five times. (b) In experiment two (E2), I performed the same set of fits as in (a) including only movement data occurring within 2000 m of the most often visited auxiliary points. (c) In experiment three (E3), I performed a series of fit as described in (a) but only using movement data not considered in (a) and (b), illustrated as grey trajectories occurring outside of the grey circles.

3.4 Results

3.4.1 Experiment one - movements near established water sources

Results from E1 (Figure 3.2a) indicate that the distance to water is on average highly influential as a predictor of the movements by every focal elephant, with a concave function indicating a back-and-forth movement pattern (Figure 3.3, second column, Water). As for the remaining physical predictors, an intermediate level of vegetation productivity (Figure 3.3, first column, NDVI) is on average a moderately influential predictor of movement for elephants AG 265 and 266, with an intermediate preferred value. In contrast, distance to auxiliary points (Figure 3.3, third column, Points) is highly influential as a movement predictor only for elephant AG 264. The function shows that AG 264 prefers closer distances to the auxiliary points, but it is important to remember that these are movements that happen while that elephant is close to the perennial water points, not when it is close to the auxiliary points themselves. So, the interpretation is that while AG 264 is moving to and from a nearby water source, it tends to do so in the direction of the auxiliary points (which are clustered in one region of the landscape).

Social influences are evident in the interactions between elephants AG 264, 265 and 268. AG 264 and AG 265 exhibit a strong influence on each other, as indicated by the fact that both functions are concave which suggests an ‘approach and retreat’ dynamic. However, the functions are asymmetrical in different ways, with AG 264 seemingly preferring to be further away from AG 265 than AG 265 prefers to be from AG 264. This would be the pattern if, for example, AG 265 repeatedly approached AG 264, which responded by retreating. AG 268 also seems to want to be close to AG 264, but in this case AG 264 appears to largely ignore AG 268.

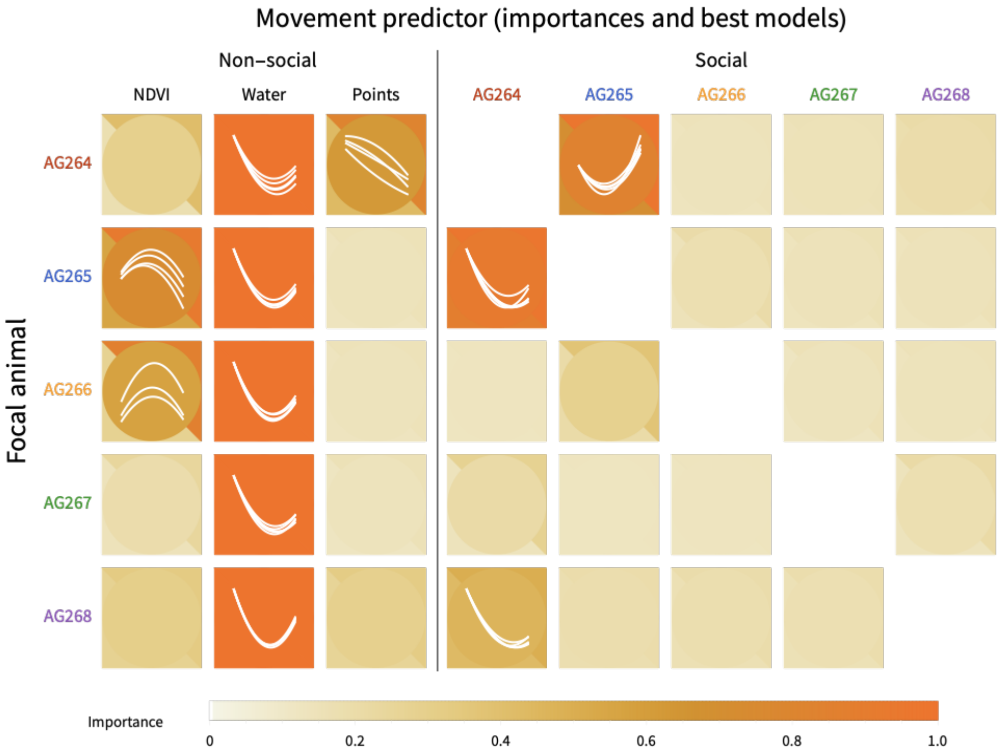


Figure 3.3 Plots represent the functional forms of the best SRSF model fits in experiment 1 estimating movement of male elephants near water.

Notes: The five focal male elephants are referred to as AG 264. The SRSF model outputs are expressed as relative preference (y axis) for choosing the next location as a function (x axis) of each of the three physical or non-social and four social predictors. Shading indicates the degree of influence that a predictor has been estimated to have on the movement of the focal individual; it expresses the statistical value of an importance score which is a cumulative Akaike weight of the models in which it appeared. The importance scores below and above the diagonal in each plot represent the lower and upper bounds of the 95 percent confidence 3 interval resulting from fitting the same combination of models, per each set of experimental conditions per each focal elephant to five randomly drawn samples of 900 movement segments. The circles represent the mean of the five fits repeated per experimental condition per individual. 1. See Table 3.2 for interpretation of the SRSF model outpost in their functional forms. 2. See Table 3.1 for behavioral and demographic descriptors of each of these elephants. 3. See Figure 3.2 for details on binning movement data into three categories.

3.4.2 Experiment two - movements near auxiliary points

Results from E2 (Figure 3.2b) indicate that none of the physical landscape predictors are influential on the movement of any of the elephants (Figure 3.4). The social variables, however, replicate the same pattern seen near water points, in which AG 264 and AG 265 have an ‘approach and retreat’ dynamic. It is less balanced, however, with AG 265 influenced more strongly by AG 264 than vice versa, yet more symmetric, with neither elephant consistently initiating or retreating.

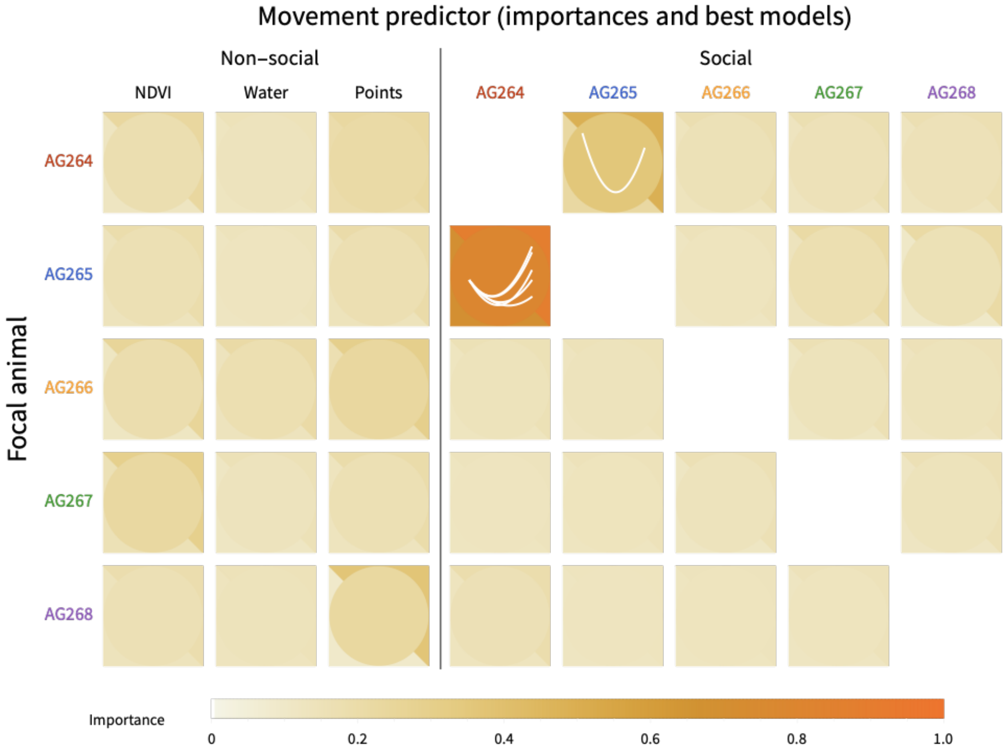


Figure 3.4 Plots represents the functional forms of the best SRSF model fits in experiment 2 estimating movement of male elephants near auxiliary points.

3.4.3 Experiment three - movements far from water and auxiliary points

Results from E3 (Figure 3.2c) are very similar to those of E2, in that the physical landscape predictors are not important in explaining the movement choices of any of the focal elephants (Figure 3.5), but the AG 264/265 pairing show the same social relationship of coming closer then moving apart, this time quite balanced and with a slight and mutual preference for the approach over the retreat. One relationship found only (and only once) in this dataset is mild evidence that AG 267 wants to stay a certain minimum distance away from AG 265. The opposite is not true for AG 265, which is not influenced by AG 267.

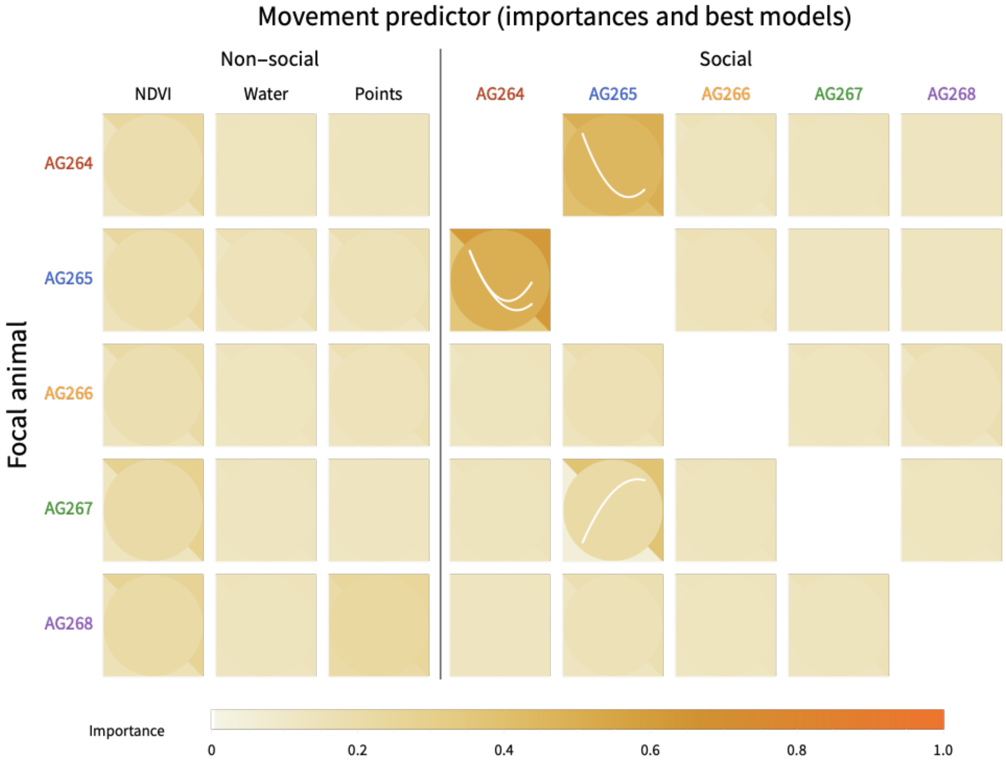


Figure 3.5 Plots represents the functional forms of the best SRSF model fits in experiment 3 estimating movement of male elephants away from water and auxiliary points.

3.5 Discussion

Using a recently developed approach (SRSF) that incorporates the social dynamics into a resource selection function model, I evaluated a unique set of GPS tracks from five male elephants inhabiting the northeast region of Etosha National Park in Namibia. My goal was to study whether the estimated patterns of movement would match known behavioral tendencies observed in areas of high visibility. I found that the global movement patterns and social dynamic estimated by the SRSF model did reflect the observed behaviors of male elephants. Below, I interpret the findings of this study in the context of the observed social dynamics and space use; their departure from my expectations; and how this work may inform our understanding of the socioecology of male elephants as well as their conservation and management.

As expected, the SRFS model estimated that water was a predictor of movement for all elephants when they were near it. As for the estimates of the remaining physical resources (i.e., vegetation productivity and auxiliary points), they were impactful only on some elephants (i.e., AG 264, 265 and 266) when they were near water. The estimated preference by elephants AG 265 and 266 for movement towards areas with intermediate vegetation productivity (as well as water points) is likely a reflection of their repeated movement between water sources and adjacent edges of the salt pan (characterized by extremely low vegetation productivity). This result does not only reveal the sensitivity of the SRFS model to a heterogeneous landscape but also may hint at the fact that relatively young, subordinate or nonmusth elephants (e.g., AG 266) may resort to foraging in areas with lesser quality of vegetation. The fact that at a larger scale of analysis vegetation productivity was not a predictor of movement for any elephant, which was not my expectation, suggests that the visited areas were relatively homogenous and neither particularly attractive or repulsive. Given that the auxiliary points landscape was assembled from explicitly searching for places of high visitation and foraging-like movement characterized by high tortuosity, it was not informative on its own (except for elephant AG 264). However, when combined with the estimates of vegetation productivity, this landscape helped me confirm that the coarse-scale distribution of consumable resources in general is not a useful predictor of high-resolution movement in the region of ENP considered in this analysis.

The social dynamics recovered by the SRSF model across the landscape matched the relative dominance hierarchy observed at water points and nearby vantage points. In other words, pairs of elephants known to interact with one another near water points were estimated to exhibit similar social behaviors at intermediate and landscape-wide scales. The push and pull interactions estimated to be occurring between elephants AG 264 and AG 265 at the time of data collection are consistent with what is respectively known about their relative social rank and reproductive status. Both are dominant adults and exhibit social rather than solitary tendencies. When in musth (at least for some portion of the data collection period), they tend to be very aggressive towards others. As a prime adult, AG 265 usually successfully displaces more mature males. Its preference to move towards locations near water that are also occupied by AG 264, which is more mature and often more aggressive, may suggest that as a high ranking male AG 265 is not intimidated by either affiliative or aggressive interaction, both of which may be invaluable learning opportunities (*128*). The counterpart to this behavior is the estimated preference by AG 264 for movement back and forth between locations occupied by AG 265 to either avoid closer interaction or more likely (given the dominant rank of AG 264) to move unencumbered by the presence of AG 265. The estimated level and type of importance of each male on the movement behavior of the other changes across the scale and the type of the landscape considered. What remains constant, however, is that these elephants are always important predictors of each other's movement.

Besides being impactful on each other, these two elephants are also impactful on behavior of more submissive or senior elephants. Specifically, AG264 is an important predictor of movement by AG 268 when AG 268 is moving in the vicinity of water. This elephant is the most senior member in this group and, according to the SRSF model estimation, it prefers moving towards locations that are relatively near AG 264. Perhaps this outcome is related to their common arrival to the same water points or an affinity by AG 268 as the most senior elephant to interact with another mature male (i.e., AG 264) who may simply be more familiar, more predictable than younger conspecifics or a long term affiliate (i.e., AG 265). Finally, AG 267, the most submissive, non-musth male in this group, unsurprisingly seems to stay away from the much more dominant AG 265 across a large region in the south, with the result that AG 265 roams in the south-west and AG 267 traverses a larger but more marginal region of ENP. In fact, AG 267 it is the only elephant traversing agriculture-dominated region bordering ENP in the north where the risk of conflict with landowners, or poachers, may be much higher. Similar movement behavior in herds of elephants in eastern Africa has been associated with lower rank of the matriarchs, or the most mature females within their social units (*94*).

The proposed explanation of the results detailed in Sections 3.4.1, 3.4.2 and 3.4.3, although informed by what is known about the ENP population and elephant behavior in general, is limited by the extent of available data (*95*, *218*, *239*). Because the focal individuals had likely interacted with other adult males and herds residing in the same region of ENP, it means that the SRSF model fitting process was estimating social behaviors on the basis of an incomplete social landscape. This in turn may have impacted the resulting estimates (as suggested in Chapter 2 of this dissertation). In addition, the relatively coarse resolution of NDVI as a representation of foraging resources may have obscured the behavioral responses of the elephants to the complex, finer-scale distribution of actual vegetation. An important but challenging future task will be to develop a reliable, fine-scale vegetation map of this large region. Despite these limitations, the SRFS model estimates indicate that the dominance hierarchy, usually only observable when elephants gather at water points, is indeed maintained in broadly similar form throughout the explored landscape (*240*).

The SRSF model can be used to tease apart and rank the contribution of various environmental and social factors in shaping movement behavior of group-living animals, such as socially bonded groups of postdispersal male elephants or between members of matrilineal herds. The novel perspective that this statistical tool adds is beyond resource preferences by individual elephants. Instead, it characterizes individual resource preference during engagement in social interaction, or competition from conspecifics or heterospecifics. This perspective, in turn, may motivate the development of practical methods for multi-individual tracking in male as well as female elephants. Or, it may inform the choice of parameters in other predictive models focused on diagnosing movement features by elephants in different types of landscape (e.g., protected areas, agricultural fields or poaching hotspots) (*41*, *225*).

In a more applied sense, understanding how groups of elephants interact across spatial and temporal scales may inform decisions by wildlife managers regarding contraception, culling, reintroduction or translocation efforts, which in a variety of social species have proven more successful when designed with regard for their existing and future social landscapes (*217*, *241*, *242*). In elephants, translocation is typically carried out to remove ‘problem’ individuals, augment population demography or rehabilitate orphaned or captive individuals. In most cases, prior behavioral research is rarely included in the decisions about which animals can be translocated (*170*). As a result, many translocation are unsuccessful due to homing behavior (i.e., return by translocated animals to their natal territories) or ensuing human-elephant conflict with newly translocated animals ((*138*); see Asian elephant example (*243*)).

Ideally, observation of social behavior as a means of informing management decisions should occur at a spatiotemporal scale relevant to the organism’s biology. However, most conservation and management operations are notoriously under-resourced (*112*). This, in turn, means that long-term behavioral observations are rarely a priority, especially in situations where elephants are endangering human life (and vice versa). Characterization of ‘past to present’ records of movement and resource use by problem animals in the context of a complex sociophysical landscape, now made possible by the SRSF model, may offer practitioners valuable, long-term information. For instance, evidence-driven decisions about which affiliates may or should not be translocated together may be more effective. In addition, questions about what destinations may be most appropriate, given the demographic and behavioral makeup of populations residing in those areas, or the surrounding land use. This in turn, may help predict and avert otherwise unforeseen aggression or trespassing by translocated elephants (*244*, *245*).

CHAPTER 4

SIMULATED POACHING AFFECTS GLOBAL CONNECTIVITY AND EFFICIENCY IN SOCIAL NETWORKS OF AFRICAN SAVANNA ELEPHANTS – AN EXEMPLAR OF HOW HUMAN DISTURBANCE IMPACTS GROUP-LIVING SPECIES

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4.2 Abstract

Selective harvest, such as poaching, impacts group-living animals directly through mortality of individuals with desirable traits, and indirectly by altering the structure of their social networks. Understanding the relationship between disturbance-induced, structural network changes and group performance in wild animals remains an outstanding problem. To address this problem, we evaluate the immediate effect of disturbance on group sociality in African savanna elephants — an example, group-living species threatened by poaching. Drawing on static association data from one free-ranging population, we constructed 100 virtual networks; performed a series of experiments 'poaching' the oldest, socially

central or random individuals; and quantified the immediate change in the theoretical indices of network connectivity and efficiency of social diffusion. Although the virtual networks never broke down, targeted elimination of the socially central conspecifics, regardless of age, decreased network connectivity and efficiency. These findings hint at the need to further study resilience by modeling network reorganization and interaction-mediated socioecological learning, empirical data permitting. Our work is unique in quantifying connectivity together with global efficiency in multiple virtual networks that feature the sociodemographic diversity of elephant populations likely found in the wild. The basic design of our simulation makes it adaptable for hypothesis testing about the consequences of anthropogenic disturbance or lethal management on social interactions in a variety of group-living species with limited, real-world data.

4.3 Introduction

In group-living animals, from insects to mammals (*246*, *247*), interactions among conspecifics with diverse social roles (*248–250*) impact individual survival (*251–254*), reproductive success (*255–257*) and adaptive behaviors (*224*, *258–260*). In species with complex organization characterized by flexible aggregates of stable social units (*122*, *261*, *262*), the loss of influential group members through natural or anthropogenic causes can be detrimental to surviving conspecifics (*126*, *263*, *264*) and to entire populations (*166*, *265*). Unlike natural phenomena, such as fire (*266*, *267*), harvest is intrinsically nonrandom (*134*, *268*, *269*). For instance, poachers profiting from pet trade prefer to capture immature individuals as the most desirable commodity (*270*), eliminating gregarious 'brokers' of social interactions (*271*, *272*). As another example, trophy hunters target individuals with prominent features, such as elephants with big tusks (*133*, *273*), killing the oldest and socioecologically experienced conspecifics (*130*, *274*, *275*).

Animal social network analysis (ASNA) can be a powerful tool in demonstrating how selective elimination of individuals with key social roles impacts closely knit animal groups. Quantifying relationships between members of a group as ‘networks of nonrandomly linked nodes’ (*276*, *277*) has revealed that while some disturbed groups break down (*278*, *279*), others stay connected (*263*, *280*). Understanding whether the relationships in remaining groups operate as prior to disturbance is based on a small number of studies. In an instance of captive zebra finches, group foraging ability decreased following repeated social disturbance (*149*). In simulated primate groups, network disturbance led to a decrease in its global connectivity and the efficiency of social diffusion but did not lead to group fragmentation (*148*). These indices depend on network structure; are based on an assumption that transmissible currency, such as information, diffuses through network links (*281*); and have been related to cohesion, the transfer of social currency and robustness to loss of influential conspecifics in animal groups (*282–284*). In light of the anthropogenic impact on ecological communities (*22*, *285–287*), evaluating the relationship between post-disturbance social structure and limitations to social resilience vis-à-vis group performance in natural animal systems is becoming increasingly important (*263*, *288*).

To explore this relationship, we considered the African savanna elephant (Loxodonta africana) — a group-living species threatened by poaching (*54*, *55*, *289*). Elephant social organization consists of several tiers, ranging from transitional clans and bonded groups of distant kin, to matrilinear core units of adults and their immature offspring (*39*); or flexible groups of postdispersal males of varying ages and kinship (*130*). While immature elephants frequently engage in affiliative interactions (*290*, *291*), mature individuals are more experienced about resource distribution and phenology (*2*, *94*) and about social dynamics (*123*, *131*, *292*). The interactions among individuals with diverse social roles across social tiers manifests as fission-fusion dynamics in response to changing sociophysical landscape (*120*, *122*). Poaching (which during the militarized wave of the past decade eliminated large subsets of populations including mature and immature elephants (*293*)), impacts demography (*294*), resource acquisition (*136*, *295*) population genetics (*238*) and various social behaviors (*132*, *296*) in affected populations.

Evidence from ASNA of data spanning periods of low and high poaching in one free-ranging population revealed that the composition and association patterns within matrilines were conserved among close but not distant surviving kin. This outcome suggests clan-level impact of poaching on network structure and resilience, with little detrimental effect at the bonded group- or core unit-levels (*125*). Whether changes in network structure in elephants relate to group functionality is difficult to test directly. However, quantifying network connectivity together with global efficiency while simulating poaching may shed new light on the theoretical capacity for dissemination of social currency and the limitation to social resilience in disturbed populations. These insights may eventually inform our understanding about the mechanisms of group performance, as well as the efforts to mitigate human-elephant conflict (*78*, *129*) and conserve this economically important but endangered, keystone species (*139*, *140*).

We characterized the immediate effect of eliminating the most influential individuals on the global structure of simulated, social networks. We used a static set of empirical association data on one free-ranging elephant population from Amboseli National Park (NP) in Kenya (*121*) because continuous data featuring network reorganization after poaching, necessary to parametrize time-varying models, do not yet exist for wild elephants. Initially, we assembled one social network using an Amboseli dataset and conducted a series of ‘poaching’ experiments by either incrementally removing 1) the oldest elephants as presumably the most experienced and prone to poaching, or topologically central individuals as the most sociable network members (*297*, *298*); or 2) by removing individuals randomly (*279*, *299*). To quantify network-wide structural changes, we evaluated four theoretical indices expressing network-wide connectivity (i.e., clustering coefficient and modularity, dependent on local neighborliness or global partitioning, respectively); as well as the efficiency of social diffusion (i.e., diameter and global efficiency, based on the distance or pervasiveness of diffusion, respectively) (*283*). To set these results in the context of a large-scale variation in demography and social interactions found in real elephant populations, we generated 100 distinct, virtual populations modeled on demographic trends in empirical data. To simulate social network formation in these populations, we built a spatiotemporally nonexplicit, individual-based model with rules informed by empirical associations (*39*, *121*). The steps of assigning social influence, conducting deletion experiments and quantifying deletion effects were as mentioned earlier.

We hypothesized that elimination of the most influential individuals, defined according to their age category or network position would lead to a decrease in global network connectedness and efficiency. Specifically, we predicted that relative to random deletions, targeted removal of the most central or mature individuals would result in a decrease in global clustering coefficient and efficiency, and an increase in diameter and modularity. We also anticipated a worsening in these outcomes as a function of the proportion of deleted individuals, resulting in an eventual network breakdown. This set of findings would be an indication of increased subgrouping at the population level, fewer interactions with immediate social partners and fewer pathways for timely and fault-tolerant transfer of social currency.

Although it was not parameterized to reflect the rate of ‘poaching’ events in absolute time and cannot be used to inform response to poaching after network reorganization, our work offers a novel perspective on the immediate response to disturbance in a large number of sociodemographically diverse populations with experience of poaching-like stress. Keeping in mind the limitations of our approach, we interpret our findings in the context of a common behavioral repertoire in wild elephant populations and offer insights about how our findings may potentially help view natural populations subject to poaching. Finally, we consider the utility of our simulation platform as a generalizable tool for testing hypotheses about the disturbance of social dynamics in other species that facilitate ecosystem functioning or impact human welfare (*300*, *301*).

4.4 Materials and Methods

We performed a series of deletions using one social network derived from association data on a free-ranging elephant population and 100 virtual networks mimicking the empirical one. Details of these experiments and underlying assumptions are described below.

4.4.1 Empirical data -specifying empirical population composition

To gather baseline information about demography and social interactions characterizing elephant sociality, we considered two dyadic association datasets from Amboseli NP originally published elsewhere (*121*). We assume that these datasets, collected at vantage points where different social units converge to drink, capture a range of social processes including events that required group cohesion and transfer of information (e.g., conflict avoidance in a multigroup gathering at a waterhole requires learning and recall about which conspecifics to affiliate with and whom to avoid (*242*)).

During the original data collection, the authors inferred proximity-based, dyadic associations at two social tiers: among individuals within 10 separate, core groups (within core group - WCG) and between 64 core groups (between core group - BCG), where each group was treated as a single social entity. However, we had a different goal — to examine population-wide dynamics. To represent associations that occurred within each core group in the population, we used the unaltered WCG association data according to the following association index (*AI*) formula: $AI_{i,j} = xi,j / (x_{ij} + d + (n - d - xi_{,j}))$. In this formula, x_{ij} is the number of times individuals *i* and *j* were seen together; *d* is the number of times neither individual was seen; *n* is the total number of times a group was observed; and by extrapolation ($n - d - x_{ij}$)) represents the number of times either individual i or *j* was seen. To express the interactions occurring between individuals from different core groups, we assembled a dyadic association matrix by combining the WCG and BCG data as (*302*) (*302*).

Although the original dataset included 64 groups, we could only focus on 10 groups for which both WCG and BCG data were available (labeled AA, CB, DB, EA, EB, FB, JAYA, GB, OA, and PC). To reflect the typical, multi-tier structure of an elephant society (*39*), we aggregated the 10 core groups into eight bond groups [i.e., B1 (core group AA, including 10 individuals); B2 (FB, 6); B3 (EA, 9 and EB, 10); B4 (DB, 4); B5 (CB, 6 and OA, 10); B6 (GB, 11); B7 (PC, 9); and B8 (JAYA, 8)] and three clan groups [i.e., K1 (bond groups B1, B2, B3 and B4); K2 (B5, B6 and B7); and K3 (B8)] using genetically determined relatedness indices and long-term, behavioral associations inferred by the authors (*121*).

4.4.2 Inferring population-wide social interactions and assembling one social network based on empirical association data

We calculated the fraction of all sightings when an individual *i* from core group *G* was seen in that group according to the following formula: $f_{i,G}$ = average $n_{i,j,G}$ /

(nG – average di,j,G) where the averages are over all the other individuals j in group G. In this formula, $n_{i,j,G}$ represents the number of times individuals i and j were seen within group G; $d_{i,j,G}$ is the number of times neither individual i nor individual j was seen within group G; and n_G is the number of times group G was observed. The denominator is, therefore, the average number of times group G was observed with either individual i, individual j or both present; and $f_{i,G}$, which falls in the interval {0,1}, can be thought of as the average fraction of these occasions when they were both present or an index of the overall sociability of individual i. This process was repeated for every individual in the population.

Using the information available for the BCG association data, we calculated the fraction of all sightings when group G was seen with group B according to the following formula: $f_{G,B} = n_{G,B} / (n_G + n_B – n_{G,}B)$. Here, $n_{G,B}$ indicates the number of times groups G and B were seen together; n_G indicates the number of times group G was seen without group B; and n_B indicates the number of times group B was seen without group G. Thus, the denominator is the number of times groups G and B were seen individually. This process was repeated for every pair of groups in the population and can be thought of as the probability of seeing a given pair of groups together. We then derived a symmetric, weighted matrix consisting of probabilities of dyadic associations between individuals from two different groups, for instance, individuals i_G and a_B from groups G and B respectively, by using the following formula: $p(i_G , a_B) = f_{i,G} \times f_{a,B} \times f_{G,B}$. Finally, using this matrix, we constructed a population-wide network of associations or links.

4.4.3 Quantifying social influence in empirically based social network

To identify influential network members serving as social centers and intermediaries (*303*), we quantified each individual's betweenness and degree scores (*298*). Given that these metrics were highly correlated, we used betweenness going forward as particularly suitable for questions about global connectivity and more importantly the efficiency of social diffusion in a society with fission-fusion dynamics (*284*, *304*). From this point onward we often refer to individuals with high betweenness scores as the most central individual. To include age as a form of social influence due to presumed disparity in socioecological experience between mature versus immature individuals, we considered four age categories. They included young adults, prime adults, mature adults and the matriarchs (*305*). Betweenness and age category were not correlated. Their definitions are detailed in Table 4.1.

4.4.4 Conducting deletions using empirically based social network

To assess how disturbance affects global structure in elephant social networks and determine the level of stress that would bring about network fragmentation, we carried out a sequence of targeted deletions by selecting 20 percent of the oldest or most central network members (together referred to as 'deletion metrics') and deleting them in a random sequence in increments of two percent. By eliminating up to 20 percent of members, we attempted to mimic the varying degree of poaching stress likely imposed on wild populations (*53*). In addition, we were motivated by evidence that many synthetic, biological systems (*306*) are organized around several, highly connected nodes, important for network development and stability (*307*). We compared the effect of targeted deletions against a null model by also deleting 20 percent of network members randomly (together referred to as ‘deletion types’) in increments of two percent (collectively referred to as ‘deletion proportions’). Each deletion proportion was replicated 1000 times per both deletion types and both metrics (i.e., betweenness centrality and age category) (*148*).

After each deletion proportion, in each deletion type and metric, we quantified four, established, theoretical indices diagnostic of social network connectivity and efficiency of social diffusion. These indices included the clustering coefficient and weighted forms of the diameter, global efficiency and modularity. Weighted variants of these indices are informative when individuals associate differently with different conspecifics, which has been reported in elephants (e.g., young adults may associate more frequently with close rather than distant kin) (*292*). Given the importance of fission-fusion dynamics in elephant populations occurring through interactions among immediate and distant kin (*119*), we quantified the clustering coefficient and weighted modularity before and after removal of socially influential elephants. By characterizing the number and weight of links within (i.e., clustering coefficient) and across (i.e., modularity) disparate subgroups or modules, we simultaneously compared the change to network connectivity at the social unit and population levels. By measuring weighted diameter and global efficiency, we aimed to illustrate the potential rapidness (i.e., diameter) and pervasiveness (i.e., global efficiency) of social diffusion. Evaluating these indices in the context of elephant social networks allowed us to identify social interactions with capacity for timely and pervasive diffusion of social currency, and their change after poaching-like disturbance. The definitions of these indices and our predictions regarding their change after deletions are detailed in Table 4.1 (*284*).

We assessed the mean value of each index as a function of the proportion, type and metric of deletion. Each deletion condition (e.g., targeted deletion of two percent of the most mature network members) was repeated 1000 times — a process theoretically unlimited in the sample size. Therefore, instead of using a comparison of means statistical test informed by a biological distribution, we quantified the difference in the effect size between means of targeted and random deletions using Hedge's g test (*308*). We expressed the differences in the mean values between all corresponding conditions using the 95 percent confidence intervals.

Table 4.1 Definitions of Social Influence Metrics and Network Indices, as well as Expected Outcomes after Deletion Experiments

Individual level metric	Definition	
Betweenness	The number of shortest paths1 passing through an individual. High value indicates high social interconnectedness and thus important theoretical role that an individual has in the exchange of social currency, such as information	
Age category	A segment of the population within a specified range of ages, including: 1) young adults (individuals <12 and < 20 years old); 2) prime adults (20-35); 3) mature adults (>35); 4) the matriarchs (the oldest or most dominant females in the core group)) used when categorical consideration of age is desired, or when data on absolute age are not available; in the empirically based population the age ranges were based on year of birth; in the virtual populations, the age range distribution was modeled to parallel the empirical distribution of ages	
Network level index		**Predictions**
Clustering coefficient	The number of triplets (where any set of three individuals are connected by either two or three links, referred to respectively as open and closed triplets, respectively) divided by the total possible number of triplets. High values have been associated with high group cohesion, little subgrouping, and resilience against disturbance-induced breakdown	deletion proportion: 0 > 0.2 deletion type: random > targeted
Diameter W	The path with the maximum weight[1] among the shortest path lengths[2] across all dyads. High values have been associated with low degree of cohesion potentially impeding rapid transmission of information	0 < 0.2 random < targeted
Global efficiency W	The inverse of the network's global efficiency, which measures the ratio between the total number of individuals and links multiplied by the network diameter[3]. High values have been associated with high probability of social diffusion in a group and thus important theoretical role in efficient transmission of information	0 > 0.2 random > targeted
Modularity W	The density of links within a module in a weighted network relative to the density of links between modules. High value indicates low group cohesion with cohesive subgroups, and susceptibility to breakdown after disturbance	0 < 0.2 random < targeted

Notes: Definitions of social influence metrics and network indices used in this publication, as well as expected outcomes for weighted (W) and unweighted indices measured after incremental deletion of the most socially influential individuals in targeted deletions, or in random deletions without consideration for their social influence. [1]Path weight - the inverse of the weight of a link, where links with highest weights are equivalent to shortest paths. [2]Shortest path - the path with the minimum number of links between any pair of individuals. [3]Diameter - the longest among the shortest path lengths in a network
Sources: (309, 310,121, 305, 277, 298, 311, 277, 279, 298, 312, 213, 314, 315, 316, 317, 284, 277)

4.4.5 Virtual data - characterizing composition and association properties in virtual populations

To evaluate the impact of poaching-like disturbance on global network structure in the context of sociodemographic diversity likely seen in wild elephant communities, we generated 100 virtual populations based on empirical population composition (*121*). Each virtual population consisted of females in the previously detailed age categories (Table 4.1) and four social tiers, namely core, bond, clan and non-kin clan group (Table B.1.1 in Appendix B.1) (*39*).

Evaluating the distribution of AIs in the empirically based network, according to age category and kinship, revealed the following patterns. 1) Individuals of any age category were most likely to associate within their core group. They were also more likely to associate with kin from the same bond group than from other bond groups; then with individuals from their clan; and lastly with non-kin (*317*). 2) In a core group, individuals of any age category were slightly more likely to associate with conspecifics from older age categories (Figure 4.1a). Since these patterns are generally consistent with the dynamics described in many elephant populations (genetic relatedness — (*317*, *318*); multilevel structure — (*121*); spatial proximity — (*292*, *319*)), we used the empirically based AI ranges for social network assembly in the virtual populations. To show the parallels, we present the ranges of dyadic associations across all age categories and social tiers in the empirically based and virtual populations (Figure 4.1 and Table B.1.1 in Appendix B.1).

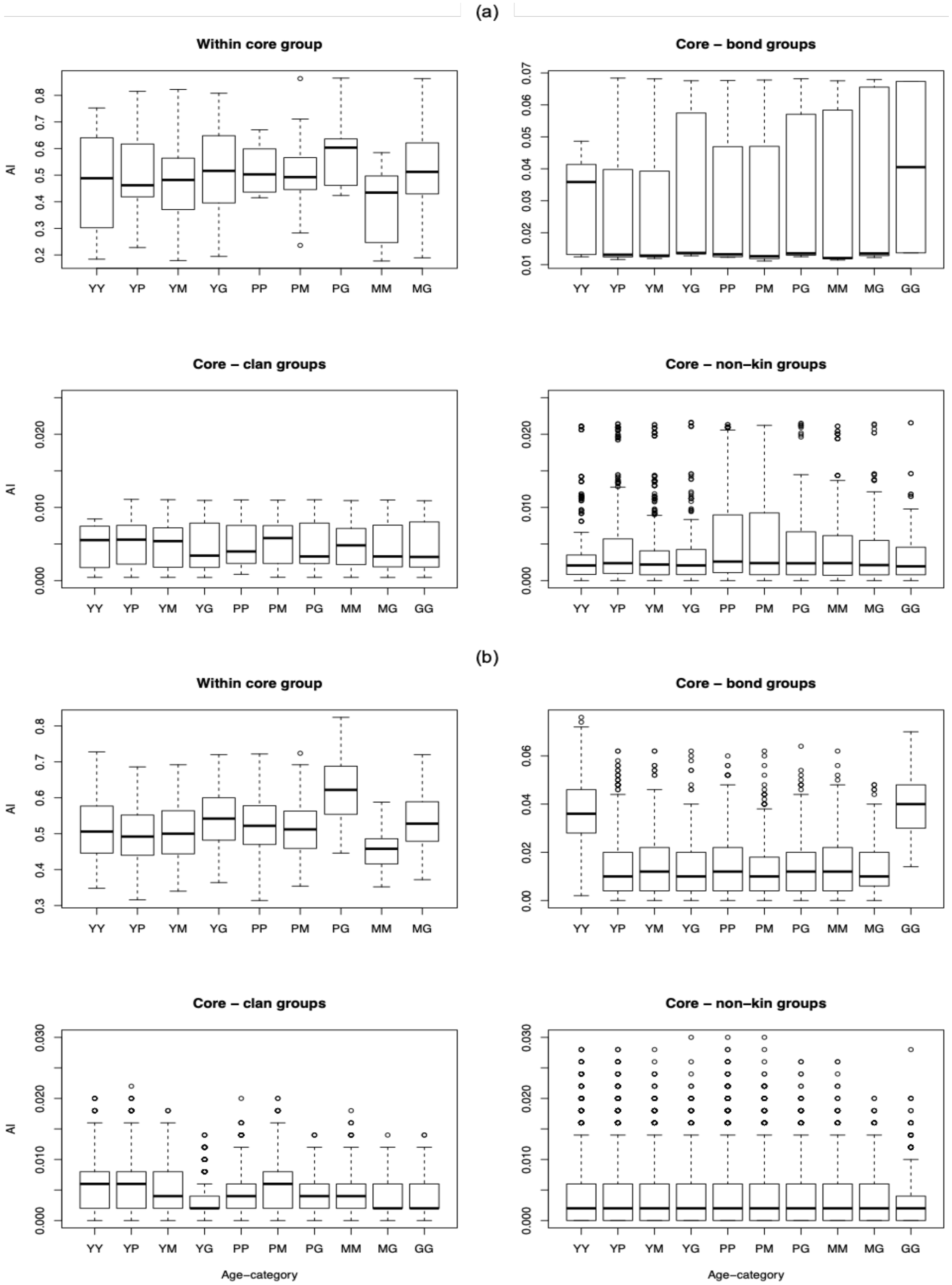

Figure 4.1 Graph representing the distribution of association indices in empirically based and virtual populations

Notes: Distribution of association indices for (a) the empirically based versus (b) virtual populations as a function of age category and kinship of the associating individuals Age categories are abbreviated using the following symbols: Y - young adult; P - prime adult; M - mature adult; G - matriarch. A detailed account of population composition in the empirically based versus virtual populations can be found Table B.1.1 in Appendix B.1.

4.4.6 Simulating virtual social networks

To simulate 100 virtual social networks, we used a spatiotemporally nonexplicit, individual-based model at two levels — between core groups and then dyads. The range of probabilities of kinship- or age-based association between two groups or individuals, respectively, were drawn from a triangular distribution mimicking empirically based data (Figure 4.1b). At each time step, each dyad in the population had the opportunity to associate. Once a core group and a dyadic association had been determined to occur, the time step was terminated and the total number of observed associations per each dyad was updated (Figure 4.2).

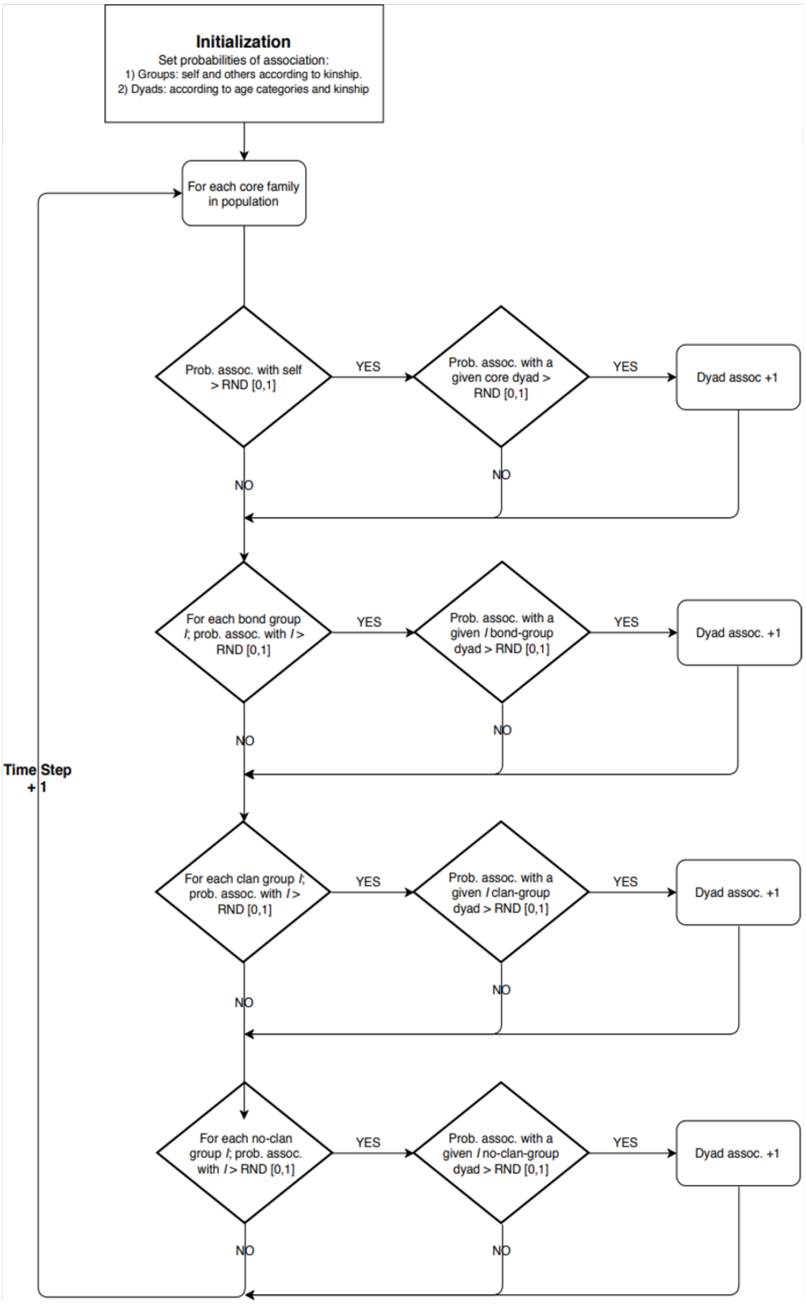

Figure 4.2 Flow chart summarizing the process of simulating social networks among virtual elephant populations

Notes: At initialization, the probabilities of association between and within groups are set according to kinship and age category (Figure 4.1). At the beginning of each time step, the set probability of association between or within each set of groups and between each dyad is compared to a randomly generated number (RDN) between {0,1}. If this probability is greater than RDN, the association is set to occur; if this probability is lower than RDN, the association does not occur, and the time step is terminated. At the end of each time step the number of times a specific dyad has formed across all previous time steps is updated (i.e., increased by one if the association had occurred, or remained the same otherwise). For the distribution of network indices as a function of the number of simulation time steps refer to Figures B.1.1 in Appendix B.1.

The networks had started to reach a plateau after 500-time steps (Figure B.1.1 in Appendix B.1). However, to study how deletions may affect the global structure of networks at different stages of development, we stopped the simulation at 100-, 200-, 300-, 400- or 500-'time steps. From these networks, we noted the age category and quantified betweenness of every individual. To compare their structure, we present graphs of the empirically based network and an example of a similarly sized virtual network (Figures 4.3). They appear similar in age category makeup and WGS associations. The empirically based network has fewer BCG associations and nodes with higher overall betweenness values than the virtual network.

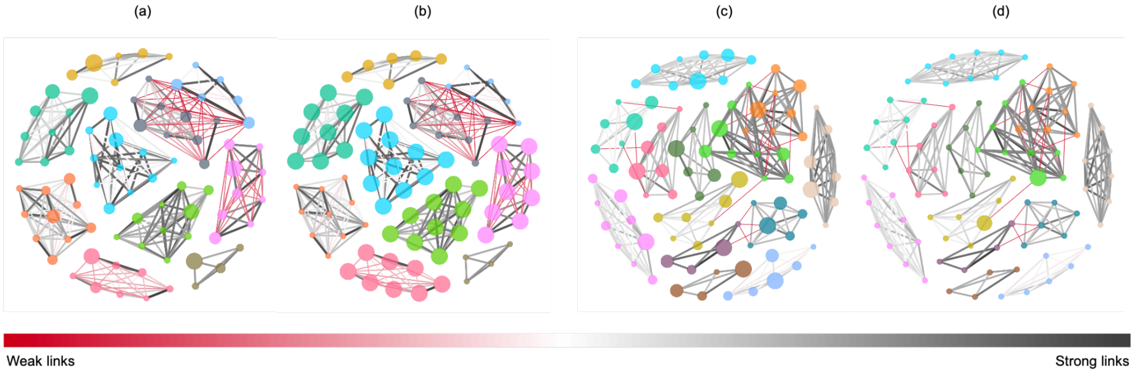

Figure 4.3 Social network graphs of the empirically based population

Notes: Color partitioning is according to a core group, considered from the perspective of either (a) age category or (b) betweenness; and a comparable example of a virtual population with the partitioning according to a core group, and either (c) age category or (d) betweenness. The nodes are ranked by size where the largest nodes indicate oldest age or highest betweenness. The links are ranked according to their relative weight. The color and thickness scheme depicting the weight of each link ranges from red/thin (low) to dark grey/thick (high weight). The links with weight less than 5 percent were filtered out for visual clarity.

4.4.7 Conducting deletions using virtual social networks

To measure if the disappearance of the most socially influential individuals changed the connectivity and efficiency in the 100 virtual networks at each of the five time steps, we performed a series of targeted and random deletions. Individuals were deleted in four percent increments, ranging from zero to 20 percent. In targeted deletions, 20 percent of individuals selected for removal had the highest betweenness or belonged to the oldest age category. During each random deletion, the same proportion of individuals as in targeted deletions was removed randomly, disregarding their betweenness or their age category. After every deletion proportion, we recalculated the following network level indices: clustering coefficient, as well as weighted diameter, global efficiency and modularity (Table 4.1). As in the empirically based portion of our study, we used the Hedge's g test to quantify the difference in the effect size between the means of all network indices across 1) the deletion proportion spectrum, 2) deletion type, 3) time step and 4) deletion metric (*308*).

Motivated by a preliminary assessment indicating a high degree of resilience to fragmentation after the deletion of the oldest or most central members, even at early stages of network formation (i.e., 100-time steps), we explored if simulated networks would break down when subject to prior elimination of relatively weak associations (*320*). Here we wanted to determine if weak associations, likely formed among individuals with high betweenness, could also be explained by age category. During this process, we manipulated only the most robust networks (i.e., 500-time steps) by filtering out the 'weakest links.' To do so, we divided the value of each link in the association matrix by the highest link value and eliminated the links with values up to three percent of the highest link in increments of one percent. After each elimination without replacement, we carried out the deletions and quantification of outcomes as described above.

The social network quantification and analysis of both the empirically based and virtual data were performed using the R statistical software, version 3.2. (R Core Team 2017). Visualization of the social networks was performed in Gephi software, version 0.9.2 (*321*).

4.5 Results

4.5.1 Empirically based network

Contrary to our expectations, the results of targeted deletions in the empirically based portion of our study revealed disparities in almost all network indices between age category and betweenness (Table B.1.2 and Table B.1.3 in Appendix B.1) and an overall unexpected level of resilience against disturbance.

The effect size statistics estimating the mean difference between age category-targeted and random deletions at each deletion proportion revealed no change in clustering coefficient, as well as weighted global efficiency and modularity. Weighted diameter decreased in targeted deletions but only at larger deletion proportions (e.g., proportions in the interval {0.1, 0.2}) (Figure 4.4). Although we did not expect these results, the removal of the oldest elephants in simulated populations appears less damaging to the network connectivity than we expected. Network efficiency, however, based on the weighted diameter results, was negatively affected by elimination of seniors.

In contrast, the effect size statistics comparing the differences between targeted and random elimination of individuals with highest betweenness, as a function of deletion proportion, showed an expected decrease in clustering coefficient and weighted global efficiency, as well as an increase in weighted diameter (Figure 4.4). Weighted modularity revealed no change relative to random deletions (Figure 4.4). This set of results indicates that the loss of the most central conspecifics, particularly if more than 10 percent of them are removed, impedes connectivity and efficiency in simulated networks.

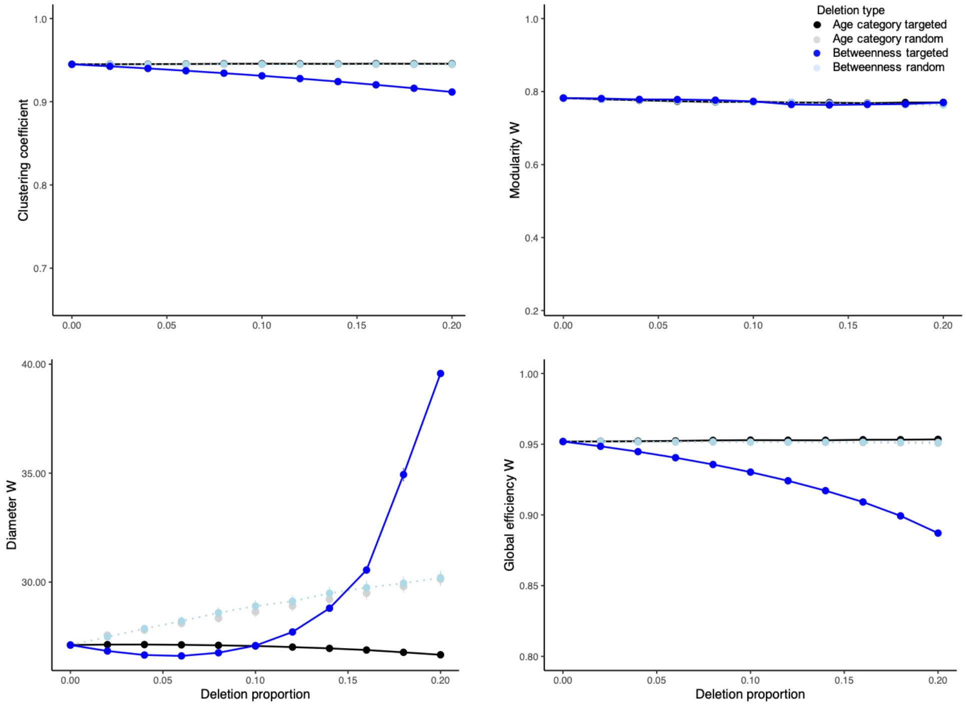

Figure 4.4 Results of deletion experiments using empirically based social networks

Notes: Graphs representing results (mean plus 95% confidence interval) of 1000 deletions per each combination of deletion proportion (i.e., 0-20%) and type (i.e., random vs. targeted) in the empirically based network. The deletions were either targeted according to age category (black series) or betweenness (blue series); or were random (grey and teal series represent random deletions without considering individual traits conducted as control conditions to age- or betweenness-targeted experiments, respectively). The network indices evaluated included clustering coefficient as well as weighted modularity, diameter and global efficiency. For a cross-species context, the minima of y-axis ranges per clustering coefficient as well as weighted modularity and global efficiency are plotted to express the minima from a similar, theoretical treatment in an egalitarian primate society (*148*). The weighted diameter index depends on group size, thus the pertinent y-axis is not expressed in a cross-species context. For results of Hedge’s g test expressing the difference in the effect size between the mean values of each network level index in targeted versus random deletions along the deletion proportion axis and per deletion type, refer to Table B.1.2 and Table B.1.3 in Appendix B.1.

4.5.2 Virtual networks

The results in the virtual portion of this study were similar to those from the empirically based portion. When age category was the focus of deletions, the effect size statistics comparing means of targeted and random deletions in the 100 virtual networks, along the time step and deletion proportion axes, revealed an increase in clustering coefficient and weighted global efficiency, and a decrease in weighted diameter. For the latter two indices, large effect size statistics were only apparent at early time steps and large deletion proportions (e.g., up to 300-time steps and proportions in the interval {0.16, 0.2}). There was no change in mean, weighted modularity between targeted and random deletions (Table B. 1.4 in Appendix B.1). Contrary to our expectation, these results suggest that removal of older individuals improved connectivity in 400- and 500-time step networks but without improving their efficiency.

When targeted deletions were performed according to betweenness, the clustering coefficient and weighted global efficiency decreased, while weighted modularity and diameter increased. The effect size statistics for these indices were large across most time steps and deletion proportions. As we expected, these results point to a decrease in connectivity and efficiency of simulated networks and importance of individuals with high betweenness in shaping these network features.

Elimination of the weakest association links with values ranging from one to three percent of the highest link in 500-time step networks led to multiple events of breakdown into at least two modules (Table B.1.5 in Appendix B.1).

Given their ‘premature’ disruption, we excluded these networks from the subsequent deletions. In the remaining filtered networks, targeted deletions of individuals with the highest betweenness, more so than age category, caused more fragmentation than random deletions. Finally, although the weakest links were rather evenly distributed between individuals of various age categories, they occurred more often among individuals from different clans (Figure B.1.2 in Appendix B.1) indicating an important role in network connectivity.

4.6 Discussion

In this study, we addressed a timely question about the response of animal groups to human disturbance by simulating poaching in African savanna elephant populations. After targeted removal of socially influential individuals, according to their age category or position in a social network (i.e., betweenness), we characterized network indices associated with cohesion and transfer of information in animal groups. We anticipated that targeted disturbance would 1) perturb theoretical indices of network connectivity and the efficiency of social diffusion immediately after disturbance and 2) increase as a function of deletion proportion (i.e., 0 - 0.2) leading to network breakdown.

Contrary to our expectations, targeted deletions according to age category resulted in improved connectivity in simulated networks. This outcome, however, instead of pointing to social influence of seniors, revealed their peripheral roles in contributing to network connectivity relative to younger conspecifics. Elimination of individuals with high betweenness led to an anticipated decrease in indices expressing connectivity and efficiency of social diffusion in simulated networks.

Unlike age category, betweenness proved to be an indicator of social influence in the context of strong links among close kin as well as weak links among distant kin. Finally, regardless of the deletion metric, the simulated networks did not break down even when subject to relatively high degree of ‘poaching’, leaving the question of a theoretical breaking point outstanding.

The disparities between age category- and betweenness-specific deletions are consistent with intraspecific behaviors in species with multilevel sociality, established dominance hierarchy and high degree of tolerance towards subordinate group members (*219*). For instance, in real elephant populations, immature individuals are rather indiscriminate in their affiliations and likely to engage with multiple conspecifics of different ages and kinship (*128*, *290*, *291*). Frequent bouts of social engagement may afford them some social skills without direct engagement of senior kin and fosters cohesion between distinct subgroups (*125*, *271*). In contrast, similarly to mature individuals in other group-living species (*322*, *323*), senior elephants may be more selective about their social partners and less sociable (*121*). Their value as social intermediaries contributing to network connectivity and efficiency may for that reason be comparable to their immature conspecifics (*125*, *130*), regardless of the wealth of socioecological experience seniors likely possess and display during social activities (e.g., such as group antipredator defense led by the matriarch — (*127*)).

This type of organization, where network stability is mediated by different categories of individuals, exemplifies a decentralized system, likely selected to buffer destabilizing effects of prolonged fission or stochastic events such as disease-induced die-off (*324*) or poaching. The notion of network decentralization, reflected in our simulation, parallels the findings by Goldenberg and collaborators who propose that the redundancy between social roles of mature elephants, prior to poaching, and their surviving offspring is a potential mechanism of network resilience against breakdown (*125*). The simulated networks in our research were also resilient to removal of the socially influential group members. Given the seemingly greater flexibility and interconnectedness in elephant populations, relative to other closely knit social species (*148*) finding hypothetical limitations to social resilience may require evaluating more intensive yet biologically meaningful ‘poaching’ disturbance than considered in our work (*325*).

Although our assessment of the effects of disturbance on social organization and resilience does not account for the dynamic or indirect responses to poaching (e.g., network reorganization or avoidance of poaching hotspots), it is a valuable first step in systems with limited real-world data. Having access to information about the proportion and type of missing group members may 1) offer basic but meaningful insights about why some poached elephant populations take exceptionally long to recover from member loss (*326*), while others recover much quicker (*327*) and 2) help reason about the fate of recovering populations. Our ideas may also be transferable to management of other group-living, keystone species (*172*, *328–331*). For instance, applied without consideration for social interactions, trophy hunting of pride lions may intensify infanticide by immigrant males (*134*, *265*, *330*) and displace distressed females to hunt in fringe habitats exacerbating conflict with humans (*172*, *332*). Prior to making decisions about lethal management or translocations of ‘problem’ individuals, wildlife managers may be well served by simulating relevant disturbance on focal populations, quantifying social network effects and adjusting management decisions for better outcomes (*241*, *277*). As another example, the use of ASNA in captive animal populations is already helping researchers characterize the dynamics of harmful agonistic interactions, such as tail biting in newly mixed groups of domestic pigs (*333*). These data may help parametrize simulated disturbance to social network structure in captive systems by taking into account traits such as genetic relatedness in group composition to determine its link to aggression and health of animal subjects. Insights from this type of assessment may improve animal husbandry and safety of farm workers (*334*, *335*).

In summary, our work confirms previous findings that although elimination of the most central network members decreases network connectivity at the population level, it does not lead to network fragmentation. Uniquely, however, our research shows that poaching-like stress in a large number of virtual elephant populations impedes the theoretical efficiency of social diffusion. A follow-up question about the relationship between the structural network changes and population performance will require simulating a dynamic process that accounts for network reorganization after poaching. In addition, to tease apart an individual's importance due to network position versus age-specific experience will require a method that accounts for interaction-mediated information transfer.

Still, our simulation platform can be easily altered to test basic hypotheses about disturbance of social interactions in wild and captive systems.

4.7 Author Contributions

1. Maggie Wiśniewska - conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; software; supervision; validation, visualization; writing-original draft preparation; writing-review and editing
2. Ivan Puga-Gonzalez - data curation; formal analysis; investigation; methodology; software; validation; visualization; writing-review and editing
3. Phyllis Lee - resources; writing-review and editing
4. Cynthia Moss - resources; writing-review and editing
5. Simon Garnier - conceptualization; writing-review and editing
6. Gareth Russell - writing-review and editing
7. Cédric Sueur - conceptualization; methodology; supervision; visualization; writing-review and editing

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APPENDIX A

SUPPLEMENTARY MATERIAL FOR ANALYSIS OF MOVEMENT IN CHAPTER 3

This appendix provides additional information about the population of male elephants evaluated in Chapter 3

A.1 Supplementary Material 1

Table A.1.1 Classification of the five collared males into several established age, reproductive and social categories. When data on absolute age in postdispersal male elephants is not available, it is segment into five categories including (O'Connell manuscript in review at Mammalogy Journal)

One Quarter (1Q)	Half (2Q)	Three Quarter (3Q)	Full (4Q)	Elder (5Q)
				
Slightly larger in size compared to age-matched females and about quarter the size of an adult bull. Relatively small, rectangular shaped head with short and thin tusks that point straight down. Shallow temporal depression.	About the same size as adult females and half the size of adult males. Head size increases and is less rectangular in shape than in 1Q. Tusks are longer, but relatively thin. Temporal depressions are still fairly shallow.	Noticeably larger than adult females. Head is larger and the hourglass shape is more apparent. Wider brow and thicker tusks that curve up and outward. Temporal depressions more pronounced.	Characterized by a heavy and muscular body with thicker, often wide-splayed tusks. Large head that forms a distinctive hourglass shape due to the broadening of the brows and tusks. Temporal depressions pronounced.	Towers over females and is noticeably larger than 4Q. Thick neck folds and a heavy, muscular body. Massive head marked by a long face and thick brow, often accompanied by very large, wide-splayed tusks. Temporal depressions are pronounced.

APPENDIX B

SUPPLEMENTARY MATERIAL FOR ANALYSIS OF SOCIAL NETWORK DYNAMICS IN CHAPTER 4

This appendix provides additional information useful for interpretation of results in Chapter 4.

B.1 Supplementary Material 1

Table B.1.1 The summary composition of 100 virtual populations with the numbers of clan, bond and core groups, as well as individuals per population; the number of bond and core groups, and individuals per clan; the number of core groups per group; and the number of individuals per bond and core groups. The distribution of age categories within each core group was the following: young adults (mean = 2 individuals, min = 1 , max = 5); prime adults (mean = 2, min = 0, max = 7); mature adults (mean = 1, min = 0, max = 3); and matriarchs (mean = 1 , min = 1, max = 1). The composition of the empirical population is included as a reference (i.e., = 10 core groups including a total of n= 83 individuals) (*121*, *305*).

Demographic group	Minimum	Maximum	Median	Empirical contrast
Clan groups per population	1	8	5	3
Bond groups per population	1	28	14	8
Core groups per population	5	86	40	10
Bond groups per clan group	1	5	3	4,3,1
Core groups per clan group	1	20	9	5,4,1
Core groups per bond group	1	5	3	1,1,2,1,2,1,1,1
Individuals per population	95	760	350	83
Individuals per clan group	10	175	74	39,36,8
Individuals per bond group	1	45	25	10,6,19,4,16,11,9,8
Individuals per core group	4	15	8	10,6,9,10,4,6,10,11,9,8

Table B.1.2. Results of Hedge's g test expressing the effect size difference between mean values of weighted forms of modularity and global efficiency indices. These statistics express the difference between targeted and random deletions in empirically based networks, along the deletion proportion axis, with deletions performed according to either age category or betweenness (*308*). Bold values indicate medium (≥ |0.5|) and large (≥ |0.8|) effect size.

Network Index	Deletion proportion	Hedge's g statistic	
		Age category	Betweenness
Modularity W	0.02	-0.0348	0.2513
	0.04	-0.0239	0.1394
	0.06	-0.1002	0.3639
	0.08	-0.0538	0.2219
	0.1	0.0380	0.1154
	0.12	0.0171	-0.4311
	0.14	0.0630	-0.1442
	0.16	0.0315	-0.1178
	0.18	0.2038	0.0303
	0.2	0.3683	0.3449
Global efficiency W	0.02	0.0750	**-1.5411**
	0.04	0.1247	**-2.2205**
	0.06	0.1565	**-2.9173**
	0.08	0.2054	**-3.5236**
	0.1	0.2066	**-4.0418**
	0.12	0.1941	**-4.6401**
	0.14	0.1994	**-5.3114**
	0.16	0.2650	**-6.0381**
	0.18	0.2883	**-6.9214**
	0.2	0.3328	**-8.1713**

Table B.1.3 Results of Hedge's g test expressing the effect size difference between mean values of clustering coefficient and weighted form of diameter indices. These statistics express the difference between targeted and random deletions in empirically based networks, along the deletion proportion axis, with deletions performed according to either age category or betweenness (*308*). Bold values indicate medium (≥ |0.5|) and large (≥ |0.8|) effect size.

Network Index	Deletion proportion	Hedge's g statistic	
		Age category	Betweenness
Clustering coefficient	0.02	0.0476	**-1.6673**
	0.04	0.0904	**-2.3356**
	0.06	0.1218	**-3.0060**
	0.08	0.1693	**-3.5128**
	0.1	0.1572	**-3.9375**
	0.12	0.12531	**-4.3778**
	0.14	0.1212	**-4.8515**
	0.16	0.1635	**-5.3056**
	0.18	0.1570	**-5.7977**
	0.2	0.1709	**-6.2864**
Diameter W	0.02	-0.2706	-0.4453
	0.04	-0.3439	**-0.5870**
	0.06	-0.4264	**-0.6470**
	0.08	-0.4898	**-0.6503**
	0.1	**-0.5604**	**-0.5966**
	0.12	**-0.6311**	-0.4333
	0.14	**-0.7000**	-0.1889
	0.16	**-0.7693**	0.1999
	0.18	**-0.8560**	**0.9766**
	0.2	**-0.9446**	**2.4932**

Table B 1.4 Results of Hedge's g test expressing the effect size difference between targeted and random deletions in virtual populations. The effect size differences, calculated as the Hedge's g test, are presented as mean values for each network index in targeted and random deletions in the virtual networks, spanning all network time step and deletion proportion increments. The deletions were performed according to age category or betweenness (*308*). Bold values indicate medium (≥ |0.5|) and large (≥ |0.8|) effect size.

		Simulation time step/Deletion proportion									
		300					500				
Deletion metric	**Network level index**	0.04	0.08	0.12	0.16	0.20	0.04	0.08	0.12	0.16	0.20
Age category	Diameter W	0.01	-0.07	-0.20	-0.37	-0.59	0.05	-0.01	-0.11	-0.28	-0.47
	Modularity W	-0.02	-0.05	-0.10	-0.18	-0.26	-0.04	-0.06	-0.13	-0.19	-0.25
	Global efficiency W	-0.04	0.04	0.19	0.39	0.63	-0.27	-0.27	-0.17	0.00	0.25
	Clustering coefficient	**0.60**	**0.82**	**0.98**	**1.11**	**1.21**	**0.53**	**0.74**	**0.89**	**1.01**	**1.13**
Betweenness	Diameter W	**1.11**	**1.53**	**1.75**	**1.86**	**1.97**	**0.76**	**1.26**	**1.60**	**1.80**	**1.95**
	Modularity W	0.22	0.55	**0.90**	**1.29**	**1.57**	0.13	0.44	**0.77**	**1.15**	**1.53**
	Global efficiency W	**-1.79**	**-1.91**	**-1.96**	**-1.97**	**-1.98**	**-1.69**	**-1.88**	**-1.94**	**-1.97**	**-1.98**
	Clustering coefficient	**-1.88**	**-1.94**	**-1.96**	**-1.97**	**-1.98**	**-1.89**	**-1.95**	**-1.97**	**-1.98**	**-1.98**

Table B.1.5 The summary of the percentages of filtered, virtual networks that broke down into two or more modules as a result of the deletions performed according to age category or betweenness. The filtering process was carried out before the onset of the deletions by dividing the value of each link in the association matrix by the highest link value and eliminating the links with values up to three percent of the highest link in increments of one percent (*320*). Only 500-time step networks were considered in these experiments.

Deletion metric	**Deletion type**	**Filtering percent**	**Deletion proportion**					**Minimum, Maximum number of modules at 0.2 deletion**
			0.04	0.08	0.12	0.16	0.2	
Age category	Targeted	1	0	0	0	0	0	1,1
		2	0	1	2	2	2	1,1.41
		3	0	0	0	0	0	1,1
	Random	1	0	0	0	0	0	1,1
		2	3	4	5	8	14	1,1.22
		3	100	100	100	100	100	1.25,1.25
Betweenness	Targeted	1	0	0	0	0	0	1,1
		2	6	14	17	19	19	1,4
		3	100	100	100	100	100	2,5
	Random	1	0	0	0	0	0	1,1
		2	1	5	7	11	16	1,1.34
		3	0	100	100	100	100	1.22,1.22

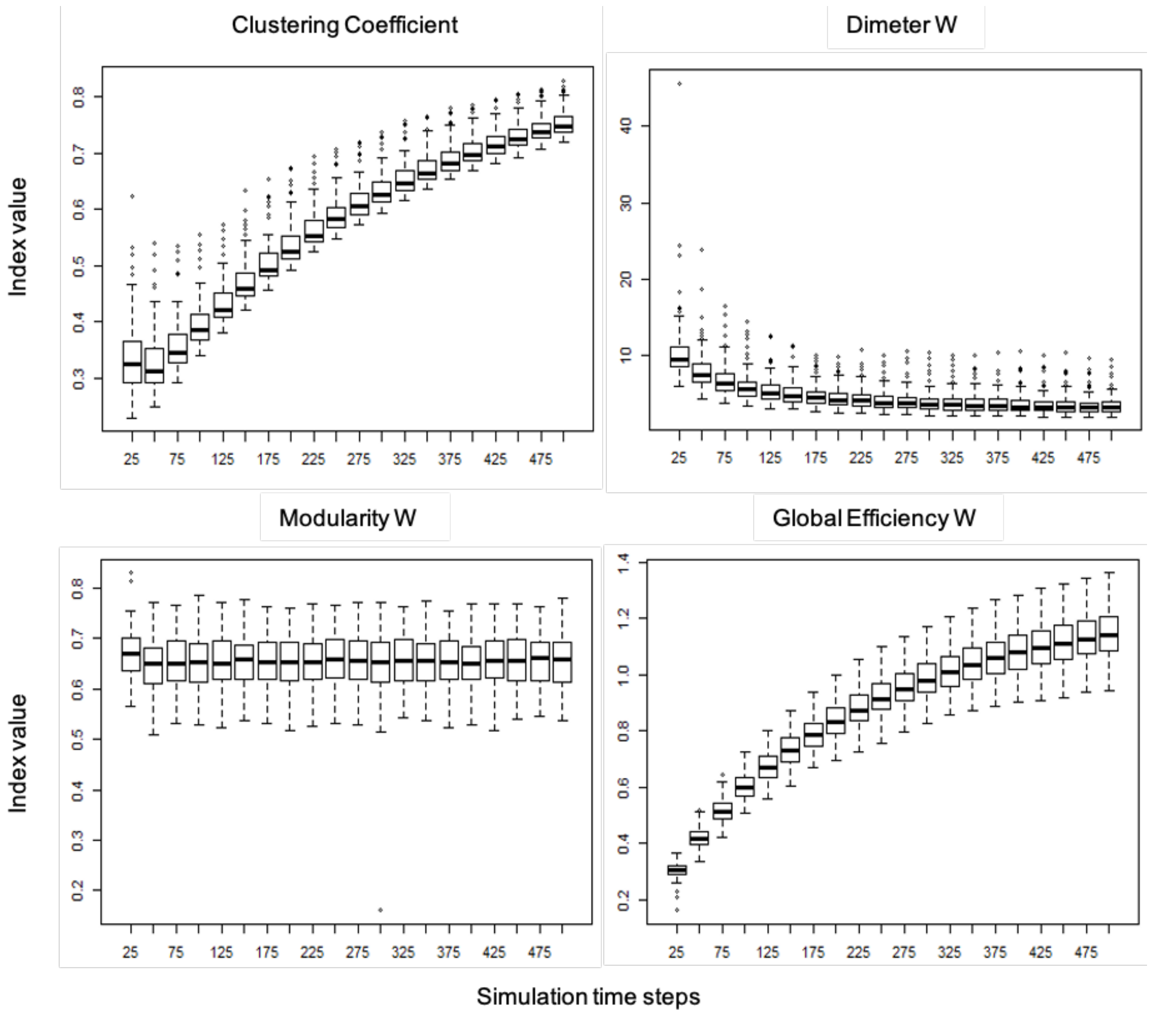

Figure B.1.1 The distribution of values per each of the network indices evaluated, including the clustering coefficient, as well as weighted diameter, global efficiency and modularity, expressed as a function of the number of simulation time steps. The 500-time step cut-off was based on when the density (or the proportion of existing interactions among network members, relative to the number of possible interactions) of the resulting networks started to reach a plateau (~ 75% median density) (*298*).

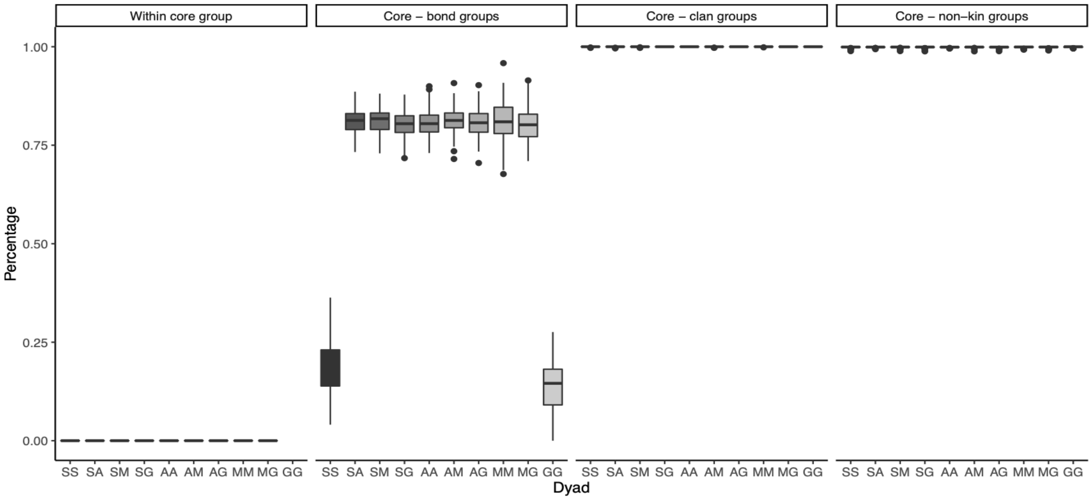

Figure B.1.2 The percentage of the weakest associations (i.e., links with values up to three percent of the highest link) filtered out from the 500-time step, virtual networks prior to deletion experiments. These links are presented according to age class in a dyad (Y = young adult; P = prime adult; M = mature adult; G = matriarch) and one of four social tiers. For the summary of filtering experiments showing percentages of filtered, 500-time step, virtual networks that broke down into two or more modules as a result of the deletions performed according to age category or betweenness, refer to Table B.1.5 in Appendix B.

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