

SOCIAL AND ECOLOGICAL INFLUENCES ON
SPOTTED HYENA (*CROCUTA CROCUTA*) FORAGING ECOLOGY

By

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ABSTRACT

In my dissertation, I use agent-based modeling and observational long-term behavioral data to elucidate how social and ecological factors affect foraging behavior of spotted hyenas, a highly social carnivore, in the Maasai Mara National Reserve, Kenya.

Group hunting is common among social carnivores, but in societies structured by linear dominance hierarchy, access to rewards from hunting are not evenly distributed among group members. In my first chapter, I explore how the inequality of resource distribution due to social rank influences the evolution of cooperative hunting in a digital evolution experimental world. The system reflects spotted hyena society, where an individuals' dominance rank affects their priority of access to critical resources with dominant individuals receiving greater benefits. I found that group hunting evolved at different rates depending on how equitably rewards were shared and high-ranking agents that benefited the most from group hunting were more likely to group hunt. These results provide insights into mechanisms that may promote cooperation in animal societies structured by dominance hierarchies.

In my second chapter, I use long-term behavioral data to investigate hyena hunting patterns and how attributes of both hunters and prey influence hunting behavior. Dominance rank, age, and sex strongly influence hyena behavior and access to resources. Additionally, prey attributes can also influence hunt success for predators. I examine how attributes of spotted hyenas and their prey affect hunting success and hunting group sizes and compare these results to previous work in this same region from 1988–1995, representing a period with lower human activity, a smaller hyena population, and more abundant prey. Prey species and prey age affected hunt success, as well as the age of the hunter when hunting alone. Hyenas hunted prey that were harder to capture in groups more often, and mean hunting group size varied by social rank and age. Group hunting was more common during this study period, possibly reflecting the increasing hyena population and decreases in easier to capture prey. These results demonstrate that attributes of predators and

their prey influence hunt success and hunt grouping behavior in spotted hyenas and are important to consider in predation studies.

In my third chapter, I investigate dietary flexibility in hyenas by comparing feeding behavior (1) contemporaneously among hyenas inhabiting areas with different ecological conditions, and (2) longitudinally across the same population as ecological conditions change in a region that has experienced decreasing wild prey and increasing livestock presence. I found that in both sites, hyenas primarily consumed the prey type that is most available. In my longitudinal comparison, I found that hyenas at one site ate more livestock, and became less reliant on resident prey, as livestock increased there over time. Long-term changes in hyena diets reflected declines in wild prey abundance and increases in livestock presence. This work demonstrates the flexibility of hyena foraging across seasons and in the face of long-term changes in prey availability.

By using agent-based simulations and empirical data, this dissertation deepens our understanding of the mechanisms influencing hunting decisions, as well as the complex social and ecological aspects that shape foraging behavior in spotted hyenas across various temporal scales. I discuss how observed changes in behavior could impact broader ecological interactions, ecosystem processes, and community ecology.

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INTRODUCTION

Feeding is foundational to animal survival, exerting one of the strongest forces on individual fitness. For large carnivores that must hunt their food, feeding involves many challenges.

Successfully finding, capturing, and consuming prey incurs many costs, such as search time and energy expenditure, the risk of injury or loss from kleptoparasites, and requires skills that may take time to learn (Creel & Creel, 1995; Kruuk, 1972; Ritwika et al., 2023; Tucker et al., 2016).

Individuals must also navigate environmental variation which causes changes in prey availability and demography across short and long temporal scales and thus must exhibit flexibility to acquire food (Höner et al., 2002; Navarro et al., 2017; Vettorazzi et al., 2022). The hunting decisions individuals must make, including prey selection and whether to hunt cooperatively, affect hunting success and ultimately fitness (Pettorelli et al., 2015).

Social carnivores must navigate additional challenges that come with group living, such as increased competition with conspecifics (Jordan et al., 2022) and increased detection by additional group members (Smith et al., 2008), scavengers, and kleptoparasites (Vucetich et al., 2004, Smith et al., 2008). There are also benefits to group living including increased hunting success, ability to hunt larger prey, and improved defense against kleptoparasites (Carbone et al., 2005; Cooper, 1991; Périquet et al., 2015). However, the costs and benefits of sociality are not felt equally by group members when societies are structured by linear dominance hierarchies. Social rank plays an important role in shaping behavior (Boydston et al., 2003; Hofer & East, 1993; Smith et al., 2008), and can have profound impacts on health, reproductive success, and longevity (Creel et al., 1997; Holekamp et al., 1996; Sapolsky, 2005; Tung et al., 2016).

In this dissertation, I investigate the foraging ecology of a gregarious carnivore, the spotted hyena (*Crocuta crocuta*), a highly flexible forager that lives in complex fission-fusion societies structured by linear dominance hierarchies. Spotted hyenas are effective hunters, and readily shift their diet to prey that are most abundant (Cooper, 1990; Cooper et al., 1999; Holekamp et al.,

1997b; Kruuk, 1972). They inhabit a wide range of habitats, from arid landscapes, montane forests, and savanna grasslands to urban areas with foraging behavior ranging from primarily hunting native ungulates to scavenging anthropogenic food sources in urban areas (Abay et al., 2011; Yirga et al., 2013; Yirga & Bauer, 2010). They compete with other sympatric large carnivores for food, primarily lions (Lehmann and Montgomery et al. 2017). Additionally, they live in societies with linear dominance hierarchies (Frank 1986). Dominance confers many benefits to high-ranking hyenas, including access to critical resources such as carcasses (Tilson & Hamilton 1984). Low-ranking individuals have lower priority of access to these resources, which leads to divergent behavior, including altered space use patterns (Boydston et al., 2003; Höner et al., 2005), hunting rates (Holekamp et al., 1997b), and association patterns with groupmates (Smith et al., 2007).

I use agent-based simulations and empirical data from long-term behavioral observations to investigate how hunting and feeding behavior varied across individual attributes and ecological conditions. Specifically, I investigate (1) how social rank and feeding tolerance influence which hunting strategies evolve in a digital system, (2) how hunter and prey attributes influence hunt success and hunting group size, and (3) how feeding behavior varies across ecological conditions in space and time.

In Chapter 1, I use agent-based modeling to explore how inequality of resource distribution due to social rank influences the evolution of cooperative hunting in a digital evolution experimental world. I designed a system that reflects the dynamics of spotted hyena societies, in which an individual's social rank affects their priority of access to critical resources, with dominant individuals receiving greater benefits. I investigate whether cooperative hunting evolves under varying levels of despotism among agents of different ranks and whether social rank influences individual agents' probabilities of hunting in groups. At the population level, I found that group hunting rates increased (1) as the rewards from hunting were shared more equally among hunters, and (2) as the relative payoff from group hunting compared to solo hunting increased. At the agent

level, higher-ranking agents were more likely to group hunt than lower-ranking agents when rewards were shared unequally. These results provide insights into mechanisms that may promote cooperative behaviors among individuals with varying social ranks in animal societies structured by dominance hierarchies.

In Chapter 2, I use long-term behavioral data to investigate hyena hunting patterns to investigate how individual attributes of both hunter and prey influence hunting behavior. Hunting behavior represents a critical component of predator-prey dynamics and attributes of both predator and prey affect prey selection and hunting success and are important to consider in predation studies (Pettorelli et al., 2015). Prey selection and hunting success rates can vary based on individual attributes such as age, sex, and social rank of predators (Cooper et al., 2007; Litvaitis et al., 1986; Ross et al., 1997; Saulitis et al., 2000) and of their prey (Fitzgibbon, 1990b; Hilborn et al., 2012; Holekamp et al., 1997b; Höner et al., 2002; Karanth & Sunquist, 1995; Stander & Albon, 1993). Among social carnivores, group hunting is common and individual attributes such as dominance rank, age, and sex can also strongly influence access to shared rewards from hunting. Thus, the differential benefits from group hunting may lead to divergent hunting behavior among individuals (as I found in agent-based simulations in Chapter 1). I investigate how individual attributes of both hunter and prey influence hunting behavior in the spotted hyena, a social carnivore that lives in fission-fusion societies that hunts both alone and with groupmates. Since spotted hyena societies have linear dominance hierarchy, where priority of access is determined by social rank, individual benefits from group hunting vary based on rank.

I investigate how prey species, prey age class, and hunting strategy influence hunting success of hyenas in the Maasai Mara National Reserve, Kenya. I also ask how prey selection influences hunting group size and how individual attributes of hunters impact solo hunt success and group hunting behavior. I then compare these results (1996-2018) to previous research on hyenas in this same region from 1988-1995 (Holekamp et al., 1997b), a period where there was less

human activity, a smaller hyena clan size, and higher prey abundance. I found that hunting success varied based on the species and age class of prey and age class of the hunter. Hunting strategies varied by prey species; hyenas tended to hunt in larger groups for species more difficult to capture. Hunting behavior also varied among individual attributes. Low-ranking hyenas tended to hunt in smaller groups than high-ranking individuals. Juveniles tended to hunt in larger groups than adults. The differences in these strategies reflect the tradeoffs individuals experience – low-ranking individuals experience higher competition in groups and juveniles have lower odds of hunting success when they hunt alone. I compare these results to previous research on hyenas in this same region from 1988-1995 (Holekamp et al., 1997b). Hunt success based on species and grouping patterns by rank and age were similar between study periods, but group hunting occurred more frequently during the later study period (1996-2018). The shift towards increased group hunting may relate to changing ecological conditions that occurred in the region over the past 3 decades. Future work in other systems investigating how predator and prey attributes affect hunting behavior and how these dynamics may change over time, due to fluctuations in both predator and prey populations and in ecological factors, will increase our understanding of the relationship between predator-prey dynamics.

In Chapter 3, I investigate how ecological conditions influence spotted hyena diets across space and time. Large carnivores are critically important in maintaining healthy ecosystems but are also highly vulnerable to anthropogenic change and face many threats globally (Ripple et al., 2014). Global ecological changes such as habitat loss, declining prey populations, conflict with humans, and climate change are all occurring at faster rates than extant species have previously experienced. Large carnivores are particularly vulnerable to anthropogenic change and come into frequent conflict with humans when livestock overlap with carnivore habitat (Inskip & Zimmermann, 2009; Treves & Karanth, 2003; Wolf & Ripple, 2017; Woodroffe & Ginsberg, 1998). Species exhibiting flexibility in behaviors (Wong & Candolin, 2015) including space use, diel activity, and diet (Farias &

Kittlein, 2008; Gaynor et al., 2018; Oriol-Cotterill et al., 2015) often cope best with rapid environmental changes (Smith et al., 2012; Suraci et al., 2019).

I use long-term observational behavioral data to compare feeding observations (1) among hyenas inhabiting two sites with different ecological conditions, and (2) in the same population of hyenas longitudinally across 31 years during a period of rapid ecological change. I compare the feeding behavior of hyenas inhabiting two areas of the Maasai Mara with different management practices: one where livestock grazing is present (Talek Region) and one without livestock grazing (Mara Conservancy). Next, I examine long-term patterns of hyena diets across 31 years in the Talek Region of the Maasai Mara. This region has undergone substantial changes in the landscape including large fluctuations in livestock grazing intensity, varying weather patterns, and changes in native herbivore abundance. I summarize prey availability, livestock presence, temperature, and rainfall to understand how the two sites compare and to look at the broader ecological changes through time. We then quantify diet using observational records of feeding behavior to examine how hyena diets compare between the two sites, and across time in the Talek Region.

Hyenas in both populations responded to seasonal changes in prey availability, consuming primarily the prey type that is most available. Hyenas in the Talek Region consumed domestic livestock and less diverse diets of resident prey species than in the Mara Conservancy. Longitudinally, in the Talek Region over 31 years, hyenas were seen feeding on resident prey less often and feeding on livestock more often. These diet changes reflected prey availability. Resident prey density declined through time and livestock counts increased. Our results complement previous work documenting the decline of herbivore populations (Green, 2015; Ogotu et al., 2005, 2009, 2011; Ottichilo et al., 2000), and adds to the body of evidence that hyenas are flexible foragers and switch to consuming prey that is most available over seasons and years. This flexibility likely facilitates hyenas' ability to persist in landscapes with high human use. We discuss the implications of dietary flexibility in large carnivores and future avenues for research.

This dissertation broadens our understanding of how social carnivores navigate complex social and ecological factors in their environment across various temporal scales. By using both simulation-based and empirical data, this work adds to our understanding of the tradeoffs faced by individuals across different attributes that impact their ability to acquire and access food. Variation among individuals and populations through time could impact broader ecological interactions and ecosystem processes.

Writing style

My research is based on the contributions and collaborations with other researchers. Chapter 1 is the product of a collaboration between researchers who are co-authors on the published manuscript. Chapters 2 and 3 arise from long-term data collected from the Mara Hyena Project, founded by Kay Holekamp and Laura Smale in 1988. These datasets were collected over decades by numerous researchers. Therefore, I use first-person plural throughout this dissertation.

CHAPTER 1:
THE EFFECTS OF SOCIAL RANK AND PAYOFF STRUCTURE ON THE EVOLUTION OF GROUP
HUNTING

ABSTRACT

Group hunting is common among social carnivores, and mechanisms that promote this behavior are a central topic in evolutionary biology. Increased prey capture success and decreased losses from competitors are often invoked as factors promoting group hunting. However, many animal societies have linear dominance hierarchies where access to critical resources is determined by social rank, and group-hunting rewards are shared unequally. Despite this inequality, animals in such societies cooperate to hunt and defend resources. Game theoretic models predict that rank and relative rewards from group hunting vs. solitary hunting affect which hunting strategies will evolve. These predictions are partially supported by empirical work, but data needed to evaluate these predictions are difficult to obtain in natural systems. We use digital evolution to assess how social rank and tolerance by dominants of subordinates feeding while sharing spoils from group hunting influence which hunting strategies evolve in digital organisms. We created a computer-simulated world to reflect social and hunting dynamics of spotted hyenas (*Crocuta crocuta*). We found that group hunting increased as tolerance increased and as the relative payoff from group hunting increased. Also, top-ranking agents were more likely to group hunt than lower-ranking agents under despotic sharing conditions. These results provide insights into mechanisms that may promote cooperation in animal societies structured by dominance hierarchies.

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INTRODUCTION

Understanding mechanisms that lead to evolution and maintenance of group hunting in animal societies is a central topic in behavioral and evolutionary ecology and the subject of much theoretical and empirical work (e.g., Carbone et al., 2005; Mesterton-Gibbons & Dugatkin, 1992; Packer, 1988; Packer & Ruttan, 1988; Stander, 1992; Tennie et al., 2009; Vucetich et al., 2004; Watts & Mitani, 2002). Group hunting occurs in diverse taxa including birds (e.g., Bednarz, 1988; Hector, 1986; Yosef & Yosef, 2010), mammals (e.g., Benoit-Bird & Au, 2009; Busse, 1978; Pitman & Durban, 2012), fish (e.g., Schmitt & Strand, 1982; Strübin et al., 2011), and arachnids (e.g., Rypstra, 1985; Tizo-Pedroso & Del-Claro, 2007). It is especially common among social carnivores (e.g., Bailey et al., 2013; Bowen, 1981; Fanshawe & Fitzgibbon, 1993; Kruuk, 1972; Stander, 1992). Group hunting can lead to improved individual energy return through a variety of mechanisms, including increased prey capture success (Creel & Creel, 1995; Fanshawe & Fitzgibbon, 1993; Holekamp et al., 1997b; Kruuk, 1972; Stander & Albon, 1993), the ability to capture larger prey items when hunting in groups (Holekamp et al., 1997b; Kruuk, 1972), and higher success at defending kills against kleptoparasites (Caraco & Wolf, 1975; Carbone et al., 2005; Cooper, 1991; Creel & Creel, 1995; Kruuk, 1972; Packer, 1986; Périquet et al., 2015; Stander & Albon, 1993; Vucetich et al., 2004).

Group hunting has many benefits compared to solitary hunting among social carnivores. However, this does not mean that each individual hunter benefits equally. Many carnivore societies are structured by dominance hierarchies and rewards from group hunting are unequally distributed based on dominance rank (Atwood & Gese, 2008; Frank, 1986; Gese et al., 1996a; Kruuk, 1972; Smith et al., 2008; Tilson & Hamilton, 1984). This occurs in spotted hyenas (*Crocuta crocuta*) in which, an individuals' social rank falls within a strict linear dominance hierarchy that determines its priority of access to critical resources and therefore confers significant fitness advantages to high-ranking individuals (Frank, 1986; Holekamp et al., 1996; Holekamp & Strauss, 2020; Kruuk, 1972; Smith et al., 2007; Tilson & Hamilton, 1984). Furthermore, like most large

gregarious carnivores, spotted hyenas live in fission-fusion societies, such that individuals spend most of their time alone or in small subgroups that change multiple times per day (Smith et al., 2008). Therefore, individuals have opportunities to hunt both solitarily and in groups as demanded by ecological and social conditions and thus are not obligate group hunters. Spotted hyenas typically hunt alone for most prey items, and although mean hunting group size is 1.5 hyenas (Holekamp et al., 1997b), they also commonly hunt in groups to capture larger or more challenging prey (Holekamp et al., 1997b; Kruuk, 1972). Because high-ranking individuals can use aggression to displace subordinates from kills, rewards are unequally distributed, with high-ranking individuals receiving most of the nutritional and energetic rewards from group hunts whereas low-ranking individuals receive little reward (Frank, 1986; Kruuk, 1972; Smith et al., 2008). Thus, rewards for cooperating are unequally distributed based on dominance rank (Gese et al., 1996a; Smith et al., 2008). Despite this inequality and these fission-fusion dynamics, individual hyenas, even those with low ranks, still hunt in groups. Research on social cognition has revealed that many animals respond negatively to inequality in reward distribution (reviewed by Brosnan & de Waal, 2014). Why do low-ranking carnivores participate in group hunts if they receive disproportionately small shares of the hunting rewards or no reward at all?

Because spotted hyenas live in fission-fusion societies in which benefits of collective action are likely to vary with social rank, these societies offer an interesting system in which to investigate the dynamics of group hunting. However, hunting dynamics are difficult to observe in nature and spotted hyenas are too long-lived to study evolution in action. Although empirical data from observational studies provide important information about the factors influencing group hunting, a deeper understanding of the evolution of this phenomenon and individual fitness outcomes is difficult to attain by observing animal behaviors in their natural habitat. Thus, theoretical and computational approaches may yield novel insights into mechanisms promoting group hunting.

Game theory improved our understanding of conditions that facilitate evolution of group hunting. Game theoretical models predict that social rank and relative rewards from cooperative vs solitary hunting affect whether group hunting is an evolutionary stable strategy (Axelrod & Hamilton, 1981; Packer & Ruttan, 1988). Although these models have some support from empirical data (reviewed by Packer & Ruttan, 1988), the game theoretical framework cannot account for complexities of biological systems such as spatial interactions, stochasticity, mutation rates, and evolutionary dynamics (Adami et al., 2016). In contrast, agent-based methods allow for such complexities to be explored and can yield insights into evolutionary dynamics that cannot be achieved by game theory alone (Adami et al., 2016). Using computational techniques such as agent-based digital evolution can enhance our understanding of natural systems to help generate and test predictions about collective behavior. Although previous digital evolution experiments have already enhanced our understanding of factors that affect the evolution of cooperative behavior in spotted hyenas (e.g., fluctuating prey availability, communication, and interspecific competitors, (Rajagopalan et al., 2011, 2019), variation in social rank has not been considered *in silico* until now.

Here we use digital evolution to examine factors influencing the evolution of group hunting in a society where access to resources is rank-based and individuals have options of hunting alone or in groups. We investigated how social rank and variation, based on differential tolerance among high-ranking hyenas for feeding concurrently with lower-ranking individuals, in the equity with which hunting rewards are shared among group members affect which strategies evolve in agents in a digital system. As also occurs among other animals living in hierarchical societies (Sapolsky & Share, 2004), there is a great deal of variation in how tolerant dominant hyenas are with respect to allowing subordinates access to critical resources (Smith et al., 2015). Here we asked specifically: 1) How does tolerance during the sharing of rewards from cooperative hunting affect the evolution of group hunting? 2) Are individuals more likely to group hunt when they are higher- or lower-ranking than other members of their group? We hypothesized that 1) group hunting would

decrease or fail to evolve altogether with decreasing tolerance (i.e., increasing rank influence on payoffs) because the per capita payoff from solo hunting would come to outweigh the group-hunting payoff for a greater proportion of agents within the system as tolerance decreases and, 2) higher-ranking individuals would group hunt more often than lower-ranking individuals because they should always receive greater per capita rewards from group hunting.

MATERIALS AND METHODS

The game environment

We used a custom-built digital environment created in MABE (Modular Agent Based Evolver) (Bohm et al., 2017) designed to reflect the social structure of spotted hyenas. The digital environment was comprised of a 60 x 60 toroidal grid where each location in the grid was occupied by an agent (3600 agents in total). Agents in the game could not move but could produce offspring after accumulating enough resources to reproduce. Each agent in the initial population was randomly assigned a unique rank, and thereafter, offspring were assigned the rank immediately below that of their parent, reflecting the maternal rank inheritance of spotted hyenas (Engh et al., 2000). Rank was used to determine resource distribution after successful group hunts (described below).

Hunting games

We ran experiments for 1,000,000 updates. Before each world update, each agent played in 5 hunting games in groups with 4 close neighbors. In one game, each agent was the central agent, playing in a game with their immediately adjacent agents, in the other four games, agents were adjacent to the north, south, east, or west of the central agent (Fig 1.1A). In the hunting games each agent made a single choice, either to group hunt for large prey, or to solo hunt for small prey. If it chose to solo hunt, the agent got the entire small payoff; if it chose to group hunt, they got a larger average per capita payoff, but shared the reward with the other agents that also chose to group hunt. Agents that solo hunted had a 50% chance of receiving the solo-hunt payoff. The success rate

for a group hunt was also 50% unless only one agent chose to group hunt; in which case the success rate was 5%. Agents that group hunted had a chance to receive a share of an accumulated group-hunt payoff based on the number of hunters who chose to hunt for large prey. Failed hunts (both solo and group) resulted in no resource gain. These success rates reflect the possibilities 1) that a single individual can choose to hunt a larger prey animal, and 2) that others in the group may not join in the hunt, and 3) the odds of succeeding when spotted hyenas attempt to hunt large prey. Hyenas have a low probability of capturing large prey, such as zebra, when hunting alone, but odds of success increase substantially with a second hunter, although hunting success does not improve much with >2 hunters (Holekamp et al., 1997b). We limited our experiments to a system where hunters capture only a single prey item at a time, because we were interested in the binary choice between the consistent payoff of a small prey vs. the payoff of a large prey (where the chance of success depends on whether others choose to cooperate). Additionally, we assumed that the social system of the agents did not evolve due to benefits of group hunting, but rather that group living preceded the evolution of group hunting, which is most likely true for spotted hyenas as it is for lions, in which group hunting was likely a consequence, but not a cause, of the evolution of sociality (Packer, 1986; Packer & Rutten, 1988).

Agent hunting decisions were determined by values encoded in their 5-site genome. The value at each genome site represented the probability that an agent would group hunt given an agent's relative rank in its hunting group (e.g., if an agent is the third-ranking agent in the hunting group, the value at the third genome site represents the probability of group hunting in that hunting game).

Fitness

An agent's reproductive success depended on how many resource points it earned from hunting. Before each world update, each agent participated in 5 hunting games. The number of resource points each agent received was equal to the average number of resource points that agent

earned from the 5 hunting games. When an agent received enough resource points, it produced an offspring at the next update. The reproduction cost was set at 50 points, the solo-hunt payoff was set at 5, and the group-hunt payoff was variable. Agents accumulated resource points until they achieved enough to reproduce. When they accumulated 50 points, they produced an offspring at the next update, after hunting games were resolved. If agents did not receive enough resource points to reproduce at that update, they carried over their points from previous updates and continued to accumulate points until they could reproduce. When an agent reproduced, it paid the reproduction cost and produced an offspring that was placed randomly into one of the 24 neighboring locations within a 2-grid cell radius of the parent agent (Fig 1.1B). We choose this design to reflect the fact that female hyenas typically remain in their natal groups throughout their lives (Frank, 1986), and that they associate most closely with their kin (Holekamp et al., 1997a). The agent at the new offspring's location died and any resources it had collected were lost so that the phenotypes reproducing faster would tend to outcompete slower-reproducing phenotypes in the population. The offspring inherited a mutated copy of the parent's genome and the rank directly below the parents' rank, following rules of maternal rank inheritance in spotted hyenas (Engh et al., 2000). All agents ranking below the new offspring were reassigned to one rank lower to maintain the linear dominance hierarchy. Mutations occurred when new agents were born at a 0.05% probability per genome site. If a mutation occurred, mutated sites were set to a new random probability (i.e., probability of group hunting, in the range [0-1]). After new agents were born, the numeric ranks of all agents in the population were updated to maintain unique rank ordering; that is, the entire population was structured by a linear dominance hierarchy where no two agents had the same rank.

Reward structure

The reward from group hunting was distributed to participating agents based on their relative rank among the group hunters. We manipulated two variables that affected the payoff

distribution: tolerance (i.e., how evenly the reward was shared among group hunters based on rank) and the payoff ratio of solo hunts to group hunts. The payoff for a successful solo hunt was 5 points for all experiments. We used two group-hunt payoffs to test the effect of the solo-hunt to group-hunt payoff ratio on which strategies evolve. The group-hunt payoff conditions were set at 2 and 1.2 times the size of the solo-hunt payoff (i.e., per capita average = 10 and 6 points, respectively). The total group-hunt payoff depended on the total number of group hunters so that the average per capita reward remained constant to approximate the relative energy gain individuals would accrue from multiple hunting bouts alone or in a group. We tested five different “tolerance” values: 1.0, 0.96, 0.88, 0.76, 0.64. Tolerance of 1 meant the payoff was shared equally among all agents who group hunted. As tolerance decreased, the payoff became increasingly skewed by social rank. For example, if three agents group hunted and tolerance was 0.64, the second-ranking agent got 64% of the payoff received by the first-ranking agent, and the third-ranking agent got 64% of the payoff received by the second-ranking agent. Note that the rank skew was determined by the relative ranks of group hunters, such that, if only the first-, third-, and fifth-ranking agents choose to group hunt, their ranks for sharing payoffs would be 1, 2, and 3 (Fig 1.2). We ran simulations for each tolerance factor for the two group-hunt payoff schemes, resulting in 10 total conditions. We ran 200 replicate simulations for each condition for 1,000,000 updates. At each update, we tracked the rate of group hunting based on relative social ranks of agents within each hunting group. We sampled each replicate every 1,000 updates and took the average group-hunt rate of the last 100,000 updates (n=101 samples). We then took the mean across the 200 replicates to calculate the final mean group-hunt rate for each experimental condition.

All data post-processing, analysis, and plotting were conducting in R (R Core Team, 2021) version 4.0.5 and RStudio (RStudio Team, 2021) version 2021.9.1.372 using the packages ‘here’ (Müller, 2020) version 1.0.1, ‘tidyr’ (Wickham & Girlich, 2022) version 1.2.0, ‘dplyr’ (Wickham et al.,

2022) version 1.0.8, 'ggplot2' (Wickham, 2016) version 3.3.6, and 'gridExtra' (Auguie, 2017) version 2.3.

RESULTS

Group-hunting rates in our population of agents were strongly influenced by the tolerance shown by dominant hyenas (Fig 1.3). When the reward was divided evenly (i.e., tolerance = 1), agents group hunted nearly 100% of the time under both payoff scenarios. As the reward from group hunting became less evenly distributed (i.e., increasingly skewed by social rank), group-hunting rates decreased within the population.

Hunting decisions were also strongly affected by relative social rank. When tolerance was low, higher-ranking agents generally group hunted at higher rates than did lower-ranking agents. When the group-hunt payoff was twice the magnitude of the solo-hunt payoff, the difference between the group-hunting rates of the highest-ranking agents and all other agents increased with decreasing tolerance, with the greatest difference at the lowest tolerance level of 0.64 (Fig 1.3A).

The relative size of the group-hunt payoff compared to the solo-hunt payoff had a substantial effect on hunting decisions (Fig 1.3). When the relative payoff from group hunting was reduced (i.e., from 2 to 1.2 times the solo-hunt payoff), agents group-hunted at similar rates only when the reward was divided evenly. However, at all other tolerance levels, group-hunting rates were lower among agents of all relative ranks compared to when the payoff was twice the size of solo hunting. At this smaller group-hunt payoff, the variance in group-hunting rates based on relative social ranks was also reduced (Fig 1.3B). There were small differences in group-hunting rates among agents of different social ranks at the lowest tolerance levels (0.64 and 0.74). The differences in group-hunting rates between agents with rank 1 and agents with ranks 2 to 5 were larger at moderate tolerance levels (0.88-0.94).

DISCUSSION

In our agent-based digital evolution system, the evolution of group hunting was strongly influenced by tolerance, social rank, and relative per capita reward from group hunting and solo hunting. These results both support previous game theoretical predictions and emulate findings from empirical studies (Packer & Ruttan, 1988). Our results also reflect tradeoffs faced by social carnivores.

Tolerance and social rank

Tolerance during distribution of hunting rewards had a strong effect on group-hunting rates in our experiments. As tolerance decreased, group hunting decreased, especially among lower-ranking agents. These results support previous experimental work. In other species, individuals are sensitive to inequity in rewards for performing the same task (Brosnan & de Waal, 2014; de Waal & Davis, 2003; Wascher & Bugnyar, 2013). Mechanisms that increase tolerance in resource sharing and improve benefits for lower-ranking individuals should promote cooperation in societies structured by linear dominance hierarchies. Further work investigating variation in social bonds among individuals could improve our understanding of cooperation in hierarchical societies. High-ranking individuals may share resources more equitably in exchange for other benefits. There is some evidence of such mechanisms in animal societies. For example, low-ranking spotted hyenas gain social and feeding tolerance by associating with high-ranking hyenas (Smith et al., 2007). Male chimpanzees share meat with males who are preferred social partners and who provide coalitionary support (Mitani & Watts, 2001; Nishida et al., 1992; Samuni et al., 2018). This increased feeding tolerance may promote participation in cooperative tasks by low-ranking individuals who form stronger bonds with, or provide more social support to, high-ranking individuals. Future work investigating how partner choice, effort, and variation in equity influence participation in cooperative tasks will further our understanding of the conditions under which cooperation evolves (Brosnan & de Waal, 2014).

Although group-hunting rates decreased with decreasing tolerance, low-ranking agents still group hunted despite the low payoff these agents received. Kin selection is another mechanism that might promote cooperation and could potentially explain why low-ranking agents sometimes cooperate in highly despotic societies (Shimoji & Dobata, 2022). Individuals that cooperate in groups containing their close relatives receive additional inclusive fitness benefits by helping kin (Hamilton, 1964). Furthermore, feeding tolerance can increase when feeding with kin (de Waal & Davis, 2003), and lower-ranking individuals may gain access to resources through higher-ranking relatives. Our experiments did not test this hypothesis; however, we set the distance offspring were placed in the world from their parent at a maximum of two cells away, meaning that offspring stayed relatively close to their parent, and were likely in one or multiple subgroups with their parent and other relatives. This close physical distance could generate a cluster of closely related agents, all of which inherited similar strategies from their parent agent, and concurrently increase inclusive fitness benefits from cooperating with kin. We expect that setting this reproductive distance farther from the parents would have a negative effect on evolution of cooperation, but more experiments are needed to test this hypothesis. Modifying the distance at which offspring can travel from their parents in digital evolution systems may provide more insights into how kin selection influences group hunting in animal societies.

There may be some conditions under which it is worth cooperating some percentage of time for lower-ranking agents. For example, if the fifth-ranking agent group hunts and the fourth- and third-ranking agents solo hunt, the fifth-ranking agent's relative rank improves among the group hunters and thus it will receive a better payoff than if all five agents group hunted. Situations such as these may explain why, in our experiments, there was little to no difference between the group-hunt rates of the second- to fifth-ranking agents across tolerance levels under both payoff conditions. Further work is needed to investigate how actions taken by individual agents vary

across hunting groups and as their relative rank and the number of group hunters vary in hunting games.

Reward from solo hunting

The relative per capita reward from group hunting vs. solo hunting also influenced group-hunting rates. As occurs in other species (e.g., Creel & Creel, 1995; Packer & Ruttan, 1988), we found that when there is greater potential for a higher per capita payoff from group hunting, this strategy should be more common. In our digital system, we kept the group- and solo-hunting success rates consistent throughout the experiments. In natural systems, the group- and solo-hunting success rates can vary spatially and temporally within and among populations due to varying ecological conditions. Chimpanzees in the Gombe forest hunt cooperatively less than chimpanzees in the Tai forest, most likely because solo hunting at Gombe is more successful than solo hunting in Tai (Boesch, 1994). Relative solo- and group-hunting success can also vary within populations due to seasonal changes in prey availability. In the Maasai Mara, Kenya, zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) abundance peaks for several months during the annual migration (Cooper et al., 1999). When these large prey are widely available, spotted hyenas have higher hunting success and are more gregarious (Holekamp et al., 1997b; Smith et al., 2008), which may affect the relative returns from alternative hunting strategies, particularly for low-ranking individuals. Solo- and group-hunt success rates can also vary with prey type (Holekamp et al., 1997b), affecting relative payoffs from hunting strategies (Packer & Ruttan, 1988). For instance, solo-hunting spotted hyenas in the Kalahari Desert have low success hunting adult gemsbok (*Oryx gazella*) but high success hunting calves (Mills, 1985), and thus should profit more by hunting in groups for adults but hunting alone for calves. In contrast, spotted hyenas in Tanzania have greater success when hunting in groups for wildebeest calves but group hunting does not increase hunt success when hunting for adult wildebeest (Kruuk, 1972). Future research is needed to understand

how varying prey availability and capture success over space and time influence evolutionary dynamics of cooperative hunting.

Our results agree with game theoretical models that the reward from cooperating must be greater than the reward from solo hunting for individuals to hunt cooperatively (Packer & Ruttan, 1988). In societies where rank determines priority of access to food, this reward must be even larger for low-ranking individuals to cooperate (Packer & Ruttan, 1988; Tilson & Hamilton, 1984). Thus, as solo-hunting success decreases, cooperation should be favored (Packer & Ruttan, 1988). Here, we tested two group-hunt payoff scenarios; one where the average per capita payoff from group hunting was twice that of the solo-hunt payoff, and one where the average per capita payoff was 1.2 times the solo-hunt payoff. Even when the mean group-hunt per capita payoff was only 1.2 times the solo-hunt payoff, group hunting still occurred, albeit at low rates, under the most despotic conditions for resource sharing. How much inequity will agents tolerate before group hunting disappears from this system?

Social carnivores face a tradeoff between relative costs and benefits gained from solo hunting vs. group hunting. Solitary foragers can be overwhelmed by groups of intra- and inter-specific competitors once a kill has been made, and thus lose control of food resources (Cooper, 1991; Fanshawe & Fitzgibbon, 1993), making solo hunting riskier and potentially less profitable than group hunting. However, hunting alone can attract less attention, and successful solo hunters may enjoy more time feeding on their prey before attracting competitors. For example, in the Maasai Mara, on average, 6 or more additional spotted hyenas were present at kills made by pairs within 10 minutes of a successful hunt, whereas hunting alone rarely attracted other hyenas (Smith et al., 2008). In our system, we did not include the potential for lost resources due to cheaters or kleptoparasites, but future studies could investigate the relationship between group size and losses due to competitors and how this tradeoff influences individuals' decisions.

CONCLUSIONS

We conducted a digital evolution experiment to investigate mechanisms promoting group hunting in a social system where reward from cooperative hunting is unequally distributed. Although this experiment presents a simplified model of a spotted hyena social system, it demonstrates the utility of agent-based digital evolution in examining complex evolutionary and behavioral dynamics across time scales and ranges of variables that are difficult or impossible to study in natural systems. This method also allows us to manipulate variables and track fitness outcomes to extents that are difficult or impossible to do with living animals. For example, our simulations ran for 1,000,000 updates which approximated roughly 20,000-50,000 generations, representing a time scale that would be impossible to measure in extant long-lived organisms. In this system, we manipulated how rewards were divided among group hunters and the per capita reward agents received from hunting based on hunting strategy, group size, and social rank. In natural systems, observers are limited to natural-occurring behaviors and cannot experimentally manipulate factors this precisely or across these ranges. Thus, digital evolution offers a powerful complement to empirical and theoretical work. In these experiments, we considered the effect of tolerance of the reward from group hunting. However, many other factors can influence the evolution and stability of group hunting such as communication, potential to cheat and punish cheaters, group size, role/effort in hunt, learned behaviors, kin selection, and partner choice (Brosnan & de Waal, 2014; Campbell et al., 2020). Thus, we close with the caveat that other factors merit investigation in future research to elucidate effects of other social and ecological variables. We suggest that doing so will further our understanding of the evolution of group hunting and of cooperative behavior more broadly.

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FIGURES

Figure 1.1. Setup of groups for hunting games and possible offspring agent locations. (A) N1 (black squares) is the location of a single agent. Grey squares represent the neighboring agents that N1 will play the 5 hunting games with during each world update. (B) The locations (grey squares) labeled with * show the possible offspring locations for a parent at location N1 (black square), as we assume offspring remain closer to their parent than do unrelated hyenas. Offspring replace the agent at their location, effectively killing off that agent.

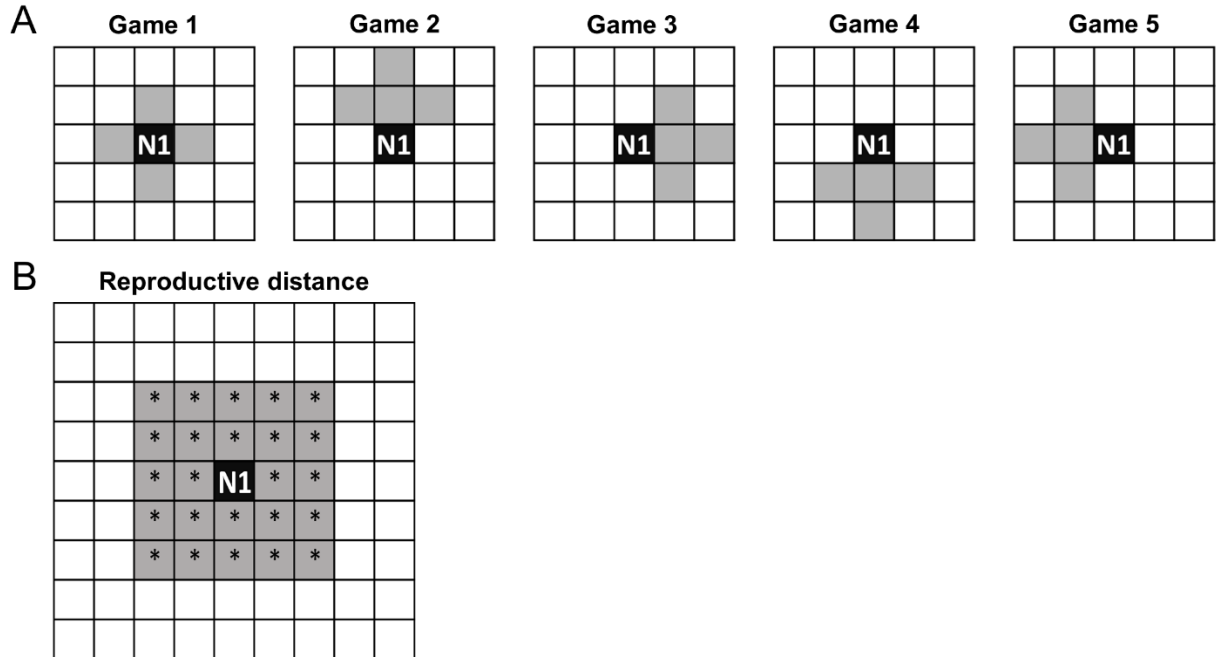


Figure 1.2. Per capita payoffs under different experimental conditions. Payoff scheme agents received for group hunting and solo hunting under different tolerance conditions (when the group-hunting payoff is 2 times the per capita payoff from solo hunting). Agents hunted in groups with four other agents and each agent decided whether to group hunt (i.e., hunt for large prey and share the reward with other agents that choose to group hunt) or solo hunt (i.e., hunt for small prey and the agent gets a smaller reward that is not shared). If an agent chose to group hunt, the payoff it received depended on its relative rank among other group hunters, the tolerance value, and how many other agents chose to group hunt. Agents received equal shares of the group-hunting payoff when tolerance = 1. As tolerance decreased, the payoff was increasingly skewed by dominance rank, with the highest-ranking agent receiving a greater proportion of the payoff. Agents received the same payoff from solo hunting regardless of rank under all tolerance conditions.

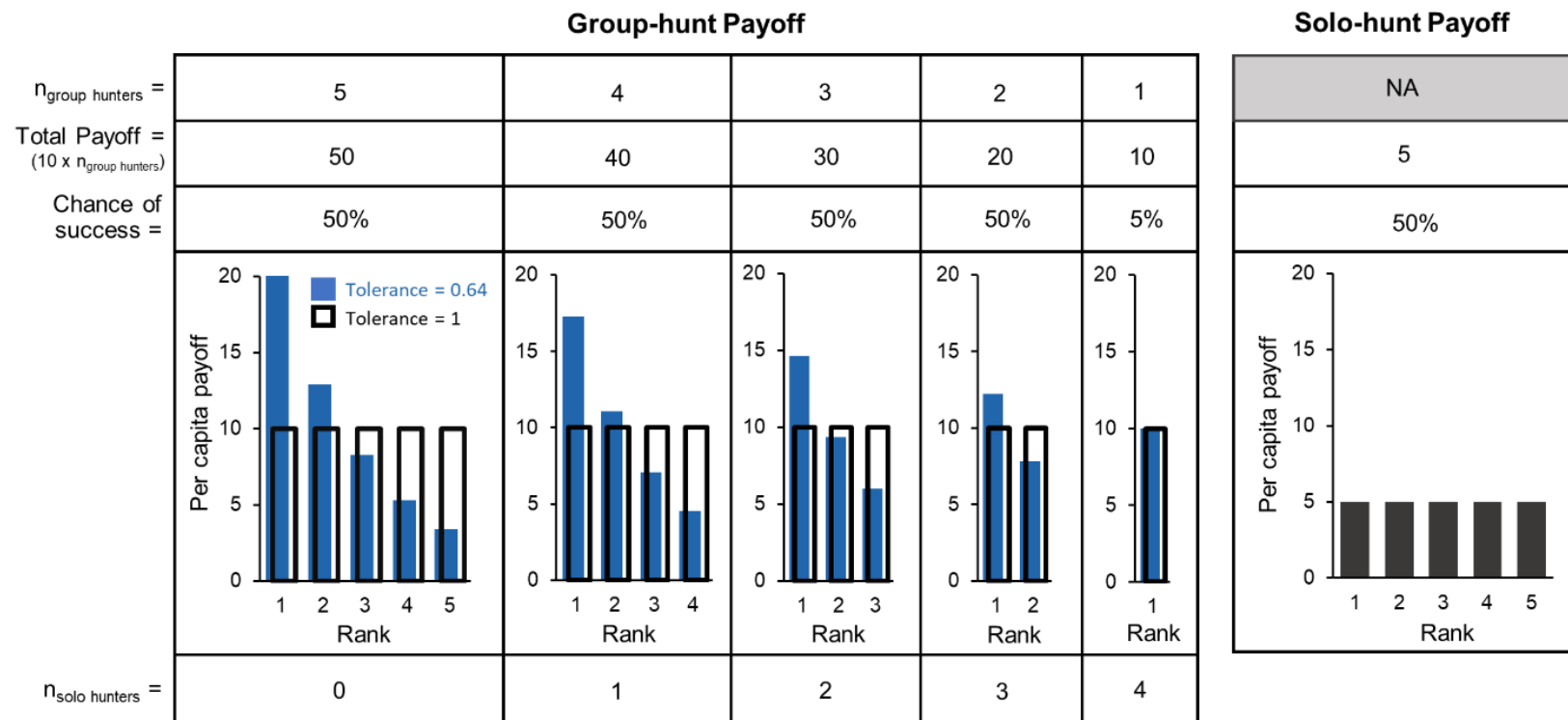
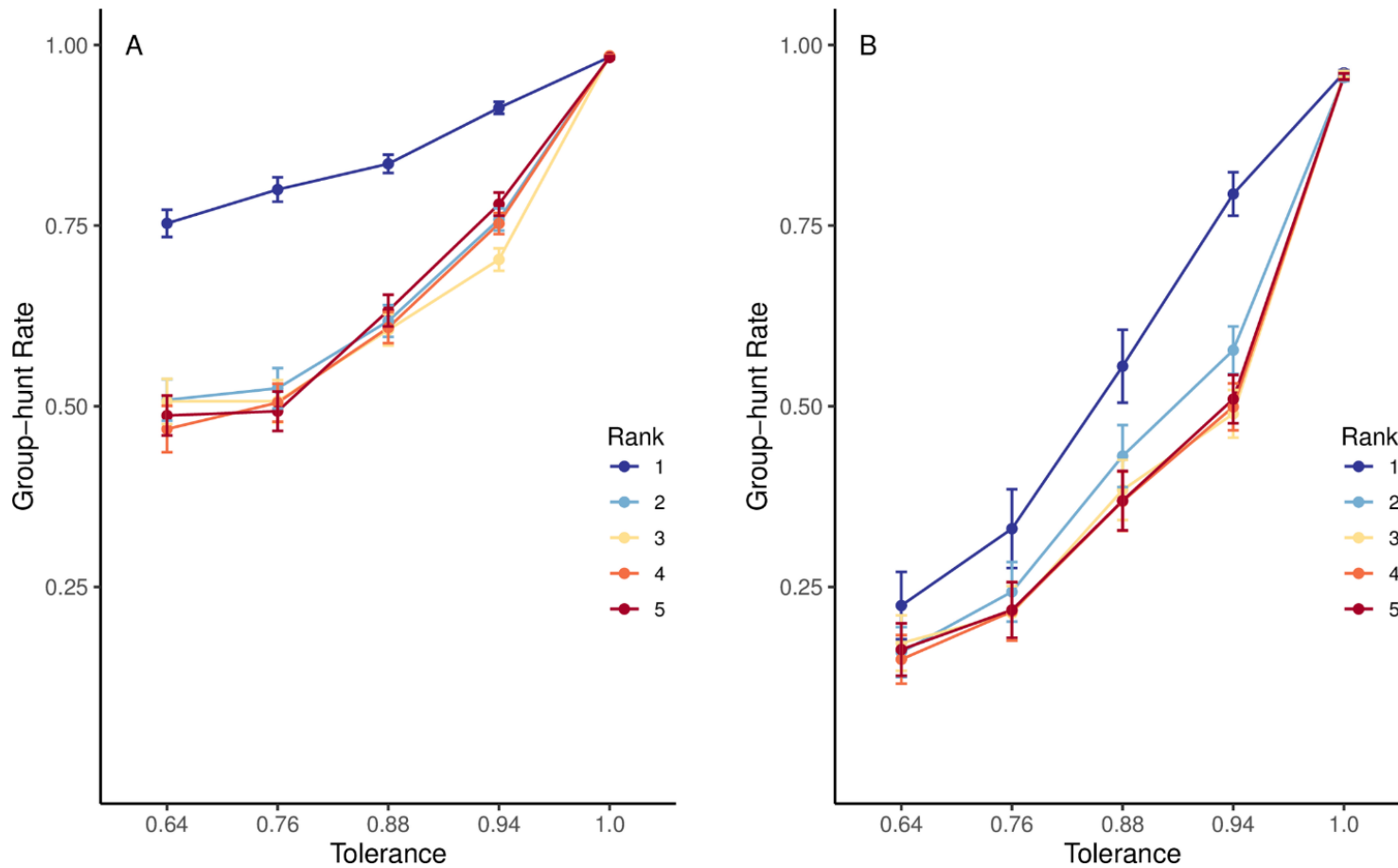


Figure 1.3. Group-hunting rates under varying tolerance conditions. The average rate of group hunting in the agent population across different tolerance levels when the group-hunting payoff is (A): 2 times the solo-hunt payoff per capita and (B): 1.2 times the solo-hunt payoff per capita. Tolerance determined how equally the reward from group hunting was shared (i.e., 1 = shared equally, 0.64 = each agent gets 64% of the reward as the agent with the rank immediately above it). Each point represents the average group-hunting rate of the agents in their respective relative rank positions within hunting subgroups (e.g., rank 1 = highest ranking agent in the subgroup). Each tolerance condition was run for 1,000,000 updates (sampled every 1,000 updates), plots represent the mean of the last 100,000 updates (n=101 samples) averaged across 200 replicates per condition. Bars represent ± 2 standard errors of the mean group-hunting rates among agents of each relative rank across each tolerance condition.



CHAPTER 2:
THE INFLUENCE OF INDIVIDUAL ATTRIBUTES ON THE HUNTING BEHAVIOR OF SPOTTED
HYENAS

ABSTRACT

Hunting behavior represents a critical component of predator-prey dynamics and exerts important influences on survival and reproduction of predators. Attributes of both predators and prey affect prey selection and hunting success and are important to consider in predation studies. Among social carnivores, group hunting is common and individual attributes such as social dominance rank, age, and sex can strongly influence access to shared rewards from hunting. In this chapter, we investigated how attributes of hunters and prey influence hunting behavior in the spotted hyena, a social carnivore that lives in fission-fusion societies that hunts both alone and with groupmates. Spotted hyena societies have linear dominance hierarchies, where priority of access is determined by social rank, and individual benefits from group hunting vary based on rank. We investigated how prey attributes and hunting strategy influence hunting success. We then asked how prey selection influences hunting group sizes, and how individual attributes of hunters impact solo hunt success and group hunting behavior. We compared these results from 1996-2018 to previous research on hyenas in this same region from 1988-1995, a period when there was less human activity, smaller hyena clan sizes, and higher prey abundance. We show that hunting success varied based on prey species, prey age class, and hunter age class. Hyena hunting strategies varied by prey species. Hyenas tended to hunt in larger groups for more difficult to hunt prey species (i.e., prey species with which hunters had lower hunting success rates). Hunting behavior also varied among individual hyena attributes, with low-ranking hyenas hunting in smaller groups than high-ranking individuals. Juveniles tended to hunt in larger groups than adults. Differences in these strategies reflect tradeoffs experienced by individual hunters – low-ranking individuals experienced higher competition in groups, and juveniles had lower odds of hunting success when

they hunted alone. We observed more group hunting from 1996-2018 than in previous years (1988-1995), and more observations of hyenas hunting more difficult to capture prey. These differences may be due to the larger clan size during our study period and declines of easier to capture prey. We demonstrate that attributes of predators and their prey exert influences on hunt success and hunt grouping behavior in spotted hyenas. We also show that hunting behavior can change in a population through time, which may be in response to demographic and ecological changes. Future work investigating how predator and prey attributes affect hunting behavior in other systems and how these dynamics may change over time will increase our understanding of the relationship between predator-prey dynamics and broader ecosystem processes.

INTRODUCTION

Predator-prey dynamics have profound consequences for ecosystem processes, community structure, food web dynamics, and for the demography and life history of prey animals, which in turn shape future predator-prey dynamics (Beschta & Ripple, 2009; Lima, 1998). Predators, particularly apex predators like large carnivores, play an especially important role in shaping communities through top-down effects via their choices of which prey species to target, and effects of predation risk on behavioral decisions made by prey animals (Creel & Christianson, 2008; Fryxell & Lundberg, 1994; Lima & Dill, 1990). Thus, hunting behavior represents a critical component of predator-prey dynamics. Hunting behavior also plays a foundational role in the lives of large carnivores, exerting important influences on their survival and reproduction. Hunting decisions, including prey selection and whether to hunt with groupmates affect hunting success and ultimately fitness.

Predator and prey attributes are important to consider in predation studies. For example, prey attributes such as age, sex, body condition, and personality can influence risk of predation (Aanes & Andersen, 1996; Fitzgibbon, 1990a&b; Murray, 2002; Réale & Festa-Bianchet, 2003). Hunting success rates and prey selection by predators also vary with prey species, sex, and age class

(Fitzgibbon, 1990b; Hilborn et al., 2012; Holekamp et al., 1997b; Höner et al., 2002; Karanth & Sunquist, 1995; Stander & Albon, 1993). Factors that influence hunting success may be highly dynamic; they are often influenced by ecological, social, and physical attributes of the species within the prey community, and may also vary with attributes of the hunters themselves (Pettorelli et al., 2015). Individual attributes of hunters, such as age, sex, and social status (Cooper et al., 2007; Litvaitis et al., 1986; Ross et al., 1997; Saulitis et al., 2000) influence hunting behavior and rates of hunting success. For example, research on bottlenose dolphins demonstrated that females had more variable diets than males, whereas males were more specialized predators (Rossman et al., 2015). Stander (1992) found that stalker roles played by lionesses during hunts varied with their morphology; slower, more heavyset lions typically assumed prey-catcher positions during hunts whereas slimmer, faster individuals functioned more often as chasers of prey, herding them toward catchers. Hunting is dangerous and requires practice and, as a result, young hunters tend to be less successful than mature adults (Caro, 1994; Hayward et al., 2007; Holekamp et al., 1997b). Across species and environments, clearly individual characteristics of the predator-prey dyad critically affects hunting success.

Group hunting, which is common among social carnivores (Bailey et al., 2013), introduces additional factors that impact both hunting success and individual fitness. While social carnivores have an enhanced ability to capture prey by hunting cooperatively (Fanshawe & Fitzgibbon, 1993; Stander & Albon, 1993), and defending prey against kleptoparasites (Creel & Creel, 1995; Périquet et al., 2015), they are also surrounded by conspecific competitors, which are their groupmates (Smith et al., 2008). As a result, both attributes of individual participants in a hunt (e.g., age, sex, dominance rank) as well as characteristics of the group (e.g., hunting party size, composition) impact individual success. For example, in carnivore societies structured by social rank, competitive ability and access to food at carcasses is not equal among individuals (Atwood & Gese, 2008; Gese et al., 1996b; Smith et al., 2008; Tilson & Hamilton, 1984). For a hunt to be successful for an individual

predator, the per capita energy intake must outweigh the energetic demands associated with prey capture and defense (Macarthur & Pianka, 1966). Although group hunting has been shown to increase hunt success and allow hunters to capture much larger prey than they could alone (Creel & Creel, 2002; Packer, 2023), the per capita benefit for low-ranking individuals may fail to outweigh the cost of inadequate nutritional gain from the kill (Holekamp & Dloniak, 2010).

Here, we use long-term behavioral data to investigate hunting patterns of spotted hyenas (*Crocuta crocuta*) and inquire how individual prey and hunter attributes influence hunting success in the Maasai Mara National Reserve, Kenya. Spotted hyenas are social carnivores that inhabit a wide range of habitats, including landscapes with diverse, seasonally variable prey bases (Kruuk, 1972; Trinkel et al., 2004). Spotted hyenas are effective hunters and most of their food is acquired through active hunting rather than scavenging (Cooper, 1990; Holekamp & Dloniak, 2010; Kruuk, 1972). Cursorial hunters who run their prey to exhaustion, spotted hyenas hunt both alone and in groups (Kruuk, 1975; Mills & Harvey, 2001). Previous work has demonstrated that hyenas cooperate to hunt in groups to take down prey much larger than themselves (Kruuk, 1975; Holekamp et al., 1997b, Hofer & East, 1993), and to defend carcasses against kleptoparasitism from lions (Lehmann & Montgomery et al., 2017). Hyena societies are structured by linear dominance hierarchies (Frank, 1986; Kruuk, 1972; Tilson & Hamilton, 1984), and dominance rank, age, and sex strongly influence hyena behavior and access to resources. High-ranking individuals have preferential access to these critical resources (Engh et al., 2000; Smith et al., 2008), and they enjoy greater fitness than their low-ranking peers (Frank, 1986; Holekamp et al., 1996; Tilson & Hamilton, 1984). Our long-term study of spotted hyenas allows an assessment of temporal variation in hunting behavior as ecological conditions change.

Using a long-term dataset gathered from a single clan of hyenas across 23 years, we first describe typical prey items and hunting scenarios for this clan of hyenas. We then examine predictors of hunting success, and model how prey attributes, predator attributes, and hunting

strategy (group vs. solo) influenced success of a given hunt. Next, we investigated predictors of hyena hunting strategy, including how prey and hunter attributes affect hunting group size. Finally, we compared our findings to previous work on hunting by hyenas from the same clan (Holekamp et al., 1997b) when the surrounding human population density was lower and ecological conditions were different from those documented more recently.

METHODS

Study site

We conducted this study in the Maasai Mara National Reserve, Kenya (henceforth “the Mara”). The Mara is a tropical savanna, primarily composed of rolling grasslands dotted with trees and riverine habitats (Sinclair & Norton-Griffiths, 1979). Precipitation follows a bimodal pattern annually, with most precipitation occurring in November–December and March–May (Green et al., 2019b; Ogotu et al., 2008). Prey availability also varies seasonally in the Mara. A diverse community of large herbivores are present year-round, and for a portion of the year (June – November), large migratory herds of wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) occupy the Mara (Bell, 1971; Craft et al., 2015; Sinclair & Norton-Griffiths, 1979). We followed one study clan, the Talek Clan, inhabiting the region near the north-eastern border of the Reserve, near the town of Talek (Fig 2.1). This clan has been under continuous observation since June 1988.

Hyena hunting behavior

Field observers collected behavioral data during twice-daily observation periods from ~0500-0830 h and again from ~1630-2000 h. Observation sessions (hereafter “sessions”) were initiated when observers encountered one or more hyenas separated from other hyenas by at least 200 m. A session ended when interactions among hyenas ceased and observers left the individual or group, or when observers lost sight of the hyenas (Lehmann et al., 2017); session duration was recorded in minutes, lasting from five minutes to several hours. Observers recorded all instances of observed hyena hunting behavior during observation sessions. Field observers followed the

definition used by Kruuk (1972) and Holekamp et al. (1997b) to classify hunting behavior - “a chase by one or more hyenas of a selected prey animal that covered at least 50 m” (Holekamp et al., 1997b, p. 3). If the chase ended in prey capture, the hunt was classified as successful. If the end of the hunt was not observed (e.g., due to darkness, hyenas running into vegetation), the hunt outcome was classified as unknown. Hyenas often “test chase” prey before attempting to hunt (Kruuk, 1972). Field observers considered test chases to be slower-paced chases that were shorter than 50 m or short rushes towards groups of prey that were not followed by longer, faster chases of a single prey animal (Holekamp et al., 1997b; Kruuk, 1972); test chases were not included in our analyses.

For each hunting attempt, field observers recorded the date, time, prey species and age class (juvenile or adult), identities of individual hyenas that participated in the hunt, and outcome of the hunt (i.e., success, fail, or unknown). Prey animals were considered adults unless observers indicated prey animal was a juvenile. Prey listed as infant, newborn, young, juvenile, or subadult were considered juvenile. For each identifiable hyena involved in each hunt, field observers assigned age, sex, and dominance rank using data collected from long-term behavioral observations. Yearly dominance rank was calculated using the outcomes of dyadic agonistic interactions via methods described in (Strauss & Holekamp, 2019). Ranks were calculated separately for natal individuals and immigrant males, then combined such that immigrants ranked below all natal individuals. We used the standardized dominance rank for individual hyenas during the year in which hunting was observed for analyses involving social rank. Hyenas less than three years of age were defined as juveniles, and individuals three years or older adults (Holekamp et al., 1997b).

We analyzed observations of hyena hunting behavior from January 1996 – December 2018. We excluded hunting attempts classified as unknown, and those for which the prey animal was not an ungulate (Rodentia, n=2; Tubulidentata, n=1), was domestic livestock (because observers intervened, when possible, to prevent livestock loss; n=3), or was unknown (n=1). Because the number of hyenas participating in a hunt often changes during a hunt (Kruuk, 1972), we used

number of hyenas present at the end of the hunt as hunting group size (Holekamp et al., 1997b), and we assumed all hunters listed in each hunting record were present until the end of the hunt. We designated each hunt as a “solo hunt” or a “group hunt” to look at the effect of hunting alone or in a group for some analyses. Hunting records with one or more unidentified hyenas were only included in analyses of solo versus group hunting, not hunting group size. For these analyses, we included hunts with unidentified group numbers because we could assign these hunts as group hunts.

Data analysis & software

First, we summarized total attempted and successful hunts by prey species, and summarized solo and group hunts by hunter age, sex, and rank. We then quantified hunting success for prey species with > 9 observed hunts and fit a generalized linear model to investigate how hunting success varied with prey species, prey age, and hunting strategy. The outcome variable was whether or not the hunt was successful (binomial distribution), and the predictor variables were prey species, prey age class (adult or juvenile), and hunting strategy (solo or group hunt). We conducted pairwise post hoc tests among species pairs to test for differences in hunting success rates. To test for evidence of temporal autocorrelation, we ran a generalized linear mixed model which included the same outcome and predictor variables in the previous model, and added two additional predictor variables: (1) Julian date as a quadratic term to account for seasonal variation in prey availability, and (2) observation session as a random variable to account for both repeated measures of the hunts observed within the same session and any unmeasured variability individual observation sessions might possess. We then focused on the top two prey species, Thomson’s gazelle (*Eudorcas thomsoni*) and wildebeest, and investigated how prey age class, hunt type (solo or group), and the interaction between these variables influenced hunt success. We ran separate models for Thomson’s gazelles and wildebeests.

We then examined whether hunter attributes influenced solo hunting success by fitting a generalized linear mixed model. The outcome variable was hunting success (or not; binomial

distribution), and predictor variables were hunter age class (adult or juvenile), sex, and standardized dominance rank, and prey age class (adult or juvenile). We included individual identity as a random effect to account for repeated measures of the same individual over time and any unmeasured variability among individual hunters. For this model, we included hunts of any identifiable prey type that was not domestic livestock.

Next, we investigated how hunting group size varied by prey species and hunter attributes. We first tested whether mean hunting group size varied for the top six prey species using a Kruskal-Wallis test and a Dunn post hoc test with Bonferroni correction to assess species pairwise comparisons. Next, we fit a generalized linear model to determine whether hunt type (solo or group) varied across prey species and age class for the top six prey species. The outcome variable was whether the hunt was a group hunt (or not; binomial distribution), and predictor variables were prey species and prey age class (adult or juvenile). We next ran a post hoc test to assess pairwise differences. We also tested whether mean hunting group size varied by hunter age class, sex, and rank using a Kruskal-Wallis test. To compare across ranks, we assigned standardized ranks to quartiles (low, mid-low, mid-high, and high), and used a Dunn post hoc test with Bonferroni correction to test rank quartile pairwise comparisons.

We performed all analyses using R version 4.3.3 (R Core Team, 2024) in RStudio version 2023.12.1.402 (Posit team, 2024). We used the 'lme4' package version 1.1-35.2 (Bates et al., 2015) to fit all models, and the 'performance' package version 0.11.0 (Lüdtke et al., 2021) to test for collinearity among predictor variables. We used the 'emmeans' package version 1.8.5 (Lenth, 2023) to run pairwise post hoc tests to assess differences in hunting success and group sizes between each prey species. We only included predictors that had a variance inflation factor < 5. We used the 'asbio' package version 1.9-7 (Aho, 2024) to run the Dunn post hoc test for multiple pairwise comparisons for the Kruskal-Wallis test. We used 'tidyr' version 1.3.1 (Wickham et al., 2024), 'dplyr' version 1.1.4 (Wickham et al., 2023), 'lubridate' version 1.9.2 (Grolemund & Wickham, 2011), and

‘stringr’ version 1.5.1 (Wickham, 2023) packages to manipulate and summarize data in R. We used ‘ggplot2’ version 3.5.0 (Wickham, 2016), ‘sjPlot’ version 2.8.14 (Lüdecke, 2023), ‘ggpubr’ version 0.6.0 (Kassambara, 2023), and ‘gridExtra’ version 2.3 (Auguie, 2017) to visualize data. We created the study area map using ArcGIS Pro (ESRI, 2021).

RESULTS

General hunting summary

Field observers documented 302 hunts by members of the hyena clan, of which 272 hunts had known outcomes (Table 2.1). Field observers identified 221 hyenas in 250 hunts (107 female, 114 male). Of the 272 hunts with known outcomes, 120 were group hunts and 152 were solo hunts. Thomson’s gazelle was the most common prey species, followed by wildebeest and zebra (Table 2.1). Field observers could determine hunting group size for 263 hunts; the mean hunting group size was 2.3 (SE=0.15) hyenas. Adults made up the majority of solo hunters, while juveniles made up a larger proportion of group hunters (Table 2.2). Females made up a larger portion of observed solo and group hunters than males, and the mean rank of group hunters was higher than that of solo hunters (Table 2.2).

Hunting success

Prey attributes: Hunting success varied among prey species, with highest success observed for Thomson’s gazelle, wildebeest, and impala, and lowest success observed for warthog, topi, and zebra (Fig 2.2). From the generalized linear model, predicted probabilities of hunting success, irrespective of hunting type or prey age, were highest for Thomson’s gazelle and wildebeest, and lowest for warthog (Table 2.3). In pairwise post hoc tests, the probability of success was higher for Thomson’s gazelle than warthogs (Odds Ratio=10.51, SE=11.85, $p = 0.04$), topi (Odds Ratio=3.92, SE=2.45, $p=0.03$), or zebra (Odds Ratio=3.43, SE=2.09, $p=0.04$). Hyenas also had better odds of success when hunting wildebeest than warthogs (Odds Ratio=0.10, SE=0.11, $p=0.04$) or topi (Odds Ratio=0.27, SE=0.18, $p=0.04$). Hyenas had better chances of success hunting juvenile than adult

prey in our model including all top 6 prey species (Table 2.4). For all top prey species, group hunting did not significantly increase the odds of success over solo hunting (Table 2.4). Julian date and observation session (as a random variable) did not influence hunting success in the model results (Table S1), and thus were not included in our final model.

When hunting Thomson's gazelles, group hunting affected hunt success for adult prey but not juvenile prey (Table 2.5a). In addition, in pairwise post hoc tests, the probability of successfully hunting a juvenile Thomson's gazelle did not differ significantly when comparing solo with group hunts (Odds ratio=1.389, SE=0.880, $p=0.604$). However, group hunting significantly increased hunting success for adult Thomson's gazelles (Odds ratio=0.165, SE=0.113, $p=0.008$) (Fig 2.3). When hunting wildebeest, the interaction between prey age and hunt type was not significant (Table 2.5b). Hunting success for wildebeest did not differ significantly between solo and group hunts. Hyenas were more likely to capture juvenile wildebeest than adults (Fig 2.3).

Hyena attributes: In solo hunts, both hunter age class and prey age class influenced hunting success (Table 2.6). Juvenile hunters had lower odds of success than adults, and hyenas had higher odds of successfully hunting juvenile prey than adult prey (Fig 2.4). There was no significant effect of either hunter rank or sex on solo hunt success (Table 2.6).

Hunting group size

Prey attributes: Mean hunting group size varied across prey types (Kruskal-Wallis $\chi^2=72.32$, $p<0.001$), with the highest average hunting group sizes observed for warthogs and zebra (Fig 2.5). Our generalized linear model showed that the odds of group hunting compared to solo hunting also varied significantly with prey species, but not with prey age class; hyenas were more likely to hunt warthogs, wildebeest, and zebra in groups than they were to hunt Thomson's gazelles (Table 2.7). Prey age class did not significantly affect the likelihood of group hunting (Table 2.7).

When comparing mean hunting group size across prey types between this study and that of Holekamp et al. (1997b), we saw differences for Thomson's gazelles, topi, and zebra (Table 2.8).

Mean hunting group size was smaller for Thomson's gazelle and zebra and larger for topi in our study compared to Holekamp et al. (1997b). Furthermore, the relative proportion of hunts that were group hunts was larger for every top prey species in our study than in that of Holekamp et al. (1997b) (Table 2.8).

Hyena attributes: Mean hunting group size varied among rank quartiles (Kruskal-Wallis $\chi^2 = 50.02$, $p < 0.001$; Fig 2.6; $n = 524$). In post hoc tests of pairwise comparisons, low-ranking hyenas hunted on average in smaller groups than hyenas in the mid-high rank quartile (Dunn post hoc test; Diff = -82.11, $p < 0.001$). On average, low-ranking hyenas also hunted in smaller groups than high-ranking hyenas (Dunn post hoc test; Diff = -129.53, $p < 0.001$). Finally, hyenas in the mid-low rank quartile tended to hunt in smaller groups than high-ranking hyenas (Dunn post hoc test; Diff = -85.24, $p < 0.001$). Mean hunting group size also differed significantly between hunter age classes (Kruskal-Wallis $\chi^2 = 18.2$, $p < 0.001$; Fig 2.7; $n = 528$), with juveniles tending to hunt in larger groups than adults. Mean hunting group size did not differ significantly between males and females (Kruskal-Wallis $\chi^2 = 2.7$, $p = 0.1$; Fig 2.8; $n = 541$).

DISCUSSION

Characteristics of both prey and predator predicted hunting success and hunting group size. For spotted hyenas, we found that hunter age, prey species and prey age, influenced hunting success. Group hunting resulted in greater success when hyenas hunted adult Thomson's gazelle, but group hunting did not enhance success when considering all common prey species together. Finally, individual attributes of both hunter and prey influenced hunting group sizes. Specifically, both hunter age and social rank, and both prey species and prey age class, affected group size during hunts. Overall, our results lend support to previous work cautioning against oversimplifying predator-prey dynamics (Pettorelli et al., 2015) and add to our understanding of how hunting behavior varies with age and social rank.

Overall, the effects of prey species and prey age class on hunting success had significant impacts on hunting success. For example, hunting success was higher for juvenile prey than adult prey for all top prey species, as seen in other systems (lions, Hayward et al., 2007; cheetahs, Hilborn et al., 2012). Two of the most common prey species for hyenas in this study, topi and warthog, had no successful hunts for adult prey. We did not find that hunting with groupmates significantly improved hunting success over hunting alone when modeling all top prey species together. This may be because the effects of prey species and prey age class on hunting success were much larger than hunting group size. We did not have enough observed hunts per prey species, age class, or hunting group size to investigate interactions among these variables. As hyenas are more likely to hunt prey species with lower hunting success rates in groups than alone, and as juvenile prey are easier to capture than adults, these effects were difficult to disentangle with our small sample sizes. For example, of the 30 observed hunts for zebra, only four were solo hunts, and none of these solo hunts were successful. Of the 14 observed warthog hunts, only one was a solo hunt, which was unsuccessful.

For the most common prey species, Thomson's gazelle, hunting group size significantly affected hunting success, but only when hunting adults. Hyenas had more success hunting adult Thomson's gazelles with clan-mates than when hunting alone but hunting success for juveniles did not improve when hunts involved multiple clan-mates. This is most likely because hunting for juvenile gazelles usually involved a solitary hunter walking in zig-zag pattern upwind to flush resting juveniles out of hiding, and clan-mates only join hunts of juveniles after the fawn has been flushed. Surprisingly, for the second most common prey type, wildebeest, group hunting did not significantly improve hunting success for adults over hunting alone. Given this, we would expect to observe less group hunting for wildebeest, since the expected per capita benefit would be reduced in a group hunt, but we found that hyenas had almost equal odds of hunting wildebeest alone or in a group. The seasonal ecology of the Mara may influence rates of group hunting. This may be

especially the case for wildebeest, since they migrate into the Mara in massive herds. When masses of wildebeest are present, hyenas are the most gregarious (Smith et al., 2008). Therefore, group hunting may increase during this time in response to high prey density while, at the same time, attempting to hunt alone may become more difficult because of hyena gregariousness.

Juvenile hyenas were less likely than adults to capture prey when they hunted alone. This is consistent with previous findings on hyena development. Their skulls are not fully developed until ~35 months (Tanner et al., 2010), and it appears to take several years to learn how to become an effective hunter (Holekamp et al., 1997b). Neither sex nor dominance rank had a significant influence on hunting success, which is consistent with Holekamp et al. (1997b). We did not have the sample size to investigate whether prey selection varied with hunter attributes, but hunter age and dominance rank may influence which prey hyenas attempt to hunt alone. Younger hyenas may choose smaller, non-ungulate prey that are easier to capture (Holekamp et al., 1997b; Mills, 1990). Since lower-ranking individuals face greater competition when feeding in groups, they may benefit more from selecting smaller prey, that is relatively easier to capture, and that they can quickly consume, to avoid attracting competitors.

Consistent with previous hunting studies (Kruuk 1972; Holekamp et al., 1997b; Trinkel, 2010), hyenas hunted more difficult prey (those with low rates of successful capture) in larger groups than they did for prey that yielded higher success. Hunting group size varied not only with attributes of prey, but also with those of the hunters themselves. Lower-ranking hyenas hunted in smaller groups than high-ranking hyenas, and juveniles hunted in larger groups than adults, consistent with results obtained by Holekamp et al. (1997b). Since juvenile hyenas are less effective hunters, they benefit more by joining clan-mates when hunting. The larger mean hunting group sizes we observed among high-ranking individuals may reflect the fact that high-ranking individuals can easily usurp food from their clan-mates, so there is little cost for them to hunt with others. In addition, high-ranking females enjoy higher reproductive success than their lower-ranking peers,

and thus have more relatives as potential hunting partners (Holekamp et al., 1997b). Furthermore, since low-ranking hyenas face greater risks of losing during feeding competition (Smith et al., 2008), low-ranking hyenas benefit less from group hunting, particularly when group-hunting does not improve the odds of prey capture over solo hunting. Earlier work revealed that low-ranking hyenas spend more time alone (Smith et al., 2008), and range farther from communal dens than do high-ranking individuals (Boydston et al., 2003), and they also forage more outside of their clan territories (Höner et al., 2005). However, when females have young cubs, social rank does not influence their space use, they become central place foragers, and they have smaller home ranges, regardless of social rank (Boydston et al., 2003). Future work investigating how reproductive state influences hunting decision among females will provide more insight into the trade-offs faced by females with den-dependent cubs.

Thomson's gazelle and wildebeest made up the majority of the observed hunts from 1996-2018, which is consistent with previous results from 1988-1995 (Holekamp et al., 1997b). However, field observers saw fewer topi hunts and more hunts of challenging prey (e.g., warthog and buffalo) in our study than did Holekamp et al. (1997b) in their earlier study of this same hyena clan. Specifically, we saw 14 warthog hunts (making them the 6th most popular prey species) and five buffalo hunts, whereas Holekamp et al. (1997b) saw only one of each. These changes may reflect the declines of resident prey species in the Talek Region since the early 1990s (Chapter 3, Green, 2015; Ogutu et al., 2005, 2009, 2011; Ottichilo et al., 2000). In Tanzania, long-term declines in easier to capture prey availability caused hyenas to consume more buffalo calves and adult wildebeest, which were more difficult to capture (Höner et al., 2002).

The overall mean hunting group size of our study was larger (2.3 hunters), than the mean hunting group size reported by Holekamp et al. (1997b) (1.5 hunters). When comparing mean hunting group sizes by species, we found that hyenas hunted Thomson's gazelle and zebra in smaller groups than they did in the late 1980s and early 1990s (as reported in Holekamp et al.,

1997b), but the group sizes in which they hunted topi increased between these same periods. These differences may be due to small sample size, particularly for zebra and topi. We cannot directly compare characteristics of groups hunting warthogs since Holekamp et al. (1997b) observed only one warthog hunt.

While solo hunts constituted the majority of hunts during both time periods, Holekamp et al. (1997b) reported a higher percentage of solo hunts (76%) than we did (56%). When comparing species, Holekamp et al. (1997b) found that zebras were the only species hunted more often in groups than by solitary hyenas. We found that zebra and warthogs were both hunted more often in groups, and the relative proportion of hunts that were group hunts increased for every species, with the most drastic increases for wildebeest, topi, and zebra. This may reflect the larger clan sizes found during our study period than during the late 1980s and early 1990s; when hyena population density is higher, it may be more difficult to separate from clan-mates such that it becomes more difficult to hunt alone.

Despite equivalent sampling effort intensities across the two study periods, field observers documented 275 hunts with known outcomes across 23 years, whereas Holekamp et al. (1997b) observed 272 hunts in just 7.5 years. This decrease in the frequency of observed hunts may reflect the greater nocturnality of hyenas in recent years due to higher pastoralist population density and increased human activity along the edge of the Reserve (Kolowski et al., 2007). Field observers were not able to observe hunts before dawn or past dusk in the current study. Globally, animals – especially apex carnivores – are responding to anthropogenic disturbance by becoming increasingly nocturnal, (Gaynor et al., 2018), and these responses to anthropogenic change can vary due to individual attributes (Hertel et al., 2017; Kolowski et al., 2007; Nevin & Gilbert, 2005). Changing activity patterns can also make prey more susceptible to predation and alter prey selection by predators, which can alter population dynamics (Brook et al., 2012; Kilgo et al., 1998; Ordiz et al., 2017).

Overall, the temporal changes we observed in hunting behavior may reflect changes in the ecology of the Talek Region. Prey populations have declined, (Ogutu et al., 2005, 2009, 2011; Ottichilo et al., 2000), temperatures have risen, and rainfall patterns have become more variable, including more periods of drought and extreme rainfall (Green et al., 2019b; Ogutu et al., 2007). Human activity and livestock grazing pressure in the Talek Region has increased during this time as well, altering habitat characteristics and herbivore grouping and populations (Green et al., 2018). Concurrent with these ecological changes, hyena populations have grown larger along the edge of the reserve, evidently in response to the decreasing lion population in this area and supplemental food in the form of livestock left behind in the Reserve unattended (Green et al., 2018). Future work comparing hunting success and prey selection between day and night would further improve our understanding of hyena foraging behavior and, more broadly, of predator-prey dynamics, particularly in systems modified by human activity.

We used observational data documenting hunting attempts in this study. These events are rare and extremely difficult to observe directly in large carnivores. For the species and environments where hunting can be observed, hunt observations are biased towards the times of day, habitats, and prey sizes where events can be most easily seen. This introduces the potential to over- and under-estimate the importance of different prey types in their diet. However, observational studies do not require invasive methods. GPS technology has greatly improved predation studies (Elbroch et al., 2018) and has been applied to a wide range of species (e.g., Miller et al., 2013; Pitman et al., 2014; Svoboda et al., 2013; Tambling et al., 2010), allowing observers to detect kill sites without direct observational methods. However, this method is expensive, requires invasive methods, and is constrained by the battery life of devices; investigators using GPS technology must balance the amount information collected gain against battery life. A combination of observational and GPS data could improve our understanding of carnivore hunting behavior at

short and long temporal scales, and improve parameter estimates for the effects of social and environmental variables on hunt success.

Together, these results demonstrate how hunting behavior and success can be influenced by traits of prey and predators and can change over time. Moreover, the changes in hunting behavior documented here reflect ecological changes in the region and demographic changes in the hyena population during this time period. Future work in other systems investigating how predator and prey attributes affect hunting behavior and how these dynamics may change over time, due to fluctuations in both predator and prey populations and in ecological factors, will increase our understanding of the relationship between predator-prey dynamics and broader ecosystem processes and community ecology.

TABLES

Table 2.1. Summary of observed ungulate hunting attempts by hyenas in the Talek clan with known outcomes, Jan 1996 – Dec 2018, Maasai Mara, Kenya.

Prey type	Genus species	Solo hunts			Group hunts		
		Total	Success	% Success	Total	Success	% Success
Thomson's gazelle	<i>Eudorcas thomsoni</i>	80	34	42.5	28	17	60.7
Blue wildebeest	<i>Connochaetes taurinus</i>	41	17	41.5	35	15	42.9
Topi	<i>Damaliscus lunatus</i>	10	3	30.0	7	2	28.6
Impala	<i>Aepyceros melampus</i>	9	4	44.4	6	3	50.0
Plains zebra	<i>Equus quagga</i>	4	0	0.0	26	5	19.2
Grant's gazelle	<i>Nanger granti</i>	2	1	50.0	0	0	-
Warthog	<i>Phacochoerus africanus</i>	1	0	0.0	13	1	7.7
African buffalo	<i>Syncerus caffer</i>	1	0	0.0	4	1	25.0
Kirk's Dikdik	<i>Madoqua kirkii</i>	1	0	0.0	0	0	-
Duiker	<i>Sylvicapra grimmia</i>	1	0	0.0	0	0	-
Eland	<i>Taurotragus oryx</i>	1	0	0.0	0	0	-
Waterbuck	<i>Kobus ellipsiprymnus</i>	1	0	0.0	0	0	-
Reedbuck	<i>Redunca redunca</i>	0	0	-	1	0	0.0

Table 2.2. Hyena age class, sex, and rank by solo and group hunts observed for the Talek clan, Maasai Mara, Kenya, January 1996 – December 2018.

	Solo hunts	Group hunts
% juvenile	20.1%	56.0%
% adult	78.1%	44.0%
% female	52.9%	62.2%
% male	47.1%	37.8%
mean rank ($\pm$ SE)	0.02 ($\pm$ 0.05)	0.40 ($\pm$ 0.03)

Table 2.3. Results from generalized linear model of the effects of hunt strategy (solo vs. group), prey age, and prey species on the probability of hunt success. Prey species are compared to Thomson's gazelle as the reference level. Group hunting (2 or more hunters) is compared to solo hunting. Juvenile prey are compared to adult prey. Odds ratios > 1 indicate increased odds of hunt success based on that respective predictor, while odds ratios < 1 indicate decreased odds of hunting successfully.

<i>Predictors</i>	<i>Odds Ratios</i>	<i>CI</i>	<i>p</i>
Group hunt	1.6	0.85 – 3.05	0.144
Juvenile prey	7.41	4.07 – 13.94	<0.001
Impala	0.41	0.12 – 1.34	0.137
Warthog	0.1	0.00 – 0.61	0.037
Topi	0.26	0.07 – 0.83	0.029
Wildebeest	0.94	0.47 – 1.87	0.86
Zebra	0.29	0.08 – 0.91	0.043
Observations	260		

Table 2.4. Predicted probability of hunting success for each prey species, averaged across group and solo hunts and adult and juvenile prey.

Prey species	Probability of success	SE	Asymptotic lower CL	Asymptotic upper CL
Thomson's gazelle	0.50	0.06	0.39	0.62
Impala	0.29	0.12	0.12	0.55
Warthog	0.09	0.09	0.01	0.45
Topi	0.21	0.09	0.08	0.45
Wildebeest	0.49	0.07	0.36	0.62
Zebra	0.23	0.10	0.09	0.46

Table 2.5. Results from generalized linear model of the effects of hunt type, prey age, and the interaction between hunt type and prey age on the probability of hunt success for (a) Thomson's gazelle and (b) wildebeest. Group hunting (2 or more hunters) is compared to solo hunting. Juvenile prey are compared to adult prey. Odds ratios > 1 indicate increased odds of hunt success based on that respective predictor, while odds ratios < 1 indicate decreased odds of hunting successfully.

(a) Thomson's gazelle

<i>Predictors</i>	<i>Odds Ratios</i>	<i>CI</i>	<i>p</i>
Group hunt	6.04	1.64 – 24.67	0.008
Juvenile prey	7.87	2.98 – 22.58	<0.001
Group hunt x juvenile prey	0.12	0.02 – 0.73	0.022
Observations	108		

(b) Wildebeest

<i>Predictors</i>	<i>Odds Ratios</i>	<i>CI</i>	<i>p</i>
Group hunt	0.83	0.21 – 3.23	0.791
Juvenile prey	6.97	1.82 – 30.86	0.007
Group hunt x juvenile prey	5.45	0.46 – 142.41	0.214
Observations	76		

Table 2.6. Results from generalized linear model of the effects of hunter age class, sex, dominance rank, and prey age on the probability of successfully solo hunting. Juvenile hunters are compared to adult hunters. Male hunters and compared to female hunters. Juvenile prey are compared to adult prey. Odds ratios > 1 indicate increased odds of hunt success based on that respective predictor, while odds ratios < 1 indicate decreased odds of hunting successfully.

<i>Predictors</i>	<i>Odds Ratios</i>	<i>CI</i>	<i>p</i>
Hunter age (juvenile)	0.24	0.06 – 0.95	0.041
Hunter sex (male)	1.82	0.56 – 5.88	0.316
Standardized rank	0.8	0.30 – 2.15	0.656
Prey age (juvenile)	8.16	3.11 – 21.38	<0.001
Observations	129		

Table 2.7. Results from generalized linear model of the effects of prey age and prey species on the probability of group hunting. Prey species are compared to Thomson's gazelle as the reference level. Juvenile prey are compared to adult prey. Odds ratios > 1 indicate increased odds of group hunting that respective prey type or age class.

<i>Predictors</i>	<i>Odds Ratios</i>	<i>CI</i>	<i>p</i>
Juvenile prey	1.09	0.61 – 1.97	0.76
Impala	1.84	0.56 – 5.70	0.295
Warthog	38.34	7.05 – 716.22	0.001
Topi	1.97	0.66 – 5.66	0.21
Wildebeest	2.47	1.32 – 4.66	0.005
Zebra	19.18	6.63 – 70.55	<0.001
Observations	260		

Table 2.8. Mean hunting group sizes and percentage of hunts that were group hunts by prey species for this study and Holekamp et al. 1997b. This study includes hunting data from January 1996 – December 2018; Holekamp et al. 1997b includes hunting data from June 1988 – December 1995 in the Talek region of the Maasai Mara, Kenya.

Prey species	<i>This study</i>			<i>Holekamp et al. 1997b</i>		
	Mean hunting group size	SE	% group hunts	Mean hunting group size	SE	% group hunts
Thomson's gazelle	1.42	0.1	25.9%	2.08	0.1	20.3%
Impala	1.69	0.5	40.0%	1.7	0.3	25.0%
Warthog	4.07	0.5	92.9%	-	-	-
Topi	2.47	0.7	41.2%	1.2	0.1	6.3%
Wildebeest	2.15	0.2	46.1%	2.92	0.3	26.2%
Zebra	5.52	0.7	86.7%	9.1	0.5	68.4%

FIGURES

Figure 2.1

Maasai Mara National Reserve, Kenya, and estimated territory of Talek hyena clan that were observed for hunting behaviors, 1996 – 2018.

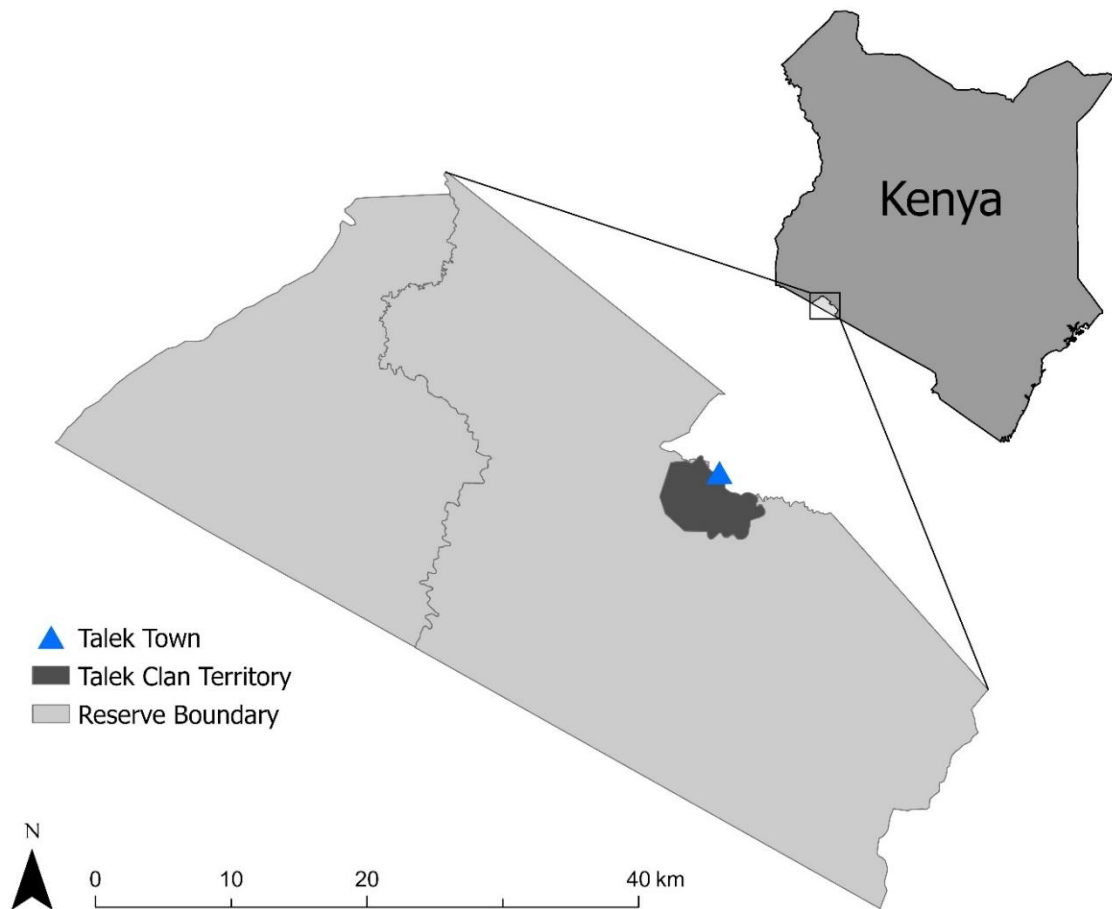


Figure 2.2. Proportion of successful hunts for top 6 prey species for Talek hyenas from January 1996 – December 2018. Species are organized from left to right by increasing mean adult body mass.

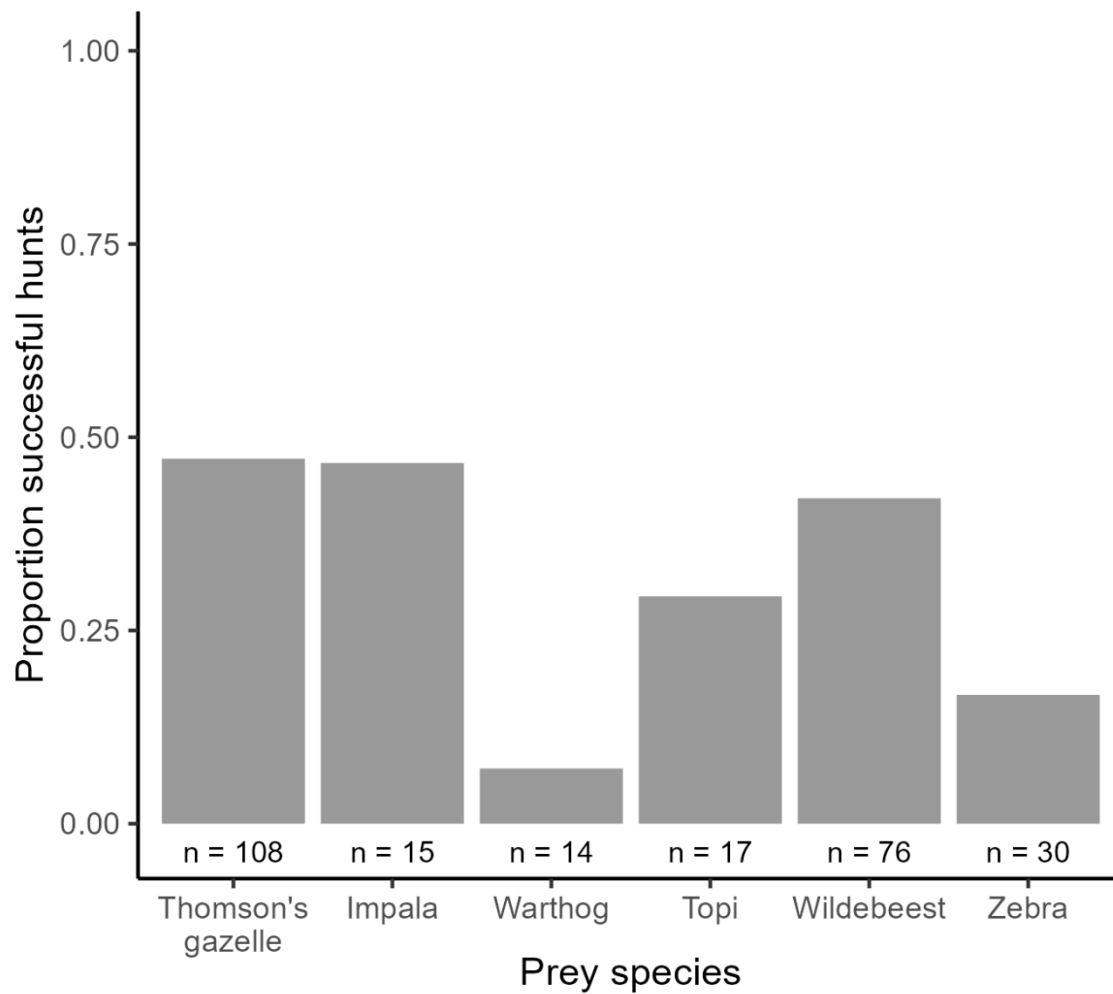


Figure 2.3. Predicted probabilities of hunt success for Thomson's gazelle (left) and wildebeest (right) by hunt type (solo or group) and adult (red) and juvenile (blue) prey. Whiskers indicate 95% confidence intervals.

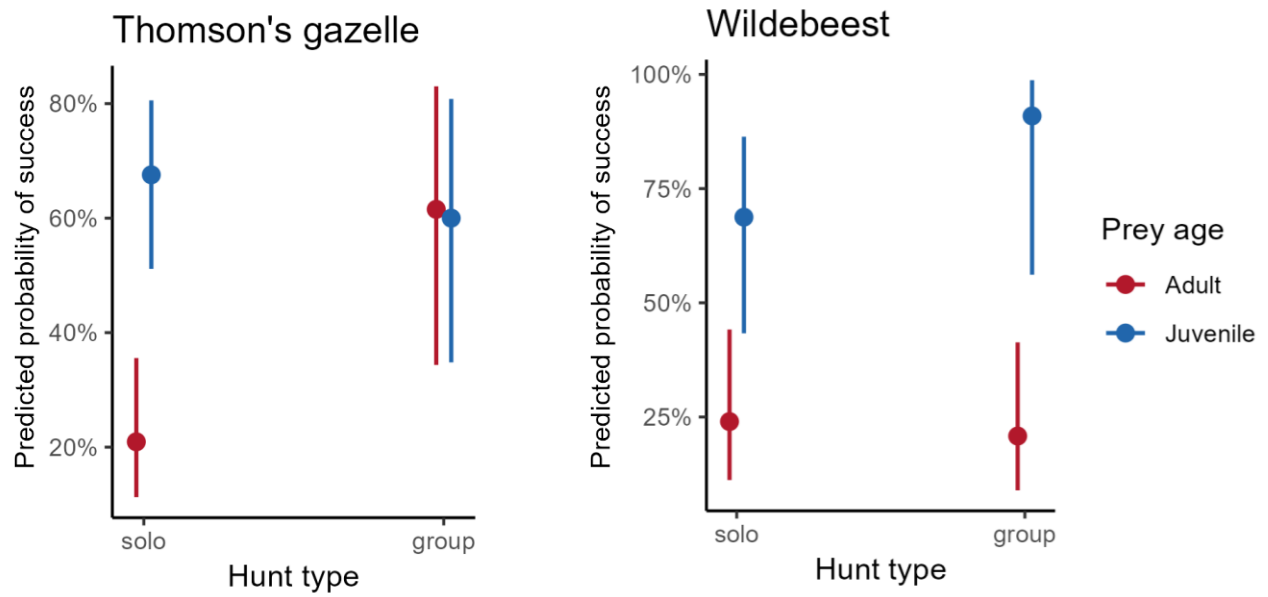


Figure 2.4. Predicted probability of successfully solo hunting by hunter age class and prey age class.

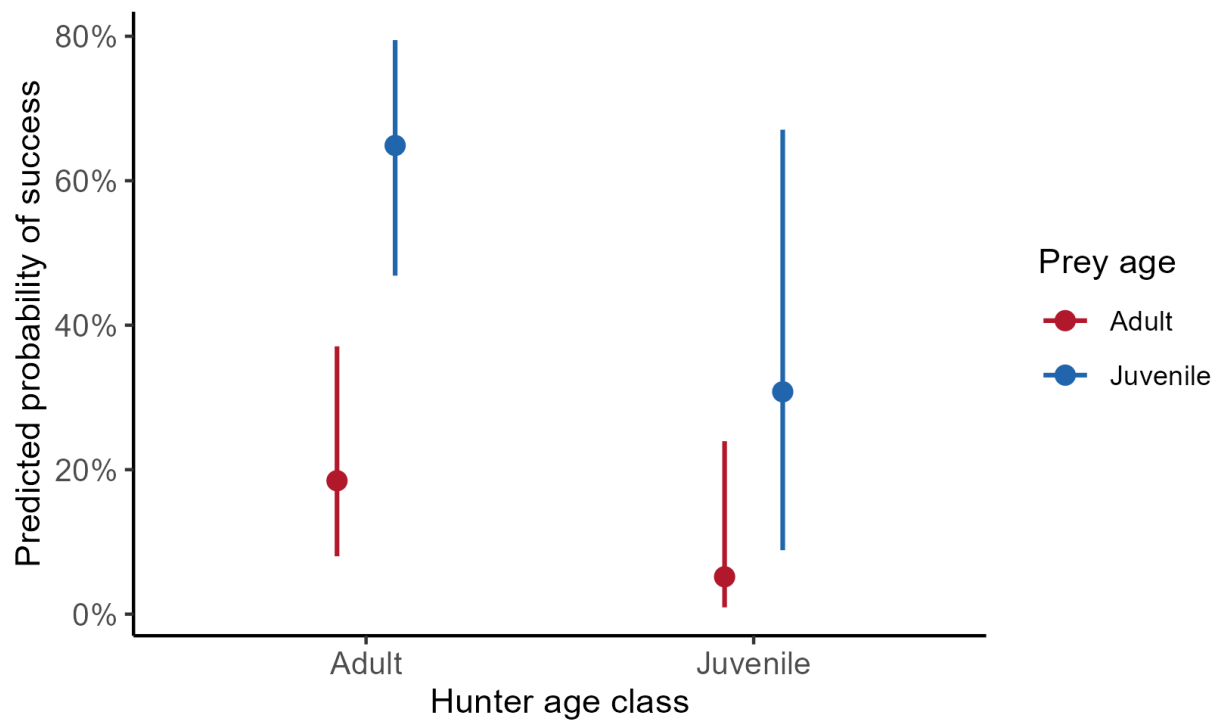


Figure 2.5. Mean hunting group size for top 6 prey species for Talek hyenas from 1996 – 2018 for hunts where group size could be determined precisely. Bars represent standard error of the mean. Species are organized from left to right by mean adult body mass.

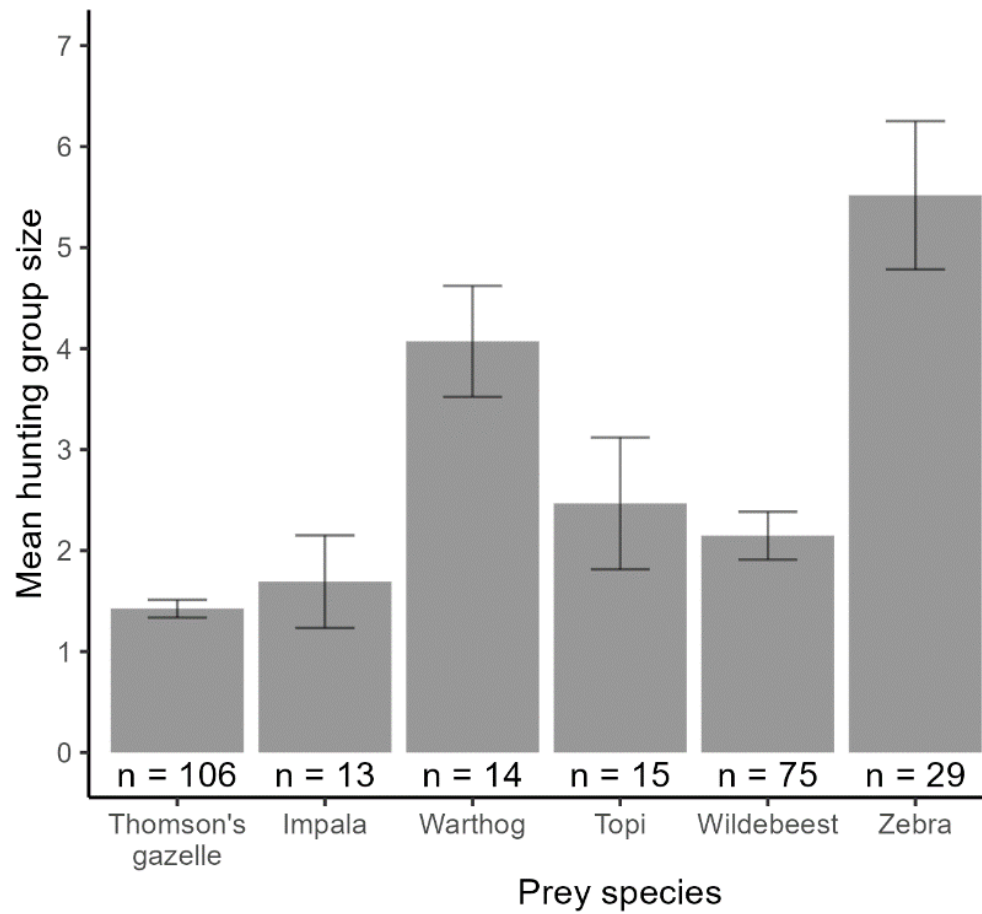


Figure 2.6. Boxplot of hunting group size based on individual hunters' rank quartile. **** indicates p-value <0.0001 for post hoc pairwise comparisons.

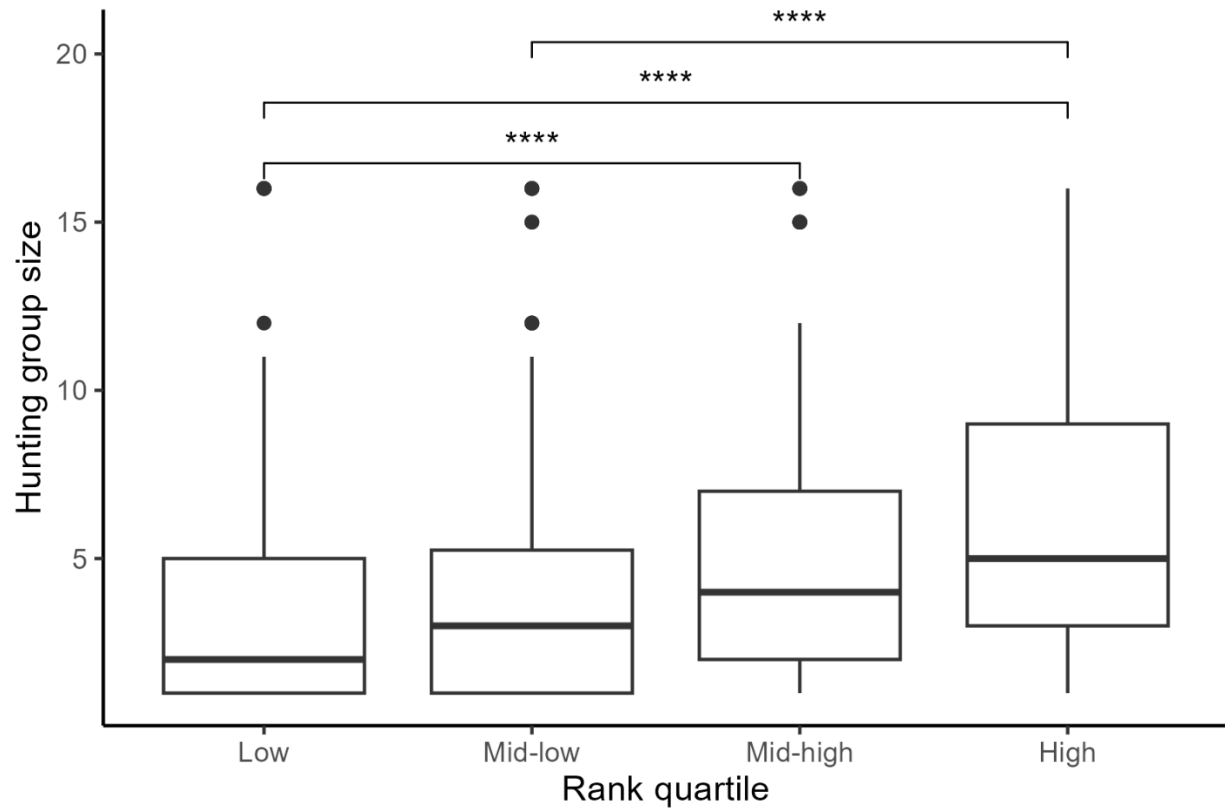


Figure 2.7. Boxplot of hunting group size based on individual hunters' age class. **** indicates p-value <0.0001 for Kruskal-Wallis test.

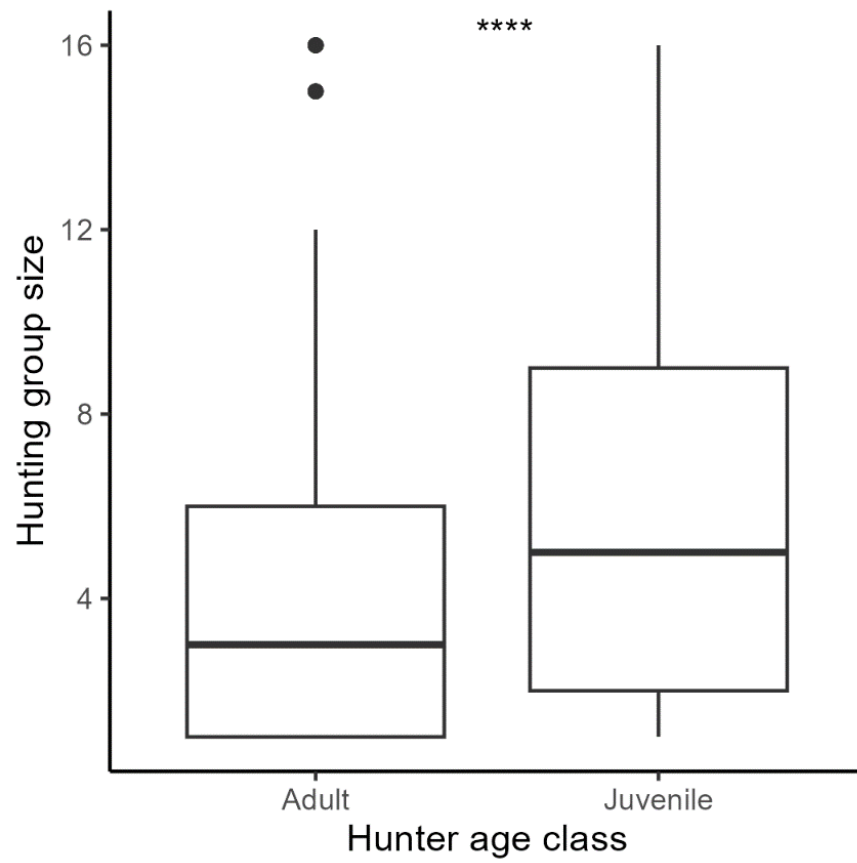


Figure 2.8. Boxplot of hunting group size based on individual hunters' sex. ns indicates p-value was not significant for Kruskal-Wallis test.



SUPPLEMENTARY INFORMATION

Table S1. Results from generalized linear mixed model of the effects of hunt strategy (solo vs. group), prey age, prey species, and Julian date (modeled as a quadratic term) on the probability of hunt success. Observation session is included as a random variable. Each prey species is compared to Thomson's gazelle as the reference level. Group hunting (two or more hunters) is compared to solo hunting, which is the reference level for hunt strategy. Juvenile prey are compared to adult prey, which is the reference level for age. Odds ratios > 1 indicate increased odds of hunt success for the specified predictor, compared to the reference level, while odds ratios < 1 indicate decreased odds of hunt success.

<i>Predictors</i>	<i>Odds Ratios</i>	<i>CI</i>	<i>p</i>
Group hunt	1.58	0.83 – 2.99	0.165
Juvenile prey	7.08	2.95 – 17.01	<0.001
Impala	0.37	0.11 – 1.29	0.119
Warthog	0.09	0.01 – 0.87	0.037
Topi	0.21	0.05 – 0.82	0.025
Wildebeest	0.77	0.36 – 1.63	0.496
Zebra	0.28	0.08 – 0.95	0.041
Julian date (1st degree)	47.72	0.27 – 8510.67	0.144
Julian date (2nd degree)	0.68	0.00 – 107.91	0.882
Observations	260		

CHAPTER 3:

HYENA FEEDING BEHAVIOR ACROSS VARYING ECOLOGICAL CONDITIONS

ABSTRACT

Large carnivores play an important role in maintaining healthy ecosystems, yet are globally threatened. They are particularly vulnerable to anthropogenic change and come into frequent conflict with humans when livestock overlap with large carnivore habitat. At the same time, native prey populations are declining for many large carnivores. Dietary flexibility can allow carnivores to cope with changes to their environment but, at the same time, may increase human-wildlife conflict. In this chapter, we investigate how ecological conditions influence the diet of spotted hyenas, a highly flexible forager and most abundant large carnivore in sub-Saharan Africa. We use long-term observational behavioral data to compare feeding observations across space and time. We compare feeding behavior of hyenas inhabiting areas of the Maasai Mara with different management practices: one where livestock grazing (Talek Region) is present and one without livestock grazing (Mara Conservancy). We then examine long-term hyena diet across 31 years in the Talek Region of the Maasai Mara; a region that has undergone changes in the landscape, including fluctuations in livestock grazing intensity, varying weather patterns, and changes in wild herbivore abundance. We summarize prey availability, livestock presence, temperature, and rainfall to understand how the two sites compare and to look at the broader ecological changes through time. We then quantify diet using observational records of feeding behavior to examine how hyena diets compare between the two sites, and across time in the Talek Region. Hyenas in both populations responded to seasonal changes in prey availability, consuming primarily the prey type that is most available. Hyenas in the Talek Region consumed domestic livestock and had a less diverse diet of resident prey species than in the Mara Conservancy. Longitudinally, in the Talek Region, hyenas were seen feeding on livestock more often as livestock presence increased. When livestock feeding increased, feeding on resident prey decreased. These changes reflect the observed declines of wild herbivores in the region. Our

results complement previous work documenting the declines of herbivore populations and adds to the body of research showing that hyenas are flexible foragers that switch to consuming prey that are most available both over seasonal time scales and across long-term ecological change. This flexibility likely facilitates hyenas' ability to persist in landscapes with high human use. Further work on dietary flexibility and behavioral plasticity on species in changing environments will improve our understanding of how species cope with ecological change.

INTRODUCTION

Large carnivores are critically important in regulating and maintaining healthy ecosystems (Ale & Whelan, 2008; Berger et al., 2001; Beschta & Ripple, 2009; Estes et al., 2011), but large carnivore populations are seriously threatened worldwide (Ripple et al., 2014). Global ecological changes such as habitat loss, shifting and/or declining prey populations, conflict with humans, and climate change are all occurring at faster rates than extant species have previously experienced. Phenotypic plasticity helps to facilitate persistence in the face of rapid or novel environmental change (Losos et al., 2001; Renaud et al., 2015; Winchell et al., 2016), and this is especially true for species with long generation times, whose environments may change significantly within a few generations. Behavior underlies much phenotypic plasticity, and it often represents animals' first response to cope with changing environmental conditions and stressors (Wong & Candolin, 2015). Examples of behavioral responses to anthropogenic change include shifts in diel activity patterns (Gaynor et al., 2018), space use (Kolowski & Holekamp, 2009; Oriol-Cotterill et al., 2015), and diet (Farias & Kittlein, 2008).

Large carnivores are particularly vulnerable to effects of anthropogenic change due to their high trophic level, which makes them sensitive to shifts in native wildlife and vegetative communities and depletion of their native prey (Dorresteijn et al., 2015; Muhly et al., 2013; Ripple et al., 2014). However, dietary flexibility is thought to play a large role in a species' ability to cope with changing environments. Species with specialized diets are more susceptible to decreases in

abundance of their primary food sources, whereas species with broader and more flexible diets can readily shift their diet in response to changes in availability of particular types of food (Navarro et al., 2017; Scholz et al., 2020). Nevertheless, maladaptive changes in foraging behavior sometimes occur because anthropogenic change outpaces evolutionary responses, decoupling links between environmental cues and effects on fitness (Lamb et al., 2017; Nisi et al., 2022).

Habitat loss and fragmentation have also created overlap between native carnivore habitat and anthropogenic land use, leading to increased rates of livestock depredation (Inskip & Zimmermann, 2009; Treves & Karanth, 2003; Wolf & Ripple, 2017; Woodroffe & Ginsberg, 1998). Anthropogenic change will continue to exacerbate the problem of livestock depredation, because the expanding human population will further restrict carnivore home ranges, increase proximity to human settlements (Ugarte et al., 2019), and deplete natural prey populations (Ripple et al., 2015; Wolf & Ripple, 2016). Livestock depredation is associated with reduced fitness for carnivores, and retaliatory killing of carnivores in response to livestock depredation has emerged as a key threat on a global scale (Ripple et al., 2014). As the effects of human-induced environmental changes increase, large carnivores that cannot readily modify their diet will face more challenges and their populations may be threatened.

Understanding how foraging behavior is altered in the face of rapid ecological change will improve our predictions regarding which species may be challenged by such changes, and thus where to target conservation efforts. Specifically, identifying how spatial and temporal variation in wild prey and livestock abundance affect prey selection in large carnivores will broaden our understanding of dietary flexibility and how it may enable other species to cope with future large-scale ecological changes. It will also provide insight into the environmental conditions that increase livestock depredation and other human-wildlife conflict, and it will thus inform conflict mitigation practices and other wildlife management strategies (Abay et al., 2011; Khanal et al., 2020; Khorozyan et al., 2015; Nelson et al., 2016; Suryawanshi et al., 2017).

Spotted hyenas (*Crocuta crocuta*) are the most abundant large carnivore in sub-Saharan Africa and exhibit high behavioral flexibility under changing habitat conditions (Holekamp & Dloniak, 2010). Hyenas are highly gregarious, generalist predators who successfully inhabit a wide range of habitat types including forests, savannas, deserts, and cities. These hyenas are highly flexible foragers that generally hunt whichever herbivore species are most available (Cooper, 1990; Cooper et al., 1999; Holekamp et al., 1997b; Kruuk, 1972). They readily switch prey types as the relative availability of local prey species changes seasonally (Cooper et al., 1999; Holekamp et al., 1997b) and across longer time scales (Höner et al., 2002). They can also persist exclusively on domestic prey or even primarily on refuse (Abay et al., 2011; Yirga et al., 2013; Yirga & Bauer, 2010). Spotted hyenas' extreme dietary flexibility makes them an excellent species in which to investigate how ecological variation affects carnivore foraging ecology, and to understand whether there are limits to this flexibility. Furthermore, hyenas are often implicated in livestock depredation but are underrepresented in livestock depredation studies (Hoffmann & Montgomery, 2022), highlighting the need for more information on how hyenas interact with livestock.

Here, we investigate feeding behavior and dietary flexibility across space and time in a population of spotted hyenas inhabiting the Maasai Mara National Reserve, Kenya (henceforth "the Mara"). The Mara is a tropical savanna with seasonal variations in prey: it both supports a diverse community of large resident mammals and, for a portion of the year, hosts large migratory herds of wildebeest and zebra (Bell, 1971; Craft et al., 2015; Sinclair & Norton-Griffiths, 1979). Anthropogenic disturbance varies considerably within the Mara: the Mara River divides the Mara into two separate management areas characterized by different ecological conditions and contrasting livestock management practices. In this study, we leverage a long-term 31-year foraging dataset collected at multiple sites within the Mara to assess predictors of dietary flexibility in spotted hyenas across the Mara landscape. We inquire how hyena feeding behavior varies (1) between two areas with different ecological conditions, one characterized by intensive livestock

grazing and one where livestock are prohibited, and (2) within a single social group across three decades of ecological change.

METHODS

Maasai Mara National Reserve

The Mara is primarily composed of rolling grasslands dotted with trees and riverine habitats (Sinclair & Norton-Griffiths, 1979). Precipitation follows a bimodal pattern annually, with most precipitation occurring in November–December and March–May (Green et al., 2019b; Ogutu et al., 2008). Temperature has less seasonal variation (Green et al., 2019b). Due to climate change, temperature is increasing, and rainfall is becoming less seasonally predictable (Green et al., 2019b; Ogutu et al., 2007). Together, these changing climatic conditions threaten primary production of grasslands, exacerbate woody plant expansion, and reduce herbivore population density and diversity (Li et al., 2020). The Mara is also under immense pressure from many anthropogenic sources (e.g., agribusiness, fencing, firewood harvesting, tourism, livestock grazing), causing population declines of resident and migratory herbivores (Green, 2015; Ogutu et al., 2005, 2009, 2011; Ottichilo et al., 2000). The declining herbivore populations have changed the prey base for large carnivores, increasing the likelihood of livestock depredation and conflict with humans, and threatening human safety and livelihood as well as carnivore populations.

Management practices differ significantly within the Mara between the west and east sides of the Mara River, which influences local community ecology (Green et al., 2018). The Eastern side of the Mara is bordered by the growing town of Talek, (hereafter “the Talek Region,” Fig 3.1), and the hyenas in this region interact with humans and livestock frequently (Green et al., 2018; Kolowski & Holekamp, 2006). Patterns and intensity of livestock grazing in and near the Talek Region have varied throughout time due to the complex interactions among ecological, social, and political influences (Butt, 2014), but overall grazing has increased in the past several decades (Green et al., 2019b). On the western side of the Mara River in “the Mara Conservancy”, livestock grazing is

prohibited and strictly enforced, such that hyenas encounter no livestock in the Reserve, and do not interact with humans except those in tour vehicles. Due partially to ecology and partially to livestock grazing practices, the grass height throughout the Mara Conservancy is generally considerably higher than that in the Talek Region (Spagnuolo et al., 2020). The differences between these regions make the Mara an excellent site for comparing concomitant dietary flexibility under different ecological conditions, and inquiring how livestock (i.e., domestic cows, sheep, and goats) influence hyena foraging ecology.

Study site and climate

We conducted our study at two sites, one in the Talek Region and one in the Mara Conservancy (Fig 3.1). The Mara Hyena Project has been monitoring the Talek clan in the Talek Region since mid-1988 and has been monitoring 3 clans (Happy Zebra, Serena North, and Serena South clans) in the Mara Conservancy since mid-2008, using the same methods at each site. Site-level weather data, including minimum and maximum temperatures and total precipitation, were recorded daily at weather stations located at each study site (Figs 3.2-3.3).

Hyena feeding behavior

We collected hyena behavioral data during twice-daily observation periods from (~0500-0830 h) and (~1600-2000 h). During these periods, observation sessions (hereafter “sessions”) were initiated when observers encountered one or more hyenas separated from other hyenas by at least 200 m. A session ended when interactions among hyenas ceased and observers left the individual or group, or when observers lost sight of the hyenas (Lehmann et al., 2017); session duration was recorded in minutes, lasting from 5 minutes to several hours.

Observers recorded all instances of hyena feeding behavior seen during sessions. A hyena was considered feeding if it was observed actively chewing and swallowing food, but not if it was carrying food, interacting with but not ingesting food, or exhibiting other signs of having fed (e.g., hyena was bloody). An observation session could contain multiple feeding observations if the

session included multiple carcasses or successful hunts. Within each session where at least one hyena fed, observers tried to collect information on the prey species, which was determined based on carcass size and coloration, horn shape, hoof shape, and other cues. However, prey species were often difficult to identify as observers needed to see the carcass prior to its decimation, and identification to species was only possible in around 50% of feeding sessions due to dense vegetation or darkness (see Results). This had the potential to over-represent observations of large prey since these carcasses take longer to consume and draw attention of more hyenas and scavengers.

To calculate monthly hyena diet profiles, we used all observations of hyenas actively feeding on identified prey species. For each month, we summarized the total feeding observations for the Talek clan in the Talek Region and all feeding observations across the three study clans in the Mara Conservancy. We then calculated monthly relative percentages of each prey species and prey type (e.g., migratory, resident) on which the hyenas in each region were observed to feed.

Prey availability

To quantify wild prey availability, we drove prey transects biweekly at 10 km/hr between 0800-1000 h. In the Talek Region, two 4-km transects were monitored within the Talek clan's territory from 1988-2019, and an additional transect was also monitored from 2005-2019. In the Mara Conservancy, six transects of variable lengths (1.5 km to 5.4 km), two in the territory of each study clan, were monitored from 2008-2019. Full details of transect methods are available in (Green et al., 2019a; Holekamp et al., 1997b). Briefly, we used a range finder to count any individual of the prey species listed in Table 3.1 that was within 100 meters of the vehicle on either side of the transect. To estimate monthly herbivore availability, we calculated the mean monthly density (animals/km²) of resident and migratory herbivores by dividing the number of each herbivore type by the transect area (transect length * 0.2 km) for each transect, then averaging across transects within each month and region.

To estimate the number of livestock grazing in the Talek Region, we performed livestock counts by systematically driving through the Talek clan's territory, recording all cows, sheep, and goats seen within park boundaries (Green, 2015). Between May 2000 and May 2008, observers performed counts up to twice daily, once between 0500-1000 h and again between 1600-2000 h. After May 2008, livestock counts were performed biweekly between 1600-2000 h (Green, 2015). To estimate livestock abundance, we summed the total livestock counted each day, then averaged across all days on which livestock counts occurred within each month.

Data analysis

To compare prey availability to hyena diet profiles, we first grouped hyena prey species into four categories: migratory herbivores, resident herbivores, livestock, and other prey (Table 3.1). Migratory herbivores include wildebeest and zebra. Although Thomson's gazelles migrate elsewhere in the Mara-Serengeti ecosystem (Bell 1971; Said et al., 2003), they are non-migratory in our study region (Green et al., 2019b) and are therefore considered resident here, as in earlier studies (Ogutu et al., 2011; Ottichilo et al., 2000). Livestock include domestic cows, goats, and sheep. Prey species that were consumed by hyenas but were not included in herbivore prey transects (e.g., small/cryptic antelope, birds, fish, other carnivores) were categorized as "other prey" and comprise only 2.6% of the feeding dataset.

We first described how hyena feeding observations relate to prey availability across both (1) space, using the 2008-2019 datasets from our study sites on both sides of the Mara, and (2) time, using the 1988-2019 dataset from the Talek Region. We calculated the percent of feeding observations involving each prey category by month, and we related this to the mean monthly prey density of each prey category. For the Talek Region, we also compared annual percent of livestock in hyena diets to mean annual livestock counts. We then compared relative proportions of resident prey in diets and tested whether the resident prey diets 1) differed between the Talek Region and the Mara Conservancy from 2008-2019 and 2) between 3 study decades (1988-1998; 1999-2008;

2009-2019) in the Talek Region using a Fisher's exact test. We used generalized linear models to investigate whether feeding on specific prey species varied across time in Talek. We fit three logistic models using the hyena feeding dataset, where one of the top three resident prey species in the Talek hyena diet was the outcome variable in each model. Our outcome variable was binomial: whether or not the feeding observation was on that particular prey species, and our predictor variable was in which decade the feeding observation occurred.

Finally, we used the hyena feeding dataset to fit three generalized linear mixed models to investigate hyena prey selection and test how hyena feeding behavior related to prey density. Our outcome variable for each model was prey category (i.e., migratory prey, resident prey, and livestock) and was binomial: whether or not the feeding observation involved that particular prey category. Our predictor variables were the scaled mean monthly prey density for each prey category, and we included year as a random variable to account for interannual variation. All analyses were run using R version 4.3.3 (R Core Team, 2024) in RStudio version 2023.12.1.402 (Posit team, 2024). We ran models using the lme4 package version 1.1-35.2 (Bates et al., 2015). We tested for collinearity among predictor variables using the 'performance' package version 0.11.0 (Lüdecke et al., 2021), and removed collinear predictors until all variance inflation factors were < 5 .

We used the 'tidyr' version 1.3.1 (Wickham et al., 2024), 'dplyr' version 1.1.4 (Wickham et al., 2023), 'lubridate' version 1.9.2 (Grolemund & Wickham, 2011; Wickham, 2023), and 'stringr' version 1.5.1 (Wickham, 2023) packages to manipulate and summarize data in R. We used 'ggplot2' version 3.5.0 (Wickham, 2016), 'sjPlot' version 2.8.14 (Lüdecke, 2023), 'ggpubr' version 0.6.0 (Kassambara, 2023), and 'gridExtra' version 2.3 (Auguie, 2017) to visualize data. We created the study area map using ArcGIS Pro (ESRI, 2021).

RESULTS

Data summary

The dataset included 7603 instances of feeding observed during 7573 observation sessions from the Talek clan (in the Talek Region) from June 1988 through December 2019, and 1950 instances of feeding during 1896 sessions from the three Mara Conservancy clans from June 2008 through December 2019. Prey type was unidentified in 44.6% (n=3390) of feeding observations in the Talek Region and in 54.7% (n=1067) of feeding observations in the Mara Conservancy. Of the observations where prey type was identifiable, wildebeest was the most common prey type on both sides of the Mara (Table 3.2). Thomson's gazelle, topi, and impala were the most common resident prey in the Talek Region, and buffalo, topi, warthog, and hippo were the most common resident prey in the Mara Conservancy (Table 3.2). Domestic cows made up 4.4% and sheep and goats 0.4% of identifiable feeding observations in the Talek Region (Table 3.2a), but livestock were never observed in the Mara Conservancy.

Cross-sectional comparison of feeding observations (2008-2019)

Hyena diets in the Talek Region and the Mara Conservancy both followed the same general pattern, where hyenas ate mostly resident prey in the first half of the year and switched to consuming mostly migratory prey when the migratory herbivores arrived during the second half of the year (Fig 3.4). When the migratory herbivores were absent, resident prey made up a larger percentage of the feeding observations in the Mara Conservancy than in the Talek Region. In the Talek Region, livestock were consumed more often when migratory prey density was lower (Fig 3.4a). In both regions, other prey made up only a small proportion of the diet and were consumed slightly more often when the migration was absent (Fig 3.4).

Observations of hyenas feeding on migratory and resident prey tended to vary with respective prey densities (Fig 3.5). Migratory herbivore density peaked from June–November in the Talek Region and from July–November in the Mara Conservancy (Fig 3.5 a & c). Feeding events

involving migratory prey were more frequent in the months when higher densities of migratory prey were present. Feeding events involving resident prey were more frequent in months with higher densities of resident prey, although resident prey density was less variable than migratory prey density (Fig 3.5 b & d). In the Talek Region, resident prey densities were higher from January–July than in August–December (Fig 3.5 b); in the Mara Conservancy, resident prey density had very little monthly variation across the year (Fig 3.5 d). The resident prey species consumed by hyenas in the Talek Region were significantly different than those consumed by hyenas in the Mara Conservancy (Fig 3.6; Fisher’s exact test, $p < 0.001$).

Longitudinal feeding observations in the Talek Region (1988-2019)

Over the last three decades in the Talek Region, hyena diets followed the same seasonal pattern described above, where hyenas ate mostly resident prey in the first half of the year and mostly migratory prey during the second half of the year (Fig 3.7). However, both migratory and resident prey densities appear to have decreased in recent years: prey densities in 1999-2008 and 2009-2019 were on average lower than in 1988-1998. Relative proportions of observations of hyenas feeding on migratory prey remained relatively consistent through time, whereas relative proportions of observations of hyenas feeding on resident prey declined across the three decades. Observations of hyenas feeding on livestock were more common in 2009-2019 than in previous years, and livestock counts were also highest during this same decade (Fig 3.8). As seen earlier (Fig 3.4), livestock counts tended to be higher in months when migratory prey densities and feeding observations were lower (Fig 3.7).

The resident prey species consumed by Talek hyenas have also changed over time (Fig 3.9; Fisher’s exact test, $p < 0.001$). Consumption of Thomson’s gazelle has decreased over time: Thomson’s gazelle made up a larger proportion of hyena feeding observations on resident prey in 1988-1998 than in 1999-2008 ($\beta = -0.391$, $p = 0.003$) and 2009-2019 ($\beta = -0.730$, $p < 0.001$). Consumption of impala has increased over time: impala made up a smaller proportion of hyena

feeding observations on resident prey in 1988-1998 than in 1999-2008 ($\beta = 1.022$, $p < 0.001$) and 2009-2019 ($\beta = 0.537$, $p = 0.011$). Relative proportions of topi in hyena diets did not significantly vary across time (1988-1998 versus 1999-2008: $\beta = -0.232$, $p = 0.172$; 1988-1998 versus 2009-2019: $\beta = 0.217$, $p = 0.179$).

Prey selection model results

In both regions, observations of hyenas feeding on migratory and resident prey tended to vary with respective prey densities. In the Talek Region, hyenas were more likely to consume migratory prey, resident prey, and livestock when those respective prey types were more abundant (Fig 3.10). The strongest association between feeding behavior and prey availability was with migratory prey. Migratory prey were consumed more often when there were higher densities of migratory prey present locally, and consumed less often when there were higher densities of either resident prey or livestock. Resident prey were consumed more often when there were higher densities of resident prey and less often when there were higher densities of migratory prey. Livestock were consumed more often when livestock counts were higher and less often when migratory prey density was higher (Fig 3.10).

In the Mara Conservancy, feeding on migratory prey was positively associated with migratory prey densities, but there was no significant relationship between feeding on migratory prey and resident prey density (Fig 3.11). Feeding on resident prey was positively associated with resident prey densities and negatively associated with migratory prey densities (Fig 3.11). As in the Talek Region, the relationship between migratory prey density and hyenas feeding on migratory prey had the largest effect size (Fig 3.11).

DISCUSSION

Our results demonstrate that hyena foraging behavior responds to ecological change across three distinct scales: seasonally, spatially, and longitudinally over three decades. Seasonally, hyenas in both regions consumed primarily migratory prey when the wildebeest and zebra migration was

present, and consumed resident prey when migratory prey were scarcer. Spatially, hyenas exposed to greater anthropogenic activity in the Talek Region consumed a less diverse range of resident prey species than did hyenas in the better protected habitat of the Mara Conservancy. Talek hyenas were the only individuals observed to regularly consume livestock. Longitudinally, the representation of livestock in the diet of Talek hyenas has increased over the last 30 years, reflecting increasing livestock grazing intensity in the region (Green, 2015). As expected, hyenas largely consume the prey category that is most available at any given time. This is consistent with previous studies demonstrating that hyenas show a functional response to local prey availability across seasons (Holekamp et al., 1997b, Cooper et al., 1999) and changes in long-term prey availability (Höner et al., 2002). In the Ngorongoro Crater, Tanzania, Höner et al. (2002) found that hyenas ate more buffalo calves and adult wildebeest as preferred prey that was easier to capture decreased.

Hyenas at both sites predominately ate migratory wildebeest and zebra during the months when the migration was present in their area. In the Talek Region, feeding on migratory prey was positively associated with migratory prey density, and negatively associated with both resident prey density and livestock count (Fig 3.10). In the Mara Conservancy, feeding on migratory prey was only positively associated with migratory prey density (Fig 3.11). Unlike in the Talek Region, where resident prey densities vary seasonally, resident prey in the Mara Conservancy are at consistently low densities year-round (Fig 3.5). In both regions, feeding on resident prey was positively associated with resident prey density and negatively associated with migratory prey density (Figs 3.10 & 3.11). Among resident prey, Thomson's gazelles were involved in a large portion of Talek hyena feeding observations, whereas Mara Conservancy hyenas were seen eating a more diverse range of resident prey species (Fig 3.6). This difference was observed despite a longitudinal shift in the Talek clan's diet away from primarily Thomson's gazelles over the last 30 years (Fig 3.9).

The impact of changing climatic factors on wildlife populations may explain some of the observed longitudinal variation in hyena foraging behavior. Our data show an increase in

temperature in the Talek region in the past 30 years (Fig 3.3), corroborating previous studies in the Mara documenting increasing temperature (Green et al., 2019b; Ogutu et al., 2007) and more extreme rainfall patterns (Bartzke et al., 2018). These changing weather patterns might have both a direct impact on hyena foraging behavior by affecting prey susceptibility to predation (Mills et al., 1995), and an indirect impact on prey densities by affecting herbivore population dynamics (Ogutu et al., 2008). Perhaps as a result, our data indicate a long-term decrease in both migratory and resident herbivore density (Fig 3.7), corroborating previous work (Green et al., 2019b; Ogutu et al., 2009, 2011, 2016; Ottichilo et al., 2000). Future work investigating how temperature and rainfall impact hyena foraging and prey availability in the Mara is important to get a more complete understanding of how current conditions influence foraging and to make future predictions.

Our data show that hyenas relied more on livestock as a food source as livestock presence increased. In the Talek Region, feeding on livestock was positively associated with livestock counts and negatively associated with migratory prey density (Fig 3.10), indicating that hyenas may replace resident herbivores with livestock when migratory herbivore density is low (Fig 3.4). The largest change in the Talek clan's diet in the last 30 years was the increase in livestock feeding (Fig 3.7 & 3.8), likely due to the increase in livestock grazing intensity in that region. Livestock loss due to carnivore depredation is a global issue, which causes major income loss and poses serious safety risks to people living near carnivores (Treves & Karanth, 2003). Livestock movement influences herbivore space use, but the impacts can vary by herd size and seasonality (Masiaine et al., 2021, Odadi et al., 2011, Kimuyu et al., 2017), therefore the complex dynamics between livestock, herbivores, and carnivores vary depending on regionally specific conditions. Research and management actions to promote human-carnivore coexistence should be location-specific, culturally sensitive, and should include knowledge, leadership, goals and perspectives from local people (Parmisa & Reid, 2021; van Eeden et al., 2018; Wilkinson et al., 2021).

In this study, we focused on differences among hyena populations across space and time, but diet can also vary widely among individuals within a social group. Hyena space use varies by age, sex, and reproductive status (Boydston et al., 2003, 2005), and individual access to critical resources such as carcasses varies with social rank (Frank, 1986; Kruuk, 1972; Smith et al., 2008; Tilson & Hamilton, 1984). These factors may influence individuals' perceptions and knowledge of their environment and lead to high inter-individual variation in foraging decisions and diet. For example, certain individual hyenas may be more likely to depredate livestock, as shown in other species (Linnell et al., 1999; Mizutani, 1993; Morehouse et al., 2016). A fecal DNA study of hyenas in the Ngorongoro Crater found that overall livestock was relatively rare in the diet, but older hyenas were more likely to eat livestock, but detections included livestock that could have been scavenged or depredated (Dheer et al., 2023). Future studies using molecular techniques such as stable isotope analysis and DNA metabarcoding could provide more highly resolved diet data to compare among individuals across different temporal scales (e.g., Massé et al., 2023; Scholz et al., 2020), and can be applied to large carnivore systems to better understand patterns of livestock depredation (Dheer et al., 2023; Thuo et al., 2020). While every method has benefits and drawbacks, incorporating multiple methods can improve diet estimates (Chiaradia et al., 2014; Nielsen et al., 2018) and elucidate foraging behavior.

Ultimately, top predators such as spotted hyenas are biodiversity indicators (Natsukawa & Sergio, 2022), and exert strong influences on ecosystem function. Their prey choices and capture success rates have cascading direct and indirect effects on sympatric populations of other large predators, mesopredators, herbivores, and primary producers as well as abiotic components of the ecosystem (Estes et al., 2011; Ripple et al., 2014). Therefore, ecological and anthropogenic changes that cause top predators to alter their diet can have profound effects on ecosystem function. Dietary niche breadth can help facilitate predator survival in changing habitats. For example, species with more dietary flexibility are more able to cope with human activities by exploiting anthropogenic

food sources (Maibeche et al., 2015; Yirga et al., 2013). Hyenas have a high niche breadth compared to sympatric carnivores (Vissia et al., 2023); other carnivores with lower niche breadth or lower tolerance for human activities may have less flexible foraging strategies. Further work on dietary flexibility and behavioral plasticity should be conducted on other species in changing environments.

TABLES

Table 3.1. Herbivore species included in prey transect counts, Talek Region (1988 – 2018) and Mara Conservancy (2008-2019), Kenya. Zebra and wildebeest were categorized as migratory prey, and all other herbivores counted were categorized as resident prey.

Common name	Genus species
<i>Migratory herbivores</i>	
Plains zebra	<i>Equus quagga</i>
Blue wildebeest	<i>Connochaetes taurinus</i>
<i>Resident herbivores</i>	
Thomson's gazelle	<i>Eudorcas thomsoni</i>
Impala	<i>Aepyceros melampus</i>
Topi	<i>Damaliscus lunatus</i>
Warthog	<i>Phacochoerus africanus</i>
Hartebeest	<i>Alcelaphus buselaphus</i>
Grant's gazelle	<i>Nanger granti</i>
African buffalo	<i>Syncerus caffer</i>
Hippo	<i>Hippopotamus amphibius</i>
Giraffe	<i>Giraffa camelopardalis</i>
Eland	<i>Taurotragus oryx</i>
African elephant	<i>Loxodonta africana</i>
Duiker	<i>Sylvicapra grimmia</i>
Oribi	<i>Ourebia ourebi</i>
Reedbuck	<i>Redunca redunca</i>
Waterbuck	<i>Kobus ellipsiprymnus</i>
Olive baboon	<i>Papio anubis</i>
Bushbuck	<i>Tragelaphus scriptus</i>

Table 3.2. Summary of hyena feeding observations where prey type was identified in the (a) Talek Region (June 1988 – December 2019) and (b) Mara Conservancy (June 2008 – December 2019), Kenya. Hyenas in the Mara Conservancy were never observed consuming livestock.

(a) Talek Region			
Prey type	Genus species	n obs	% obs
Blue wildebeest	<i>Connochaetes taurinus</i>	2120	50.32
Thomson's gazelle	<i>Eudorcas thomsoni</i>	606	14.38
Plains zebra	<i>Equus quagga</i>	411	9.76
Topi	<i>Damaliscus lunatus</i>	286	6.79
Cow	<i>Bos taurus</i>	185	4.39
Impala	<i>Aepyceros melampus</i>	179	4.25
Giraffe	<i>Giraffa camelopardalis</i>	79	1.88
African buffalo	<i>Syncerus caffer</i>	64	1.52
Savanna elephant	<i>Loxodonta africana</i>	48	1.14
Common warthog	<i>Phacochoerus africanus</i>	47	1.12
Invertebrate	Arthropoda, Taenia*	35	0.83
Grant's gazelle	<i>Nanger granti</i>	16	0.38
Common eland	<i>Taurotragus oryx</i>	15	0.36
Sheep/goat	<i>Ovis aries</i> , <i>Capra hircus</i>	15	0.36
Bird	Aves*	14	0.33
Rodent/hare	Rodentia, Lagomorpha*	13	0.31
Spotted hyena	<i>Crocuta crocuta</i>	12	0.28
Bat-eared fox	<i>Otocyon melgalotis</i>	9	0.21
Nile crocodile	<i>Crocodylus niloticus</i>	9	0.21
Reptile	Testudines, Squamata*	8	0.19
Hippo	<i>Hippopotamus amphibius</i>	7	0.17
Hartebeest	<i>Alcelaphus buselaphus</i>	6	0.14
Olive baboon	<i>Papio anubis</i>	5	0.12
Jackal	<i>Canis</i> spp.*	5	0.12
Mongoose	Herpestidae*	5	0.12
Domestic dog	<i>Canis familiaris</i>	4	0.09
Kirk's Dikdik	<i>Madoqua kirkii</i>	3	0.07
Common Reedbuck	<i>Redunca redunca</i>	2	0.05
Waterbuck	<i>Kobus ellipsiprymnus</i>	2	0.05
Domestic cat	<i>Felis catus</i>	1	0.02
Catfish	<i>Clarias gariepinus</i>	1	0.02
Lion	<i>Panthera leo</i>	1	0.02

*highest identifiable taxonomic level

Table 3.2 (cont'd).

(b) Mara Conservancy

Prey type	Genus species	n obs	% obs
Blue wildebeest	<i>Connochaetes taurinus</i>	457	51.76
Plains zebra	<i>Equus quagga</i>	102	11.55
African buffalo	<i>Syncerus caffer</i>	58	6.57
Topi	<i>Damaliscus lunatus</i>	53	6.00
Common warthog	<i>Phacochoerus africanus</i>	41	4.64
Hippo	<i>Hippopotamus amphibius</i>	36	4.08
Impala	<i>Aepyceros melampus</i>	33	3.74
Thomson's gazelle	<i>Eudorcas thomsoni</i>	25	2.83
Invertebrate	Arthropoda*	21	2.38
Giraffe	<i>Giraffa camelopardalis</i>	18	2.04
Savanna elephant	<i>Loxodonta africana</i>	14	1.59
Spotted hyena	<i>Crocuta crocuta</i>	8	0.91
Bird	Aves*	6	0.68
Olive baboon	<i>Papio anubis</i>	2	0.23
Hartebeest	<i>Alcelaphus buselaphus</i>	2	0.23
Lion	<i>Panthera leo</i>	2	0.23
Nile crocodile	<i>Crocodylus niloticus</i>	2	0.23
Common eland	<i>Taurotragus oryx</i>	1	0.11
Rodent/hare	Rodentia, Lagomorpha*	1	0.11
Waterbuck	<i>Kobus ellipsiprymnus</i>	1	0.11

*highest identifiable taxonomic level

FIGURES

Figure 3.1. Maasai Mara National Reserve, Kenya, and study area locations for quantifying hyena feeding and prey availability, 1988 – 2019.

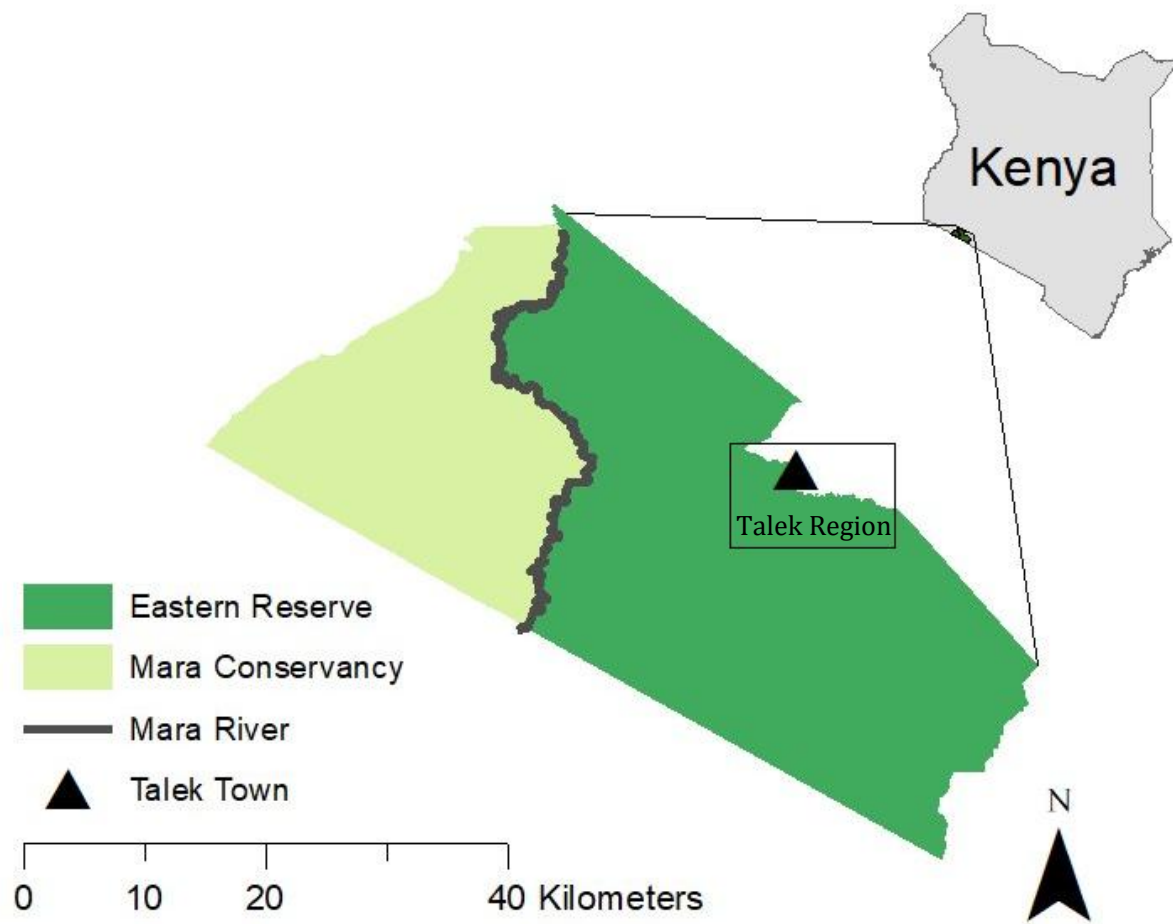


Figure 3.2. Mean monthly maximum (solid line) and minimum (dashed line) temperature $\pm$ SE and mean monthly precipitation $\pm$ SE (grey bars) from 2009 – 2019 for the (a) Talek Region and (b) Mara Conservancy, Kenya.

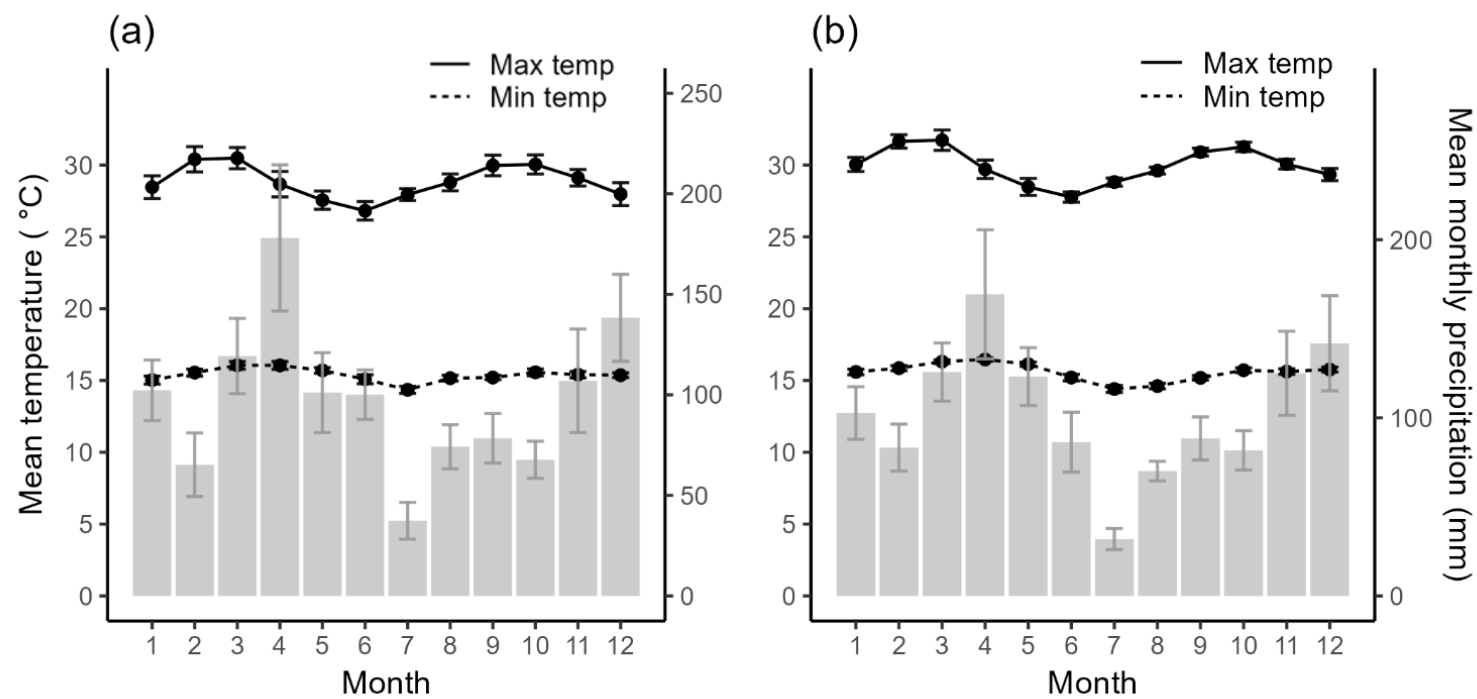


Figure 3.3. Mean annual maximum (solid line) and minimum (dashed line) temperature $\pm$ SE and cumulative annual precipitation (grey bars) for the (a) Talek Region from 1989 – 2019 and (b) Mara Conservancy from 2009 – 2019, Kenya. Data from the first years of study in the Talek Region (1988) and the Mara Conservancy (2008) were excluded from annual weather summaries because data collection began mid-year and did not contain a full year of data.

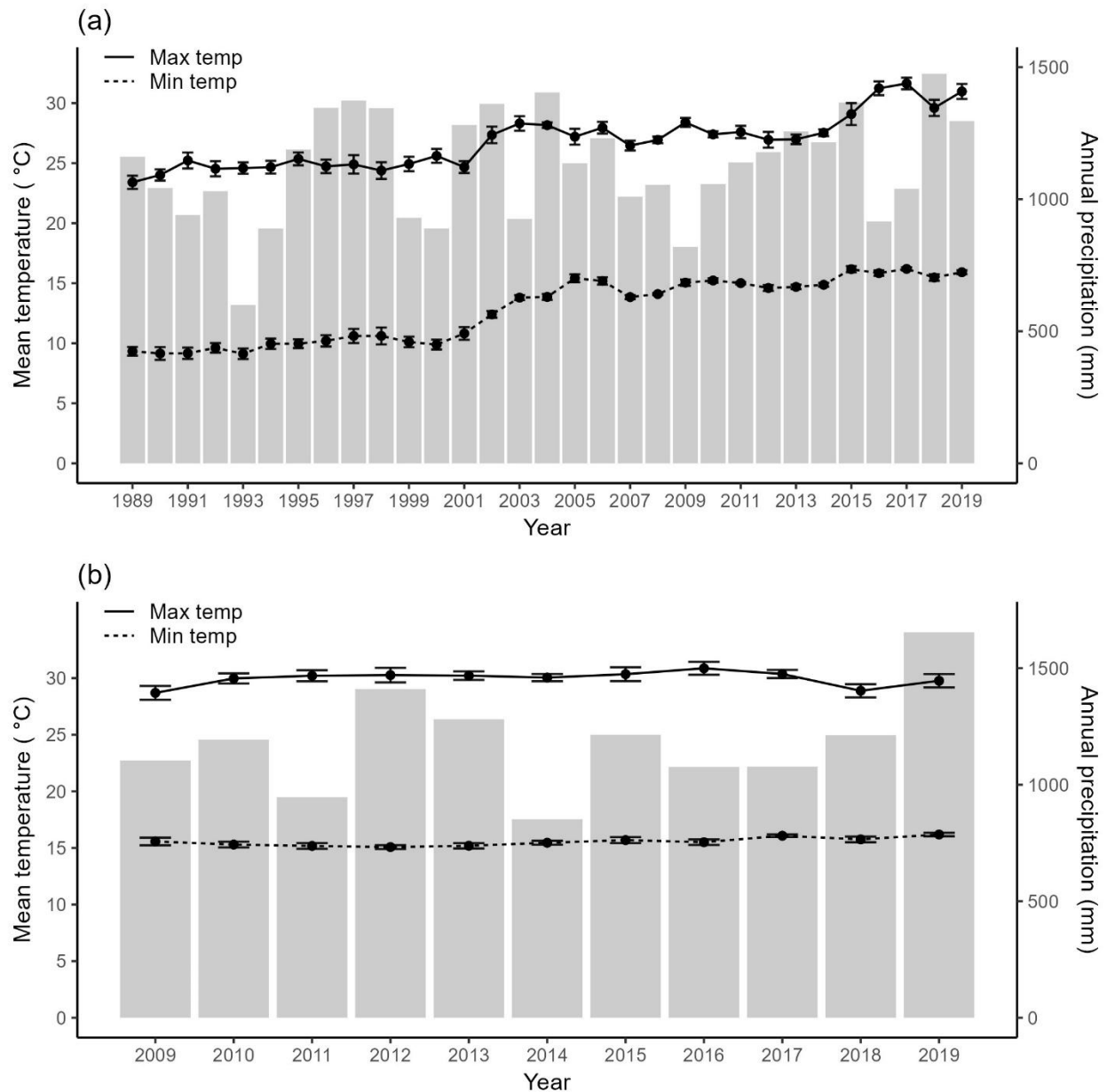


Figure 3.4. Monthly proportion of hyena feeding observations on migratory herbivores (red), resident herbivores (orange), livestock (light blue), and other prey (dark blue) from July 2008 to December 2019 in the (a) Talek Region and (b) Mara Conservancy, Kenya. Migration season is indicated by the black brackets (June – November for the Talek Region; July – November for the Mara Conservancy).

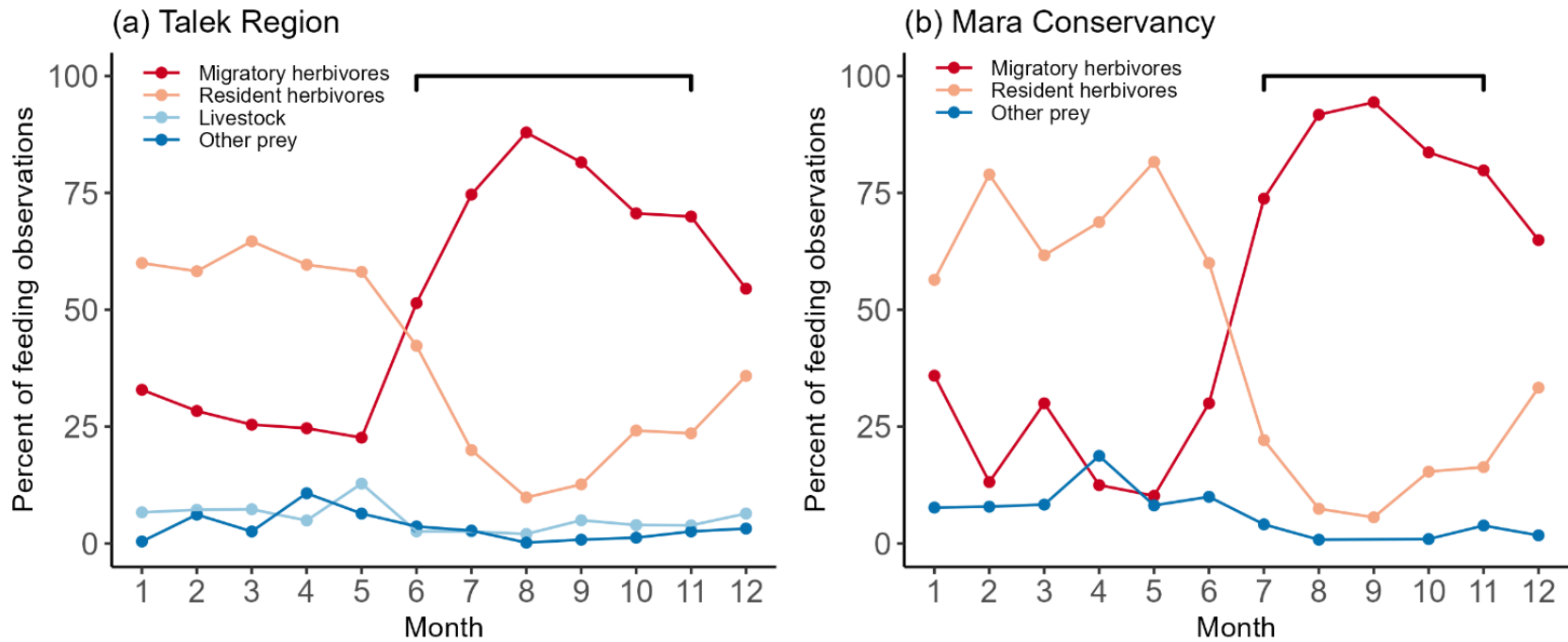


Figure 3.5. Monthly mean prey density $\pm$ SE (dashed line) and proportion of hyena feeding observations (solid line) from July 2008 to December 2019, separated by region and prey type. Feeding events of migratory herbivores (solid red) and mean monthly migratory herbivore density (dashed red) in the (a) Talek Region and (b) Mara Conservancy, Kenya. Feeding events of resident herbivores (solid orange) and mean monthly resident herbivore density (dashed orange) in the (c) Talek Region and (d) Mara Conservancy.

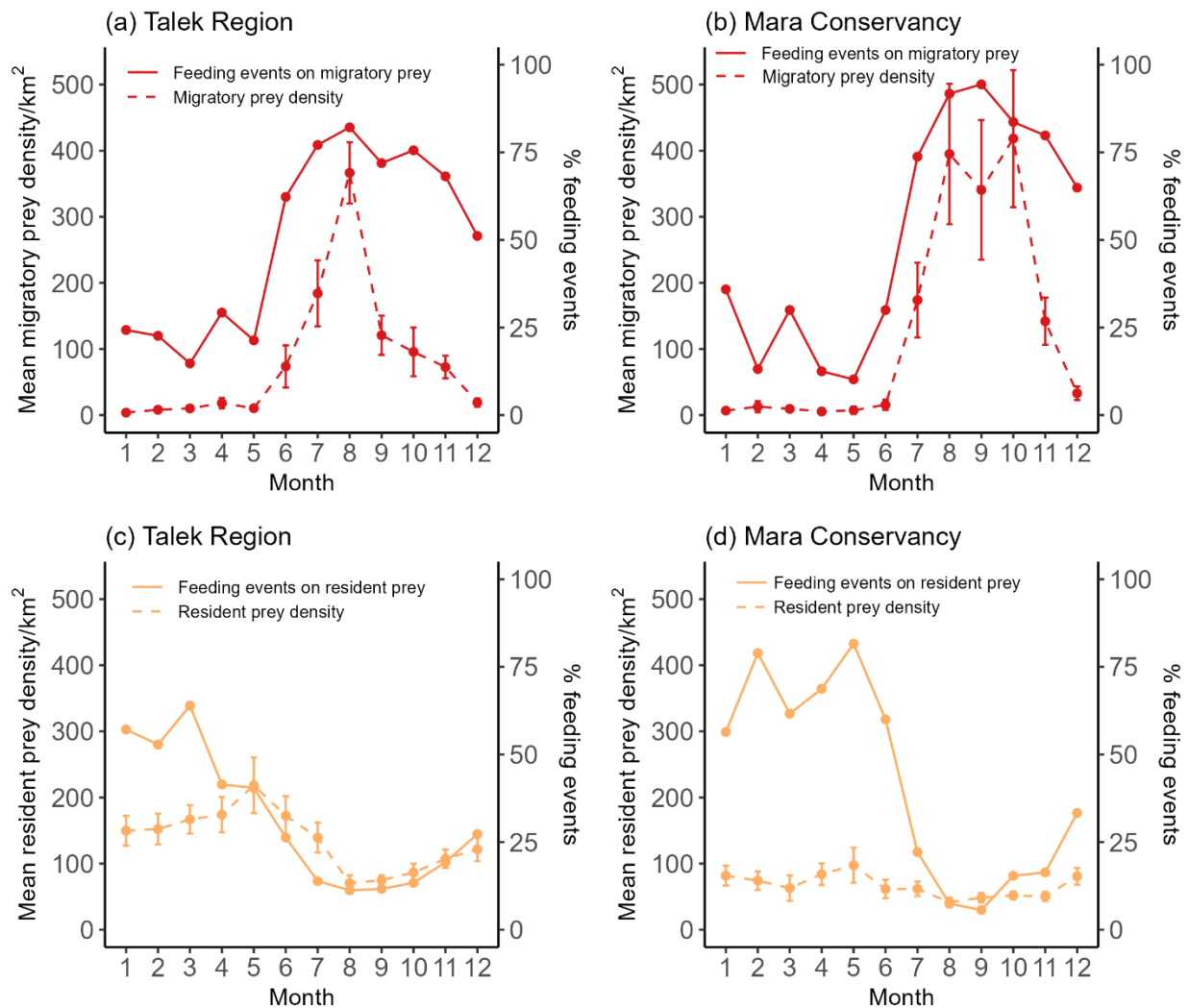


Figure 3.6. Monthly proportion of hyena feeding observations on different resident prey species from July 2008 to December 2019 in the (a) Talek Region and (b) Mara Conservancy, Kenya. The category “other antelope” included dik dik, hartebeest, reedbuck, and waterbuck.

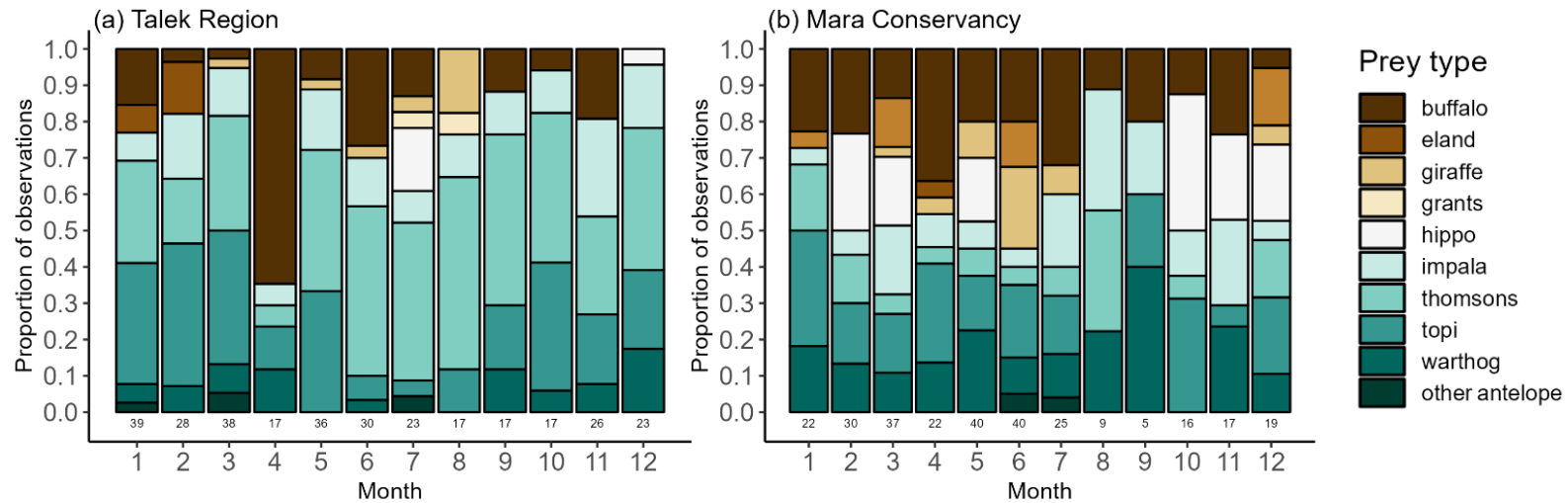


Figure 3.7. Monthly mean prey density and proportion of hyena feeding observations in the Talek Region, Kenya: 1988 – 1998 (light blue), 1999 – 2008 (medium blue), and 2009 – 2019 (dark blue): (a) migratory herbivore density, (b) migratory herbivore feeding observations, (c) resident herbivore density, (d) resident herbivore feeding observations, (e) livestock counts, and (f) livestock feeding observations. Error bars represent $\pm$ SE of mean monthly prey density and livestock counts.

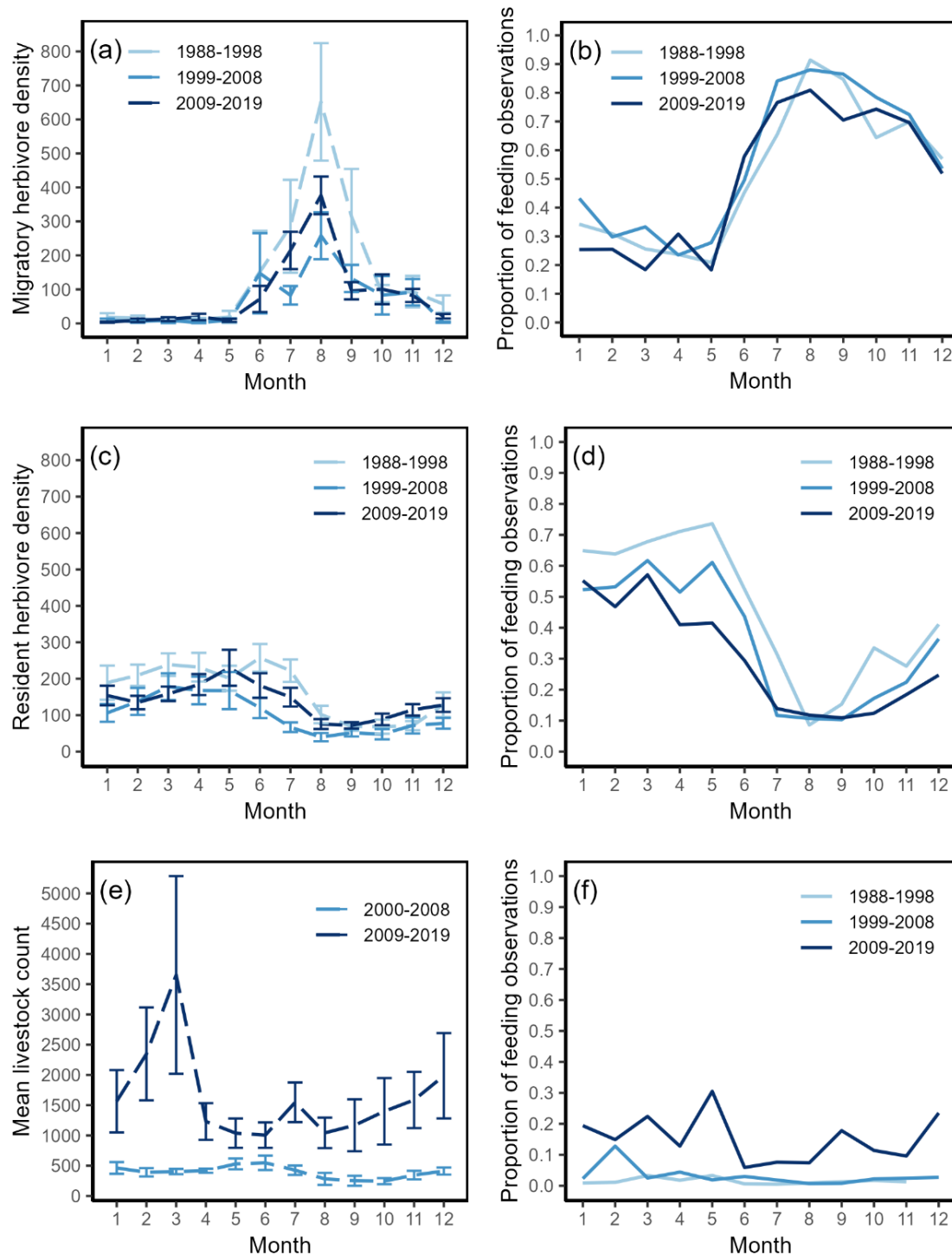


Figure 3.8. Mean annual livestock counts $\pm$ SE (dashed line) and annual proportion of hyena feeding observations on livestock (solid line) in the Talek Region, Kenya from 2000 – 2019.

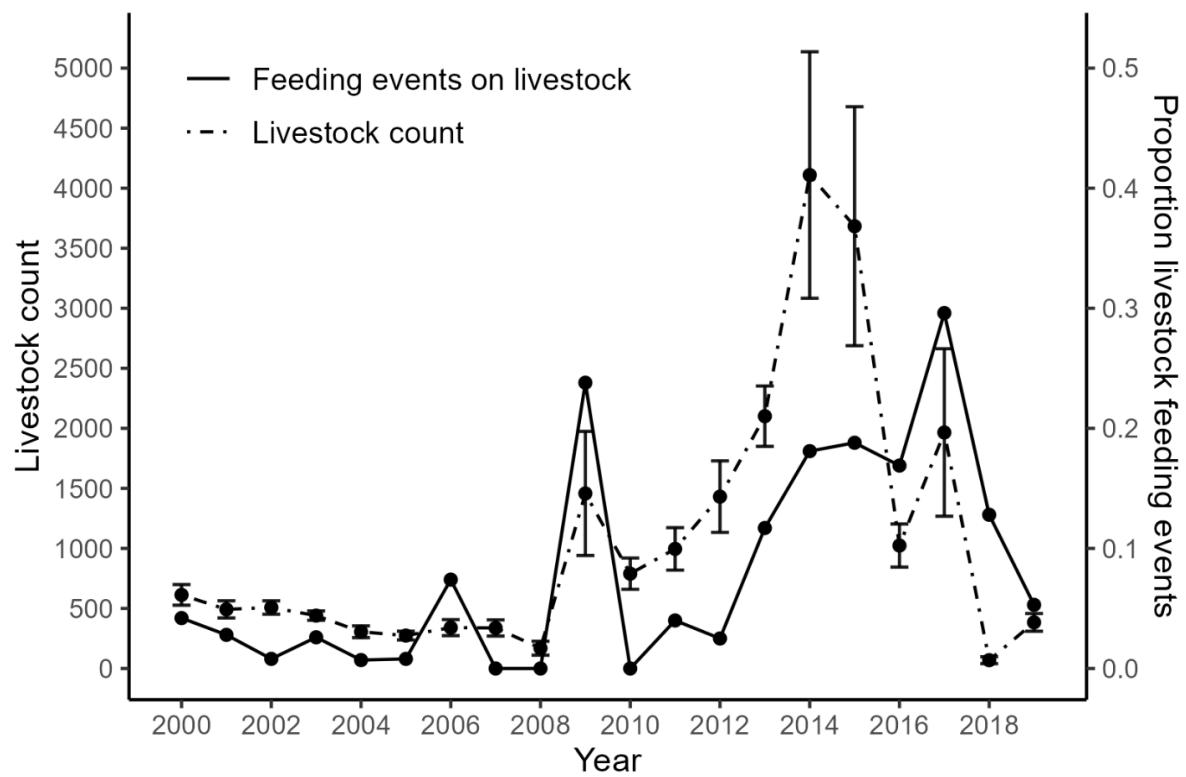


Figure 3.9. Monthly proportion of hyena feeding observations on different resident prey species by decade in the Talek Region, Kenya. The category “other antelope” includes dik dik, hartebeest, reedbucks, and waterbucks.

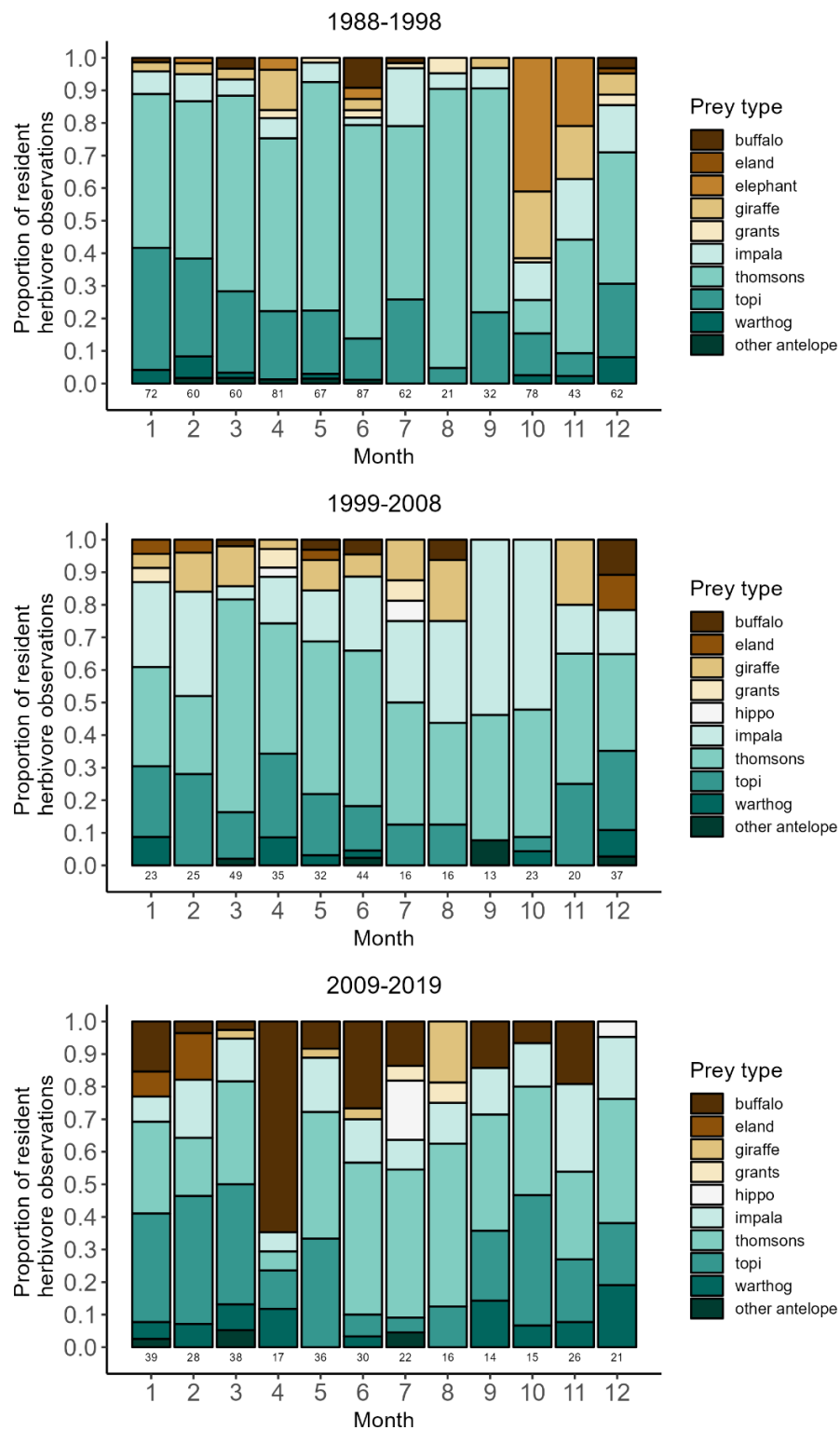


Figure 3.10. Forest plot showing odd ratios and 95% confidence intervals of the fixed effects from models of observed hyena feeding behavior on migratory herbivores and resident herbivores in the Talek Region, Kenya. Odds ratios > 1 indicate increased odds of feeding on that respective prey type, while odds ratios < 1 indicate decreased odds of feeding on that prey type. *** indicates p-value of < 0.001, ** indicates p-value of < 0.01, and * indicates p-value of < 0.1.

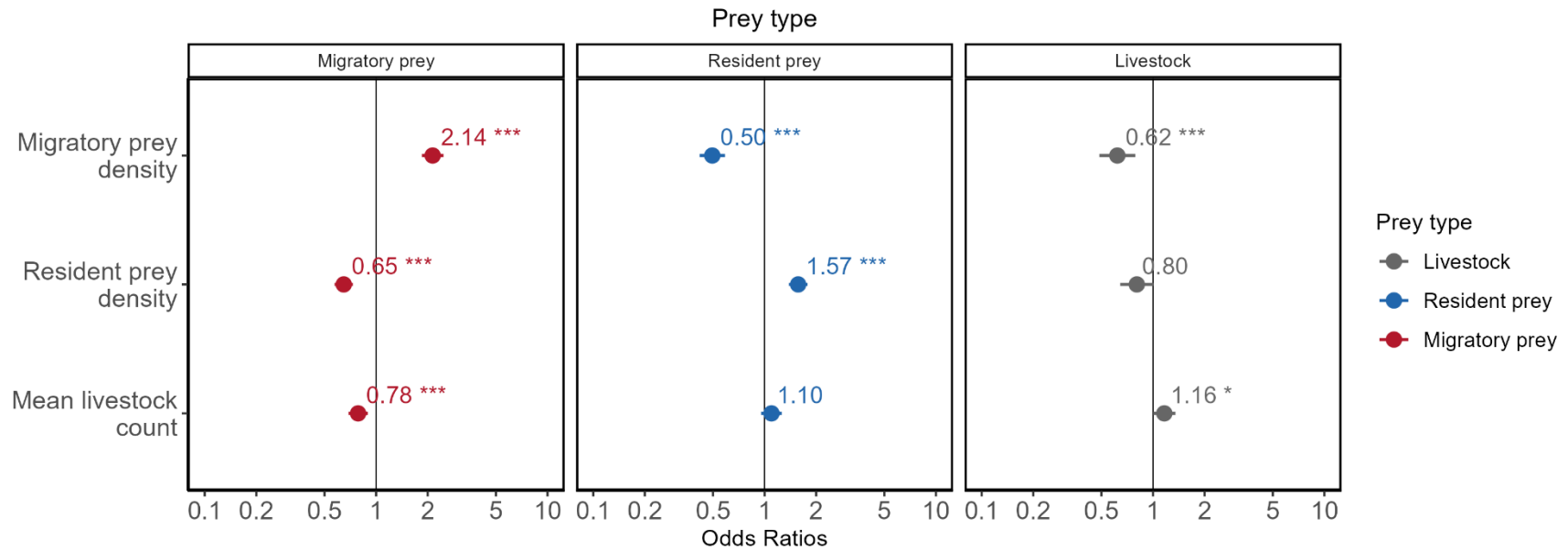
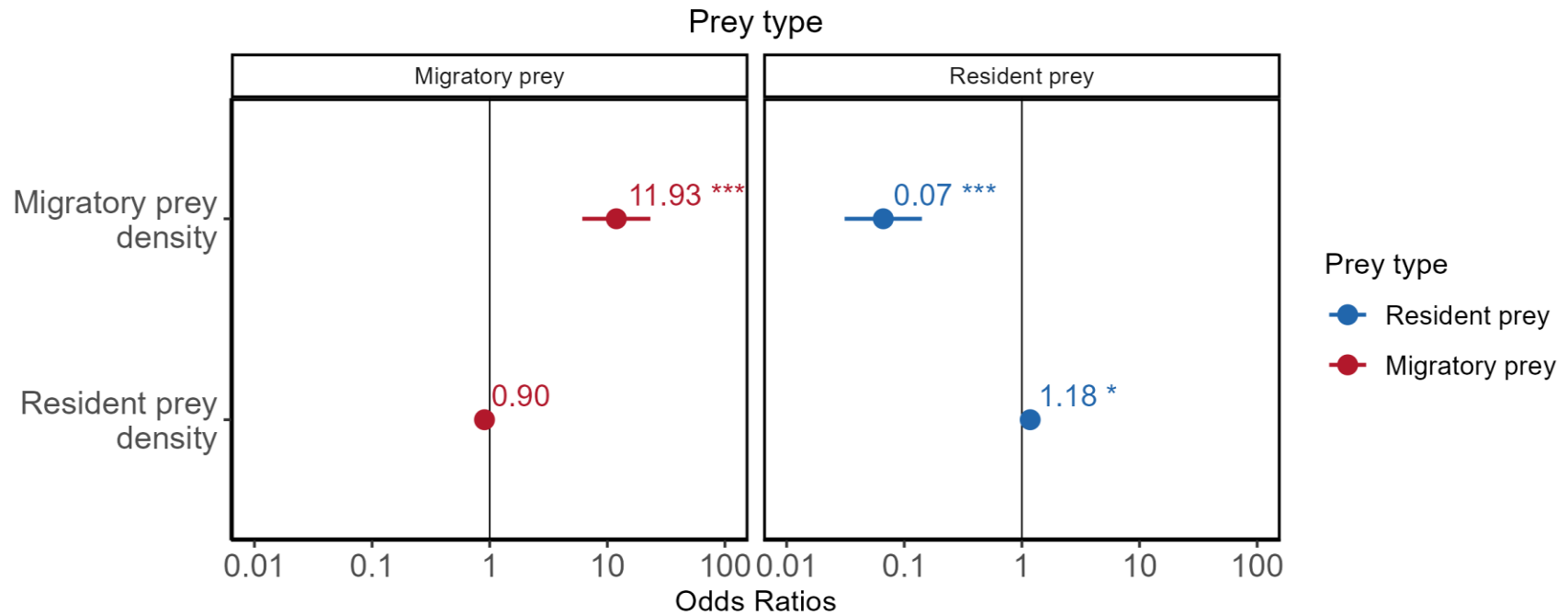


Figure 3.11. Forest plot showing odd ratios and 95% confidence intervals of the fixed effects from models of observed hyena feeding behavior on migratory herbivores and resident herbivores in the Mara Conservancy, Kenya. Odds ratios > 1 indicate increased odds of feeding on that respective prey type, while odds ratios < 1 indicate decreased odds of feeding on that prey type. *** indicates p-value of < 0.001, ** indicates p-value of < 0.01, and * indicates p-value of < 0.1.



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