SEX AND INDIVIDUAL DIFFERENCES IN AGONISTIC BEHAVIOR
OF SPOTTED HYENAS (*CROCUTA CROCUTA*):
EFFECTS ON FITNESS AND DOMINANCE

By

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ABSTRACT

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Agonistic behavior can be observed across all taxa arising from a common need to compete over limiting resources. Within species, individual variation of agonistic behavior can allow individuals to acquire and maintain limiting resources leading to higher reproductive success or fitness. However, what is often overlooked in studies of agonistic behavior is submissiveness, and how this aspect of agonistic behavior relates to aggressiveness. Further, historical studies of agonistic behavior among social mammals are biased towards studies of male agonistic behavior, often ignoring aspects and effects of female agonistic behavior. Here, I address these knowledge gaps through a long-term study of a free living highly gregarious mammal, the spotted hyena (*Crocuta crocuta*). Spotted hyenas offer an excellent model system for studying variation in aggressive and submissive behavior within individuals and between sexes, as they live in complex societies formed around a female dominated, or matrilineal, hierarchy that is enforced through constant agonistic interactions. For this dissertation, I utilized 30 years' worth of consistently recorded behavioral data collected by Dr. Kay E. Holekamp and her team from free living hyenas residing within the Masai Mara National Reserve, Keyna. Because this dissertation involved many collaborations with other scientists, I use "we" throughout this abstract to describe participation in each chapter. In Chapter 1, we describe sexually dimorphic traits within spotted hyenas that fit common mammalian patterns, as well as numerous traits that violate mammalian norms, including sex

differences in agonistic behavior. In particular, adult female spotted hyenas are significantly more likely to emit unsolicited acts of aggression down the hierarchy than adult breeding males, and females do so significantly more ferociously, or intensely. For Chapter 2, we analyzed rates and intensities of unprovoked aggressive and submissive acts emitted by adult females to determine if these two behaviors were individually consistent, as well as testing the hypothesis that these two behaviors may represent separate traits within individuals. Here we found that the intensity at which females emit aggressive and submissive behaviors are consistent, and that these traits were not correlated within individuals. Further, both consistent aggressive intensity and submissive intensity were correlated to adult female fitness, such that individuals expressing high or low extremes of these behaviors had lower annual offspring survival. Then in Chapter 3, we assessed drivers of female dominance within spotted hyenas. Within this chapter we tested two hypotheses 1) that intrinsic sex differences in agonistic behavior drives female dominance and/or 2) social support facilitates female dominance in this species. Further, we assessed these hypotheses among juvenile age classes to determine if drivers of female dominance occurred prior to sexual maturity and subsequent male dispersal. We found that females are intrinsically more aggressive both as cubs and adults, and adult males more submissive whether provoked or not. Further, social support during agonistic encounters is more likely to occur when acting against a female than a male, and adult females can dominate males with or without support. In completion, my dissertation provides interesting insights to sexual and individual variation on agonistic behavior among a social mammal.

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I am proud to finally be writing this dissertation, as this will be the greatest achievement of my professional career. It has not come easy, and considering my past, it seems implausible that I have made it this far. Fifteen years ago, I was a 25 year old high school dropout, living on the fringes of society with no friends, digging through dumpsters for food and things to sell, and lying to my family about how far I had fallen, as I just could not admit my failure and ask for help. Thankfully, a close cousin, who had gone through her own trials and tribulations, sought me out and convinced me to come clean and turn my life around. What resulted has been a journey of joy, heartache, wonder, and loss. However, now at age forty I find myself finally achieving a dream that I had shared only with my father, and with a life I can be proud of.

I want to first thank those that helped me to begin my journey: my cousin Bridgette, my aunt Beth, my uncle Bill, and my grandfather Joe, without whom none of this would have ever happened. Despite my years of deceiving my family about my failure, they accepted me, and guided me onto a new path. Had it not been for all of them I don't believe I would still be alive, let alone have received my GED and pursued a PhD. Bill and Joe, I know you have passed on, but please know how much I appreciate your support both in life and in death.

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student. She even encouraged me to apply to the University of New Mexico and helped me through the application process. It was thanks to her that I was able to seek out new mentors at UNM: Dr. Astrid Kodric-brown, who believed in me enough to allow me to join her behavior lab, Dr. Joe Cook, who allowed me to join the undergraduate research program and work in the biological museum collections, and Dr. Blair Wolf, who invited me along in his field work. All of these experiences shaped me into the scientist I wanted to become. Of course, the two individuals who had the greatest impact on my undergraduate career were Chuck Hayes and Shannon Maccoy-Hayes, who honestly stepped in as a secondary set of parents while I attended UNM, whether it was applying for fellowships, helping me learn how to complete field research, or acting as a shoulder to cry on when I failed. Without them I would have never considered applying to the graduate program at Michigan State University, let alone succeed.

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Agonistic behavior is represented across all taxa due to competition for resources within and between species (Hsu et al 2006). With respect to aggressive behavior, variation in aggressive behavior can increase fitness by increasing access to food (Lim et al 2014), mates (Kwek et al 2021), territory (Perrone et al 2019) and offspring defense (Krieg & Getty 2020). Within social species, agonistic behavior can also act as a form of communication that can lead to stable hierarchies (Holekamp & Strauss 2016), which also leads to fitness advantages for individuals of higher rank (Strauss & Holekamp 2019). Agonistic behavior also presents a fitness trade off through the loss of energy (Xu et al 2018) and time, and of course risk of injury (Georgiev et al 2013). Many of these costs may well explain why agonistic behavior may vary between sex, as typically the sexes have differential investment in gametes, parental care, and competition for access to mates (Hunt et al 2009; Safari & Goymann 2021).

Additionally, variation in agonistic behavior among individuals within a species can be due to many reasons, such as underlying genetic differences (Heyne et al 2014), hormonal and neurotransmitter variation (Nelson & Trainor 2007), and variation in ontogeny (Haller et al 2014). For example, allelic variation between individuals in genes contributing to brain development can have lasting effects on agonistic behaviors (Mejia et al 2002). Additionally, variation in gene expression, through epigenetic modifications, has been linked to expression of aggressive behavior (Mustafin et al 2019). Many of these factors in turn can be affected by differences in ontogeny, such as variation in in-utero exposure to hormones (Dela-Cruz & Pereira 2012), or maternal care (Veenema 2009), or even interactions with group mates during juvenile development (Nelson & Trainor 2007; Haller et al 2014).

While a great deal is known about the evolutionary history, current utility, ontogeny, and mechanism of agonistic behavior, there is still much to investigate. In some cases, variation in agonistic behavior that may be shared across species are overlooked due to variation in scientific interest. For example, female agonistic behavior and competitive ability has only received major focus and funding in the past half century (Björkqvist & Niemelä 1992). This may be because males are typically the more easily observed sex, as male-male competition over mates is more common across taxa (Safari & Goymann 2021), and female mate choice can lead to competitive traits in males (Hunt et al 2009). This may have biased the early scientific community to focus on male aggression over female aggression. However, studies have come to light presenting the importance of female aggression (Stockley & Campbell 2013), including in taxa where females are the dominant sex within social groups or where sex roles appear reversed (Safari & Goymann 2021).

Another area of agonistic research that needs greater focus is that of individual variation in agonistic behavior in free living social species; particularly as the goal of many behavioral ecologists is to compare and contrast natural human behavior to natural animal behavior. Variation in consistent [is this a correct phrasing?] individual differences, or personalities, in agonistic behavior has been identified in many social mammalian species (Gosling & John 1999). However, within animal studies of agonistic personalities, an area that is often overlooked is the difference between aggressive behavior and submissive behavior, and the separate effects these two agonistic behaviors may have on social interaction and fitness. This could be due to the focus of aggressive behavior on dominance relationships, where dominants "win" by using aggressive behavior to elicit a submissive response (Gammel et al 2003; De vries el al 2006). However, it has been postulated that these agonistic traits may in fact vary independently within an individual (Nelson & Kriegsfield 2017). This independent variation of aggressive and submissive traits within and

individual may well be supported by varying mechanism underlying these components of agonistic behavior (Kiser et al 2012; Lischinsky & Lin 2020).

Therefore, we would like to present a model social mammalian species and study system that can, to some extent, approach the issues presented here. The spotted hyena (*Crocuta crocuta*) is a large mammalian carnivore, which persists in complex social groups that appear evolutionary convergent with cercopithecine primates (Holekamp 2017). The hyena social groups, called clans, present a strict matrilineal dominance hierarchy (Holekamp et al 1996). Females are philopatric, or stay with their natal clans for life, while males disperse upon reaching sexual maturity (Holekamp and Smale 1998a). These clans can be quite large compared to many mammalian carnivore groups, but they exist in fission fusion societies (Smith et al 2008) that maintain strict territorial boundaries between other spotted hyena clans (Boydston et al 2001). Within these territories, females will give birth at a natal den and following 2 weeks of cub maturation the mothers will transfer cubs to a communal den shared by other members of the clan (Holekamp & Smale 1998b). Here, cubs will develop together both physically and socially. Spotted hyenas also express a complex repertoire of agonistic behaviors that have already been shown to present individual consistency (Yoshida et al 2016). Most importantly, a population of spotted hyenas has been under study for behavioral assays for the past 30 years by the Mara Hyena Project, Kenya. This population has provided the data for this dissertation.

It the first chapter we review sex differences in spotted hyenas to find a mosaic of dimorphic traits, some of which conform to mammalian norms and some of which contrast. For example, sex differences in dominance are apparent in neonates and adulthood but are less prominent in intermediate developmental stages. Additionally, the virilization, development of male characteristics (Glickman et al 2006), of the female spotted hyena also raises questions about sex differences in behavior and morphology.

In chapter 2, we utilized a long-term dataset of over 50,000 dyadic agonistic interactions among spotted hyenas that included acts of unsolicited aggressive and unsolicited submissive behaviors, to quantify consistent individual variation in these behaviors. Further, we linked these individual differences to current evolutionary utility by assessing how individually consistent traits effected offspring survival.

In chapter 3, we examined the mechanisms that underly variable patterns of female dominance across ontogeny. Our focus here was on two mechanistic hypotheses explaining the occurrence of female dominance: that either females dominate males because they receive more social support than males, and/or they are inherently more aggressive than males. Again, we used the Mara Hyena Project's 30 years behavioral database to determine how sexes differ in rates of agonistic behaviors within adult of each sex, and followed by determining if these patterns were present during juvenile development. Then we determined how often males and females within each age-class win dyadic agonistic encounters. Last, we analyzed how much social support members of each sex and age-class receive during agonistic encounters from their groupmates, and how this support affects fight outcomes.

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CHAPTER ONE:

SEX DIFFERENCES IN SPOTTED HYENAS

ABSTRACT

The apparent virilization of the female spotted hyena raises questions about sex differences in behavior and morphology. We review these sex differences to find a mosaic of dimorphic traits, some of which conform to mammalian norms. These include space-use, dispersal behavior, sexual behavior, and parental behavior. By contrast, sex differences are reversed from mammalian norms in the hyena's aggressive behavior, social dominance, and territory defense. Androgen exposure early in development appears to enhance aggressiveness in female hyenas. Weapons, hunting behavior and neonatal body mass do not differ between males and females, but females are slightly larger than males as adults. Sex differences in the hyena's nervous system are relatively subtle. Overall, it appears that the 'masculinzed' behavioral traits in female spotted hyenas are those, such as aggression, that are essential to ensuring consistent access to food; food critically limits female reproductive success in this species because female spotted hyenas have the highest known energetic investment per litter of any mammalian carnivore. Evidently natural selection has acted to modify traits related to food access, but has left intact those traits that are unrelated to acquiring food, such that they conform to patterns of sexual dimorphism in other mammals.

INTRODUCTION

Spotted hyenas (*Crocuta crocuta*) are large mammalian carnivores that occur throughout sub-Saharan Africa. They exhibit many unique and fascinating characteristics, such as living in large, complex societies where they must compete and cooperate with non-kin as well as kin. However, the aspect of the biology of spotted hyenas that many people find most intriguing is the apparent 'masculinization' of females. This female virilization manifests itself in several obvious ways. For example, in contrast to the situation characteristic of most other mammalian species, female spotted hyenas are larger than males, they are socially dominant to males, and they exhibit genitalia that are astonishingly male-like. These 'sex role-reversed' traits coexist in the same individuals with other sexually dimorphic traits that are much like those exhibited by virtually all 'typical' female mammals, such as dogs, antelope, rats and baboons. The hyena's chimeric blend of feminine and 'masculinized' traits is particularly intriguing because it raises so many questions about how and why some traits have been 'masculinized' in this species whereas others have not. Here we summarize existing information about sexually dimorphic traits in the behavior and morphology of spotted hyenas. We will consider sexually dimorphic traits in adults of this species, including both those that are "reversed" from patterns found in most other mammals and those known to show the same patterns of dimorphism typical of other mammals. Wherever possible, we also briefly review what is known about the development of sexually dimorphic traits in spotted hyenas. Finally, we discuss the adaptive significance of sexually dimorphic traits in this species.

SEX DIFFERENCES IN BEHAVIOR

Sex differences in space use, territory defense and dispersal

Spotted hyenas live in sTable Aocial groups, called 'clans', that may contain up to 130 individuals. They defend group territories against encroachment by neighboring

conspecifics. They engage in border patrols and 'wars' with neighboring clans. In contrast to many other mammals that defend group territories, female hyenas initiate and lead most territorial advertisement and defense efforts. Females are more likely than males to lead border patrols and clan wars, and females tend to scent-mark along territorial boundaries at higher hourly rates than do adult males. (Henschel & Skinner 1991; Boydston et al. 2001). Thus, female hyenas are willing to assume more risks and expend more energy during territorial defense than are males. These sex differences are consistent with the hypothesis that male and female clan members derive different selective benefits from advertisement and defense of group territories. Defense of food resources appears to be the primary function of territoriality in spotted hyenas (Kruuk 1972; Henschel & Skinner 1991). Indeed, it appears that natural selection has favored female spotted hyenas to maintain boundaries of a territory that supports enough herbivore prey to feed themselves and their young throughout the year.

In other respects, the territorial and space-use behavior of spotted hyenas resembles that of other territorial mammals. For instance, during territorial encounters between residents and aliens, residents are more likely to attack same-sex than opposite-sex intruders (Boydston et al. 2001). As also occurs in most other social mammals, male spotted hyenas disperse from their natal clans after they reach reproductive maturity whereas females are philopatric and spend their entire lives in the natal clan (Smale et al 1997; Honer et al. 2007). No measures of space use are sexually dimorphic among young hyenas until these animals are approximately 30 months of age, which is roughly 6 months after they reach reproductive maturity. Late in the third year of life males start making exploratory excursions into the territories of neighboring clans whereas females do not; these sex differences in space-use persist throughout the remainder of the life span; males are found farther from the geographic center of their natal territory than are females, and the

mean size of individual home ranges is larger for males than females (Boydston et al. 2005). As adults, male spotted hyenas travel 17.7 km/day whereas females travel only 12.36 km/day (Kolowski et al. 2007).

Sex differences in reproductive behavior

Although copulation is rather challenging for male spotted hyenas because of the female's unusual external genitalia (see below), otherwise spotted hyenas exhibit the same suite of sex differences in reproductive behavior as those typical of other mammals. For instance, males approach females at higher rates than vice versa (Szykman et al. 2007), although, in contrast to most other male mammals, male spotted hyenas appear to be extremely nervous when courting females. Copulation involves the male mounting the female and inserting his erect penis into the female's flaccid clitoris. Both males and females mate promiscuously (Szykman et al. 2007).

Hyenas are born in litters that usually contain only one or two cubs, but maternal investment in each cub is enormous. As occurs in most mammals, female spotted hyenas do all the parenting; the low social status of sires effectively prevents them from being able to assist their offspring even to the same small extent as males can assist their young in other polygynous, group-living mammals (e.g., baboons, Buchan et al. 2003). Spotted hyena cubs rely exclusively on their mother's milk during the first six months of life, and although they then start eating some solid food, cubs continue to rely largely on milk until they are weaned, which typically occurs at 12-20 months of age (Kruuk 1972; Hofer & East 1995; Holekamp et al. 1996); this represents an extremely protracted lactation period relative to those of other carnivores of similar body mass. For example, canid and felid species the same size as, or larger than, spotted hyenas wean their young when they are only 1.1 to 6 months of age, including species as large as wolves, lions, and tigers (Watts et al. 2009). The milk produced by spotted hyenas is also unusually rich; it has the highest

protein content of milk from any fissiped carnivore (Hofer & East 1996), a fat content

exceeded only by that of milk produced by palearctic bears and sea otters, and a higher

gross energy density than the milk of most other terrestrial carnivores (Hofer & East 1995).

Due to the high energy content of their milk and the long period of lactation, spotted hyenas

have the highest energetic investment per litter of any mammalian carnivore (Oftedal &

Gittleman 1989; Hofer et al. 2016). It follows that two critical factors affecting cub growth

and survival are maternal access to food (Swanson et al. 2009; Holekamp & Strauss 2020)

and nursing frequency (Hofer et al. 2016), both of which vary with maternal social rank.

Sex differences in aggression and dominance among adults

Adult female spotted hyenas are socially dominant to all adult males not born in the

females' natal clan, so females can straightforwardly displace immigrant males from desired

resources such as food (Kruuk 1972; Mills 1990). Natal animals of both sexes acquire ranks

immediately below those of their mothers via a prolonged learning process early in

development, so they can dominate all immigrant males. However, most males disperse

before breeding and behave submissively to all new hyenas encountered outside the natal

territory. Thus, the mechanisms by which adult social rank is acquired differ between male

and female hyenas. Females maintain their natal ranks as long as they live in the natal clan;

females do this largely by behaving aggressively to lower-ranking clan-mates. In contrast,

when males disperse to new clans, they assume the lowest possible rank in the new clan,

where they follow a queuing convention in which the most recent immigrant is the lowest

ranking animal in the entire clan (East & Hofer 2001; Smale et al. 1997). Males only

improve their status when higher-ranking immigrants die or engage in secondary dispersal,

which occurs in roughly 40% of males (Van Horn et al. 2003).

Although some have argued that female dominance among spotted hyenas is strictly

due to more social support for females than males (e.g., Vullioud et al. 2019), compelling

evidence indicates that behaviors associated with the acquisition and maintenance of social rank are strongly sexually dimorphic in this species, and in fact require no social support. Female spotted hyenas emit aggressive acts at higher rates than do males (Figure 1.1 a), they emit more intense aggressive acts (Figure 1.1 b), they are more tenacious fighters (Figure 1.2), and they exhibit unambiguous "role-reversed" sex differences in aggressive behavior from a very young age. Thus, in contrast to most mammals, female spotted hyenas are substantially more aggressive than males (Szykman et al. 2003; McCormick & Holekamp in review). This notion is also supported by wounding data obtained from the several hundred spotted hyenas we have immobilized in Kenya (Figure 1.3). These data show clearly that adult females bear many more wounds, on average, than do adult males; this is the opposite of the pattern found in most other mammals (e.g., primates, Smuts 1987; rodents, Michener 1988). Interestingly, the sex difference in wounding among hyenas does not emerge until adulthood, as males and females 24 months of age or less do not differ in wounding frequency (Figure 1.3). If most wounds were caused by prey animals during capture, we would expect male and female hyenas to show similar rates of wounding because adults of both sexes are equally successful at hunting their own prey (Holekamp et al 1997). However, the finding that females sustain so many more wounds than males is consistent with the idea that most wounding occurs during fights over carcasses. Males almost invariably defer to females at kills whereas other females often do not (Kruuk 1972), and fights among males are typically far less intense than those among females. Our wounding data are consistent with both these behavioral tendencies.

Ontogenetic development of sex differences in aggression

Sex differences in aggressive behavior emerge during the first days of life in young spotted hyenas. Newborn spotted hyenas often fight vigorously with their siblings during the first days or weeks after birth to establish intra-litter ranks (Frank et al. 1991; Smale et al.

1999; Wachter et al. 2002; Wahaj and Holekamp 2006). Once intra-litter ranks have been established, the rates and intensities at which siblings fight decline; intra-litter aggression rates also decline with increasing maternal rank (Golla et al. 1999; Smale et al. 1999). When litters are of mixed sex, females dominate their male siblings 67 to 84% of the time (Smale et al 1995; Golla et al. 1999; Wahaj et al. 2006; Benhaiem et al. 2012). Thus, female spotted hyenas evidently come into the world behaving more aggressively than their male peers.

This trend persists throughout ontogeny. The proportion of dyadic fights with lower-born adult females won by hyenas 6-36 months of age is significantly greater for young females than for their male peers (Smale et al. 1993). Subadult females also dominate lower-born adult females more consistently than do subadult males. That is, although young males can often displace lower-born adult females from desired resources, their rank relationships with lower-born adult females often remain unstable until males disperse from their natal clans (Smale et al. 1993). Furthermore, juvenile females are more persistent than their male peers in their attempts to outrank adult females. For instance, juvenile females are more likely than their male peers to counter-attack lower-born females who attack them (Figure 1.2; also see Smale et al. 1993). Thus, although aggression rates come to be strongly affected by social rank in adulthood (McCormick & Holekamp 2022), sex differences in aggressive behavior are apparent from birth in this species.

Exposure to androgens early in development appears to enhance aggressiveness in female spotted hyenas. In the wild, both juvenile and adult females whose mothers have higher androgen concentrations during gestation are considerably more aggressive than are same-age females exposed to lower androgen concentrations *in utero* (Dloniak et al 2006; Holekamp et al. 2013). Furthermore, experimental exposure to anti-androgens during development *in utero* reduced female aggressiveness later in life among captive hyenas at

the Berkeley hyena colony. Pregnant females were treated throughout gestation with a cocktail of anti-androgens (AA: flutamide and finasteride), and the behavior of the offspring from those pregnancies was assessed throughout development. For many years after the AA-treated hyenas reached adulthood, investigators were unable to identify any obvious effects of the prenatal AA-treatment on aggressive behavior. In particular, AA-treated females were always the winners over control and AA-treated males in single-bone dyadic tests, wherein two hyenas compete for a single bone tethered to a fence within an enclosure. However, as the Berkeley Hyena Project neared its end, the bone dyad test was modified to include two bones. Only two double-bone dyad tests were completed before the colony closed, one with a control female and the other with an AA-treated female, where each was paired with an untreated male. In their single-bone dyad tests with these same males, both females always won, securing all bones for themselves by aggressively displacing the males from proximity to the tethered bones. However, whereas the control female secured both bones for herself in the double-bone test while keeping the male at bay, the AA-treated female allowed the male to have the second bone and feed on it beside her. No untreated captive females or females in the wild ever share food with unrelated males, so even with a sample size of only one, the experimental treatment effects here were highly suggestive. A video showing both control and treatment trials is available in the Supplementary Materials.

The striking sex differences seen in aggression and dominance in spotted hyenas have clear adaptive value, as higher rates of aggressive behavior enhance reproductive success among females (McCormick & Holekamp in review; Yoshida et al. 2016; Watts et al. 2009) but not among males (Hofer & East 2012). Furthermore, the establishment of dominance over other females has a much greater influence on the fitness of females than males. Similarly, although rank reversals among adult females are rare in this species,

improving one's social status via rank reversals is far more critical to females than males, as the effects of rank reversals are amplified in later generations (Strauss & Holekamp 2019). The uniquely heavy energetic demands of lactation in this species (Oftedal and Gittleman 1989) cause improved access to food resources, often accomplished via aggressive displacement of group-mates from carcasses, to be far more important for female than males (Holekamp & Strauss 2020), and females are clearly willing to fight to maintain or improve their priority of access to food.

SEX DIFFERENCES IN MORPHOLOGY

Body size and shape

Sexual size dimorphism is common among mammals; in most species, including most other mammalian carnivores, males on average are larger than females. In contrast, the spotted hyena is one of the rare species in which females are generally larger than males. We took 14 different body measurements from several hundred wild hyenas in Kenya, and found that, although many body size measures differ only by 1 to 5 % between the sexes, and although distributions of most size measures overlap for males and females, these sex differences are strongly statistically significant (Swanson et al. 2013). The largest sex differences in body size in spotted hyenas appear in measures of head and neck circumferences, body mass and girth, indicating that adult females are roughly 10% brawnier than males. These traits are larger in adult female hyenas than adult males even when the two sexes are fed identical diets while housed alone throughout development in captivity, allowing us to rule out a strictly environmental explanation for this dimorphism (Swanson et al. 2013). Because the fundamental frequencies of some hyena vocalizations vary with girth measurements and because girth is strongly sexually dimorphic in this species, adult females have deeper voices than adult males in their whoop and groan

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vocalizations (Theis et al. 2007; Mathevon et al. 2010), so these calls inform listeners about the sex of callers.

Female spotted hyenas are larger than males because they grow faster, rather than exhibiting a longer period of growth (Swanson et al. 2013). Eleven sets of male and female littermates born as mixed sex twins at the Berkeley hyena colony did not differ in mass at birth; on average, both sexes weighed 1.5 kg at birth (Figure 1.4 a). However, there was a significant effect of litter size on mass at birth, with singletons being heaviest and members of triplet litters being lightest (Fig 4b). Early in postnatal life males and females appear to grow similarly, but between weaning and reproductive maturity their ontogenetic growth trajectories diverge. Female growth rates increase relative to those of males as animals approach sexual maturity. Traits that mature before divergence of these ontogenetic trajectories are monomorphic, whereas traits that mature later are dimorphic (Swanson et al. 2013). Although it is difficult to distinguish young males from young females, in adulthood, female spotted hyenas are visibly brawnier than their male peers (Figure 1.5).

The teeth of a spotted hyena, particularly the incisors and canine teeth, are its primary weapons, but neither the canines nor the incisors differ significantly between the sexes in spotted hyenas (Van Horn et al. 2003). However, in adulthood, the height of the lower canine tooth tends to be slightly larger in females than males, so if any sexual dimorphism exists at all in weaponry in this species, females may have a slight advantage.

External Genitalia

The external genitalia of female spotted hyenas are unique among mammals. The clitoris is greatly elongated to form a fully erectile structure (Figure 1.6), with a single urogenital tract passing from the tip of this structure into the caudal region of the abdomen (Matthews 1939; Racey & Skinner 1979; Neaves et al. 1980). The female's enlarged clitoris is not as slender as the male's penis (Glickman et al. 2005), and the clitoris is slightly

shorter (mean = 17 cm) than the male's penis (mean=19 cm) (Drea et al. 2002; Neaves et al.1980). Furthermore, the glans of the phallus is blunt and barrel-shaped in females whereas it is angular and pointed in males (Figure 1.7; Cunha et al. 2003; Frank et al. 1990). Nevertheless, the female's external genitalia look remarkably like those of the male (Figures 1.5, 1.6 & 1.7). In female spotted hyenas, these unusual genitalia are present at birth. 'Masculinization' of their genitalia is not as strictly androgen-dependent (Drea *et al.* 1998; Cunha et al. 2005; Conley *et al.* 2020) as it is in other mammals (Herman *et al.* 2000). Initial prenatal development of the external genitalia in both sexes is largely free of androgenic influence (Glickman et al. 2006); however, elevated androgen concentrations in late gestation influence the development of both genital morphology and behavior (Drea et al. 2002; Dloniak et al. 2006; Holekamp et al. 2013). Furthermore, AA-treatment of pregnant females reduces the developmental influence of androgens on their fetuses (Conley et al. 2020). No adult females in other species of the hyena family have unusual genitalia, so the enlargement of the clitoris is unique to spotted hyenas. In contrast to other carnivores, including the other hyena species, the female spotted hyena has no external vaginal opening. Instead, she urinates, copulates, and gives birth through the tip of her elongated clitoris. Her vaginal labia are fused together and filled with fat and connective tissue to form a bi-lobed structure (Figure 1.6) that resembles the scrotal sac and testes of the male (Frank et al. 1990).

Although the spotted hyena's clitoris and penis are similar in length, their internal anatomies are strikingly different to match their different functions (Cunha et al. 2005). The male urethra needs only to allow for the passage of urine and ejaculate, but in addition to passing urine, the female urogenital (UG) canal that traverses the clitoris must enable her to receive the male during copulation and to give birth to cubs that weigh approximately 1.5 kg. In contrast to the male urethra, which is narrow and surrounded by the corpus

spongiosum, the female UG canal is more pleated, voluminous and expandable because it is surrounded by loose connective tissue, which facilitates the birthing process. The spotted hyena's penis and clitoris are retractable organs as a result of retractor muscles that span their lengths. However, the position of the retractor muscles relative to the urethra and the UG canal are quite different in the two sexes, with the retractor muscles being ventral to the urethra and dorsal to UG canal in males but not females. If not for this sex difference, the retractor muscles within the clitoris would surely be damaged during parturition, because the distal clitoris tears along its ventral midline (Fig. 6) during the first birth of a cub, which has a cranial diameter substantially exceeding the diameter of the clitoral meatus. Interestingly, the differences in the internal anatomies of the penis and clitoris are androgen dependent, as indicated by the effects of anti-androgens that were administered to pregnant dams starting in early gestation. Most striking was the finding that the internal penile anatomy of AA-treated males was almost completely "feminized" – the urethra was more pleated and voluminous, because it was surrounded by loose connective tissue rather than the corpus spongiosum, and the retractor muscles had shifted from the ventral to dorsal position relative to the urethra (Cunha et al. 2005). Many of the external differences between the penis and clitoris (as described above) were also erased by *in utero* AA-treatment, in that the penis was reduced in length, and the shape of the glans was feminized. This alteration proved to be functionally significant, because the males that had received the most intensive anti-androgen treatment during fetal development were incapable of copulating with receptive females (Drea et al. 2002).

In both sexes, the phallus is erect during greeting ceremonies, but during copulation, only the penis is erect while the clitoris is flaccid and retracted. The location of the clitoral opening is far more rostral than in more typical mammals, and as such, males perform penile "flips" that are used to locate the flaccid and retracted clitoris, and then pull the

opening caudally so that he can intromit. The ability of an AA-treated male to reach the clitoral opening was largely negated by the reduced length of his feminized penis. And the AA treatment also feminized the perineal muscles that contribute to the flipping behavior, i.e., the bulbocavernosus (BC) muscles (Forger et al. 1996). As a result, anti-androgen treated males are more likely to misdirect their flips (NJ Place and SE Glickman, unpubl.). Similar to the internal anatomy of the phallus, the morphology of the BC muscles is sexually dimorphic in spotted hyenas and *in utero* AA-treatment feminized the BC muscles in males. The BC muscles are innervated by spinal motoneurons located in Onuf's nucleus (see below), and the male advantage in the number of motoneurons was negated in AA-treated males.

Nervous system

Sex differences in behavior are of course mediated by differences in the nervous system. One would therefore expect to see a mosaic pattern of typical and atypical sex differences in the spinal cords and brains of spotted hyenas, as we do in the behavior and morphology of these animals. Regions such as those mediating sexual behavior (e.g., male-typical mounting and erection of the phallus), aggression and dispersal are of special interest in this regard. Although there are major obstacles impeding research on the hyena's nervous system, we are aware of five such studies. We begin with three that focused on specialized subpopulations of cells within the nervous system, and then turn to two that have taken a broader "whole brain" approach.

The first study to compare the nervous systems of male and female hyenas described spinal motor neurons located in Onuf's nucleus (Forger et al. 1996). These cells project to muscles at the base of the penis, and in most mammals they are more numerous in males than females (Sakamoto 2014). This is also the case in hyenas; adult males have approximately 20% more Onuf's neurons than do females; this difference is present at birth,

and prenatal AA-treatment feminizes the nucleus in males (Forger et al. 1996). These data might suggest that hyenas are not unusual with respect to Onuf's nucleus. However, both male and female hyenas frequently engage in greeting ceremonies in which the erect phallus of one animal is presented to another for sniffing (Figure 1.5), so perhaps motor neurons in Onuf's nucleus play a role in this behavior in both sexes (Forger et al. 1996). As male hyenas face unusual challenges associated with copulation that females do not, these behaviors may depend on the additional neurons found in the male's Onuf's nucleus. This suggests that the development of the motor neurons projecting to muscles controlling the phallus in females follows the same 'rules' as the development of the phallus itself; this in turn suggests considerable masculinization via androgen-independent mechanisms. The additional development of Onuf's nucleus in males may be mediated by androgens produced in the testes, which is the case for the phallus (Glickman et al. 2006).

The first sub-cortical region of the brain examined in spotted hyenas is the sexually dimorphic nucleus (SDN) in the preoptic area (Fenstemaker et al. 1999), which is larger in males than females in the many species in which it has been examined (McCarthy et al. 2017). This is also the case in spotted hyenas. In other species the SDN is associated with mounting, intromission and ejaculation, as well as partner preference (reviewed by Pfaff and Baum, 2018). Although the motor coordination of copulation may seem especially challenging for male hyenas, it can be decomposed into the same basic elements as seen in other species, and it is directed towards females. It is therefore not surprising that the sex difference in the SDN of hyenas would resemble that found in other mammals, i.e., that it is larger in males than in females. However, the two-fold sex difference in the hyena's SDN is considered modest compared to those in other species (Fenstemaker et al. 1999).

Rosen et al. (2006) assessed sex differences in four forebrain regions of captive hyenas with respect to the density of fibers containing the peptide vasopressin (VP). In

many other species, VP innervation of the forebrain, particularly that of the lateral septum, is associated with social behaviors such as aggression and dominance (Albers 2012), and VP innervation of the lateral septum is consistently greater in males than in females (De Vries and Panzica 2006). Rosen et al. (2006) found no sex differences in the sub-paraventricular region of the hypothalamus, anterior hypothalamic region, or anterior supraoptic region, nor was there a significant sex difference in the lateral septum, but they observed a bimodal distribution of VP fibers in this brain region in males. Specifically, they found that VP fibers were heavily concentrated in the lateral septum of all three females examined and in two of the four males, but that these fibers were virtually absent in the other two males. These authors suggested that in a natural setting VP may contribute to the heightened aggression of adult females relative to adult males that have dispersed from their natal clans, but that their two captive males with elevated VP, which were both living with peers, may have been in a pre-dispersal state, in which their aggressive behavior had not yet declined to facilitate immigration into a neighboring clan.

Sex differences have also been examined with respect to whole brains, endocranial volumes and "virtual brains" of spotted hyenas (Mann et al., 2018; Arsnov et al. 2010). Mann et al. (2018) reached the conclusion that "females have smaller brains despite having bodies that are (on average) longer and heavier," whereas Arsnov et al. (2010) found no evidence of a sex difference in overall brain size but did see regional sex differences. The methods used to collect and analyze data were quite different in these two studies so it is difficult to compare them.

Mann et al. (2018) found no sex difference in the weight of brains dissected from nine hyenas in Northern Kenya or in endocranial volumes in a collection of 60 skulls in the British Museum of Natural History (BMNH), but they did find a difference, favoring males, in a sample of 19 skulls in the Museum of Vertebrate Zoology (MVZ) at UC Berkeley. Body

lengths were greater in females than males in the BMNH collection, but there was no difference in the MVZ collection. These patterns thus suggest a difference favoring males in the BMNH sample because body size was greater in females, and in the MVZ sample because brain size was smaller in females. Reasons for these inter-population differences are not obvious. By contrast, Arsnov et al. (2010) found no evidence of a sex difference in overall brain sizes measured from a sample of 22 adult hyena skulls in the Michigan State University Museum. Here, brain volumes were measured in 'virtual' brains (endocasts) created from CAT scans of skulls; these volumes were divided by skull basal length to take body size into account. There were many differences between the protocols used by Mann et al. (2018) and Arsnov et al. (2010) that might account for what appear to be conflicting results. For example, the former study evaluated sex differences in brain size and in body length but not in brain size corrected for body length, while authors of the latter study used skull length as a proxy for body size and conducted their analysis on the corrected values.

When Arsnov et al. (2010) examined regional brain volumes (as a proportion of total brain volume) in virtual hyena brains, they found clear and interesting differences between the sexes. Specifically, the anterior cerebrum was larger in males than females, and the posterior cerebrum was larger in females than males. The latter difference is difficult to interpret because this portion of the brain contains a multitude of subregions that have a diverse array of functions but that were impossible to delineate with the endocast method. The anterior cerebrum contains primarily frontal cortex, which is associated with a variety of measures of social cognition, as well as inhibitory control. However, no differences between male and female hyenas have been found to date in either of these domains in behavioral tests (Benson-Amram and Holekamp 2012; Johnson-Ulrich and Holekamp 2017).

CONCLUSIONS

In the domains of both behavior and morphology we find in spotted hyenas a mosaic of traits: some conform to sex differences in other mammals whereas others do not (Table 1.1). We find that spotted hyenas exhibit sexually dimorphic behavior that conforms to mammalian norms with respect to space-use, dispersal behavior, sexual behavior, and parental behavior. However, we also find sex differences that are reversed from mammalian norms in the hyena's aggressive behavior, social dominance, and territory defense. Neither weapons nor hunting behavior differ between males and females, but sexual size dimorphism is distinctly reversed from mammalian norms. However, as in other mammals, the SDN in spotted hyenas is larger in males than in females (Fenstemaker et al. 1999). Similarly, the number of motoneurons innervating the perineal muscles associated with the phallus is sexually dimorphic in the conventional manner (Forger et al. 1996). Several features of VP immunoreactivity in the spotted hyena forebrain are similar to what has been described in other mammals (Rosen et al. 2006). However, contrary to what has been reported in many other species (De Vries and Panzica, 2005), the density of VP innervation of the lateral septum is not sexually dimorphic. Whether there are sex differences in overall brain size remains controversial. In any case, it is clear that 'sex role-reversed' or 'masculinized' traits coexist in the same females with other sexually dimorphic traits that are like those exhibited by virtually all 'typical' female mammals.

The female spotted hyena's chimeric blend of feminine and 'masculinized' traits raises questions about how and why some traits have been 'reversed' in this species whereas others have not. Overall, it appears that the behavioral traits that have been 'masculinzed' in female spotted hyenas are those critical to ensuring consistent access to food resources, which is the critical factor limiting reproductive success in females of this species (Holekamp & Strauss, 2020). Aggressive behavior, social dominance and territory

defense are all very important in this regard. Furthermore, because body size is not a good predictor of fight outcomes among spotted hyenas (Smale et al. 1993), larger body size does not help female hyenas win fights; instead, larger body size most likely helps females capture larger prey to help satisfy the enormous energetic demands imposed by pregnancy and lactation. Evidently natural selection has acted to modify those traits related to food access from the ancestral condition, but has left unchanged those behavioral and morphological traits that are unrelated to accessing food, such that they conform to patterns of sexual dimorphism in other mammals. The adaptive significance of the female's odd genitalia remains uncertain, although they may play a role in allowing females to select which sperm fertilize her ova.

FIGURES AND TABLES
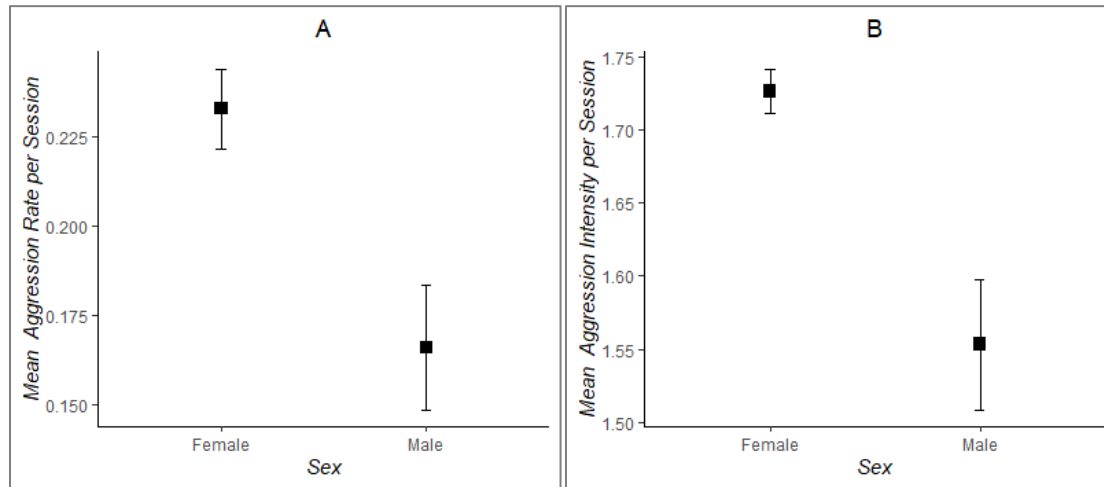
Figure 1.1: **Sex differences in the mean A) rates of emission of aggressive acts by adult hyenas (Wilcox Rank Sum Test: p < 0.001), and B) intensity of aggressive behaviors observed (Wilcox Rank Sum Test: p < 0.001) in the wild emitted by adult natal females and immigrant males.** We controlled for social rank, time observed, and immigration status. Sampled hyenas include 57 adult immigrant males and 128 adult females. Error bars represent 95% confidence intervals.
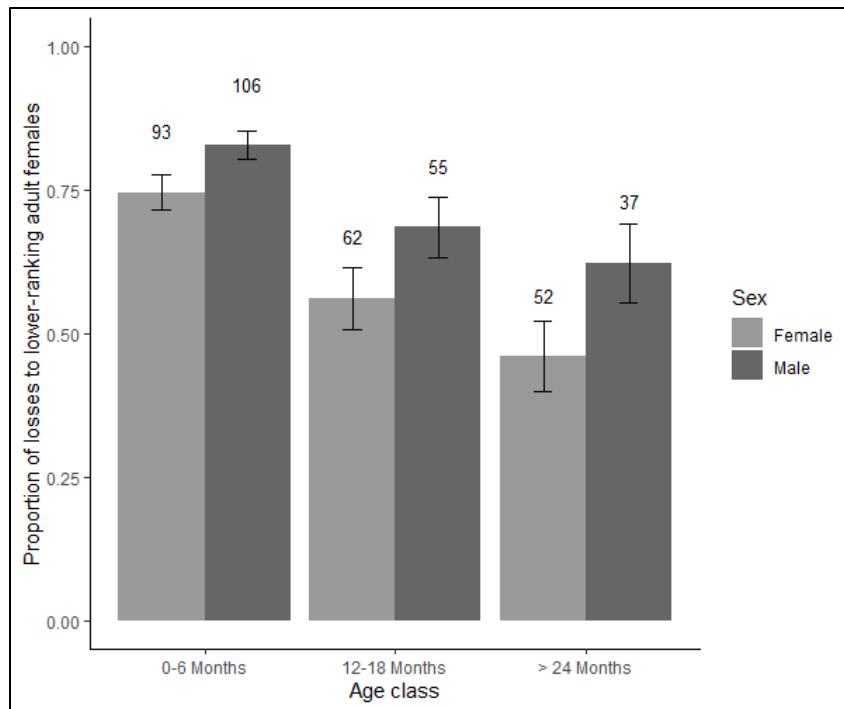
Figure 1.2: **Sex differences in losses by juvenile hyenas in aggressive interactions initiated by lower ranking adult females.** In these fights, females are more tenacious and less likely to lose than are their male peers. Bars represent the proportion of fights lost per individual in each sex and age class, error bars represent standard error of the mean, and the numbers above the error bars represent the number of individuals observed. Females are represented by pale gray bars, and males by dark gray bars. The age categories here were 0-6 months, 12-18 months, and 24-36 months. Significant differences were found based on both sex (ANOVA, F=9.71, P=0.002) and age class (F=19.05; P<0.001).
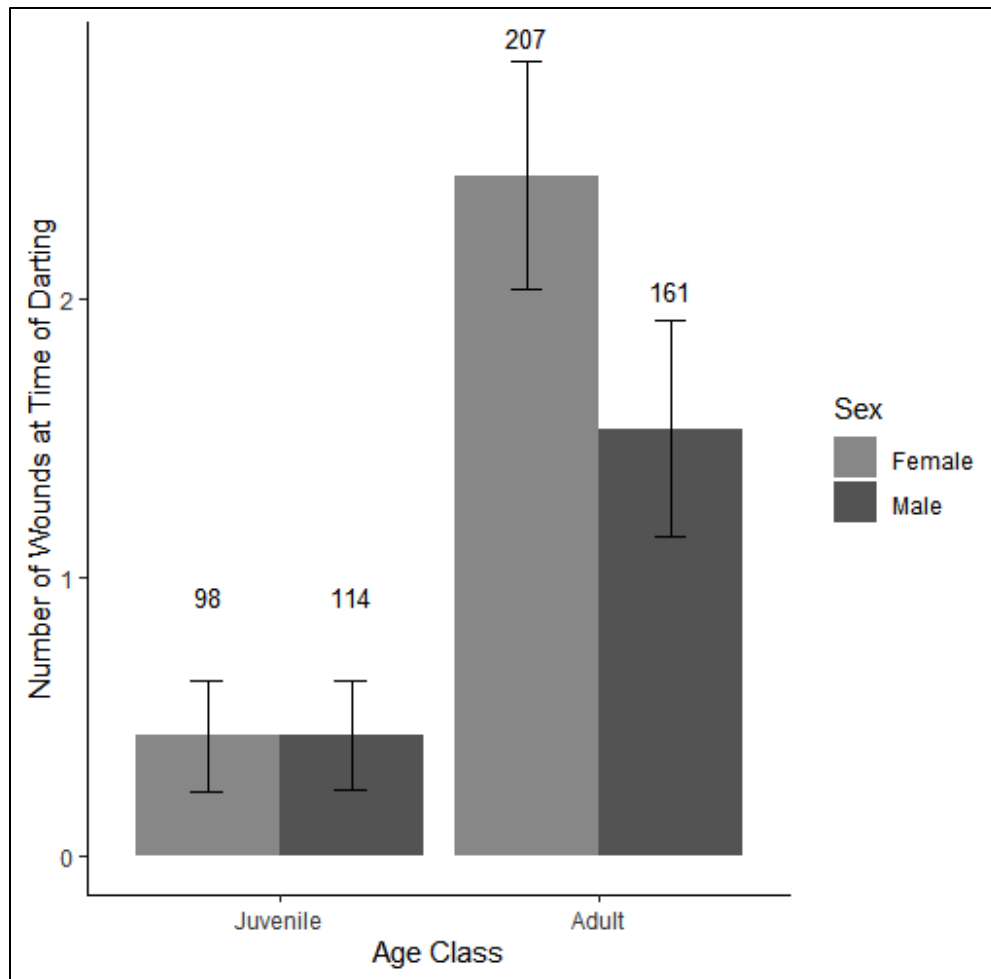
Figure 1.3: **Sex differences in the mean number of wounds among juvenile (less than 24 months) & adult (older than 24 months) spotted hyenas of each sex.** Error bars represent 95% confidence intervals. Numbers over the error bars indicate individuals sampled. Significant differences were found based on sex (ANOVA, F=5.17, P=0.024), age class (F=72.34, P<0.001), and an interaction between sex and age class (F=6.64, P=0.01).
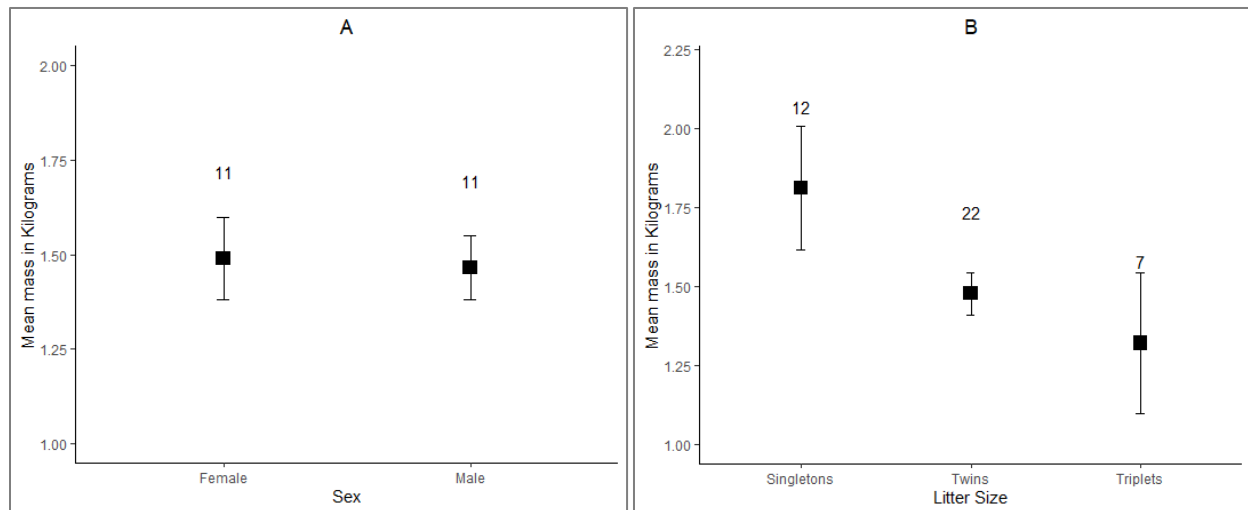
Figure 1.4: **A) There is no sex difference in body mass at birth among twin cubs born in mixed sex litters in captivity at the Berkeley Hyena Colony (Wilcox Rank Sum Test: p = 0.553); each litter contained one male and one female cub. B) Litter size does have a significant effect on cub birthweights (Kruskal Wallace Test: p = 0.0007).** Error bars represent 95% confidence intervals. Numbers over the error bars indicate individuals sampled.
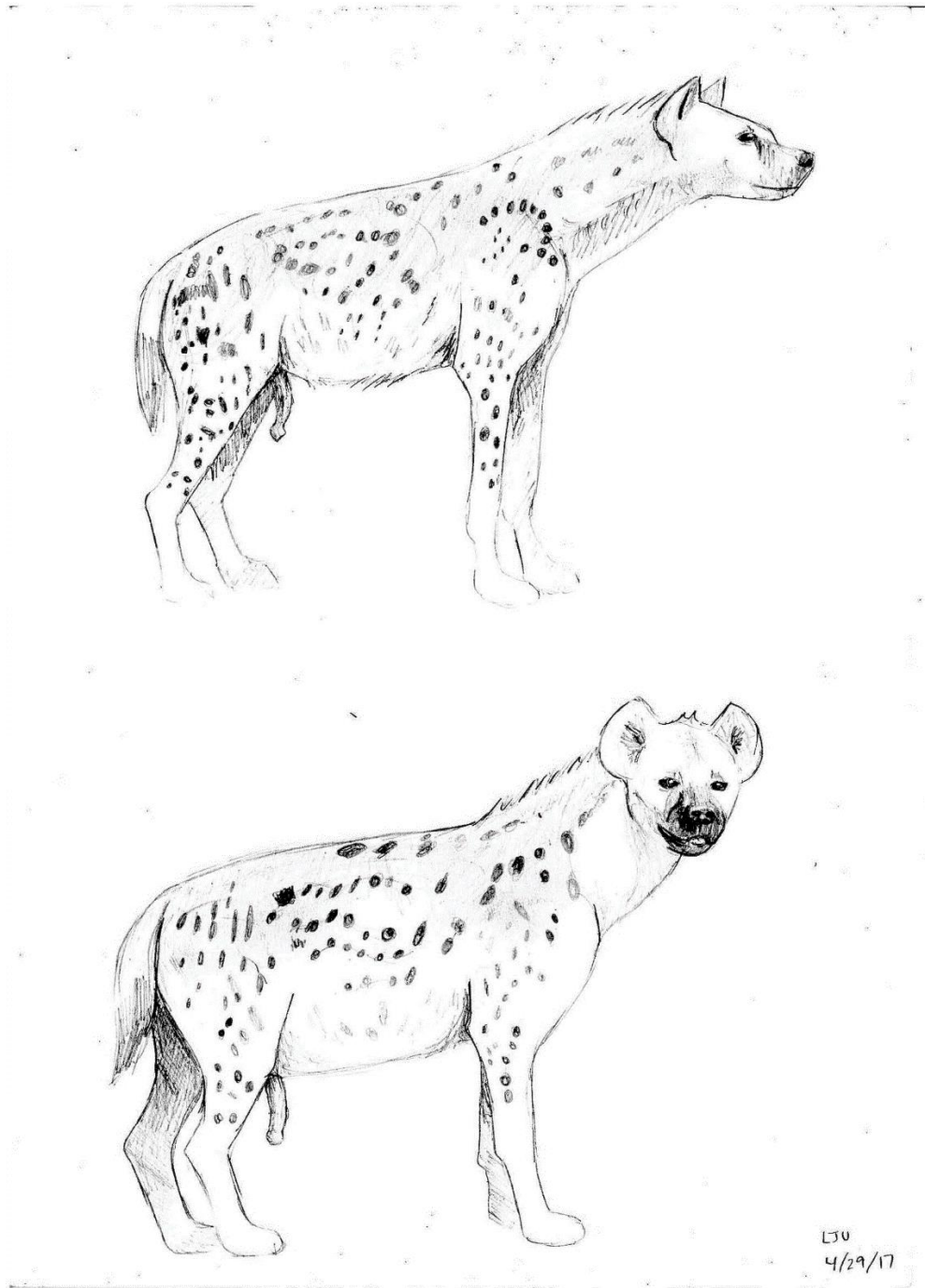
Figure 1.5: **Adult male (top) and adult female hyena (bottom) showing sex differences in body shape and genital morphology.** Drawings by Lily Johnson-Ulrich.
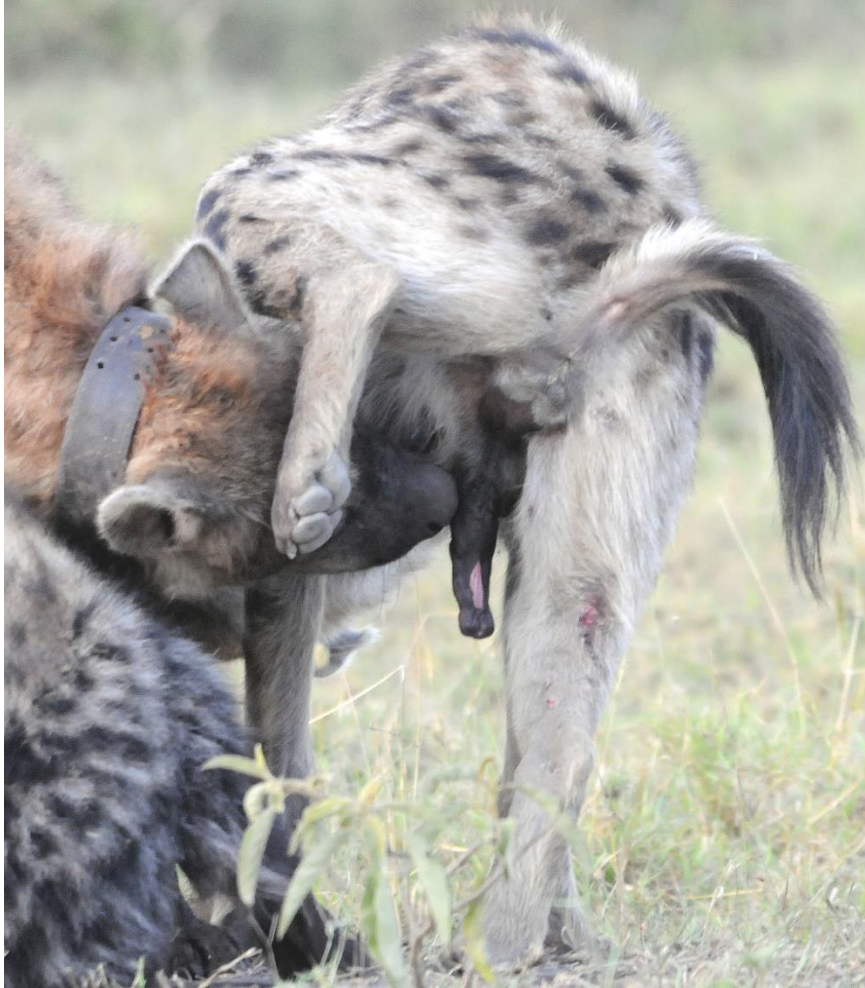
Figure 1.6: **External genitalia of the female spotted hyena seen while this female engages in a greeting ceremony with another female, who sniffs her anogenital region.** The vaginal labia form structures that resemble the male's scrotal sac; the clitoris is elongated and fully erectile. The strip of pink scar tissue running down the posterior surface of the clitoris was caused by tearing during parturition, indicating that the female has borne at least one litter in the past. Photo by K.E. Holekamp.
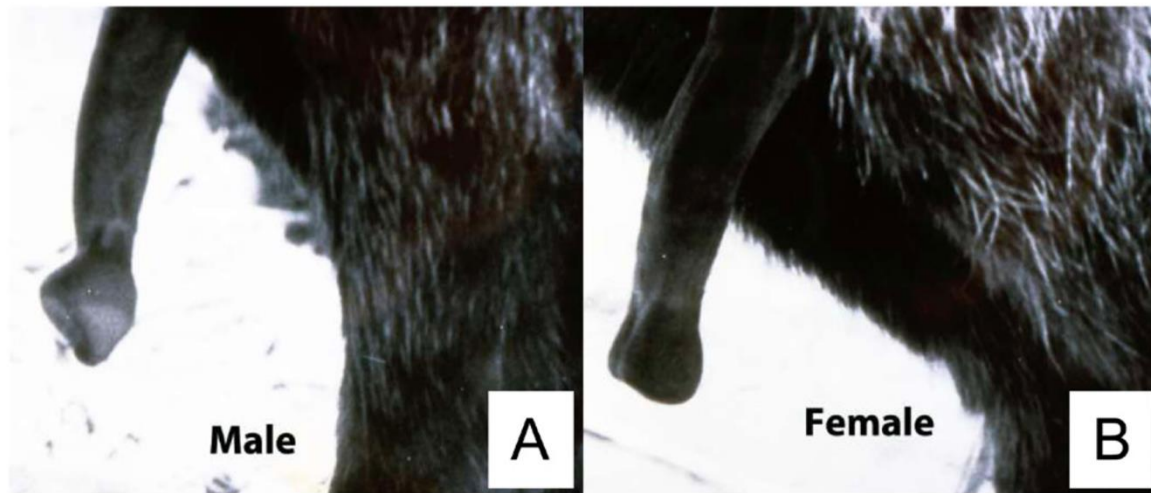
Figure 1.7: The gross anatomy of the male and female genitalia of the spotted hyaena. Shown are the penis (A) and clitoris (B) in the erect state. Photos by S.E. Glickman.

Table 1.1: **A summary of traits reviewed here, indicating which conform to a typical mammalian pattern of sexual dimorphism, which exhibit a 'role-reversed' pattern of dimorphism, and which show no sex differences.** SDN stands for sexually dimorphic nucleus of the hypothalamus.

Category	Normal mammalian pattern	Role-reversed pattern	No sex difference
Behavior	Space-use Dispersal behavior Sexual behavior Parental behavior	Aggressive behavior Social dominance Territory defense	Cognition Hunting
Morphology	Onuf's nucleus SDN	Body size	Weaponry

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CHAPTER TWO:

AGGRESSIVENESS AND SUBMISSIVNESS IN SPOTTED HYENAS: ONE TRAIT OR TWO

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ABSTRACT

Aggressive and submissive behaviors are commonly assumed to represent two extremes of a single personality trait, often labelled "aggressiveness." However, most studies focus exclusively on submissive behavior elicited by conspecific aggression, and on rates at which aggressive and submissive behaviors are emitted, without considering either unsolicited submissive behavior or the intensity of the actions themselves. Utilizing a long-term dataset spanning 27 years of dyadic agonistic interactions among spotted hyenas, including counts and intensities of all unsolicited acts of aggressive and submissive behavior, we assessed consistency within individuals in these behaviors. We found that counts of acts of both aggression and submission emitted by adult female hyenas vary with context, that neither measure is consistent within individuals over time, and that both are strongly affected by social rank, suggesting that neither of these rate measures represent personality traits. Although rank influences the intensity of submissive acts, intensity of aggressive acts does not vary with rank. Intensities of aggressive and submissive acts also vary with context, but both are consistent within individual females regardless of age, suggesting that both intensity measures may represent personality traits. We found no significant correlation between individual lifetime averages of intensities of aggressive and submissive behavior, supporting the hypothesis that these may represent different traits rather than opposite ends of a single spectrum. Lifetime rates at which females emitted acts

of aggression and submission were uncorrelated with fitness, but analysis of the average intensity of aggressive or submissive acts emitted by adult female hyenas suggests that lifetime reproductive success may be lower at both ends of the spectrum of behavioral intensity than in its center after controlling for rank, suggesting the action of stabilizing selection.

INTRODUCTION

In animal societies structured by linear dominance hierarchies, outcomes of dyadic agonistic interactions are usually determined by the subordinate's behavior in response to an aggressive act, and the aggressor is considered to "win" the altercation if it receives a submissive response (De Vries 1998, Gammel et al. 2003, De vries el al. 2006). This means that more dominant individuals win more aggressive altercations, and less dominant individuals submit more often. Therefore, some have suggested that a subordination hierarchy might be a more useful concept than a dominance hierarchy (e.g., Rowell 1974). Furthermore, many highly cited articles on agonistic behavior (e.g., Lewin et al. 1939, Bernstein 1981, Drews 1993, Sapolsky 2004, Tiedens & Fragale 2003) can be interpreted to suggest that aggressive and submissive behaviors represent two ends of a single continuum (Figure 2.1 a) based on the number of agonistic interactions an individual wins or loses in a dominance relationship. However, this common assumption of a negative correlation between aggressive and submissive behavior spectra usually only considers "solicited" submissive behavior, which occurs in response to conspecific aggression. Here instead we focus exclusively on "unsolicited" submissive behavior, which is spontaneous appeasement behavior not emitted in response to a preceding aggressive act directed at the actor by a groupmate.

An alternative hypothesis (Fig I.B) suggests that aggressiveness and submissiveness may represent two independent personality dimensions, such that

individuals vary consistently in these traits in different ways, and that the traits may even have different effects on fitness. Here we suggest that the study of spontaneous acts of aggression and submission can shed light on whether aggressiveness and submissiveness represent one personality dimension or two. As emphasized by Nelson & Kriegsfield (2017), this is not a trivial semantic issue, but rather an important conceptual one, because our assumptions about whether aggression and submission represent one behavioral dimension or two influence the way both the proximal mediation of agonistic behavior and its survival value are assessed (Schlinger and Callard, 1990). For example, the hormonal mediation of the aggressive and submissive components of an agonistic interaction may differ (Leshner and Moyer 1975). In fact, the hypothesis that aggression and submission represent independent personality dimensions is supported by research on the neural and genetic correlates of aggressive behavior in humans and laboratory animals, suggesting underlying mechanisms that may be shared across mammalian taxa (de Almeida et al. 2005; Ferrari et al. 2005; Kiser et al. 2012, Lischinsky & Lin 2020); this work suggests that aggressiveness and submissiveness may either be uncorrelated, or even positively correlated if both indicate general reactivity to social stimuli. However, we know very little about whether aggression and submission represent one dimension or two in free-living non-human mammals, in part because addressing such questions demands access to detailed long-term data sets that quantify both rates and intensities of agonistic acts.

Quantification of personality traits in highly social free-living mammals typically requires intensive long-term study to record behavioral data, such that repeated measures of a specific trait can be obtained from each individual to assess its consistency within individuals. Animal personality traits are characterized by consistency within individuals over time and among contexts (e.g., Sih & Bell 2007). Here we use detailed, longitudinal data documenting rates and intensities of unsolicited aggressive and submissive behaviors in a

wild population of spotted hyenas (*Crocuta crocuta*) that we have followed for many years in Kenya. In contrast to many other field studies of free-living mammals, we record not only the number of unsolicited acts of aggression and submission observed, but also the intensity of these behaviors. By focusing on unsolicited behaviors, we hope to assay the consistency of the individual's spontaneous behavior, rather than its reactive behavior, which may be controlled by a different set of underlying mechanisms.

The spotted hyena is unique among mammalian carnivores in that its social structure resembles that of many cercopithecine primates (Holekamp 2017). However, in contrast to cercopithecine primates, adult female hyenas dominate all immigrant males (Kruuk 1972), who sire most cubs in hyena societies (Engh et al. 2002, Van-Horn et al. 2004). Much like cercopithecine primate groups, spotted hyena clans are structured by matrilineal, linear dominance hierarchies in which cubs acquire social ranks just below those of their mothers (Engh et al. 2000, Strauss et al. 2020); in fact, cubs acquire the entire social networks of their mothers in a complex process of non-genetic inheritance (Ilany et al 2021) that is maintained via learning through successive generations (Engh et al. 2000, Strauss et al. 2020). This well-studied clan structure permits us to analyze unsolicited aggressive and submissive behavior within the context of a dominance hierarchy, and control for each subject's social rank at the time of each observation. This in turn allows us to determine whether unsolicited aggressive and submissive behaviors are individually consistent across time and contexts, as expected of a personality trait, and whether differences in these behaviors are driven primarily by social rank, or whether both rank and individual differences affect their occurrence.

Some personality traits have already been defined and assessed in spotted hyenas, including boldness, sociability, and aggressiveness (Yoshida et al. 2016; Gosling 1998; Greenberg and Holekamp 2017). In particular, Yoshida et al. (2016) found that

aggressiveness was consistent over time within individual hyenas, based on the intensity of their aggressive behavior, but not on the rates at which they emit aggressive acts. These studies? also found that rates, but not intensities, of aggressive acts were positively correlated with fitness in female spotted hyenas. Specifically, after calculating a lifetime measure of aggressiveness for each individual, they found that the offspring of more aggressive females survived better than did offspring of less aggressive females, after controlling for social rank. However, these analyses were completed with much smaller datasets than we have now, they failed to consider submissive behavior at all, and they focused exclusively on actions directed down the hierarchy.

Our primary goal here was to determine whether individuals are consistent with respect to the rates and intensities at which they emit spontaneous aggressive and submissive behaviors. If submissiveness represents a personality dimension distinct from aggressiveness, then observations of social interactions involving unsolicited acts of submissive behavior should reveal individual consistency through repeated measures across time and across multiple contexts. Our second goal was to test the hypothesis that spontaneous or "unsolicited" submissiveness represents a different personality trait from unsolicited aggressiveness. Unsolicited submissive acts obviate the need for aggression, because they function to make clear to a potential aggressor that the submitting hyena recognizes its status as lower than that of the potential aggressor. We tested this hypothesis by determining whether submissiveness and aggressiveness are negatively correlated within individuals, uncorrelated within individuals, or positively correlated, as might occur if both reflect overall emotional or social reactivity. Either of these latter findings would oppose the notion that aggressiveness and submissiveness are negatively correlated. Finally, we inquired whether these traits have significant independent effects on offspring survival after controlling for social rank. Although past work indicated that higher

rates of aggressive behavior enhance reproductive success among females (Yoshida et al. 2016; Watts et al. 2009), here we use data collected over nearly three decades to inquire whether either rates or intensities of aggressive and submissive behavior affect fitness when social rank is included in the same model. If these are truly two separate traits, then the two traits may have different effects on fitness, suggesting an evolutionary mechanism for maintaining individual variation in agonistic behavior within a social species where rank is known to have large effects on fitness (Holekamp et al 1996; Hofer & East 2003). We focus exclusively on dyadic agonistic interactions because fitness effects of coalitionary aggression have been well studied previously (Smith et al 2010; Vullioud et al; Strauss & Holekamp 2020), and because coalitionary aggression in the fission-fusion societies of spotted hyenas is so variable that it cannot be used to assess individual consistency in agonistic behavior. Finally, we focus exclusively on aggressive and submissive behaviors not elicited by a preceding agonistic action; we refer to these as spontaneous or "unsolicited" behaviors.

METHODS

Observations of behavior

Observational data were collected between 1989 and 2016 from one large social group, or "clan," of hyenas inhabiting the Talek region of the Masai Mara National Reserve, Kenya. Individuals were identified based on their unique spots and other identifying marks, such as scars and ear damage. The sex of each individual was determined based on the shape of the glans of its erect phallus (Frank et al. 1990), and ages of natal animals were determined based on cub appearance when first seen (Holekamp et al. 1996). Mother offspring relationships were based on observations of cubs nursing (Holekamp and Smale,

1998) and genotyping through microsatellite profiling (Engh et al. 2000; Van Horn et al. 2004), allowing for a count of the total number of cubs produced during a female's lifetime.

Observations were made daily from vehicles for 3-4 hours around dawn and again around dusk. We defined an observation session as finding one or more hyenas separated from others by at least 200m, as described previously (Yoshida et al. 2016); observation sessions lasted from 5 minutes to several hours. However, sessions lasting 5 minutes were typically those where the observer stopped only to identify hyenas and then moved on. Therefore, we restricted our analyses to observation sessions lasting 10-minutes or longer. Additionally, we restricted our dataset to include only those observation sessions in which at least 2 hyenas were present. During each observation session, we identified all hyenas present to calculate group size, and used all-occurrence sampling (Altmann 1974) to record all aggressive and submissive acts. We then restricted our analyses to acts that were clearly not occurring in response to a preceding agonistic behavior directed at the actor by a groupmate. All observation sessions were excluded from our analyses in which observers were unable to conduct complete all-occurrence sampling of agonistic behaviors due to either poor observation conditions or the presence of at least one hyena we were unable to identity. We also recorded the context in which each agonistic interaction occurred as either with "food" at a kill or carcass, at a "den," or elsewhere ("other"), where hyenas were generally traveling or resting together. Sessions at natal dens and where mating occurred were not included due to the rarity of observing individuals in these contexts' multiple times during their lives. Because agonistic behavior might vary with local food availability, we assessed average prey abundance twice each month by counting prey along multiple 4 km transects within the Talek clan's territory (Green et al. 2019). Monthly

prey count data were assigned as either high or low, depending on whether they were higher or lower in that month than the average prey availability during that year.

Social ranks were assigned based on wins and losses in dyadic agonistic encounters between individuals within the study clan each year. From this a dominance matrix could be calculated annually for adults of each sex (Strauss and Holekamp 2019a). Cubs were assigned their mother's rank until they reached reproductive maturity at 24 months of age, at which point females were classified as adults and entered the adult female hierarchy with their own ranks. After male spotted hyenas reach reproductive maturity they typically disperse to new clans, where they join the hierarchy in the new clan at the lowest possible rank position, below all natal individuals and other immigrant males that arrived earlier, only ascending in rank when males ahead of them in the immigrant queue die or disperse to new clans (East et al 2003). All ranks were assigned annually. Although rank is fairly stable over long periods within our study clans, births and deaths do lead to small shifts. To help control for this, every newly reproductive female that was alive at some point in the year for which a rank matrix was calculated was assigned a rank below that of her mother. Ranks were then standardized by dividing numerical ranks by the number of hyenas present in the clan in that year, and then centered from -1 to 1. Finally, given the philopatric nature of female spotted hyenas, and our ability to assess their lifetime reproductive success, the data used in our analyses only include observations of aggressive and submissive acts emitted by adult (>24 mo) females. This allowed us to count the number of lower-ranking individuals than the acting hyena present in each observation session in our analyses of aggressive behavior, and to count higher-ranking individuals present with the actor in our analyses of submissive behavior.

Counts of aggressive and submissive behavior

Because we considered only dyadic interactions, we were able to avoid any confounding effects of support from groupmates during agonistic encounters. Counts of aggressive or submissive behaviors emitted during dyadic agonistic interactions within each observation session involved assessing how many times a hyena either aggressed upon a groupmate or submitted to a groupmate, respectively, during an observation session without any immediately preceding agonistic action from any groupmate. To ensure we were recording only spontaneous behavior, we removed cases in which any agonistic behavior involving the actor occurred during the preceding minute of observation. The groupmate to which aggressive or submissive behavior was directed was identified based on its proximity, the actor's body orientation, and the actor's viewing direction. However, all acts were excluded from our data set for which an actor directed its spontaneous behavior at multiple groupmates concurrently, or if for any other reason we could not identify the intended recipient of the behavioral act.

We considered all unsolicited aggressive and submissive acts regardless of whether they were directed up or down the hierarchy. From counts within observation sessions, hourly rates could be calculated and corrected for both observation time and number of groupmates present with the focal hyena. Thus, an hourly rate of behavior, controlled for opportunity to emit that behavior, was calculated for each adult female in each observation session as (# Actions emitted / Number of group-mates present / (Observation Session length in minutes/60)).

Intensities of aggressive and submissive behavior

We recorded the intensity of both aggressive and submissive acts on separate three-point scales, with three being the most intense. The aggressive behaviors we recorded included (1) intention movements to attack, such as head waves, (2) threat and

attack behaviors without bodily contact, such as lunges, jaw snapping and chases, and (3) physical contact that might result in injury, such as biting and tackling. Similar intensity categories for unsolicited submissive behaviors were also assigned, from lowest to highest as (1) minor appeasement signals, such as flattening the ears back against the head or head-bobbing, (2) postural changes such as folding the entire body into a submissive posture with tail down between the legs, and (3) 'groveling,' or crawling on one's belly and carpals (Kruuk 1972). Descriptions of these behaviors can be found on page 1 of the Supplementary Materials. Vocal signals were not included as acts of aggression or submission because the meanings of most hyena vocalizations have yet to be determined, and some vocalizations have been observed to occur in several different social contexts (e.g., East & Hofer 1991; Theis et al. 2007).

Correlation between aggression and submission within individuals

If we found that an agonistic measure was consistent across time or context within individuals, we referred to it as a personality "trait," then compared consistent submissive and aggressive traits within a single model. That is, we assessed the correlation between measures (either counts or intensities) of aggressive and submissive acts within individuals. Hourly rates of behavior within observation sessions were aggregated for each female to calculate her mean lifetime rate of emitting aggressive or submissive behavior, starting when she reached 24 months of age; then we normalized the data by taking the square root of the rate calculation. To calculate mean lifetime intensities of aggressive and submissive acts emitted by each female, we aggregated the intensity scores for all her acts of aggression or submission, which were normally distributed. We also utilized these mean lifetime rates and intensities of aggressive and submissive behavior in our assessment of effects on fitness.

Assessment of fitness

Each female's lifetime reproductive success was calculated by counting her offspring that survived at least to 24 months, which is the age at which spotted hyenas are physiologically competent to breed (Glickman et al. 1992). These numbers were then divided by the mother's age at death in years to calculate an annual lifetime rate at which her offspring survived to sexual maturity, and to normalize the data we calculated the square root of each value. Here we focused only on females in our dataset for which we knew both their birth and death dates, allowing for analyses of 72 females.

For any behavioral measure that was consistent over time within females, we considered lifetime reproductive success in relation to each female's lifetime mean value of that behavioral measure. We used the mean lifetime values of aggressive and submissive acts calculated for each adult female as described above, from all sessions in which she was observed starting when she was 24 months old. By calculating rates of behavior corrected for the number of other hyenas present, we were also able to assess effects on lifetime reproductive success of aggressiveness or submissiveness with social rank as a separate predictor; rank is well known to have large effects on fitness in female spotted hyenas (Holekamp et al. 1996, Swanson et al 2011; Turner et al. 2020). To account for slight changes in rank across a female's lifetime, we calculated a mean lifetime rank for each female as her mean rank across all observation sessions in which she was present in the clan as an adult. These mean lifetime ranks, and lifetime mean rates and intensities of aggressive and submissive behavior, were included as factors in each fitness model to distinguish their effects on offspring survival from those of social rank alone.

Data analysis

Given our interest in individual differences, we chose to utilize a mixed model approach for quantifying individual variation, allowing us to treat individual identity as a

random factor in our models, and compare the fit of models with and without this random factor included (Dingemanse & Dochtermann 2013). For both number of acts (counts) and intensities of agonistic behaviors, we built models for analyzing the individual-level fixed effect of standardized social rank (Tables 2.1 & 2.2). We also included relevant session-level fixed effects as predictors in the model, including the total number of hyenas present, the context of the session (food, den or other), prey density (high or low) in the month when the observation occurred to account for variation in motivation to interact over food resources, and the proportion of hyenas present in each observation session that were either lower-ranking than the actor for aggressive behavior, or higher-ranking than the actor for submissive behavior. Age was also included in these models to determine whether a female's agonistic behavior was consistent over time after the onset of adulthood. For each female this included all observations between 24 months of age and her death. The median age at time of death for females surviving to 24 months in our sample was ~7 years of age.

Analyses of all models were conducted in R Version 4.0.0 and R Studio Desktop Version 1.2.5042. Collinearity diagnostics for fixed model predictors were done during model selection using the R package olsrr (Hebbali 2020), ensuring that variance inflation factors did not exceed 4, and that condition indices between variables were within acceptable limits to avoid collinearity among fixed factors. All social factors (rank, proportion of targets, and group size) were tested for interaction effects, and if these were found to be significant, they were included in the final model (Tables 2.1 & 2.2).

For final analyses of count and intensity data we utilized the MCMCglmm package in R (R Core Development Team 2020; Hadfield 2010). This Bayesian approach allowed for visual inspection of trace plots to determine whether each model converged to make a good approximation of the posterior distribution for each fixed factor. Fixed effects were tested for significance based on the distribution of their 95% credible intervals, and a pMCMC value

indicated whether or not a result was statistically significant. A model factor was only

considered significant if its credible interval failed to overlap zero and its pMCMC was less

than 0.05. We also tested the significance of a random effect of hyena identity (ID) by

looking at the difference in deviance information criterion values ($\Box$DIC) between models

fitted with and without individual ID included as a random effect. The ID was considered

significant, indicating individual consistency, if $\Box$DIC was -10 or more (Hadfield 2010,

Burnham and Anderson 2002). Because our counts of acts were calculated even for

observation sessions in which focal individuals did not interact with any groupmates

present, we utilized zero-inflated Poisson distribution within our MCMCglmm count models.

Within these models, length of each observation session was included as a predictor to

control for the amount of time the focal individual had in which to act. MCMCglmm models

of behavioral intensity were analyzed using the family = "ordinal" specifications given that

the categorical levels of our defined intensities (1 to 3) had a natural order (Hadfield 2010).

Following this, to determine whether rates or intensities of aggressive and

submissive behavior were correlated within individuals, we used the R base linear model

package "lm" to compare lifetime mean values within individuals of each behavioral

measure (counts of aggressive and submissive acts or intensities of those acts) if deemed a

potential personality trait. We did this using the aggression measure as the dependent

variable and the submission measure as the independent variable for each comparison (R

Core Development Team 2020).

Finally, we used the R package "lm" to assess reproductive success of each female

in relation to her mean lifetime value of each behavioral measure, along with the female's

mean lifetime social rank. If the correlation between the behavioral trait and reproductive

success was found to be significant when mean rank was included in the model, the lifetime

reproductive success of females was then plotted against the lifetime mean for the

behavioral measure, as calculated from all observation sessions involving that focal female during her adulthood. A best fit line was then fitted to the distribution, considering three polynomial relationships (linear, quadratic, and logarithmic) in an initial analysis. The best fit was then kept, and results plotted using ggplot2 (Wickham et al. 2019).

RESULTS

Aggressive behavior

For models predicting counts of unsolicited aggressive acts, we used 43,157 observation sessions involving 128 adult females who had an opportunity to aggress upon at least one groupmate during each session. The mean length of all observation sessions used here was 46.4 minutes, with an SEM of 0.16. This dataset included sessions in which the female had the opportunity to act because a groupmate was present with her, but failed to do so, leading to a count of zero aggressive acts by that female in that observation session. Within this dataset we recorded 10,732 aggressive acts, with 15% directed up the hierarchy and 85% directed downward. The mean number of opportunities to attack when at least one groupmate was present per female was 332 over her lifetime, with a range of 20 to 1,740.

Counts of aggressive acts by adult females

Count of aggressive acts in observation sessions, when controlled for session length, showed some level of consistency within individuals, as the random factor of ID improved model fit (D DIC = -47). However, it also appeared that the number of times a female directs aggressive acts toward groupmates is driven largely by rank, contextual factors, age, and group size (Figure 2.2 a,b,c,d). First, social rank significantly affected counts of aggressive acts (pMCMC = 0.002). Second, counts of aggressive behavior were higher in the presence of food than in other contexts (pMCMC < 0.001; Figure 2.2 b). Third, we observed a significant interaction between the proportion of targets present who were

lower-ranking than the actor and overall group size in affecting the likelihood of females

emitting aggressive acts (pMCMC < 0.001); females emitted aggressive acts more often as

the proportion of lower-ranking groupmates increased, but how often they emitted

aggressive acts declined as group size increased (Figure 2.2.c). Fourth, age was a

significant predictor of counts of aggressive acts (pMCMC = 0.034), suggesting variation

over time (Figure 2.2 d), though the effect size was small, and difficult to see in Figure 2.2 a.

Finally, prey density was not correlated with the number of times an individual emitted

aggressive acts during an observation session (pMCMC = 0.97)

Intensities of aggressive acts by adult females

The model for intensity of female aggression was improved by including the random

factor of ID (DDIC = -42), indicating individual consistency between measures. Within this

model only two factors appeared to significantly affect the intensity of aggressive acts

displayed by adult females (Figure 2.3 a,b): females emitted more intense aggression in

food-related than other contexts (pMCMC < 0.01), and when group sizes were larger than

when they were smaller (pMCMC < 0.01). However, rank was not a significant predictor of

aggression intensity (pMCMC = 0.556), nor were age (pMCMC = 0.756), proportion of lower

ranking targets present (pMCMC = 0.156), or relative prey density (pMCMC = 0.289).

Submissive behavior

For models predicting counts of unsolicited acts of submission we used data from

35,858 observation sessions involving 136 females who had an opportunity to submit to at

least one groupmate without first being attacked or threatened in each session. Overall,

mean session length here was 46 minutes. As with the aggression count dataset, the

unsolicited submission count dataset included zero counts when at least one groupmate

was present, but the focal animal never submitted to it. Within these sessions we observed

4,345 spontaneous submissive behaviors, and we used these to assess the intensity of

submissive acts, approximately 17% of which were directed down the hierarchy, and 83% directed up the hierarchy. The mean number of opportunities per female to exhibit unsolicited submission during an observation session with at least one other group mate present was 290 over her lifetime, with a range of 20 to 1,141.

Counts of submissive acts by adult females

When the random factor of ID was included in the model predicting counts of unsolicited submissive acts by females, after controlling for session length, we found that ID improved model fit (D DIC = -200). However, counts of unsolicited submissive acts were also related to context, age, and rank (Figures 2.4 a,b,c). That is, the number of times adult females emitted unsolicited acts of submission was higher in food-related (pMCMC <0.001) and other (pMCMC < 0.001) contexts than at dens. Rank significantly affected counts of submissive acts emitted (pMCMC < 0.001 Figure 2.4 b), and females performed fewer submissive acts as they aged (p < 0.001 Figure 2.4 c). In contrast to our analysis of aggression counts, here we found no interaction between the proportion of targets present and group size, so the interaction term was dropped from the model. Group size (pMCMC = 0.257), proportion of lower-ranking targets present (pMCMC = 0.777, and prey density (pMCMC = 0.314) had no significant effects on counts of unsolicited acts of submission, despite being included in the best model.

Intensities of unsolicited submissive acts by adult females

As when modeling intensity of aggressive acts, the model predicting intensity of all submissive acts by adult females was improved by including the random factor of ID (DIC = -35). Females performed more intense unsolicited submissive acts during observation sessions with food present, than during sessions in other contexts (pMCMC < 0.001; Figure 2.5 a,b). Rank also had a significant effect on the intensity of unsolicited submissive acts emitted by females (pMCMC = 0.04). However, as in our analyses of intensity of aggressive

acts, age had no significant effect on the intensity of submissive acts (pMCMC = 0.318), so this trait was consistent within individuals. The proportion of higher-ranking targets present with the actor also had no effect (pMCMC = 0.449), nor did group size (pMCMC = 0.506) or prey density (pMCMC = 0.08).

Correlation between aggression and submission within individuals

As the counts of both aggressive and submissive acts were affected by both context and age, they were not consistent over time (Figures 2.2 a & 2.4 a), so these should not be considered personality traits; therefore, we did not assess the correlation between these two count measures. Indeed, counts of both types of behavior appeared more closely related to social rank than to individual differences. However, as the intensity with which a female emitted either aggressive or submissive acts remained consistent as she aged (Figures 2.3 a & 2.5 a), and as model fit was also significantly improved for both by adding the random factor of ID, we compared our two intensity measures to determine whether they were correlated. When we compared the mean lifetime intensities of aggressive behavior to mean lifetime intensities of submissive behavior within individuals, we found no correlation between intensities of these two types of acts (p = 0.31).

Fitness consequences of aggression and submission

To assess correlations between each of our four agonistic traits and fitness, we ran separate models assessing the relationship between each mean trait value and the number of cubs produced in a female's lifetime that survived to 24months. Models included mean lifetime rates and intensities of aggressive or submissive behaviors, and mean lifetime rank. We found no significant interaction between mean lifetime rank and mean lifetime aggression rate in our model assessing the relationship between aggression counts, rank, and fitness, so the interaction term was dropped, and this improved model fit. The effect of aggression count on offspring survival was not significant (p = 0.284), but social rank was

highly and positively correlated with offspring survival (p = 0.007). We found a similar

pattern with respect to the relationship between counts of submissive behavior and offspring

survival. The interaction between rank and submission rate was not significant, so the term

was dropped. Submission rate was not correlated with offspring survival (p = 0.217), but

rank was positively correlated with annual offspring survival (p = 0.008).

Interestingly, mean lifetime aggression intensity did show a pattern related to annual

offspring survival. Within this model mean lifetime aggression intensity had a polynomial

relationship with annual offspring survival (p = 0.001), such that fitness was higher for

individuals with midrange values of aggression intensity and lower for individuals on the

extremes of the distribution, whereas rank presented a positive statistical trend with fitness

in a linear relationship (p = 0.06). However, we did find a significant interaction between

rank and aggression intensity in relation to annual offspring survival (p = 0.002). For

individuals who have average lifetime intensities of aggressive behavior closer to the center

of the distribution, as their rank increases their annual offspring survival increases.

However, for individuals presenting extreme average lifetime intensities of aggressive

behavior on either end of the distribution, increased rank does not have a significant

positive correlation with annual offspring survival. As rank was not a predictor of aggression

intensity in our individual consistency analysis (Figure 2.3 a), we have included a model

excluding rank when modelling the relationship between annual offspring survival and mean

lifetime aggression intensity; here again we found the relationship between the mean

lifetime intensity and annual offspring survival to be significant (p = 0.016) presenting a

polynomial relationship between annual offspring survival and mean lifetime aggression

intensity independent of rank (Figure A.2.1).

In our model assessing the relationship between mean lifetime submission intensity

and annual offspring survival, we found a trending interaction between rank and submission

intensity (p = 0.07). In this interactive model, individuals with lower average lifetime submission intensities see a positive benefit of rank, but individuals with higher average lifetime submissive intensities do not see the positive benefit of rank. Withing this model rank was also positively correlated with fitness (p = 0.0499), but submission intensity was uncorrelated (p = 0.864). However, in a follow-up analysis in which we controlled for rank as done earlier with aggressive behavior by Yoshida et al. (2016), by only analyzing intensity of submissive acts directed up the hierarchy, we did observe a significant relationship between mean lifetime submission intensity and annual offspring survival. Here again we found that fitness was lower on the extremes of the intensity distribution (Figure A.2.2).

DISCUSSION

We found that the intensities, but not counts, of spontaneous acts of aggression and submission are consistent within individuals across time, suggesting that they represent true individual differences or personality traits. We found that the intensity of unsolicited agonistic behavior varies strongly with context, with more intense aggressive and submissive behaviors occurring during feeding sessions than in other contexts. This is unsurprising given that aggressive competition over food is both intense and common in this species. Individual plasticity is clearly apparent in our data, given the important effects of rank, context, and other factors on our behavioral measures. However, intensities of unsolicited aggressive and submissive acts did not vary with age among adult female spotted hyenas (Figures 2.3 a & 2.4 a), and model fit was improved by including individual identity, suggesting strong consistency within individuals over time (Hadfield 2010). Further, although social rank clearly has effects on how often individuals emit aggressive or submissive acts, rank was not a significant predictor of the intensity of their aggressive acts, a result also obtained earlier by Yoshida et al. (2016).

Yoshida et al (2016) did not assess submissive behavior at all, but we found that

rank had a significant effect on submission intensity. This appeared to be strongly related to

contextual variation, such that lower-ranking hyenas performed more intense submissive

behaviors over food and at dens than elsewhere (Figure 2.5 b). Regardless, even in this

model we observed individual consistency based on ID, and we did not see an effect of age,

suggesting consistency within adults. This pattern warrants further investigation, but even

so, we find it fascinating that intensity of agonistic behaviors seems to show true individual

consistency across time. Similarly, Yoshida et al. (2016) found that aggressiveness was

consistent over time within individual hyenas, based on the intensity of their aggressive

acts, but not on the rates at which they emit aggressive acts.

Based on the significant effects of rank, age, group size, and proportion of targets

present with the focal female on our count measures, we conclude that rank is likely the

driving factor leading individuals to emit aggressive and submissive acts at higher or lower

rates. Thus, social rank is positively correlated with the probability of emitting aggressive

acts (Figure 2.4 a) and negatively correlated with the probability of emitting submissive acts

(Figures 2.3 a). Although including ID improved model fit in analyses of counts of agonistic

acts, suggesting some degree of individual consistency (Hadfield 2010), age-related

variation in count measures indicates considerably less consistency in these measures

across time within individuals than in measures of intensity.

Our results also reveal that intensities of aggressive and submissive agonistic acts

are not correlated within individuals. Our results thus support Nelson and Kriegsfield's

(2017) hypothesis that an individual's aggressiveness is not necessarily predictive of its

submissiveness when considering only spontaneous actions rather than those elicited by

groupmates. They suggest that the intensity of an individual's aggressive and submissive

acts may be largely independent of one another, which is inconsistent with the notion that

these traits represent opposite ends of a single continuum. Our data also argue against the idea that aggressiveness and submissiveness are negatively correlated. Further analyses will be required to determine whether these traits are truly independent of one another, as we can only discern clearly here that they are not correlated.

Mean lifetime rates of unsolicited aggressive and submissive acts do not appear to have any significant relationship to offspring survival when considered in the same model with effects of social rank. In all our analyses of fitness, the lifetime mean rank of the individual was strongly and positively correlated with annual offspring survival. It is interesting that rates of submissive and especially aggressive behavior have no effects on fitness within our analyses, because this finding opposes an earlier result indicating that lifetime rates of aggressive behavior are positively correlated with fitness (Yoshida et al. 2016). However, Yoshida et al. (2016) controlled for rank differently than we did here; they included as potential targets only the number of individuals of lower rank present with the actor in each observation session whereas ours included all clanmates present. Furthermore, their data set included only sessions in which at least one individual of lower rank was present in assessment of aggression, and they assessed only aggressive acts directed down the hierarchy. In contrast, our data set included all sessions in which two or more hyenas were observed together, and we included acts directed both up and down the hierarchy.

Our results also differed in another important respect from those reported in earlier studies. Strauss and Holekamp (2020) conducted a study of coalitionary aggression by spotted hyenas, where they found that only 6% of coalitionary attacks among adult females were directed up the hierarchy whereas 94% of such attacks were directed down the hierarchy, effectively functioning to maintain the status quo. Similarly, in earlier studies of dyadic aggression among adult male hyenas (Holekamp & Smale 1998) and adult female

hyenas (Smale et al. 1993), respectively, fewer than 3% of aggressive acts in dyadic interactions with clan-mates were directed up the hierarchy, and 97% were directed downward. By contrast, in the current study we found that 15% of aggressive acts were directed up the hierarchy, which seems surprising in comparison to the earlier studies. We believe that is because, although all actors were adult females in our analyses, we included all acts of aggression directed against all clanmates present with the actor in observation sessions so long as their identity, age and rank were known. Similarly, we were surprised to find that 17% of submissive acts were directed down the hierarchy, and 87% directed up it. To assess the consistency of aggressiveness and submissiveness, we included all such behavior occurring during observation sessions for which we had complete data. Our adult female subjects were thus able to attack or submit to any other clan-mate, and our data set included cases in which adult females attacked cubs of higher-ranking females than themselves when their mothers were absent or appeased to lower-ranking animals.

Finally, we found that mean lifetime intensity of unsolicited aggressive acts was associated with reproductive success. In general, individuals whose mean lifetime aggression intensity measures represented extreme values on either end of the intensity distribution had lower offspring survival rates than did animals in the middle of the distribution, even though mean lifetime rank interacted with mean lifetime intensity of aggressive acts when included in the same model. Within this model it appeared that higher rank enhanced fitness for those individuals with mean lifetime aggressive intensity values near the center of the intensity distribution, but the benefit of higher rank was lost for individuals presenting extremely high or extremely low levels of aggressive intensity. This polynomial relationship between mean lifetime intensity and annual offspring survival can be easily observed in Supplement Figure A.2.1. This figure and its related analyses highlight the detrimental effects of consistently presenting extreme levels of aggressive behavior. On

the other hand, individual submission intensity did not appear to be correlated with fitness, as we observed no significant relationship between offspring survival and submission intensity unless we control for rank in the same way as done by Yoshida et al. (2016) (Supplement Figure 2.2). These patterns warrant more investigation, particularly given that we do observe individual consistency across time in the intensity with which females emit acts of aggression and submission.

It has been postulated that personalities in many nonhuman animals involve fitness tradeoffs (Smith & Blumstein 2008), and in humans it has been shown that extreme personality traits have costs (Gutierrez et al. 2013). Similarly, among non-human primates, extremely aggressive individuals suffer reproductive costs (e.g., Alberts et al. 1992; Packer et al. 1995). Additionally, individuals on the extremes of these trait distributions, particularly on the positive extreme, may be suffering additional physical costs (Lane & Briffa 2017). It is possible that individual variation in unsolicited aggressive and submissive traits observed in female spotted hyenas may buffer individuals somewhat from rank effects on fitness, perhaps by affecting social bond strength or access to resources, or by reducing social stress. In any case, it appears that stabilizing selection may favor adult female hyenas whose aggressive and submissive behaviors fall in the middle range of their respective spectra.

FIGURES AND TABLES
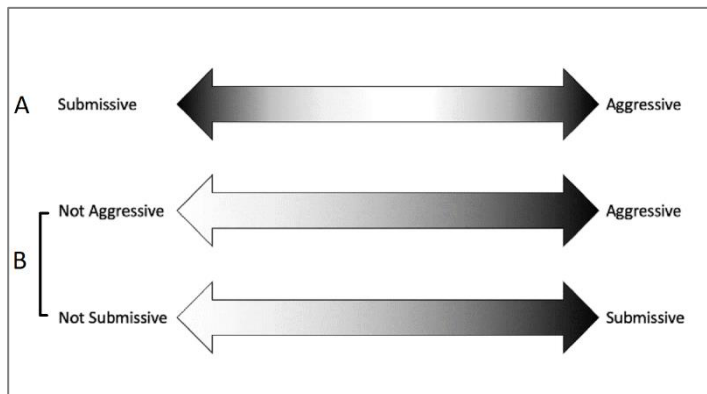
Figure 2.1: Two models of agonistic behavior. Aggressive and submissive behaviors can be conceptualized either as (A) opposite ends of a single behavioral continuum, or (B) as two separate aspects of an individual's behavior. (Modified from Nelson & Kriegsfield, 2017).

Table 2.1: MCMCglmm model description for biological and random factors predicting the number of times female hyenas emit unsolicited acts of aggression or submission in observation sessions, with definitions of fixed and random effects.

Variable of Interest	Fixed effects	Definition	Random effects	Interaction Effects
Count of Behavior (Sum of aggressive or submissive acts within each session, with a zero inflated Poisson distribution)	**Duration**	*Number of minutes within an observation session*	**Session** (Observation session number as a factor)	Group Size X Proportion Targets
	Context (Den, Food, or Other)	*Food (a kill or carcass present), den (an active hyena den present), other (all other sessions)*	**ID** (Identity of the individual hyena)	
	Standardized Rank	*Rank of the individual in the hierarchy controlled for number of ranked individuals in the clan*		
	Age	*Age of the individual on the date of the session*		
	Group Size	*Number of hyenas present during an observation session*		
	Proportion Targets	*Ratio of number of ranked individuals (in relation to the acting hyena) divided by the Group Size in a session*		
	Prey Density (High or Low)	*Monthly average of prey transects counts compared to the annual average of prey transect counts*		

Table 2.2: MCMCglmm model for predicting intensity of unsolicited acts of aggressive or submissive behavior emitted by female hyenas, with definitions of fixed and random effects.

Variable of Interest	Fixed effects	Definition	Random effects	Interaction Effects
Intensity of Behavior (Ordinal scale 1, 2, or 3, with 1 being lowest and 3 being highest, for aggressive or submissive acts)	**Context** (Den, Food, or Other)	*Food (a kill or carcass present), den (an active hyena den present), other (all other sessions)*	**Session** (Observation session number as a factor)	None Observed
	Standardized Rank	*Rank of the individual in the hierarchy controlled for number of ranked individuals in the clan*	**ID** (Identity of the individual hyena)	
	Age	*Age of the individual on the date of the session*		
	Group Size	*Number of hyenas present at within an observation session*		
	Proportion Targets	*Ratio of number of ranked individuals (in relation to the acting hyena) divided by the Group Size in a session*		
	Prey Density (High or Low)	*Monthly average of prey transects counts compared to the annual average of prey transect counts*		

Figure 2.2: Model assessing fixed predictors of the number of aggressive acts emitted by adult females.
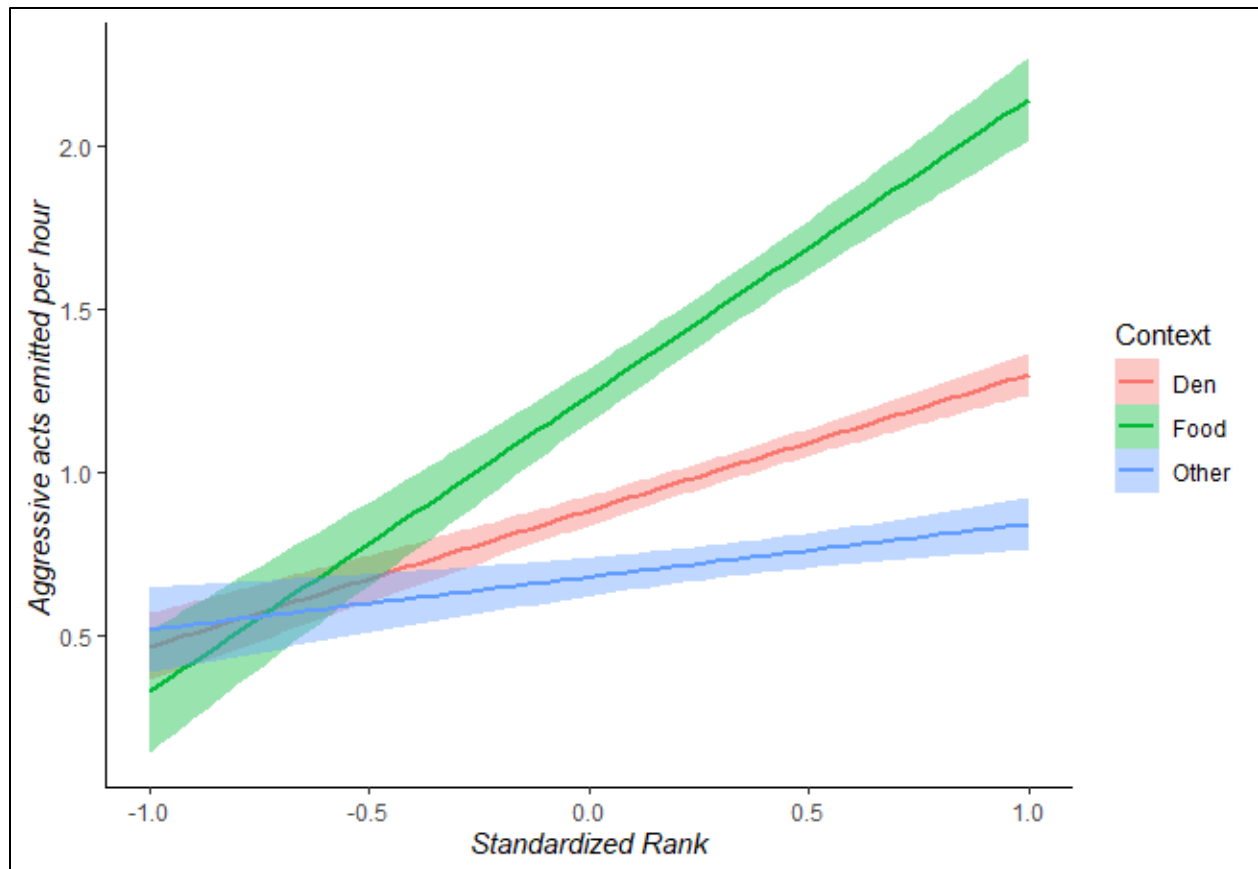
Figure 2.3: Aggressive acts emitted by adult females per hour (Count/Duration) in different contexts based on their standardized rank in the observation session. The shaded areas surrounding the lines represent 95% confidence intervals.
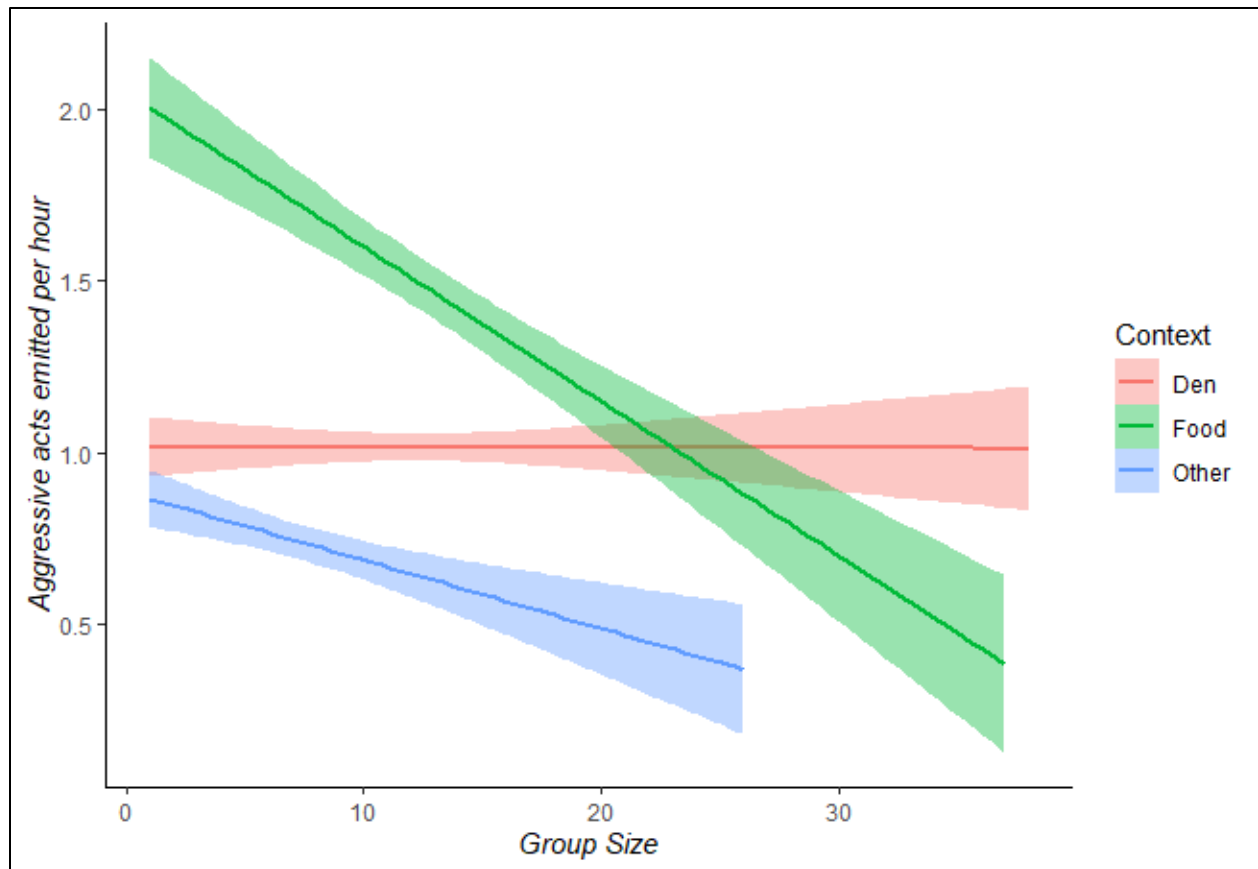
Figure 2.4: Aggressive acts emitted by adult females per hour (Count/Duration) in different contexts based on the group size present in the observation session. The shaded areas surrounding the lines represent 95% confidence intervals.
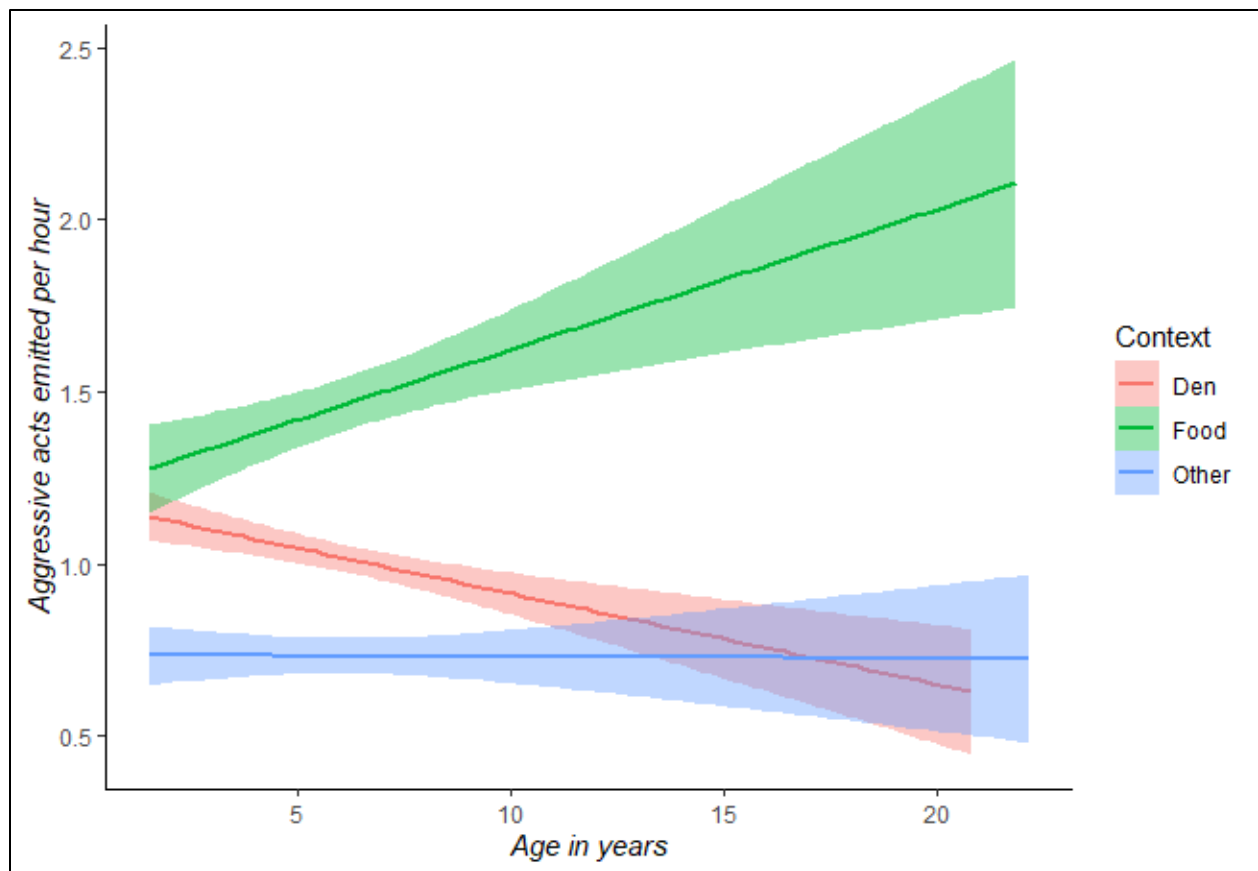
Figure 2.5: Aggressive acts emitted by adult females per hour (Count/Duration) in different contexts based on the age in years of the individual in each observation session where it was present. The shaded areas surrounding the lines represent 95% confidence intervals.
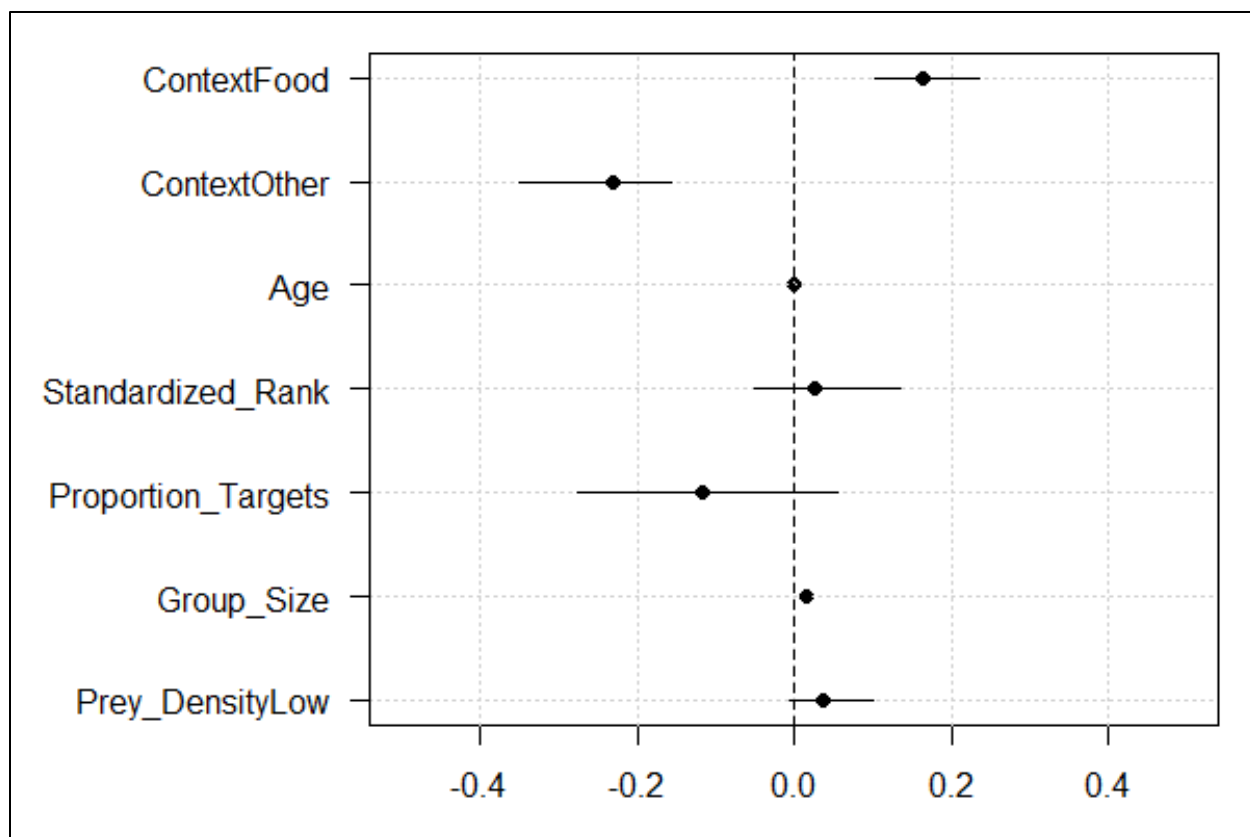
Figure 2.6: Model assessing fixed predictors of intensities of aggressive acts emitted by adult female hyenas
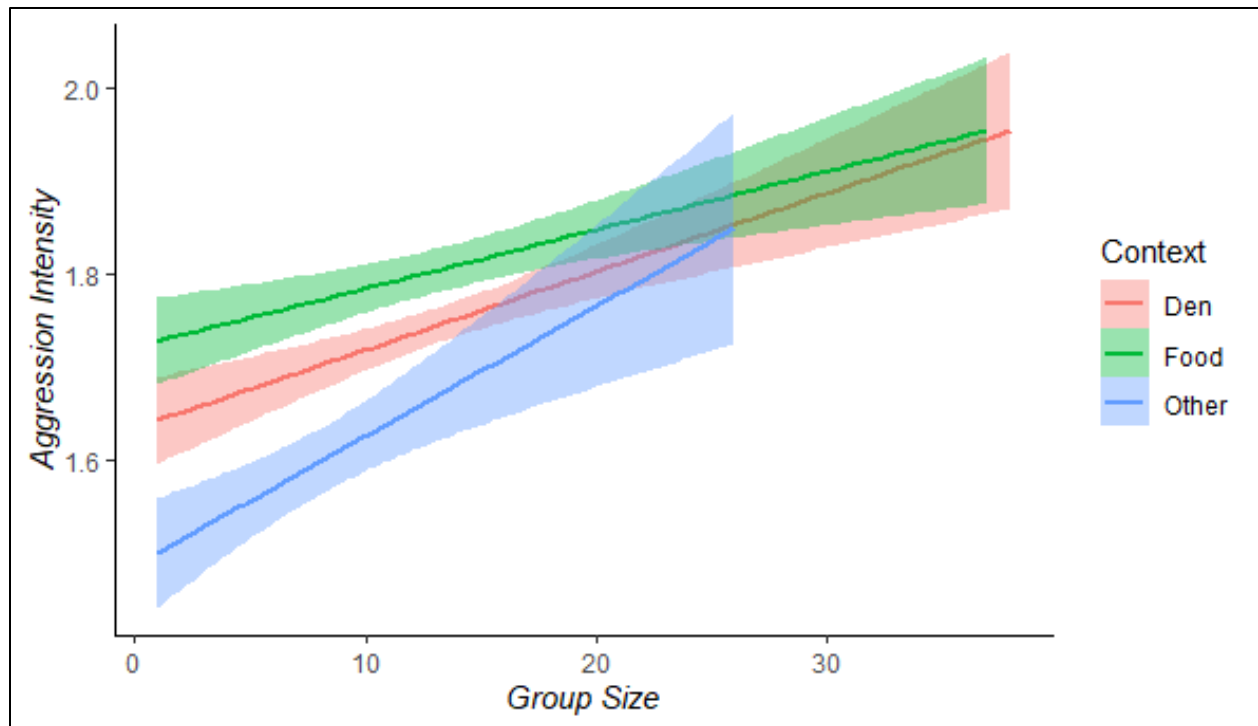
Figure 2.7: Mean intensity of aggressive acts emitted by females in observation sessions taking place in different contexts based on the group size, or number of hyenas present in an observation session. Colored areas surrounding the lines represent 95% confidence intervals.
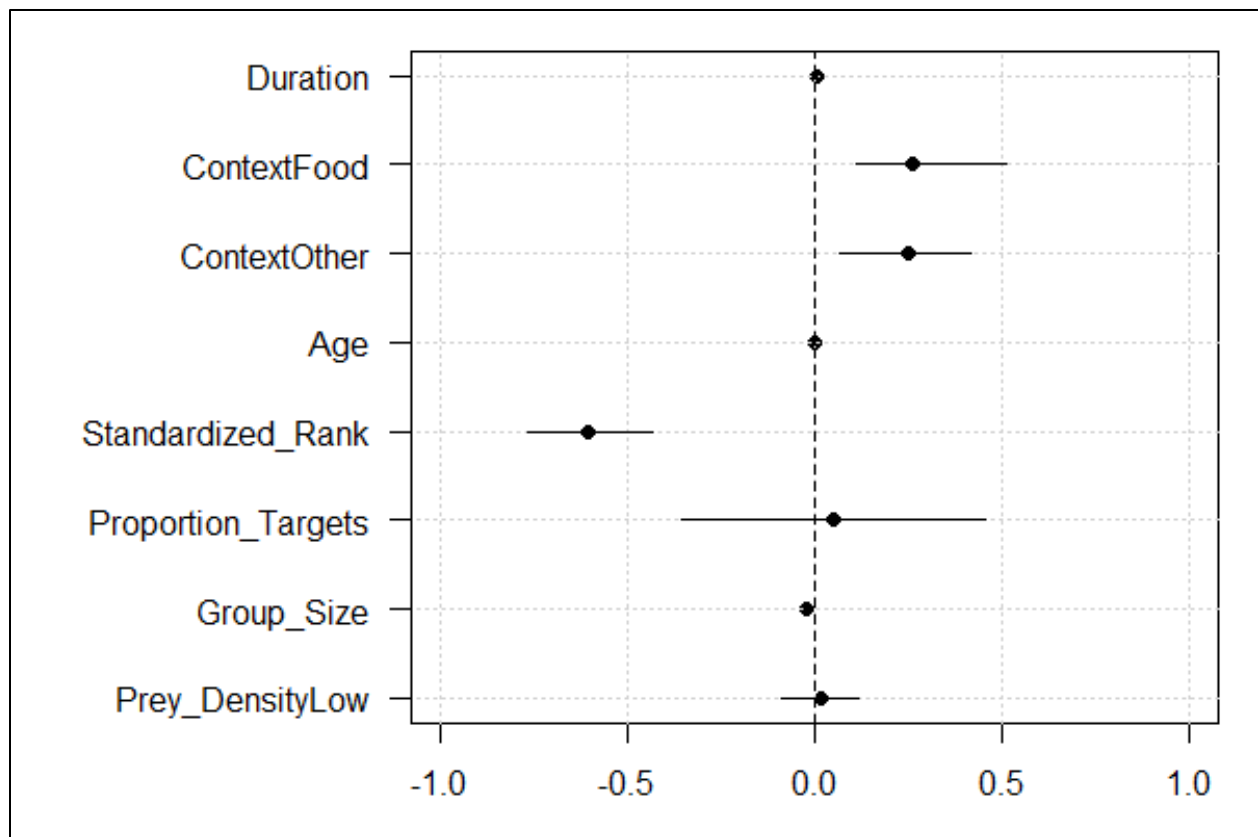
Figure 2.8: Model assessing fixed predictors of the number of submissive acts emitted by adult females.
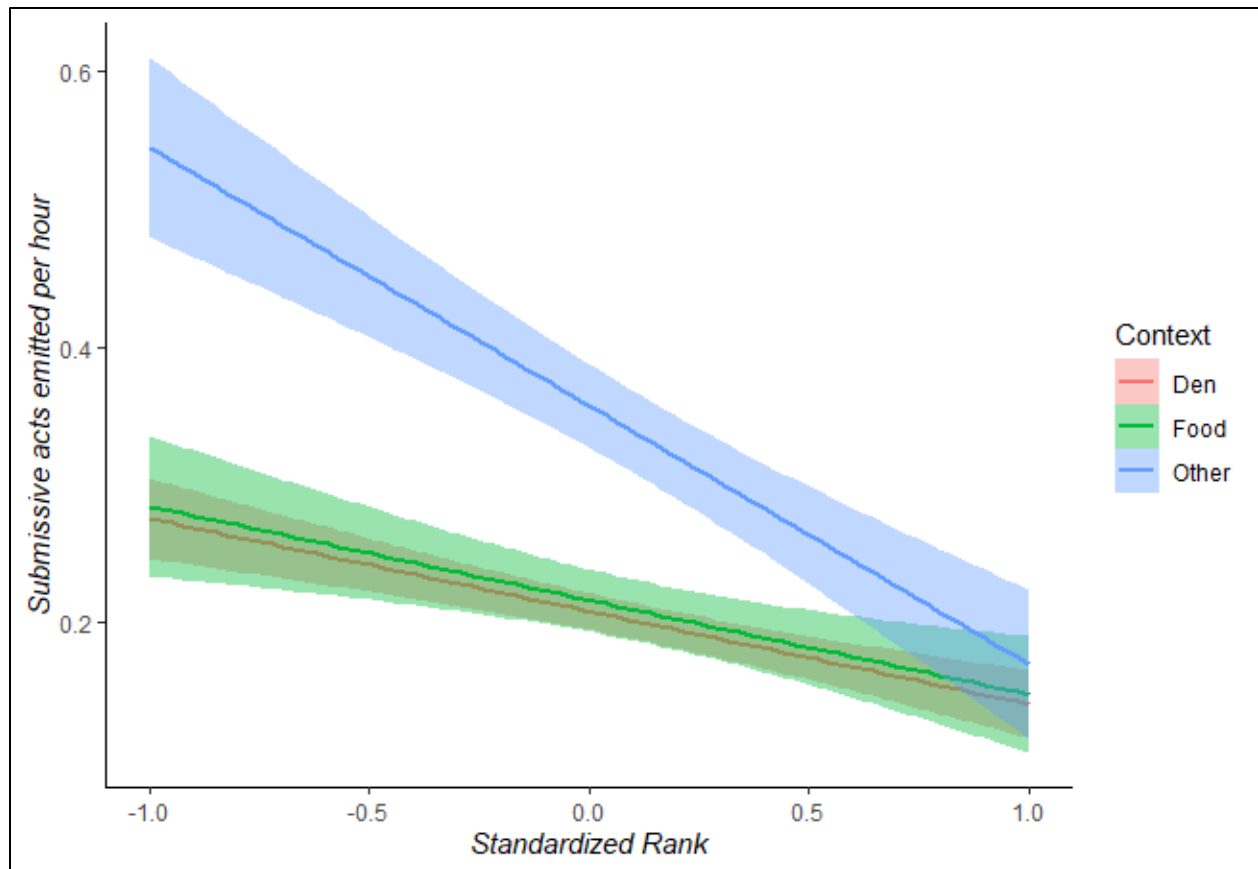
Figure 2.9: Submissive acts emitted by adult females per hour (Count/Duration) in different contexts as a function of their standardized ranks. The shaded areas surrounding the lines represent 95% confidence intervals.
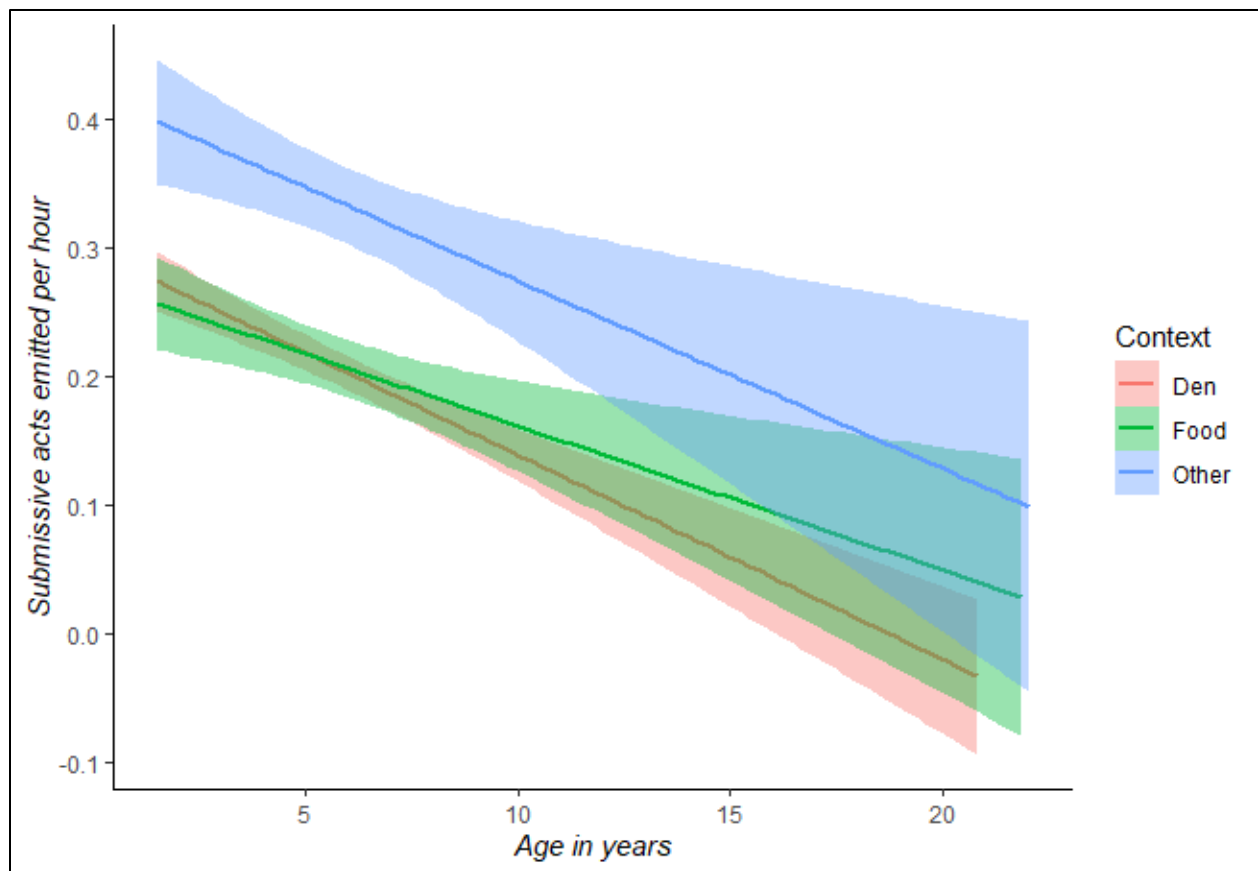
Figure 2.10: Submissive acts emitted by adult females per hour (Count/Duration) in different contexts based on the age in years of the individual in the observation session. The shaded areas surrounding the lines represent 95% confidence intervals.
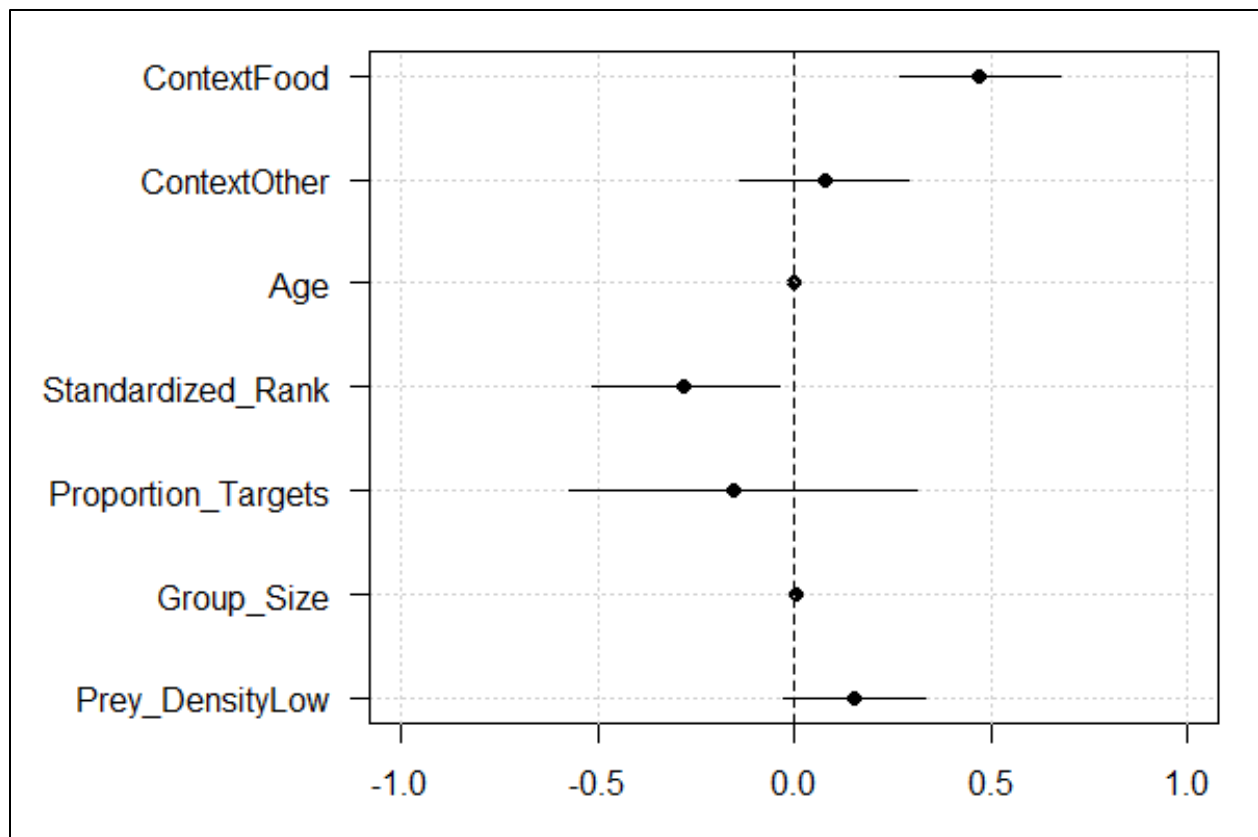
Figure 2.11: Model assessing fixed predictors of the intensity of unsolicited submissive acts emitted by adult females.
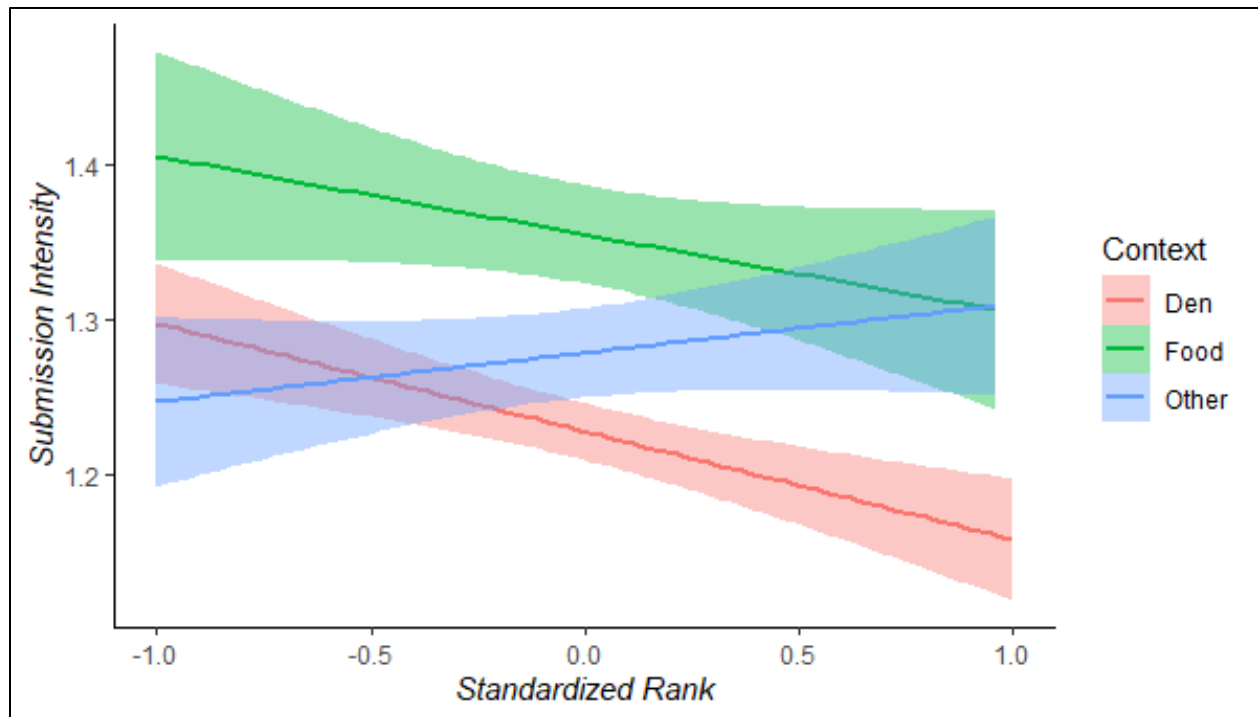
Figure 2.12: Mean intensity of submissive acts emitted by females in observation sessions based on their rank in the session taking place in different contexts. Colored areas surrounding the lines represent 95% confidence intervals.

APPENDIX

Agonistic behaviors emitted by spotted hyenas

Unsolicited Aggressive Behaviors

Stand over (st ov): t1. One animal stands with head high and muzzle pointed down at shoulders of a second individual. Lower intensities may involve an approach with head up and ears forward, sometimes with tail bristled. Refer to this lower intensity as "pointing".

Point (pt): t1. Hyena adopts the exact same posture as an adult who is standing over another, but is too small or too far away to put its head over the back or shoulders of the conspecific against which it is behaving aggressively. Point should be used instead of "stand over" in any case where a youngster is too small to physically stand over the other animal or when the aggressor is approaching with head up and ears forward.

Head wave (hewa): t1. This is an intention movement to bite or lunge in which the aggressor moves its head unidirectionally toward the opponent to signal that it will escalate its aggression if the opponent hyena persists in its current behavior. The amount of movement is what differentiates this from a lunge.

Push: t2. One animal uses its body to push another.

Lunge: t2. One hyena, often with ears cocked forward, suddenly moves quickly toward another hyena, as if to bite; this may be done from either standing or lying position.

Chase: t2. Running pursuit. Note that a chase can also be a t3 if it ends in a tackle or if there is any other form of physical contact.

Snap: t2. Aggressor closes mouth rapidly near a conspecific, often making a snapping noise, but without any physical contact. Please record snap, not "attempt t3 bite."

Bite: t3. One animal's teeth make physical contact with another hyena. Multiple bites that occur in rapid succession during a single aggression should be considered one t3 bite.

Bite shake (bsh): t3. One animal grips the skin of the back or shoulders of another with teeth, and violently shakes its head from side to side, sometimes with an upward pulling motion.

Unsolicited Submissive Behaviors

Back off (bo): s1 - The animal withdraws a step or two from a particular individual, but does not run or flee

Ears back (eb): s1 - Ears are flattened backward against the top of the head. The more extreme the appeasement, the more radically they are flattened, but any clear flattening of the ears is recorded as a signal by one hyena to another indicating that it perceives itself as subordinate to the other hyena.

Head bob (hb): s1 - Head wagging up and down or sideways.

Grin: s2 - Retracting the lips to reveal the teeth, but the mouth is not open.

Open mouth appease (oma): s2 - One animal puts his/her open mouth up to the other animal's mouth. An open mouth appease involves the same motor patterns as a defensive parry, but occurs spontaneously rather than in response to aggression.

Submissive posture (sp): s2 - The animal stands or walks with its head lowered, body hunched and bent around toward the recipient, butt tucked under, and tail down between the legs. This often (but not always) occurs in conjunction with ears back and lips retracted in a grin.

Run/flee: s2 - An animal runs from another individual or moves swiftly 2 or more body lengths away (Note: While it does happen, these are rarely unsolicited. All of these are triple checked to be sure that this was clearly not solicited by a preceding aggression)

Carpal crawl (cc): s3 - The threatened animal crawls on its front carpal joints, with hind legs bent. (Also known as "grovel.")
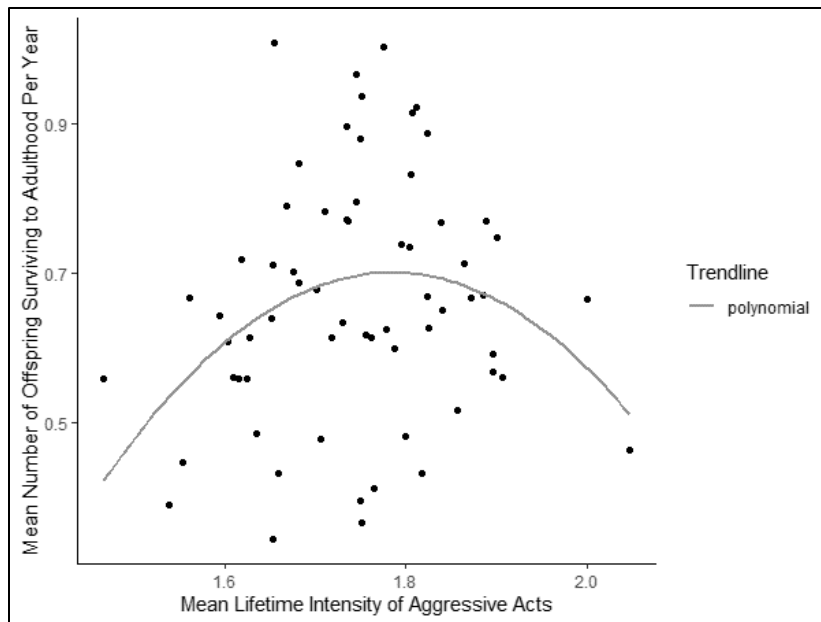
Figure A.2.1: Lifetime reproductive success (number of cubs born that survived to 2 years of age) varies with mean lifetime intensity of aggressive acts emitted by individual female hyenas (p = 0.016). The best fit line for the distribution was a quadratic polynomial.
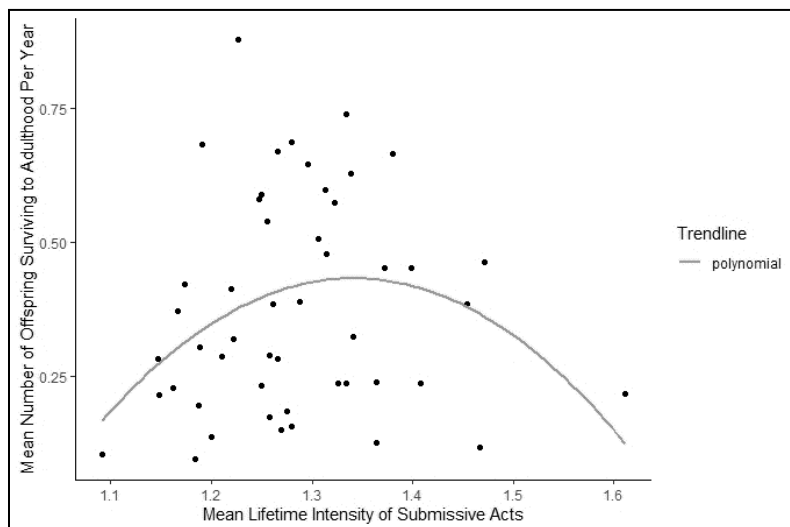
Figure A.2.2: Lifetime reproductive success (number of cubs born that survived to 2 years of age) varies with mean lifetime intensity of submissive acts emitted by individual female hyenas up the hierarchy (p = 0.024). The best fit line for the distribution was a quadratic polynomial

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CHAPTER THREE:

EVALUATING DRIVERS OF FEMALE DOMINACE IN THE SPOTTED HYENA

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ABSTRACT

Sex-based dominance relationships where females are dominant over males are rare among mammals. Mechanistic hypotheses explaining the occurrence of female dominance suggest that females dominate males because 1) they are intrinsically more aggressive or less submissive than males, and/or 2) they receive more social support than males. Here, we examine the mechanisms that underly these variable patterns of female dominance across ontogeny in spotted hyenas (*Crocuta crocuta*), and we use 30 years of detailed behavioral observations from the Mara Hyena Project to evaluate these two hypotheses. Among adult hyenas, we find that females spontaneously aggress at higher rates than males, whereas males spontaneously submit at higher rates than females. Once an aggressive interaction has been initiated, females are slightly more likely than males to elicit submission from members of the opposite sex during cub and adult life-history stages, but not as subadults. We also find that aggressing males receive social support at higher rates than aggressing females, and that regardless of actor sex, aggressors are 2-3 times more likely to receive support when attacking a female than when attacking a male. Receiving social support does not help males elicit submission from females, although it does slightly help females elicit submission from other females. Finally, our results show that females are more likely than males to win fights against the opposite sex, regardless of whether or not they are supported by group-mates. Overall, we find support for both

mechanisms hypothesized to underlie dominance in this species: 1) male and female hyenas clearly differ in their spontaneous aggressive and submissive tendencies, and 2) social support does play an important role in dominance within a clan. Nevertheless, our results suggest that social support is not sufficient to explain sex-biased dominance in hyenas. Although social support can certainly influence fight outcomes among females, adult females can easily dominate immigrant males without any social support.

INTRODUCTION

Dominance hierarchies are common in animal societies and have profound fitness consequences for individuals in many different species (Strauss et al. 2022). Interestingly, in some animals, one sex is typically dominant over the other, prompting questions about the evolutionary and mechanistic origins of this sex bias. Male dominance, where males exert power or influence over females, is very common in mammals and has thus been studied extensively (Darwin 1871, Carpenter 1942, Schjelderup-Ebbe 1935). A diverse array of traits facilitates male dominance, including larger body size (Cassini 2020), superior weaponry (Rico-Guevara & Hurme 2019), higher androgen concentrations (Nelson 2005), and more frequent and intense expression of aggressive behavior (Nelson 2005). These sexually dimorphic, male-biased traits are often correlated (e.g., male aggression levels and circulating testosterone; Muller 2017), and in most cases provide an advantage in both intra- and inter-sexual competition (Nelson 2005).

Female dominance, where females exert power or influence over males, is uncommon in mammals but occurs in various Malagasy primates (Lewis 2020), meerkats (*Suricata suricatta*; Russel et al. 2004), and spotted hyenas (*Crocuta crocuta*; Kruuk 1972). Compared to the factors influencing male dominance, those mediating female dominance in mammalian societies remain poorly understood. Nevertheless, three proximate mechanisms leading to female dominance over males have been proposed: (1) intrinsic

attributes, or sex-based differences in ability to use force (e.g., body size, physical strength, aggressiveness; Watts et al. 2009); (2) extrinsic, or derived, attributes, or sex-based differences in social support (e.g., coalition and alliance partners; Vullioud et al. 2019), and (3) leverage, or sex-based differences in resources that cannot be taken by force (e.g., fertilizable eggs; Lewis et al. 2019).

Spotted hyenas are an ideal system in which to examine the phenomenon of female dominance, as female dominance over males has been particularly well described in this species (Kruuk 1972; Holekamp & Strauss 2020; East et al. 2003). Spotted hyenas live in mixed-sex matrilineal societies called 'clans,' which are characterized by low within-group relatedness, female philopatry, and male dispersal (Smale et al 1997; Holekamp et al. 2012, Van Horn et al. 2004). Past studies of spotted hyenas have supported both the intrinsic attributes hypothesis (e.g., Frank et al 1989) and the derived attributes, or social support, hypothesis (Vullioud et al 2019).

Although we were unable to assess the leverage hypothesis here, we were able to address both the intrinsic attributes hypothesis and the social support hypothesis. The "intrinsic attributes hypothesis" posits that intrinsic behavioral and physiological differences between the sexes contribute to female dominance. Under this hypothesis, females have enhanced fighting abilities due to selection favoring females who can obtain priority of access to resources for themselves or their offspring (Watts et al. 2009), or as a by-product of intense selection on female-female competition over resources (Clutton-Brock & Huchard 2013). In support of this hypothesis, sex differences in aggressive behavior in spotted hyenas emerge early in life during the neonatal period (Smale et al. 1995; Golla et al. 1999; Wahaj and Holekamp 2006; Benhaiem et al. 2012). As adults, female spotted hyenas are larger than males (Swanson et al. 2013) and aggress at higher rates and intensities when attacking lower ranking hyenas than do immigrant males (McCormick et al. 2021). These

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higher rates of aggressive behavior are associated with superior reproductive success among females (McCormick & Holekamp 2022; Yoshida et al. 2016; Watts et al. 2009), but not among male spotted hyenas (Hofer & East 2001).

The "derived attributes hypothesis" suggests that differential social support allows females to dominate males. Under this hypothesis, female dominance over adult males arises when females have more social support than males, such as when males disperse to join a new clan but arrive lacking any kinship ties or social bonds in the new group. Consistent with this hypothesis, Vullioud et al. (2019) found that the outcomes of dyadic interactions between spotted hyenas in Ngorongoro Crater, Tanzania were best predicted by which individual could potentially receive more social support from groupmates, and this was true even after statistically controlling for sex and body size. Additionally, support from social allies during agonistic encounters aids in rank acquisition (Engh et al. 2000) and facilitates rank reversals among adult females (Strauss & Holekamp 2019), highlighting the importance of social support in determining dominance.

Here we interrogate both the intrinsic attributes hypothesis and the social support hypothesis in explaining the tendency for females to dominate males among spotted hyenas. Although these hypotheses are not mutually exclusive, they are often characterized as being in conflict, with some suggesting that female-biased dominance in hyenas can be explained by the social support hypothesis alone (Vullioud et al. 2019). To clarify the contributions of these different mechanisms to female-biased dominance in spotted hyenas, we test predictions of both hypothesized mechanisms, and evaluate whether differences between the sexes in social support are sufficient to explain sex-related patterns of agonistic behavior in this species.

We focus first on agonistic interactions among adult hyenas, where female dominance is most clearly expressed. The intrinsic attributes hypothesis predicts that

females should emit aggressive acts at higher rates than males, and that males should exhibit submissive behavior (both in response to a threat and in the absence of a threat) at higher rates than females. The social support hypothesis predicts that females should receive social support at higher rates than males, and that females acting aggressively towards males while receiving social support should be more likely to elicit submissive responses from their targets than females acting alone. After evaluating the predictions of these two hypotheses in adults, we then take an ontogenetic perspective by examining the co-occurrence of these mechanisms and female-biased dominance in younger hyenas that have yet to reach sexual maturity.

METHODS

Study species

Female spotted hyenas invest heavily in the rearing of offspring (Hofer & East 1996; Laubach et al. 2021; Watts et al. 2009; McCormick et al. 2021). They usually bear litters of 1 or 2 cubs; when twin cubs are born, neonatal females dominate males in 67% to 84% of mixed-sex twin litters (Smale et al. 1995; Golla et al. 1999; Wahaj and Holekamp 2006; Benhaiem et al. 2012). During the first 2 years of life, juveniles of both sexes assume the social ranks and entire social networks of their mothers (Strauss et al. 2020; Smale et al. 1993; Holekamp & Smale 1993; Ilany et al. 2021). Young animals of both sexes generally retain their maternal ranks as long as they remain in the natal clan, resulting, on average, in parity between the sexes with respect to dominance rank among cubs and subadults. Full-blown female dominance over males emerges after reproductive maturity and male dispersal.

One to six years after they become reproductively mature, most male spotted hyenas disperse to join new social groups (Smale et al. 1997; Höner et al. 2007), a process that induces a suite of physiological, behavioral, and social changes (Holekamp & Sisk

2003). It also generates two classes of adult males in most hyena clans: immigrant males who have arrived from other clans and adult natal males who have not yet dispersed. Immigrant males are subordinate to all females and natal males in the group (Kruuk 1972), but long-term immigrants sire the vast majority of offspring (Engh et al. 2002, Van-Horn et al. 2004). Immigration into a new clan by a male spotted hyena coincides with an increase in the frequency with which he exhibits extreme submissive behavior (Smale et al. 1997); it also coincides with an elevation in circulating testosterone concentrations and onset of adult testicular function (Holekamp & Sisk 2003; Curren et al. 2013). Finally, by joining a new group of unfamiliar conspecifics, dispersing males not only experience a drastic decline in their priority of access to food resources (Smale et al. 1997), but they also lose most or all their established social relationships (Vullioud et al. 2019).

Study population

In this study, we used data collected between 1988 and 2018 from three clans of spotted hyenas inhabiting the Masai Mara National Reserve, Kenya. Individual hyenas were identified by their unique spots and other marks, such as scars and ear damage. The sex of each individual was determined based on the shape of the glans of its erect phallus (Frank et al. 1990), and ages of natal animals were determined to +/- 7 days based on cub appearance when first seen (Holekamp et al. 1996). We classified hyenas in their first year of life as cubs; these individuals are largely dependent on their mothers for food and on dens for refugia (Holekamp & Smale 1998). We classified hyenas in their second year of life as sub-adults; these individuals are weaned on average at 13 months, and they no longer use dens, but remain heavily dependent on their mothers for access to food and protection (Watts et al. 2009). We classified hyenas two years of age and older as adults; hyenas of both sexes are physiologically able to breed at 2 years of age (Glickman et al 1992). As a result, there are three categories of resident adult hyenas within each clan: females, natal

males that have not yet dispersed, and immigrant males that have successfully left their natal clan to join a new one. Here, a dispersing adult male was considered to have successfully immigrated into a new clan after he was observed in the clan's territory for at least 6 months and observed interacting with clan residents at least 3 times (Engh et al. 2002).

Observations were made daily from vehicles for 3-4 hours around dawn and again around dusk. We defined an observation session as observing one or more hyenas separated from others by at least 200m (Holekamp et al. 1997; Yoshida et al. 2016). In each session, we identified all hyenas present, and we used all-occurrence sampling (Altmann 1974) to record aggressive and submissive acts. We restricted our analyses to observation sessions lasting 10 minutes or longer, and at which 2 or more hyenas were present, and we excluded observation sessions that occurred at natal dens. We also restricted our analyses to agonistic interactions in which observers identified all hyenas involved in the interaction, and we excluded agonistic interactions classified as "baiting", a type of stereotyped sexual aggression between adult males and females where multiple males cooperatively attack a lone female. Baiting behavior does not affect intersexual dominance relationships in spotted hyenas (Szykman et al. 2003).

Calculating rates of unsolicited aggressive and submissive behaviors

To assess spontaneous aggressive and submissive behavior, we counted the number of aggressive or submissive acts emitted by each individual present in each observation session. Aggressive behaviors included intention movements to attack, threat and attack behaviors without bodily contact, and physical contact that might result in injury. Submissive behaviors included appeasement signals like flattening the ears back against the head or head-bobbing, postural changes such as folding the entire body into a submissive posture with tail down between the legs, and "groveling," or crawling on one's

belly and carpals (Kruuk 1972). Descriptions of all agonistic behaviors in this dataset can be found in the Supplementary Materials. For aggressive behavior, we only included acts of spontaneous aggression and did not count acts of aggression that were immediate responses to a prior aggressive act directed at the focal individual, such as counterattacks or redirection onto a third party. For unsolicited submissive behavior, we only included spontaneous submissive acts that were emitted in the absence of an immediately preceding aggressive act directed at the focal individual.

Calculating dominance

An individual was considered to successfully dominate another individual during an aggressive encounter if the recipient of an aggressive act emitted a submissive response. This resulted in a binary variable, successful vs unsuccessful attack, indicating whether or not the recipient hyena emitted a submissive response. It should be noted that, if a recipient does not respond with a submissive behavior, it does not necessarily mean that the aggressor was dominated; instead, it simply means that the threat was not successful in eliciting a submission signal from the recipient.

Calculating social support

An individual was considered to have been supported during an agonistic interaction if another hyena present either acted simultaneously with it to attack a target or joined it in an ongoing attack. This resulted in a binary factor, supported vs unsupported aggression, indicating whether or not the aggressor received support from 1 or more clan-mates during an agonistic encounter. We used this binary variable of social support to assess sex differences in social support and to assess the effect of social support on dominance.

Modeling rates of aggression and submission

To compare variation in spontaneous aggressive and submissive behavior between sexes and across ontogeny, we built separate mixed models for each age class (cubs,

subadults, adults) that included the sex of the acting individual ("actor") as the independent

variable and counts of aggressive and submissive behaviors as the dependent variables.

The number of hyenas present in the observation session was included as a covariate to

control for known effects of group size on rates of social behavior (McCormick & Holekamp

2022). The duration of the observation session was included as an offset to account for

variation in observation time. The observation session ID was included as a random

intercept to control for contextual variation among sessions. Models were built using a zero-

inflated Poisson approach within the glmmTMB package in R (Mollie et al. 2017), and we

report estimated incidence rate ratios (IRR) in which we set females as the reference group.

These IRR values are calculated from exponentiating the model estimates comparing males

to the female reference category, such that an IRR of 2 would be interpreted as males

exhibiting the modeled behavior 2 times more often than females (Long & Freese 2006).

Modeling dominance and social support

To ascertain whether successfully dominating another group member was driven by

the sex of the actor or the sex of the recipient, we built logistic regression models including

actor sex and recipient sex as independent variables and dominance (successful vs.

unsuccessful attack) as the binary dependent variable. This allowed for both intra- and inter-

sexual comparisons of whether or not the aggressive act elicited a submissive response.

We included an interaction between actor sex and recipient sex, and we included

observation session ID and actor ID as random intercepts.

To assess whether members of one sex received more social support than members

of the other sex, we built logistic regression models that included actor sex and recipient

sex as independent variables, and support (supported vs. unsupported) as the binary

dependent variable. We again included an interaction between actor sex and recipient sex

as a fixed effect, as well as observation session ID and actor ID as random intercepts.

To determine whether social support during an agonistic encounter affected the

supported hyena's ability to successfully dominate a member of the opposite sex, we built

logistic regression models including actor sex, recipient sex, and support (supported vs.

unsupported) as independent variables and dominance (successful vs. unsuccessful) as the

binary dependent variable. We also included a three-way interaction between actor sex,

recipient sex, and support, as well as observation session ID and actor ID as random

intercepts.

To address all these questions, we built a separate mixed model for each actor age

class (adults, subadults, and cubs) to track dominance and social support throughout

ontogeny. Aggressive acts were separated by actor age and filtered to require actors to

aggress on individuals of their own age class or older (for example, the subadult model

includes subadult actors and both subadult and adult recipients). All models for dominance

and social support were logistic regression models fit using the glmer function in the lme4

package (Bates et al. 2015). If we found a signification interaction between any explanatory

variables at $\alpha = 0.05$, we further stratified our analysis based on both actor sex and recipient

sex to determine if the sex difference was driven by the actor or the recipient.

All formal models were built using R-software (R Core Team 2021). All models were

tested for violations of dispersion, within-group deviation of uniformity, homogeneity of

variance (Levene Test), and influence of outliers using the DHARMa package (Hartig 2021).

Inclusion of relevant random intercepts (observation session ID and actor ID) was checked

by calculating the intraclass correlation coefficient (ICC). If a random intercept did not

account for sufficient variation in the model (ICC < 0.001), it was dropped. Finally, all

models were assessed using two-tailed tests with an alpha = 0.05.

RESULTS

Spontaneous aggressive behavior

We built three separate age-stratified models of sex differences in spontaneous aggressive behavior: cubs (actors < 1 year old), sub-adults (actors 1-2 years old) and adults (actors > 2 years old). A summary of the data for counts of spontaneous aggressive behaviors can be found in Table A.3.1. Among adults, comparisons of incidence rate ratios (IRR) revealed that adult natal males emitted aggressive acts at roughly half the rate of females (IRR = 0.485; 95% CI = 0.415, 0.566; p < 0.001), and immigrant males (IRR = 0.193; 95% CI = 0.172, 0.216; p < 0.001) at roughly one fifth the rate of females (Figure 3.1). We found no sex difference in rates of aggression among sub-adults (IRR = 0.924; 95% CI = 0.736, 1.16, p = 0.496; Figure 3.1). In cubs, we found that male cubs exhibited marginally lower rates of aggression than female cubs (IRR = 0.835; 95% CI = 0.694, 1.01; p = 0.0566; Figure 3.1).

Spontaneous submissive behavior

We built three separate age-stratified models of sex differences in unsolicited submissive behavior: cubs (actors < 1 year old), sub-adults (actors 1-2 years old) and adults (actors > 2 years old). A summary of the data for counts of spontaneous submissive behaviors can be found in Table A.3.1. Among adults, comparisons of incidence rate ratios (IRR) revealed that adult natal males emitted spontaneous acts of submission roughly 2.5 times more often than adult females (IRR = 2.54; 95% CI = 2.23, 2.88; p < 0.001), and immigrants at roughly 4.5 times the female rate (IRR = 4.43; 95% CI = 4.07, 4.83; p < 0.001) (Figure 3.2). We found no sex difference in submission rates among either cubs (IRR = 0.932; 95% CI = 0.768, 1.13; p = 0.485; Figure 3.2) or sub-adults (IRR = 0.901; 95% CI = 0.770, 1.05; p = 0.194; Figure 3.2).

Variation in successful acts of dominance

In our initial models of dominance (successful vs. unsuccessful attack) in most age classes (cub, sub-adult, adult), we found a significant interaction between actor sex and recipient sex (Figure A.3.1, Table A.3.3). A summary of the number of acting individuals by sex and age class for this model can be found in Table A.3.2. Given the significant interaction, we thus stratified our further analyses by recipient sex and actor sex to investigate the effects of both actor sex and recipient sex separately.

Eliciting submission

In our models stratified by recipient sex (Table A.3.4), we investigated the effect of actor sex on the probability of the actor eliciting a submissive response. Among adults, when recipients were females, adult immigrant male actors were less likely than adult female actors to receive a submissive response (OR = 0.0869; 95% CI = 0.0512, 0.148; p < 0.001; Figure 3.3 a), but adult natal male actors were just as likely as adult female actors to receive a submissive response (OR = 0.981; 95% CI = 0.767, 1.26; p = 0.881; Figure 3.3 a). When recipients were either immigrant or adult natal males, adult male and adult female actors were equally likely to elicit a submissive response (Figure 3.3 a, Table A.3.4). In both subadults and cubs, male and female actors were equally likely to elicit a submissive response regardless of recipient sex (Figure 3.3 a, Table A.3.4).

Offering submission

In our models stratified by actor sex (Table A.3.5), we investigated the effect of recipient sex on the probability of the recipient responding with a submissive act. In adults, when the aggressors were females, adult immigrant male recipients (OR = 1.71; 95% CI = 1.52, 1.93; p < 0.001) and adult natal male recipients (OR = 2.34; 95% CI = 1.29, 4.23; p < 0.001) were far more likely to submit than adult female recipients (Figure 3.3 b). When adult immigrant males were the aggressors, both adult immigrant male recipients (OR = 12.8;

95% CI = 4.23, 38.4; p < 0.001) and adult natal male recipients (OR = 8.76; 95% CI = 2.00, 38.4; p < 0.001) were far more likely to submit than adult females recipients (Figure 3.3 b). When adult natal males were the aggressors, both sexes were equally unlikely to offer a submissive response (Figure 3.3 b, Table A.3.5).

Among sub-adults, when females were the aggressors, male recipients were more likely than female recipients to offer a submissive response (OR = 1.31; 95% CI = 1.03, 1.66; p = 0.0259; Figure 3.3 b). When males were the aggressors, male and female recipients were equally likely to offer a submissive response (OR = 1.05; 95% CI = 0.811, 1.38; p = 0.682; Figure 3.3 b). Among cubs, male recipients were more likely than female recipients to offer a submissive response to both female aggressors (OR = 1.41; 95% CI = 1.19, 1.66; p < 0.001) and to male aggressors (OR = 1.88; 95% CI = 1.59, 2.22; p < 0.001; Figure 3.3 b).

Variation in receipt of social support

Next, we inquired whether there were sex differences in receiving social support or being targeted by coalitionary social support during aggressive acts. A summary of the number of acting individuals by sex and age class, acting with or without support, for this model can be found in Table A.3.2. There was no significant interaction between actor sex and recipient sex in any of our initial models of social support (supported vs. unsupported) in all three age classes (cub, sub-adult, adult), so the interaction term was not included in the final models, and main effects were reported (Figure A.3.2, Table A.3.6).

Receiving social support as an actor

Among adult actors, we found that both adult immigrant males (OR = 1.86; 95% CI = 1.50, 2.30; p < 0.001) and adult natal males (OR = 2.06; 95% CI = 1.72, 2.47; p < 0.001) were roughly twice as likely as adult females to receive social support during an aggressive

act (Figure 3.4a). However, males and females were equally likely to be supported during attacks among both cubs and subadults (Figure 3.4 a, Table A.3.6).

Being targeted by socially supported aggressors

Across all age classes, females were more likely than males to be the targets of aggression when actors were supported (Figure 3.4 b). Among adult recipients, both immigrant males (OR = 0.303; 95% CI = 0.272, 0.338; p < 0.001) and adult natal males (OR = 0.406; 95% CI = 0.305, 0.539; p < 0.001) were far less likely than females to be targets of socially supported aggressors (Figure 3.4 b). Male recipients were also less likely than females to be targets of socially supported aggressors among both cubs (OR = 0.323; 95% CI = 0.288, 0.364; p < 0.001; Figure 3.4 b) and subadults (OR = 0.323; 95% CI = 0.288, 0.364; p < 0.001; Figure 3.4 b).

Effects of social support on dominance

Finally, we inquired whether social support during an aggressive encounter was associated with dominance outcomes. In our initial model of dominance (successful vs. unsuccessful attack) in adult hyenas, we found a significant three-way interaction between actor sex, recipient sex, and social support (Figure A.3.3, Table A.3.7). To assess the effect of social support on whether or not an actor was successful in a dominance interaction with a recipient of the opposite sex, given this evidence of effect modification, we stratified the data by actor sex and age class and report estimates from each stratified model for each age class. We report inter-sex comparisons of the effect of social support on dominance outcomes below and report all other comparisons in Table A.3.8.

Among adults, we found that support had no effect on how likely immigrant males (OR = 0.58; 95% CI = 0.08, 4.47; p = 0.603) or adult natal males (OR = 0.73; 95% CI = 0.29, 1.89; p =0.522) were to elicit a submissive response from adult females (Figure 3.5). Interestingly, supported adult females were slightly less likely to elicit a submissive

response from immigrant males than unsupported adult females (OR = 0.68; 95% CI = 0.47, 0.99; p = 0.042; Figure 3.5). When adult females aggressed on adult natal males, there was no effect of support on the dominance outcome (OR = 0.30; 95% CI = 0.01, 5.48; p = 0.420; Figure 3.5). Among subadult aggressors, supported males were more likely than unsupported males to elicit a submissive response from female recipients (OR = 2.18; 95% CI = 1.53, 3.13; p < 0.001), but support had no effect on the odds of subadult females eliciting a submissive response from males (OR = 0.62; 95% CI = 0.27, 1.40; p = 0.248; Figure 3.5). Finally, among cubs there was no effect of support on the odds of male aggressors eliciting a submissive response from females (OR = 0.96; 95% CI = 0.70, 1.30; p = 0.773), or on the odds of female aggressors eliciting a submissive response from males (OR = 1.37; 95% CI = 0.85, 2.21; p = 0.194; Figure 3.5).

DISCUSSION

Here we evaluated intrinsic attributes and social support as two non-mutually exclusive hypotheses explaining sex-biased dominance in spotted hyenas. In support of the intrinsic attribute hypothesis, we found that, without provocation, adult females were more aggressive than adult males (Figure 3.1), and that adult males were more submissive than adult females (Figure 3.2). Interestingly, adult natal males also appeared to be more aggressive and less submissive than immigrant males (Figures 3.1 & 3.2). Earlier during ontogenetic development, the pattern of intrinsic behavioral differences between the sexes was less clear, especially among subadults. However, female cubs were marginally more aggressive than their male counterparts (Figure 3.1). These results support the earlier conclusion by McCormick et al. (2020) and Watts et al. (2009) that female spotted hyenas are the more aggressive sex, even after controlling for opportunities to act aggressively towards clan-mates within each observation session. That adult males were more likely than adult females to submit without any observed provocation suggests another important

intrinsic difference between the sexes, one that was also documented earlier by Smale et al. (1993). Although this difference emerges as hyenas reach sexual maturity and the typical age of dispersal, the fact that adult natal males were more submissive than adult natal females indicates that this pattern of adult male submissiveness is not driven purely by dispersal-induced changes in social support, as has been suggested (Vullioud et al. 2019).

In further support of the intrinsic attributes hypothesis, both immigrant males and natal males were more likely than females to submit to females (Figure 3.3 b). If this sex-biased pattern in submission was driven exclusively by the actor's and recipient's relative positions in the clan's dominance hierarchy, we expected that only immigrant males would differ significantly from natal individuals of both sexes because natal males retain their maternal ranks before dispersal (Strauss et al. 2020). However, as early as the first year of life we observed that males were more likely than females to offer submission spontaneously, regardless of the sex of the aggressor (Figure A.3.1 b). We also observed the pattern of more submissive males during the sub-adult phase of life (S1C). These findings, particularly when considered in light of the striking sex differences in dominance within mixed-sex twin litters (Smale et al. 1995; Golla et al. 1999; Wahaj and Holekamp 2006; Benhaiem et al. 2012), lead us to conclude that the patterns associated with female dominance start to emerge long before sexual maturity, and before dispersal by males.

In regard to the social support hypothesis, we found that social support was not sufficient to explain patterns of sex differences in agonistic behavior or dominance. If social support was the basis of female dominance over males, we expected to see that females received support at higher rates than males, and that this support aided them in dominating males. Instead, adult females were considerably more likely than either immigrant males or natal males to act alone as aggressors (Figure 3.4 a), and females elicited submissive responses from immigrant and natal males when acting alone just as readily as when acting

with support (Figure 3.5). Despite the lack of evidence for the social support hypothesis as the sole determinant of female dominance among spotted hyenas, our results indicated that social support did shape agonistic interactions in some interesting ways. Support improved the likelihood of adult females successfully dominating other adult females (Figure A.3.3); previous work revealed that coalitionary aggression is an important mechanism producing rank change among female hyenas (Strauss & Holekamp 2019). Most strikingly, hyenas of all age and sex classes were more likely to act alone when aggressing against males than against females (Figure A.3.2), suggesting that the increased threat posed by female opponents can be diminished by social support from groupmates.

Surprisingly, we found that social support had a greater effect on the outcomes of interactions involving cubs and sub-adults than those involving adults (Figure A.3.3 b & S.3.3 c). Here, support generally increased the likelihood that cubs would receive a submissive response during an agonistic encounter regardless of actor sex or recipient sex. Some of this support involved mothers helping cubs win fights as part of the process of rank acquisition in the clan's dominance hierarchy (Engh et al 2000; East et al. 2009; Strauss et al. 2020). However, winning fights by cubs was clearly also affected by the male tendency to concede defeat more readily than females when attacked.

Although our results suggest that social support is not sufficient to explain female dominance over male hyenas, they point to social support and intrinsic sex differences as dual influences on dominance in this species. Of particular interest in distinguishing the contributions of these two hypotheses are our results for natal adult males, who have reached sexual maturity but have not yet dispersed to join a new clan. If social support is the sole driver of differences in behavior between the sexes, natal males should behave similarly to adult females, as they both have access to all the social support of their natal clans (Vullioud et al. 2019). In contrast, if intrinsic differences between the sexes are the

sole drivers of sex-biased dominance, natal males should behave similarly to immigrant males. However, the aggressive and submissive behavior of natal males supports neither of these predictions. Instead, natal males offered unsolicited aggression (Figure 3.1) and submission (Figure 3.2) at rates intermediate between immigrant males and adult females, implicating both social support and intrinsic sex differences as dual concurrent drivers of sex-biased dominance in this species.

In fact, as occurs in so many other mammalian? species (Dehnen et al. 2022; Lewis, 2020), there are likely to be multiple determinants of female dominance in spotted hyenas. We consider the problem of female dominance in these animals in light of the general framework suggested by Lewis (2002) for assessment of female power in animal societies. Lewis (2002) divides power into two categories, dominance, and leverage, depending on the nature of the asymmetry between actor and recipient giving rise to the power (Lewis 2002. Lewis uses the term 'dominance' when the base of power is an asymmetry in physical capacities affecting the ability to use force. Female dominance is intrinsic among adult hyenas insofar as females are larger and more aggressive than males (Swanson et al 2013; McCormick et al 2021; Figure 3.1), and males also concede defeat much more readily than do females (Figure 3.2). However, female dominance in this species is also based on social support, which helps cubs, often with support from their mothers, elicit submission from larger hyenas, and also helps females win fights against other females (Engh et al. 2000; Strauss & Holekamp 2019). Thus, larger body size, and greater aggressiveness are intrinsic traits that enhance a female hyena's likelihood of winning fights with groupmates, but the number of kin or other social allies available as potential supporters to a particular aggressor also affect its ability to win fights (Smith et al. 2010; Vuillouid et al 2019).

Economic 'leverage' is another important form of power among female hyenas because neither their ova nor their affiliative relationships can be taken by force. For

instance, some researchers have argued, and we strongly agree, that aggression among immigrant males is low because a close relationship with a female is a nontransferable resource that cannot be acquired through physical contests between males (e.g., East et al. 1993; Hofer & East 2001). The complete control females have over mating in this species has presumably favored the submission of males to females, the queuing convention observed among immigrant males, and the lack of selection for physical contests among males (East et al., 1993; Hofer and East, 1995). Adult female spotted hyenas thus enjoy both dominance and leverage over males simultaneously. Females may also issue rewards to or withhold rewards from males, for example, by mating with them or tolerating them while feeding concurrently from a carcass (Smith et al. 2007).

In summary, we conclude, as did Kruuk (1972), Frank (1986) and Mills (1990) before us, that female spotted hyenas are the more aggressive and socially dominant sex, and that males are inherently more likely than females to submit in response to aggression. Some of these determinants of female dominance can be observed during early post-natal ontogeny, well before sexual maturity or male dispersal. As the weaker members of intersexual dyads, males emit a great deal of unprovoked submissive behavior, and they concede defeat more readily in fights. Patterns of social support did not explain these differences between males and females—adult females more frequently attacked groupmates without support than did adult males, and females were also clearly able to dominate males without social support. Nevertheless, support helped individuals of both sexes and in multiple age classes to dominate formidable females, and thus, support is crucial to rank acquisition (Engh et al 2000; East et al. 2009; Holekamp & Smale 1991), it reinforces the established kin-structured dominance hierarchy among natal individuals (Smith et al. 2010, Holekamp et al. 2012, Vullioud et al. 2019), and it influences competition among females (Strauss & Holekamp 2019).
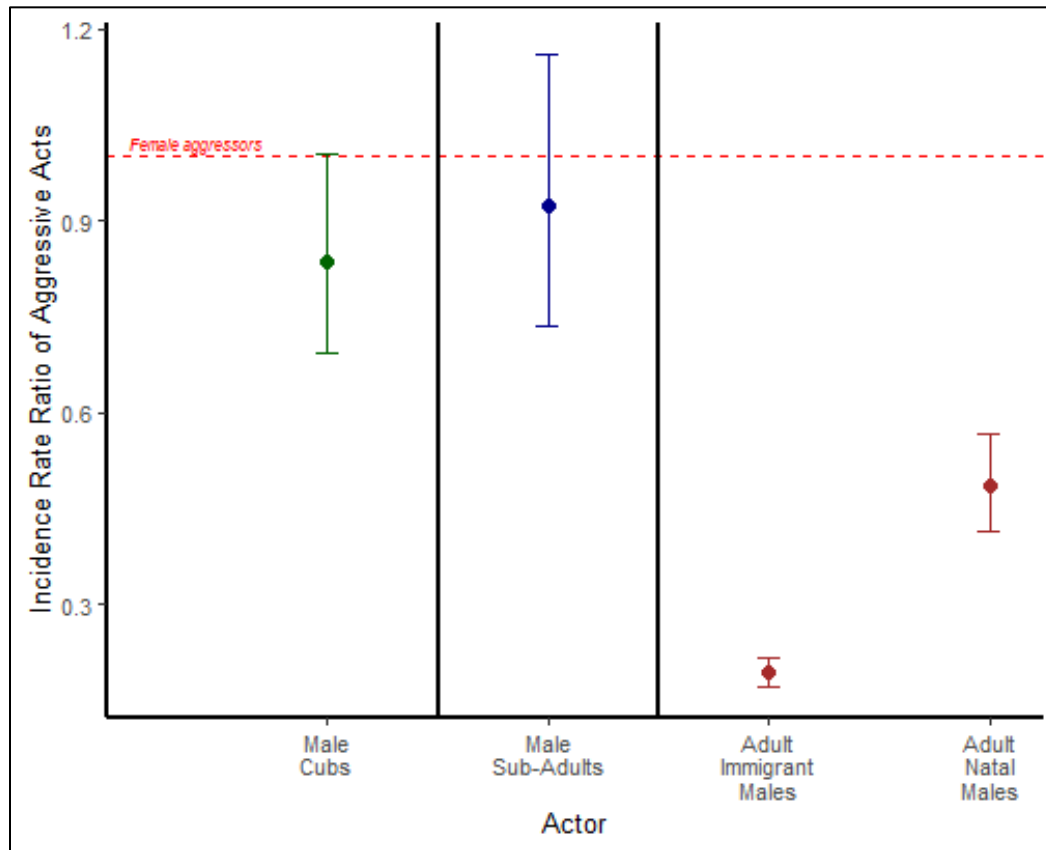
Figure 3.1: Incidence rate ratios of spontaneous aggressive acts emitted by male cubs (green), male sub-adults (blue), adult immigrant males (brown) and adult natal males (brown). Each is compared to a female aggressor reference group of the same age class, represented by the red dashed line. Points represent the estimated incidence rate ratios from three separate mixed models separated by bold black lines (actors who are cubs, actors who are sub-adults, and actors who are adults), and error bars represent 95% confidence intervals around the incidence rate ratio.
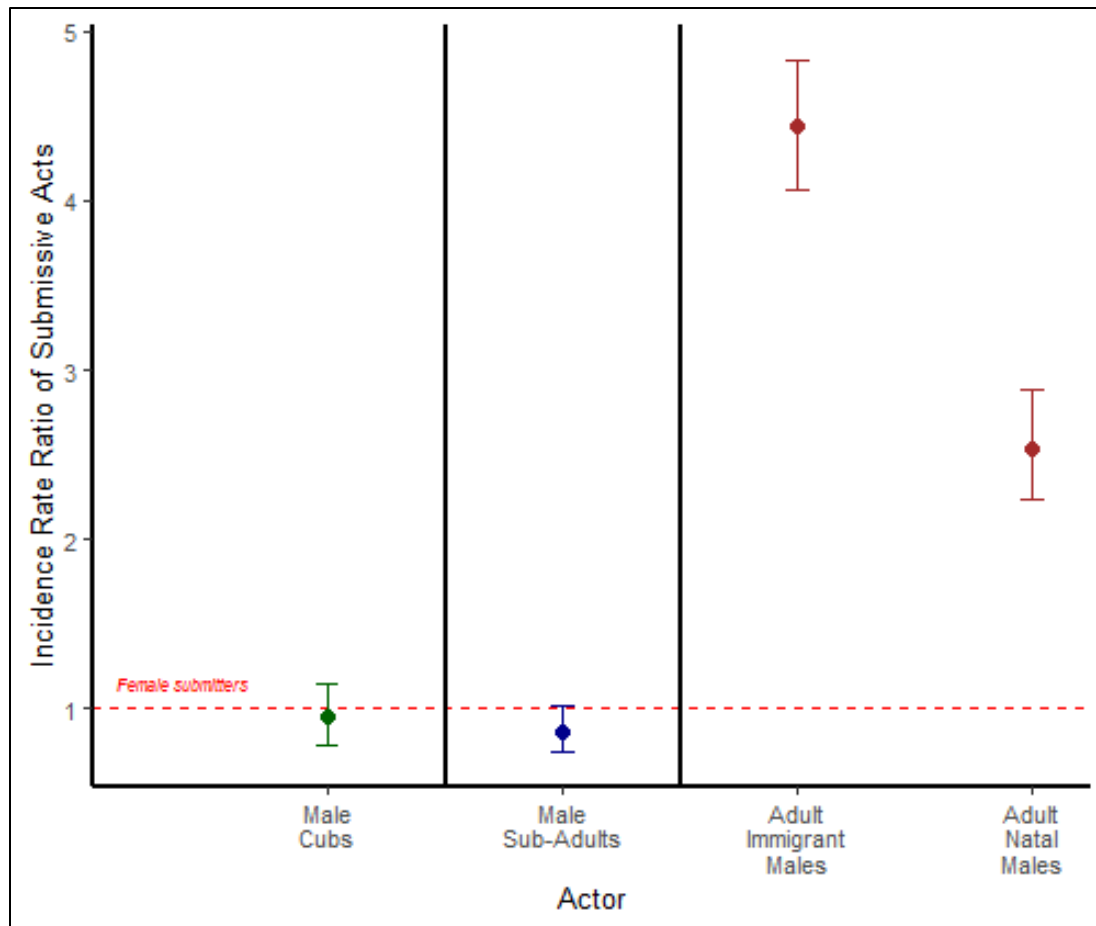
Figure 3.2: Incidence rate ratios of spontaneous submissive acts emitted by male cubs (green), male sub-adults (blue), adult immigrant males (brown) and adult natal males (brown). Each is compared to a female actor reference group of the same age class, represented by the red dashed line. Points represent the estimated incidence rate ratios from three separate mixed models separated by bold black lines (actors who are cubs, actors who are sub-adults, and actors who are adults), and error bars represent 95% confidence intervals around the incidence rate ratio.
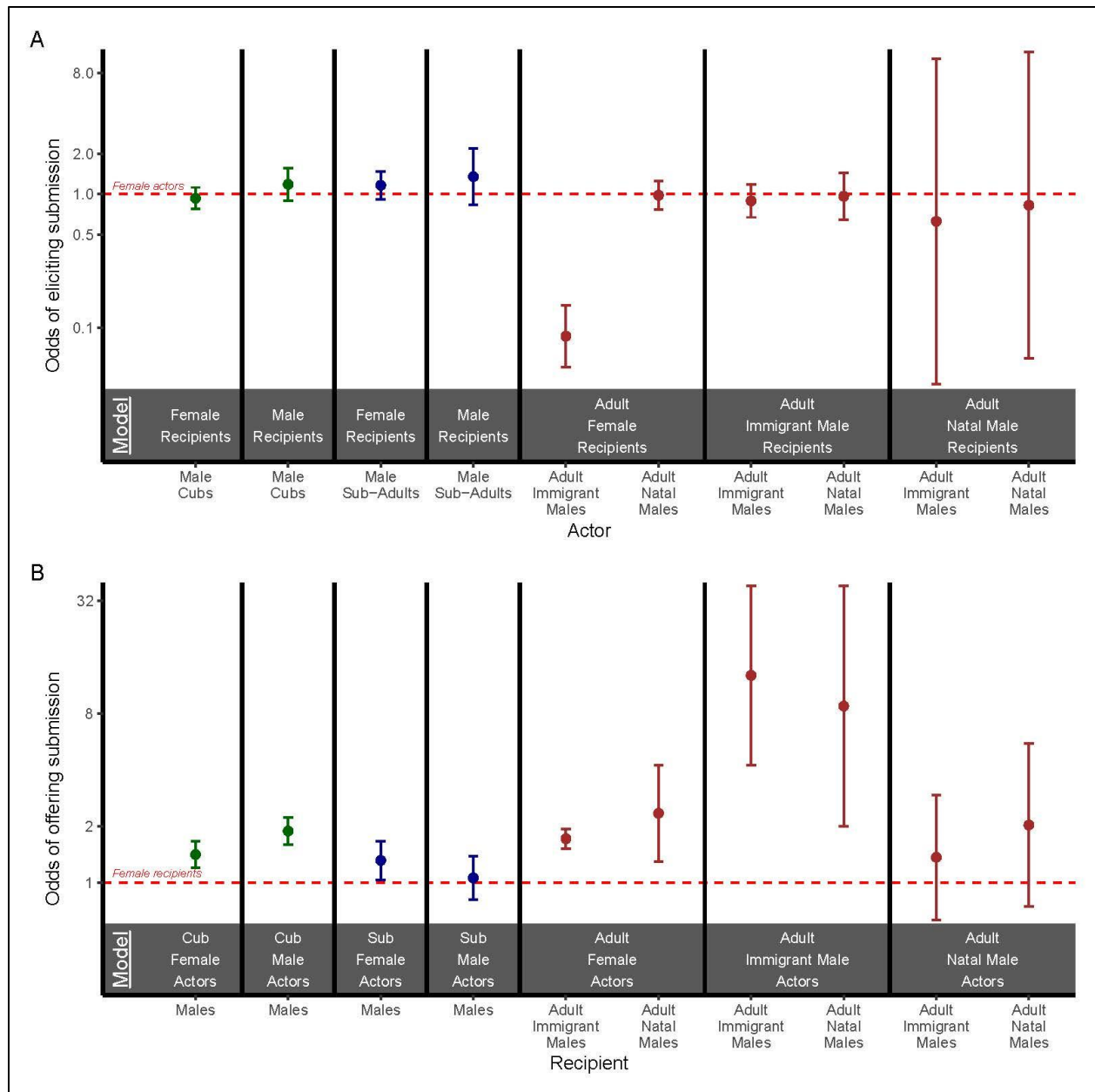
Figure 3.3: A. Likelihood of an actor eliciting a submissive response in models stratified by both actor age and recipient sex. B. Likelihood of a recipient offering a submissive response to an aggression in models stratified by both actor age and actor sex. A-B. Models are separated by bold black lines, and age is depicted by color where cub actors are green, sub-adult actors are blue, and adult actors are brown. Points represent the odds ratio and error bars represent 95% confidence intervals around the odds ratio. Each point is compared to a female reference group of the same age class represented by the red dashed line.
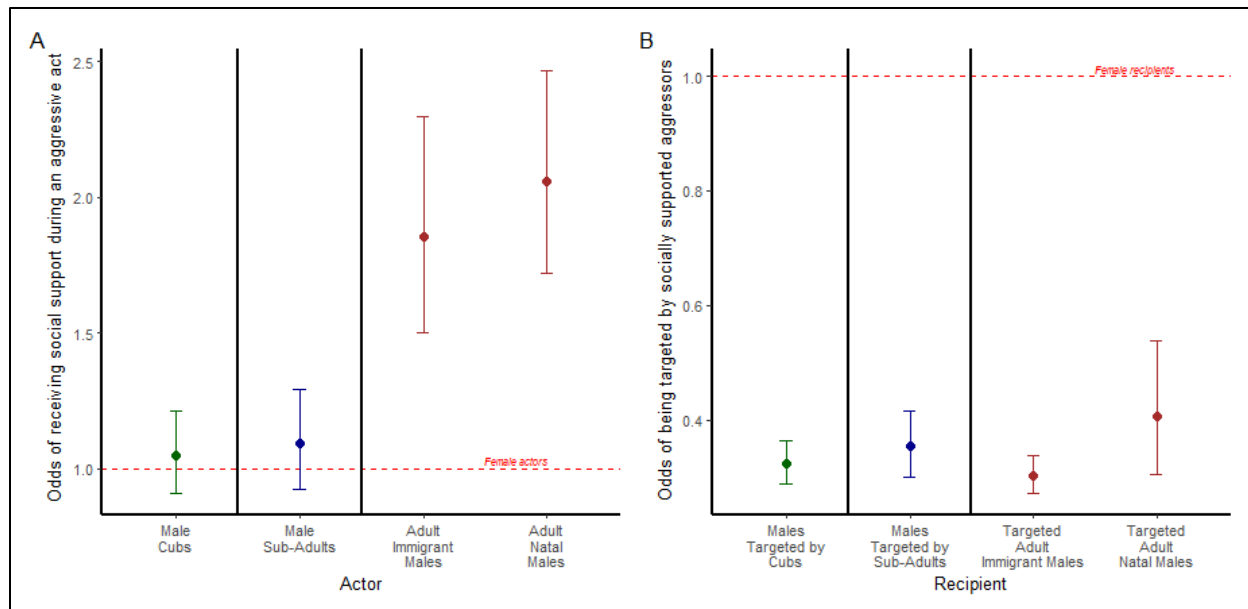
Figure 3.4: A. Likelihood of the acting aggressor receiving social support in an aggression. B. Likelihood of an individual being targeted by an actor with social support. A-B. Models are separated by bold black lines, and age is depicted by color where cub actors are green, sub-adult actors are blue, and adult actors are brown. Points represent the odds ratio and error bars represent 95% confidence intervals around the odds ratio. Each point is compared to a female reference group of the same age class represented by the red dashed line.
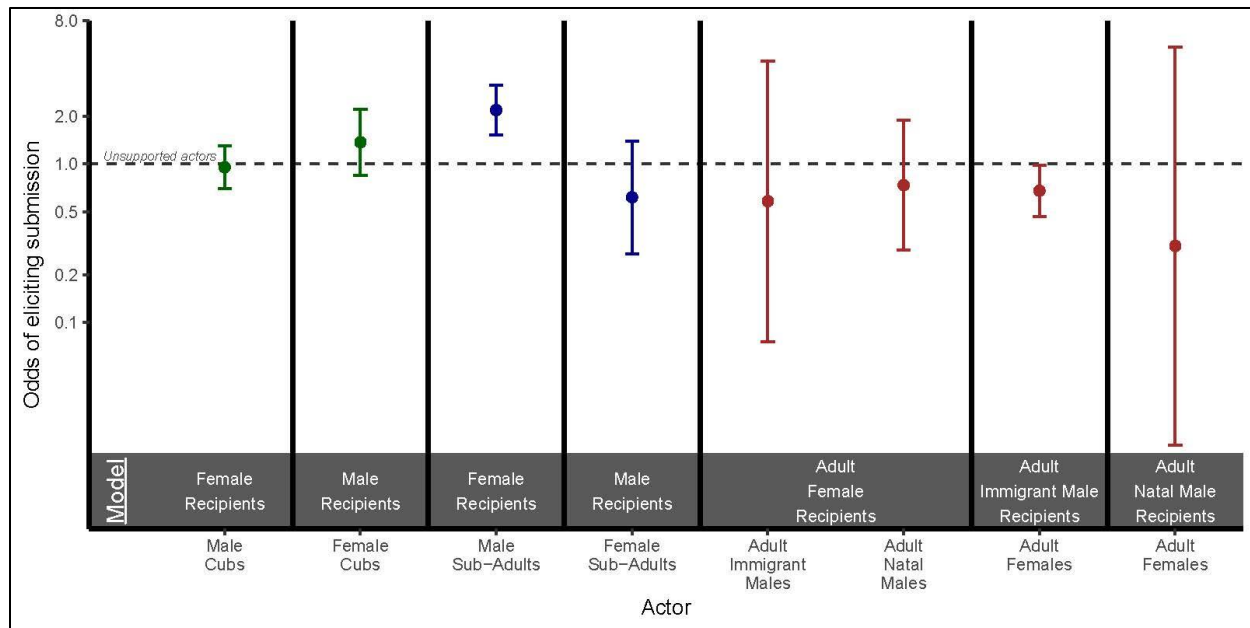
Figure 3.5: Likelihood of a supported versus unsupported actor eliciting a submissive response from a recipient of the opposite sex by actor's age and sex during an aggressive encounter. Models are separated by bold black lines, and actor's age is depicted by color where cubs are green, sub-adults are blue, and adults are brown. Points represent the odds ratio and error bars represent 95% confidence intervals around the odds ratio. Each point is compared to an unsupported actor reference group represented by the black dashed line.

APPENDIX

Agonistic behaviors emitted by spotted hyenas

Aggressive behaviors

Stand over (st ov): One animal stands with head high and muzzle pointed down at shoulders of a second individual. Lower intensities may involve an approach with head up and ears forward, sometimes with tail bristled. We refer to this lower intensity as "pointing".

Point (pt): Hyena adopts the exact same posture as an adult who is standing over another, but is too small or too far away to put its head over the back or shoulders of the conspecific toward which it is behaving aggressively. Point is used instead of "stand over" in any case where a youngster is too small to physically stand over the other animal or when the aggressor is approaching with head up and ears forward.

Head wave (hewa): This is an intention movement to bite or lunge in which the aggressor swings its head toward the opponent to signal that it will escalate its aggression if the opponent persists in its current behavior.

Push: One animal uses its body to push another.

Lunge: One hyena, usually with ears cocked forward, suddenly moves quickly toward another hyena, as if to bite; this may be done from either standing or lying positions.

Chase: Running pursuit.

Snap: Aggressor closes mouth rapidly near a conspecific, often making a snapping noise, but without any physical contact.

Bite: One animal's teeth make physical contact with another hyena.

Bite shake (bsh): One animal grips the skin of the back or shoulders of another with its teeth, and violently shakes its head from side to side, sometimes with an upward pulling motion.

Submissive behaviors

Back off (bo): The animal withdraws a step or two from a particular individual, but does not run or flee.

Ears back (eb): Ears are flattened backward against the sides of the head. The more extreme the appeasement, the more radically they are flattened, but any clear flattening of the ears is recorded as a signal by one hyena to another indicating that it perceives itself as subordinate to the other hyena.

Head bob (hb): Head wagging up and down or sideways.

Grin: Retracting the lips to reveal the teeth, but the mouth is not open.

Defensive parry (dp): One animal puts his/her open mouth up to the other animal's mouth/head to parry an oncoming attack.

Open mouth appease (oma): One animal puts his/her open mouth up to the other animal's mouth. An open mouth appease involves the same motor patterns as a defensive parry, but occurs spontaneously rather than in response to aggression.

Submissive posture (sp): The animal stands or walks with its head lowered, body hunched and bent around toward the recipient, butt tucked under, and tail down between the legs. This often (but not always) occurs in conjunction with ears back and lips retracted in a grin.

Run/flee: An animal runs from another individual or moves swiftly 2 or more body lengths away. (Note: While it does happen, these are rarely unsolicited. All of these are triple checked to be sure that this was clearly not solicited by a preceding aggression.)

Carpal crawl (cc): The threatened animal crawls or walks on the carpal joints of its forelegs, with hind legs bent and ears flattened back. (Also known as "grovel.")

Spontaneous aggressive and submissive behavior

Table A.3.1: **Aggressive and submissive data used in our analyses of the number of aggressive and submissive acts**. Rate is calculated per observation session per individual as (the number of spontaneous actions emitted / the number of hyenas present as possible targets of the action / duration of the session). Spontaneous actions are defined as agonistic actions occurring without social support that were not immediately proceeded by an observed threat.

Behavior Measured	Actor's Age-Sex Class	Number of Individuals	Number of Observation Sessions	Combined Duration (hours)	Number of Behaviors	Mean Behavior Rate	SD
Aggressive Acts	**Adults**						
	Female	227	38141	25746.48	3813	0.038	0.30
	Natal Male	187	17132	11338.68	612	0.017	0.16
	Immigrant Male	156	7149	4831.27	391	0.013	0.15
	Sub-Adults						
	Female	225	7917	5319.25	456	0.017	0.16
	Male	226	7313	4866.2	471	0.021	0.21
	Cubs						
	Female	378	10312	8063.77	556	0.015	0.13
	Male	309	11462	9128.02	633	0.015	0.15
Submissive Acts	**Adults**						
	Female	293	31022	21067.55	1642	0.027	0.23
	Male	208	13722	9012.18	2920	0.055	0.36
	Immigrant Male	181	6186	4176.98	709	0.12	0.67
	Sub-Adults						
	Female	258	6420	4332.28	469	0.034	0.29
	Male	284	6110	4071.73	413	0.028	0.21
	Cubs						
	Female	329	7682	6175.3	416	0.016	0.13
	Male	381	8873	7228.05	517	0.017	0.16

Variation in successful acts of domination

Table A.3.2: **Sample size of the number of acting individuals stratified by age, actor sex, recipient sex and presence/absence of support for the actor during ongoing aggressive interactions.** These data were used for models describing <u>variation in successful acts of domination</u>, <u>hyenas receiving social support</u>, and <u>effects of social support on dominance</u>.

Actor Age Class	Actor Sex	Recipient Sex	Actor Support	Count of Actors	Count of Sessions	Count of Actions
Adult	Female	Female	Supported	222	1539	2526
			Unsupported	247	3298	9894
		Immigrant Male	Supported	193	687	889
			Unsupported	244	3613	8516
		Natal Male	Supported	25	24	25
			Unsupported	81	145	289
	Immigrant Male	Female	Supported	41	35	43
			Unsupported	41	77	105
		Immigrant Male	Supported	74	185	248
			Unsupported	117	730	1513
		Natal Male	Supported	24	27	34
			Unsupported	39	62	108
	Natal Male	Female	Supported	120	267	408
			Unsupported	135	354	643
		Immigrant Male	Supported	78	134	168
			Unsupported	118	305	630
		Natal Male	Supported	44	49	75
			Unsupported	88	132	229
Cub	Female	Female	Supported	272	813	1298
			Unsupported	300	1224	3311
		Male	Supported	261	503	709
			Unsupported	298	1362	3709
	Male	Female	Supported	318	834	1348
			Unsupported	330	1345	3199
		Male	Supported	290	540	821
			Unsupported	352	1360	4267
Sub-Adult	Female	Female	Supported	197	595	952
			Unsupported	218	934	1991
		Male	Supported	129	214	266
			Unsupported	199	723	1423
	Male	Female	Supported	183	486	767
			Unsupported	214	740	1543
		Male	Supported	125	188	253
			Unsupported	196	510	1177
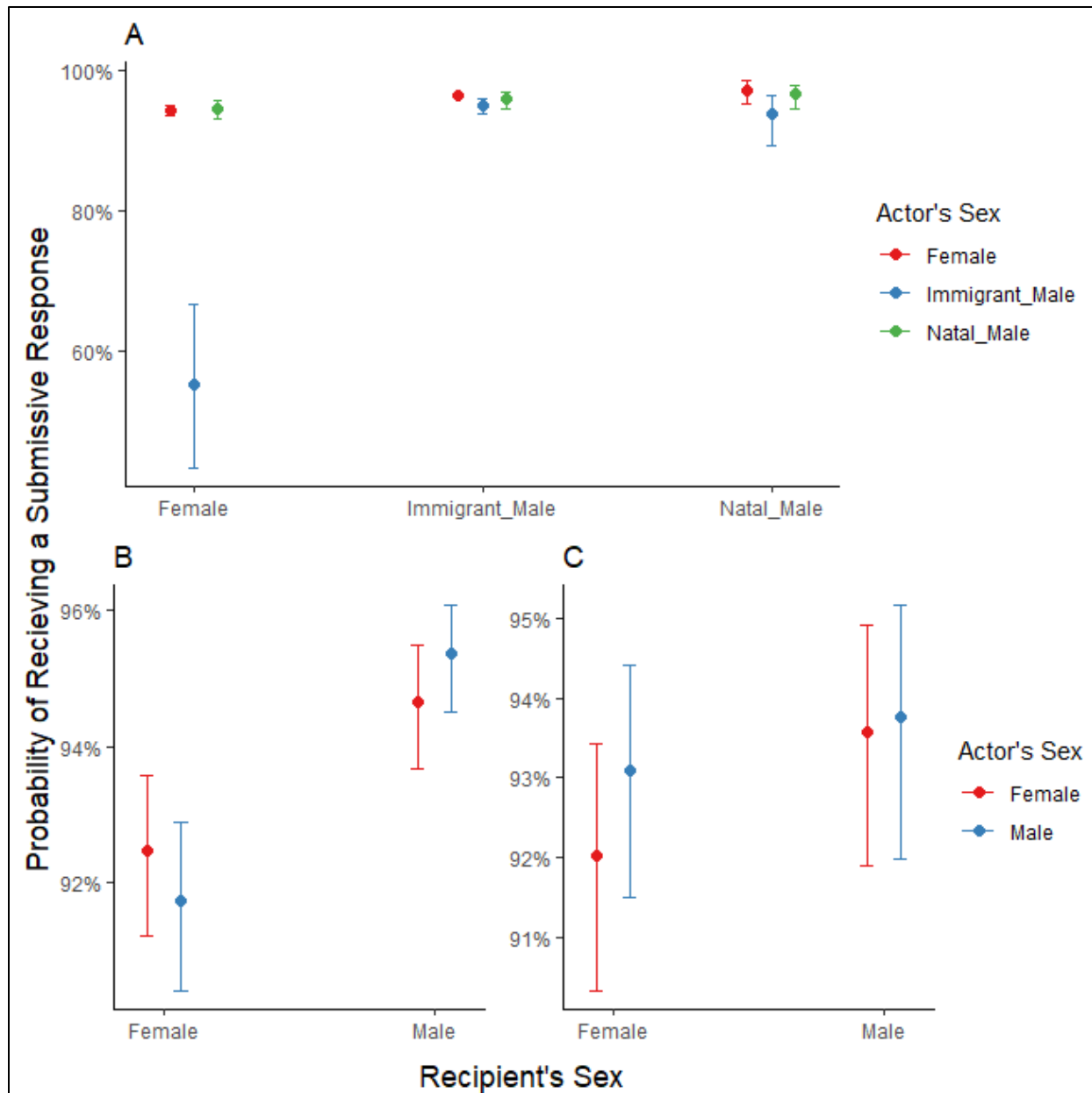
Figure A.3.1: **Probability of adults (A), cubs (B), and sub-adults (C) successfully eliciting a submissive response to an aggressive act based on actor sex and recipient sex.** Colors correspond to the actor's sex during interactions. Points represent the estimated marginal mean probabilities, and error bars represent the 95% confidence intervals.

Table A.3.3: **Estimate of the effect of actor sex and recipient sex on the likelihood that an actor's threat elicits a submissive response from the recipient.** Estimates are log-odds ratios of the effect of actor sex or recipient sex relative to females, and come from the full interactive model displayed in Figure A.3.1.

Age Class	Fixed Effects - *Reference group: Females*	Log-Odds	SE	P-Value
Adult	*(Intercept)*	2.789	0.065	< 0.001
	Actor: Immigrant Male	-2.572	0.247	< 0.001
	Actor: Natal Male	0.070	0.121	0.561
	Recipient: Immigrant Male	0.505	0.060	< 0.001
	Recipient: Natal Male	0.769	0.291	0.008
	Actor: Immigrant Male x Recipient: Immigrant Male	2.231	0.267	< 0.001
	Actor: Natal Male x Recipient: Immigrant Male	-0.203	0.195	0.299
	Actor: Immigrant Male x Recipient: Natal Male	1.717	0.475	< 0.001
	Actor: Natal Male x Recipient: Natal Male	-0.305	0.393	0.437
Cub	*(Intercept)*	2.509	0.086	< 0.001
	Actor: Male	-0.102	0.089	0.252
	Recipient Sex: Male	0.365	0.084	< 0.001
	Actor: Male x Recipient: Male	0.250	0.114	0.027
Sub-Adult	*(Intercept)*	2.445	0.107	< 0.001
	Actor: Male	0.157	0.114	0.169
	Recipient: Male	0.234	0.119	0.050
	Actor: Male x Recipient: Male	-0.125	0.175	0.475

Table A.3.4: **Estimate of the effect of actor sex on the likelihood that their threat elicits a submissive response from the recipient.** Estimates are odds ratios of the effect of actor sex relative to female actors, and come from models stratified by actor age and recipient sex. Model numbers do not correspond across tables.

Age Class	Recipient Sex	Model	Actor Sex: *Reference group: Females*	Odds Ratio (Actor Sex)	SE	P-value	95%CI Low	95%CI High
Adult	Female	1	Immigrant Male	0.087	0.024	< 0.001	0.051	0.148
			Natal Male	0.981	0.123	0.881	0.767	1.256
	Immigrant Male	2	Immigrant Male	0.892	0.129	0.431	0.671	1.185
			Natal Male	0.965	0.196	0.860	0.647	1.438
	Natal Male	3	Immigrant Male	0.628	0.895	0.744	0.038	10.279
			Natal Male	0.826	1.111	0.887	0.059	11.539
Cub	Female	4	Male	0.932	0.089	0.457	0.773	1.123
	Male	5	Male	1.185	0.169	0.235	0.896	1.567
Sub-Adult	Female	6	Male	1.166	0.142	0.208	0.918	1.481
	Male	7	Male	1.352	0.332	0.219	0.836	2.186

Table A.3.5: **Estimate of the effect of recipient sex on the likelihood that they offer a submissive response to a threat.** Estimates are odds ratios of the effect of recipient sex relative to female recipients, and come from models stratified by actor age and actor sex. Model numbers do not correspond across tables.

Age Class	Actor Sex	Model	Recipient Sex: *Reference group: Females*	Odds Ratio (Recipient Sex)	SE	P-value	95% CI Low	95% CI High
Adult	Female	1	Immigrant Male	1.714	0.106	< 0.001	1.518	1.935
			Natal Male	2.341	0.706	0.005	1.296	4.229
	Immigrant Male	2	Immigrant Male	12.790	7.215	< 0.001	4.234	38.640
			Natal Male	8.766	6.604	0.004	2.002	38.379
	Natal Male	3	Immigrant Male	1.361	0.534	0.432	0.631	2.936
			Natal Male	2.028	1.040	0.168	0.742	5.541
Cub	Female	4	Male	1.409	0.119	< 0.001	1.194	1.663
	Male	5	Male	1.881	0.161	< 0.001	1.591	2.224
Sub-Adult	Female	6	Male	1.312	0.160	0.026	1.033	1.666
	Male	7	Male	1.057	0.142	0.682	0.811	1.376
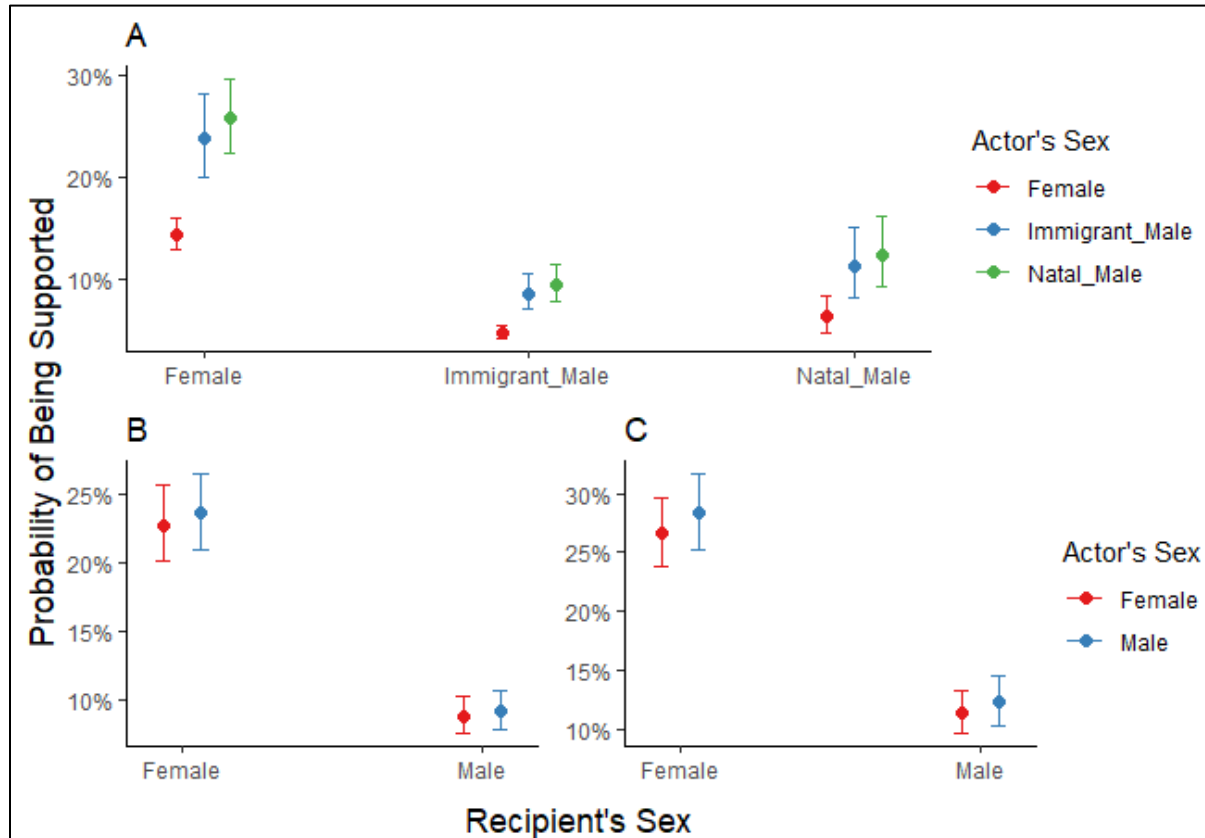
Figure A.3.2: **Probability of adults (A), cubs (B), and sub-adults (C) being supported during aggressive interactions based on the sex of the actor and the sex of the recipient.** Points represent the estimated marginal mean probabilities, and error bars represent the 95% confidence intervals.

Table A.3.6: **Estimate of the effect of actor sex and recipient sex on the likelihood that they receive social support during an aggression**. Estimates are log-odds ratios of the effect of actor sex and recipient sex relative to females, and come from the full model displayed in Figure A.3.2.

Age Class	Fixed Effects – *Reference Group: Females*	Log-Odds	SE	P-value
Adult	*(Intercept)*	-1.782	0.065	< 0.001
	Actor: Immigrant Male	0.619	0.109	< 0.001
	Actor: Natal Male	0.723	0.092	< 0.001
	Recipient: Immigrant Male	-1.193	0.055	< 0.001
	Recipient: Natal Male	-0.902	0.145	< 0.001
Cub	*(Intercept)*	-1.222	0.081	< 0.001
	Actor: Male	0.048	0.073	0.511
	Recipient: Male	-1.128	0.060	< 0.001
Sub-Adult	*(Intercept)*	-1.017	0.076	< 0.001
	Actor: Male	0.090	0.085	0.293
	Recipient: Male	-1.040	0.083	< 0.001

Effects of social support on dominance

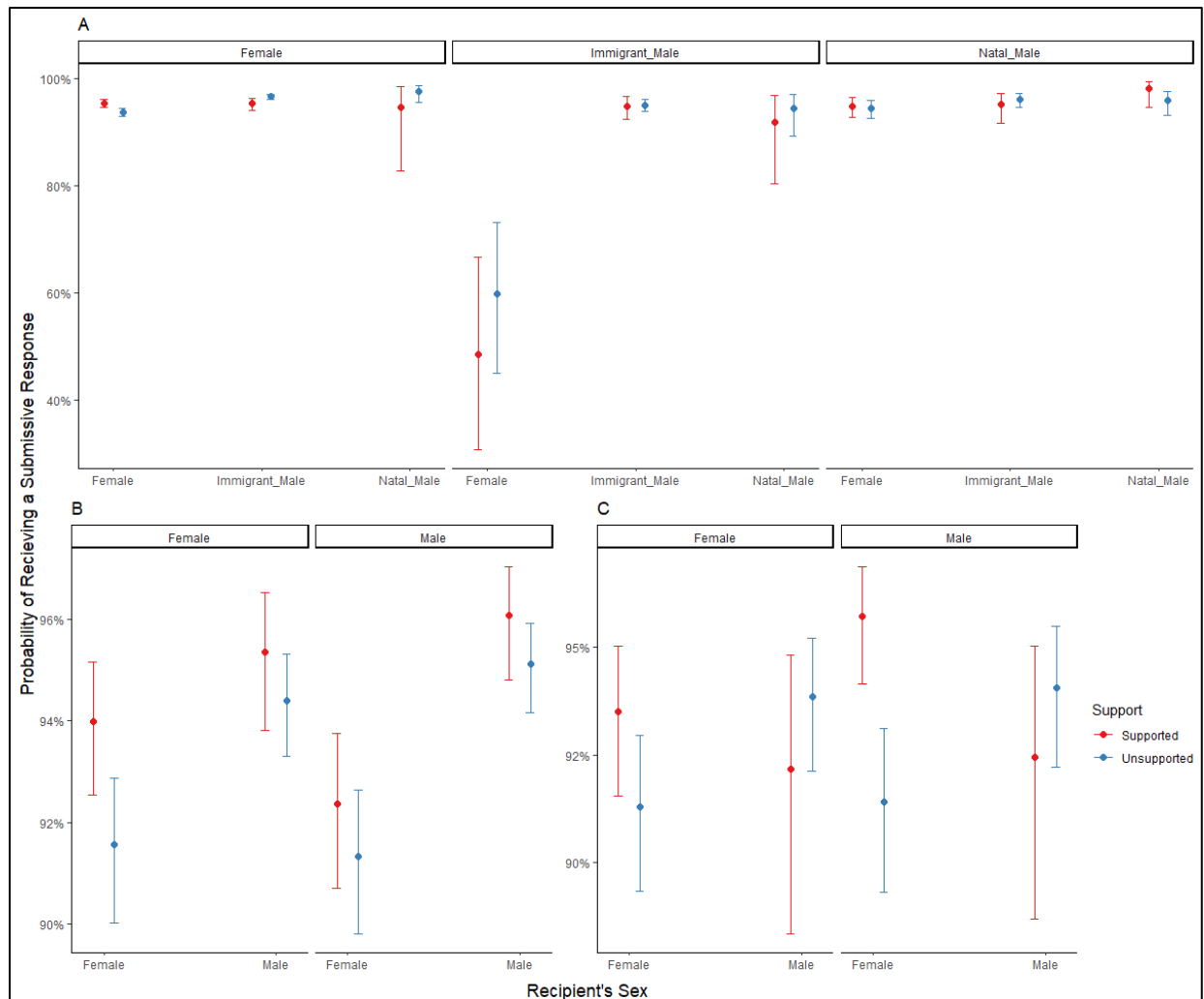**Figure A.3.3: Probability of adults (A), cubs (B), and sub-adults (C) successfully eliciting a submissive response to an aggressive act based on actor sex, recipient sex, and the presence of social support**. Colors correspond to whether or not the aggressive interaction was supported. Points represent estimated marginal mean probabilities, and error bars represent the 95% confidence intervals.

Table A.3.7: **Estimate of the effect of actor sex, recipient sex, and social support on the likelihood that an actor's threat elicits a submissive response from the recipient.** Estimates are log-odds ratios of the effect of actor sex or recipient sex relative to females, and the effect of social support, and come from the full interactive model.

Age Class	Fixed Effects *Reference Group: Supported Females*	LogOdds	SE	P-Value
Adult	*(Intercept)*	3.028	0.089	< 0.001
	Actor: Immigrant Male	-3.087	0.393	< 0.001
	Actor: Natal Male	-0.117	0.192	0.541
	Recipient: Immigrant Male	-0.009	0.136	0.949
	Recipient: Natal Male	-0.166	0.667	0.804
	Support: Unsupported	-0.325	0.078	< 0.001
	Actor: Immigrant Male x Recipient: Immigrant Male	2.982	0.455	< 0.001
	Actor: Natal Male x Recipient: Immigrant Male	0.069	0.362	0.848
	Actor: Immigrant Male x Recipient: Natal Male	2.649	0.921	0.004
	Actor: Natal Male x Recipient: Natal Male	1.177	0.877	0.180
	Actor: Immigrant Male x Support: Unsupported	0.786	0.497	0.114
	Actor: Natal Male x Support: Unsupported	0.242	0.240	0.313
	Recipient: Immigrant Male x Support: Unsupported	0.637	0.148	< 0.001
	Recipient: Natal Male x Support: Unsupported	1.136	0.726	0.118
	Actor: Immigrant Male x Recipient: Immigrant Male x Support: Unsupported	-1.056	0.556	0.058
	Actor: Natal Male x Recipient: Immigrant Male x Support: Unsupported	-0.314	0.427	0.462
	Actor: Immigrant Male x Recipient: Natal Male x Support: Unsupported	-1.209	1.065	0.256
	Actor: Male x Recipient: Natal Male x Support: Unsupported	-1.833	0.967	0.058
Cub	*(Intercept)*	2.750	0.118	< 0.001
	Actor: Male	-0.256	0.137	0.061
	Recipient: Male	0.273	0.171	0.110
	Support: Unsupported	-0.365	0.118	0.002
	Actor: Male x Recipient: Male	0.432	0.226	0.056
	Actor: Male x Support: Unsupported	0.225	0.156	0.149
	Recipient: Male x Support: Unsupported	0.167	0.192	0.384
	Actor: Male x Recipient: Male x Support: Unsupported	-0.256	0.257	0.319
Sub-Adult	*(Intercept)*	2.666	0.145	< 0.001
	Actor: Male	0.440	0.185	0.017
	Recipient: Male	-0.201	0.241	0.404
	Support: Unsupported	-0.314	0.139	0.024
	Actor: Male x Recipient: Male	-0.400	0.341	0.241
	Actor: Male x Support: Unsupported	-0.428	0.213	0.044
	Recipient: Male x Support: Unsupported	0.573	0.270	0.034
	Actor: Male x Recipient: Male x Support: Unsupported	0.426	0.387	0.272

Table A.3.8: **Estimate of the effect of social support on the likelihood that the actor elicits a submissive response from the recipient during intersexual aggressive interactions**. Estimates are odds ratios of the effect of social support relative to unsupported actors, and come from models stratified by actor age, actor sex, and recipient sex.

Age Class	Actor Sex	Recipient Sex	Model	Supported: *Reference group: Unsupported Actor*	Odds Ratio (Social support)	SE	P-value	95% CI Low	95% CI High
Adult	Female	Female	1	Actor Supported	1.418	0.114	< 0.001	1.211	1.660
		Immigrant Male	2	Actor Supported	0.678	0.130	0.042	0.466	0.987
		Natal Male	3	Actor Supported	0.304	0.449	0.420	0.017	5.477
	Immigrant Male	Female	4	Actor Supported	0.583	0.606	0.604	0.076	4.474
		Immigrant Male	5	Actor Supported	1.782	0.689	0.135	0.835	3.803
		Natal Male	6	Actor Supported	0.019	0.053	0.162	0.000	4.985
	Natal Male	Female	7	Actor Supported	0.735	0.353	0.522	0.286	1.886
		Immigrant Male	8	Actor Supported	2.317	1.880	0.300	0.472	11.368
		Natal Male	9	Actor Supported	25.57	55.55	0.136	0.362	1807
Cub	Female	Female	10	Actor Supported	1.522	0.197	< 0.001	1.181	1.962
		Male	11	Actor Supported	1.371	0.333	0.194	0.851	2.208
	Male	Female	12	Actor Supported	0.955	0.152	0.773	0.700	1.304
		Male	13	Actor Supported	1.069	0.216	0.741	0.720	1.587
Sub-Adult	Female	Female	14	Actor Supported	1.354	0.202	0.042	1.011	1.813
		Male	15	Actor Supported	0.617	0.258	0.248	0.272	1.399
	Male	Female	16	Actor Supported	2.190	0.401	< 0.001	1.530	3.134
		Male	17	Actor Supported	0.794	0.280	0.514	0.398	1.587

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SYNOPSIS

Of particular interest to the scientific community is the dramatic variation in expression of agonistic traits within social species, particularly the dynamic aggressive and submissive interactions among individuals and between males and females (Nelson 2007). Many scientific studies of agonistic behavior focus on aggression within the context of conflict over resources, with submissive behavior being expressed by an animal in response to being aggressed upon to reduce or end the conflict (De Vries 1998, Gammel et al. 2003, De vries el al. 2006), rather than the spontaneous expression of these behaviors in the absence of resource-based conflict. However, even as early as Darwin's *Expression of Emotions in Man and Animals* (1872), it was recognized that these two types of behaviors may occur spontaneously in the absence of overt conflict. In regard to aggressive behavior, Darwin describes the following as an example of spontaneous aggression: "The appearance of a dog approaching another dog with hostile intentions, namely, with erected ears, eyes intently directed forwards, hair on the neck and back bristling, gait remarkably stiff, with the tail upright and rigid." Similarly, in regard to spontaneous submissive behaviors in dogs, Darwin says: "These consist in the head and whole body being lowered and thrown into flexuous movements. The ears fall down and are drawn somewhat backwards...The lips hang loosely, and the hair remains smooth." It is not that the scientific community in the past century has deliberately overlooked the fact that spontaneous or 'unsolicited' aggressive and submissive behaviors do occur (Nelson 2007), but resource-based conflicts occur very commonly in virtually all gregarious animals, and each of these usually involves an attack to which the target animal responds with submissive behavior. Thus, it is not surprising that the bulk of scientific literature on agonistic behavior focuses on easily observed aggressive acts and submissive responses during resource-based conflicts, as this permits us to

identify a clear "winner" and an equally clear "loser" in each dyadic agonistic interaction. In addition, perhaps stemming from the fact that most human societies are patriarchies (Orr et al. 2020), there has historically been a bias in the literature on agonistic behavior focusing on males, particularly given that male-male conflict over mates is so common among animals (King et al 2013; Cassini 2021). In many species big flashy males, many sporting substantial weapons, are considerably easier to observe, than females, which are typically smaller and less aggressive than male conspecifics. Despite this, much recent research has shown that aggressive females may compete for mates, and that they can also often increase their fitness through defense of territory and offspring (Clutton-Brock 2009; Clutton-Brock & Huchard 2013; Holekamp & Sawdy 2019) and also through acquisition and maintenance of social rank in animal societies structured by dominance hierarchies (Holekamp & Strauss 2016; Strauss & Holekamp 2019). Individual variation and sex differences in aggressive and submissive behavior are of particular interest to me, and I therefore wished to investigate these sources of variation in my dissertation. To do this I chose a free-living species in which aggressive and submissive behaviors were already well-described (Kruuk 1972), and in which females are believed to be particularly aggressive, the spotted hyena (*Crocuta Crocuta).*

The goal of this final chapter is to synthesize the three empirical chapters of my dissertation, showing not only how they relate to one another and how they represent a coherent whole, but also how they shed new light on agonistic behavior in my study species. I also wanted to advance the field of behavioral ecology by assessing the fitness consequences of agonistic behavior, examining the ontogenetic development of such behavior, and inquiring whether intrinsic sex differences in agonistic behavior and/or other variables maintain female dominance in my study species.

In chapter one of my dissertation, working in conjunction with several experts in the field of hyena biology, I documented sex differences in numerous morphological and behavioral traits that are sexually dimorphic in this species, and inquired whether each sex difference found conformed to the norms found in most other mammals or whether instead they occurred in patterns that clearly opposed mammalian norms. With respect to morphological traits, we found that, unlike most female mammals, adult spotted hyena females are larger on average than adult males, particularly in neck and head circumference, body mass, and girth, even when males and females are fed the same diet and housed alone (Swanson et al. 2013). However, the weaponry that hyenas use, their jaws and very robust teeth, do not differ significantly between the sexes (Van Horn et al. 2003). Female spotted hyenas also have uniquely "masculinized" external genitalia among mammals, in that the clitoris is elongated into an elongated and erectile phallus-like structure that appears to be remarkably similar to the male's penis (Glickman et al. 2006). The female's labia are fused together and filled with connective tissue and fat, such that they are at least superficially similar in appearance to the male's testes (Frank et al. 1990). However, despite males and females having similar external genitalia, the nervous system mediating sexual behaviors in this species conforms to a more typical mammal pattern, at least with respect to the hypothalamic nuclei known to mediate sexual behavior in other mammals (Forger et al. 1996; Fenstemaker et al. 1999). Furthermore, as occurs in most mammals, adult males are more likely than females to initiate mating bouts (Szykman et al. 2007), though the act of mating itself is very challenging for male hyenas given the unique genital morphology of female conspecifics.

Hans Kruuk (1972) documented long ago that female spotted hyenas are socially dominant to most adult males (Kruuk 1972), which is very rare among mammals, otherwise

occurring only in various lemurs, a few mole-rat species, and bonobos (Holekamp & Engh 2009). Spotted hyenas exhibit a matrilineal dominance hierarchy in which rank is passed from mother to offspring via an elaborate learning process early in life via a process dubbed "maternal rank inheritance" even though there is no literal genetic inheritance of rank in this species (Engh et al. 2000). Interestingly, although both sexes "inherit" their mothers' social ranks so long as they remain in their natal clans, all but a tiny handful of male spotted hyenas males disperse from their natal clans after reaching reproductive maturity, and become socially integrated in neighboring clans (Holekamp and Smale 1998a), whereas females almost always spend their entire lives in their natal clans. Because patterns of dispersal behavior in spotted hyenas conform to the sexually dimorphic patterns of dispersal seen in the vast majority of other mammals, only females retain their mothers' social ranks throughout their lives.

Finally in Chapter One, we found that adult female spotted hyenas are significantly more aggressive than immigrant males, emitting aggressive acts at higher rates than adult males, even after controlling for relative position in the hierarchy (Chapter 1: Figure 1.1 a). Further, adult female spotted hyenas attack opponents with more ferocity, or intensity, than do immigrant males (Chapter 1: Figure 1.1 b), such that females are more likely to make bodily contact with their opponents than males are; this is also reflected in the higher numbers of fresh wounds and scarring found on adult females than adult males (Chapter 1: Figure 1.3).

Having found that female spotted hyenas appear to be the much more aggressive sex, and given that females remain in their natal clans until they die, I next turned my attention in Chapter Two to individual variation among adult females, focusing on adult lifetime repeated measures of aggressive and submissive behaviors, as well as on the

effects of these behaviors on offspring success. I focused exclusively on unsolicited

aggressive and submissive behaviors emitted by individual adult female hyenas, calculating

both the number of aggressive acts each female directed toward lower-ranking group

mates, and the number of submissive acts directed toward higher-ranking individuals. I also

calculated mean lifetime intensity scores for the aggressive and submissive acts emitted by

adult female hyenas. This allowed me to inquire whether aggression and submission were

negatively correlated in spotted hyenas, as is so often assumed in the literature. I was

intrigued by alternative hypotheses put forward by Nelson (2007) suggesting that

aggressive and submissive behaviors might actually be uncorrelated or that they might in

fact be positively correlated, as when individuals vary in their overall reactivity in social

situations (Chapter 2: Figure 2.1 b).

Using 30 years with of data documenting agonistic interactions from the Mara Hyena

Project, I was able to inquire in Chapter Two whether or not either rates or intensities of

agonistic acts represent personality traits in spotted hyenas; this requires some level of

individual consistency across time or contexts (Sih et al 2004; Sih et al 2008; Koski 2011).

Here I found that the rate at which a female acted either submissively or aggressively was

related to many situational and social factors within our observation sessions, and that rates

of aggressive and submissive acts varied within individuals across time and among

contexts. I therefore ruled out rates of agonistic behaviors as personality traits. However,

the intensities of emitted aggressive and submissive acts did exhibit consistency across

time and did not appear to be affected by most situational factors, and they thus appear to

present personality traits.

I found that, although intensities of aggressive and submissive behaviors were

consistent within individuals, they were not correlated within individuals, indicating that the

common assumption of a negative correlation was false, at least among spotted hyenas.

Next, because aggression and submission did appear to represent separate spectra rather

than a single continuum as Nelson (2007) suggested, I inquired whether these traits had

separate effects on fitness by correlating each trait within individual females with the

average number of offspring each female was able to rear to sexual maturity in her lifetime.

I found that both aggression intensity scores and submission intensity scores were

positively correlated with annual offspring survival among adult female spotted hyenas.

With respect to both aggression & submission, my findings here suggested that fitness is

lower at both ends of each spectrum of behavioral intensity, indicating the action of

stabilizing selection on agonistic behavior in adult female hyenas.

Given both findings regarding agonistic variation from Chapters One and Two, as

well as the importance of aggressive and submissive behaviors in the lives of spotted

hyenas, in my final empirical chapter I chose to inquire whether intrinsic sex differences in

agonistic behavior are drivers of female dominance over males in this species. My interest

in this question stems from reading about a competing hypothesis suggesting that females

dominate males in spotted hyena due exclusively to social support of females but not males

(Vullioud et al 2019). This seemed unlikely to me given our findings in Chapter One.

Furthermore, Vuilloud et al. (2019) claimed that female dominance does not become

apparent in this species until after male dispersal triggers an "ontogenetic switch" such that,

when males emigrate from one clan and immigrate into another they lose all of their support

from their genetic relatives in their natal clans. Therefore, here I chose to test both proposed

hypotheses across multiple age classes of spotted hyenas, including the "cub" phase (< 1

year of age) where individuals utilize the communal den for shelter and are dependent on

their mothers, the sub-adult phase (> 1 year < 2 years of age) where individuals are no

longer dependent on the communal den but are still dependent on their mothers, and in

adults (< 2 years of age) including both adult females, immigrant males, and adult natal-

males that have not yet dispersed to new clans. Together with some of my lab mates, I first

described intrinsic sex differences in agonistic behavior within each sex and age class.

Here, we found that females were more likely to emit unsolicited aggressive behaviors than

peer-aged males both during the cub phase, and in the adult phase compared to both adult

natal males and immigrant males (Chapter 3: Figure 3.1). Further, adult females were

significantly less likely to emit unsolicited submissive behaviors than either adult natal males

or immigrant males (Chapter 3: Figure 3.2). In short, females appeared to be more

aggressive than males even as cubs, and adult males were inherently more submissive

than adult females regardless of whether or not they had dispersed. Next, we inquired

which sex was more likely to elicit a submissive response (i.e. a successful act of

domination or "winning" a fight) from the opposite sex, as well as which sex was more likely

to offer up a submissive response in response to an aggressive act. Here we found that the

odds of eliciting a submissive act were only significantly different when comparing adult

female actors to immigrant male actors, such that immigrant males were less likely to get a

female to submit than was a female interacting with another female (Chapter 3: Figure 3.1

a). However, we also observed that males were more likely than females to submit to cubs

regardless of the sex of the cub actor; males were also more likely to submit to female

subadults, and of course to adult females (Chapter 3: Figure 3.1 b). Essentially, males

appear to be more willing to submit in response to an attack than are females in any age

class.

Next, we determined which sex received more social support during ongoing

agonistic encounters and found, contrary to the social support hypothesis proposed by

Vuilloud et al (2019), that adult females received less social support than either adult immigrant or adult natal males (Chapter 3: Figure 3.4 a). Interestingly, across all age classes females were more likely than males to be targets of aggressive acts by coalitions (i.e., individuals enjoying social support) (Chapter 3: Figure 3.4 b). Finally, we assessed whether this social support was related to successfully eliciting a submissive response from a member of the opposite sex, and found that it only improved the ability of sub-adult males to dominate females (Chapter 3: Figure 3.5), which may be primarily driven largely by maternal support during feeding bouts (Holekamp & Smale 1998b). In fact, it appears that adult females might actually be more successful when acting alone than with social support against immigrant males. In short, it appeared that this dominance pattern may be driven primarily by intrinsic sex differences in behavior, with more aggressive females and more submissive males, rather than social support received during agonistic encounters. Just as importantly, these sex differences underlying female dominance emerge early in ontogeny, well before male dispersal.

In conclusion, spotted hyenas present a wide variety of sexually dimorphic traits that violate common sexual norms among mammals, particularly females' enhanced aggressiveness and social dominance over males. Further, female agonistic traits appear to be individually consistent, at least in regard to the intensity with which individuals emit unsolicited aggressive and submissive behaviors. In addition, these behaviors appear to coexist within individuals on separate spectra, such that they are not correlated with individuals, and both aggression intensity and submission intensity have significant effects on fitness. Finally, intrinsic sex differences in the agonistic behavior of spotted hyenas appear to play an important role in female dominance over males, and these patterns emerge well before male dispersal.

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