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The roots of male-female socio-sexual bonds in spotted hyenas, *Crocuta crocuta* (Carnivora, Hyaenidae)

Master thesis

Zagreb, 2024.

Sveučilište u Zagrebu
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Temelji muško-ženskih socio-seksualnih veza u pjegavih hijena, *Crocuta crocuta* (Carnivora, Hyaenidae)

Diplomski rad

Zagreb, 2024.

Ovaj rad je izrađen na Leibniz Institute for Zoo and Wildlife Research u Berlinu, pod mentorstvom dr. phil. nat. Olivera Hönera, te komentorstvom izv. prof. dr. sc. Zorana Tadića. Rad je predan na ocjenu Biološkom odsjeku Prirodoslovno-matematičkog fakulteta Sveučilišta u Zagrebu radi stjecanja zvanja sveučilišni/a magistar/magistra eksperimentalne biologije.

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Tijekom proteklih nekoliko godina, dinamika borbi za moć između mužjaka i ženki kao i njihovi sukobi oko reproduktivne i društvene kontrole zaokupili su sve veću pozornost i znanstvene zajednice i društva u cjelini. Ova međuigra između spolova je od velikog značaja te se je pojavila kao istaknuta tema istraživanja. U svom sam diplomskom radu istraživala strategije ponašanja koje mužjaci koriste za izgradnju društvenih odnosa sa ženkama kod pjegave hijene, društvenog sisavca gdje ženke imaju visoku društvenu i reproduktivnu kontrolu. Istražila sam kako mužjaci prilaze ženkama i kako ženke reagiraju na različite stilove prilaska. Otkrila sam da se prilasci mužjaka mogu okarakterizirati kao ležerni, oprezni ili prikradajući te da ti stilovi mogu utjecati na učestalost ispoljavanja agresije i kod mužjaka i kod ženki. Osim toga, otkrila sam da ti stilovi prilaska, u kombinaciji s osobnim karakteristikama kod oba spola, igraju ulogu u oblikovanju ukupnog ishoda tih muško-ženskih interakcija. Moj diplomski rad pokazuje kako različiti prilasci i signali mogu poslužiti kao pokazatelji namjere mužjaka i posljedičnih odgovora ženki, dok također istražuje kako različiti prilasci mogu objasniti razlike u muškom reproduktivnom uspjehu.

Ključne riječi: pjegava hijena, prilazak, agresija mužjaka, socio-seksualne veze.
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Master thesis

The roots of male-female socio-sexual bonds in spotted hyenas, *Crocuta crocuta* (Carnivora, Hyaenidae)

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Over the past few years, the dynamics of power struggles between males and females and their conflicts over reproductive and social control have captured increasing attention from both the scientific community and society as a whole. This interplay between the sexes is of considerable significance and has emerged as a prominent research topic. In my thesis, I investigated the behavioural strategies that males use to build social relationships with females in a social mammal, the spotted hyena, where females have both high social control and high reproductive control. I analysed how males approach females and how females respond to the different approach styles. I found that male approaches can be characterised as casual, cautious, or sneaky, and that these styles may influence the likelihood of aggression in both males and females. Additionally, I found that these approach styles, combined with the life history traits of both sexes, play a role in shaping the overall outcome of male-female interactions. My thesis shows how different acts and signals could serve as indicators for male intentions and subsequent female responses, while also exploring how distinct approaches may explain the differences in male reproductive success.

Keywords: spotted hyena, approach, male-to-female aggression, socio-sexual bonding

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Contents

1.Introduction

1.1 Sexual conflicts

Males and females often have differing levels of investment in reproduction, each aiming to enhance their own fitness while still focusing on the success of any resulting offspring (Aloise King et al., 2013).

Based on Bateman's principle regarding the potential mating rates between the sexes, males typically invest fewer resources per offspring compared to females (Wedell et al., 2006). This leads to their higher mating rates, as they are thought to have a natural inclination towards promiscuity, with their mating opportunities being restricted mainly by access to females (Bateman 1948, Aloise King et al., 2013). Conversely, females, particularly mammals, invest significantly in offspring, and their mating rates are constrained by their reproductive biology, including lengthy periods of pregnancy and lactation (Aloise King et al., 2013). Consequently, females are expected to be inherently more selective than males when it comes to choosing mates (Bateman 1948, Aloise King et al., 2013).

Due to this difference in the minimal investment required for a successful offspring, sexual conflicts arise (Kokko and Jennions, 2008), defined by Parker (2006) as conflicts between the evolutionary interests of individuals of the two sexes.

1.2 From coercion to social bonds – male and female mating tactics

Male tactics to obtain mating opportunities

A direct example of such a disparity in interests is sexual coercion, which is comprised of forced copulation, harassment, and intimidation (Clutton-Brock and Parker, 1995).

Although the terminology surrounding involuntary copulation itself is difficult and leads to the question of the anthropomorphic conception of nonhuman behaviours, what generally characterises coercion is the exhibition of aggression or intimidation by males towards females to compel copulation against her will (Gowaty, 2019).

In numerous species exhibiting pronounced intersexual dimorphism, typically characterised by larger body sizes in males, sexual coercion can emerge as the primary reproductive strategy employed by males (Clutton-Brock and Parker, 1995). This is observed in various species, including the Sumatran orangutan (Fox, 2002), chimpanzees (Watts, 2022), northern elephant seals (Le Boeuf and Mesnick, 1991) as well as in non-mammalian vertebrates such as reptiles, fish and birds (Gowaty, 2019).

South American sea lions (Cappozzo et al., 2008) and sea otters are among the species where males engage in harassment by repeatedly attempting to copulate with females, which can then lead to injuries or even death (Clutton-Brock and Parker, 1995, Harris et al., 2010), while chacma baboons and chimpanzees use intimidation as a form of sexual coercion and punishment for refusing to mate with them (Clutton-Brock and Parker, 1995, Baniel et al., 2017).

Female counter strategies

Despite the risk of injury or even death, females tend to resist copulation attempts through defensive actions such as fighting back, running away, or hiding (Gowaty, 2019).

In some species, females can invest in bonding with certain males as a behavioural strategy to counter male coercive attempts. For example, female Sumatran orangutans (Wilson and Mesnick, 1997) and savanna baboons form protective bonds and mate with adult males who provided protection to them and their offspring (Clutton-Brock and Parker, 1995).

Social bonds in mammals

Affiliative relationships or bonds can develop between males, females, or both, including within family groups and beyond, while this widespread formation of bonds is thought to be driven by natural selection (Seyfarth and Cheney, 2012). The benefits of bonds vary widely, ranging from improved reproductive success (Silk et al., 2010), increased birth rates and offspring survival (Cameron et al., 2009), to improved stress resistance, and health advantages for all individuals involved (Yee et al., 2008).

Bottlenose dolphins have been observed to engage in sexual coercion (Scott et al., 2005) as well as in the formation of temporary consortships (Owen et al., 2002). Consortship, described as a temporary socio-sexual association between a male and a female during a female's estrus period, is also observed in rhesus macaques. This consortship can last for several days, following which females have the opportunity to form new consortships with different males (Weingrill et al., 2000).

In addition to short-term associations, long-lasting bonds are observed as well. They are present in many group-living animals such as baboons (Silk et al., 2010) and other cercopithecines (Smith et al., 2010), chimpanzees (Langergraber et al., 2007), dolphins (Connor, 2007) and elephants (Moss et al., 2013), as well as spotted hyenas (Kruuk, 1972).

1.3 Bonds in spotted hyenas

Spotted hyenas are highly social animals, living in predominantly female-dominated social groups, which in hyenas are referred to as clans (Kruuk, 1972). Clans can consist of as many as 130 individuals (Vullioud et al., 2019) and are usually ruled by one alpha female (but see Davidian and Höner, 2021).

Females have complete control over copulation and can exercise mate choice (Watts et al., 2009; Vullioud et al., 2019). Reproductive control is possible as a result of extreme masculinization of the female external genitalia; the spotted hyena is the only extant mammal in which females have no vaginal opening and mate and give birth through a pendulous penis-like clitoris, also known as "pseudo-penis" (Cunha et al., 2014). Because of this untypical anatomy, copulation without the complete cooperation of the female is close to impossible (East et al., 1993) so males tend to adopt behavioural strategies that align with female preferences by investing in affiliative relationships (Höner et al., 2007).

Previous studies (Höner et al., 2007) on the spotted hyena found that females show a preference for males who were either native to or joined their clan subsequent to the female's own birth, which reduces the chance of inbreeding within the clan. As a result of these preferences, most males leave their natal clan to breed. Prior to selecting a breeding clan, be it their birth clan or a new one, adult males undertake exploratory trips into the territories of clans they were not born into. They do this as a response to the female mate preferences mentioned above, while also opting for clans with the greatest number of young females (Höner et al., 2007).

It has been proposed that females prefer to mate with males they are familiar or socially bonded with (Szykman et al., 2001). By choosing a clan with predominately young females, males can thus form lasting affiliative relationships with females as both parties spend more time together within the clan, all while their tenure in the clan increases (Höner et al., 2007).

This aligns with a previous study, focusing solely on immigrant males, that noted a tendency for assortative mating based on female age and male reproductive tenure: old females were more tolerant of long-tenured immigrant males, while young females were more receptive to shorter-tenured immigrant males (East and Hofer, 2001; East et al., 2003). Specifically, younger females were often seen biting or chasing away males with a long tenure in favour of short-tenured males, whereas older females exhibited more direct aggression towards males with shorter tenures but were threatening towards both short- and long-tenured males (East and Hofer, 2001). While East and Hofer (2001) and East et al. (2003) did not consider male behaviour or the possibility that a male's approach style might reflect his intentions in their research, Szykman et al. (2003) did note that females tend to react aggressively when approached by a group of males exhibiting aggressive behaviour, a strategy termed ‘baiting’.

Male hyenas occasionally resort to behavioural tactics to influence female mate selection through displays of aggression, although the efficacy of these tactics remains uncertain (East et al., 2003; Szykman et al., 2003), since males who harassed females rarely experienced any advantages in terms of their reproductive success (East et al., 2003).

1.4 Goals and predictions

So far, no empirical study has examined how males and females develop friendly bonds in spotted hyenas. My focus was on the context that influences the foundation of any relationship: the approach between individuals. I explored if males differ in their ability to bond with females by studying interactions between a male and a female in contexts when a male approached a female that was either resting (e.g., sitting or lying) or suckling her cubs. This context is interesting because males tend to approach females when they are limited in their movement (by lying down or suckling their cubs) and probably less attentive to their surroundings which makes them more accessible to approaching males.

I focused on characterising male approach styles and identifying the outcome of the interaction, all while addressing three specific questions.

Question 1: Do male hyenas vary in the way they approach females: can these approaches correspond to distinct styles and do they correlate with certain types of male behaviours following the approach?

- **Prediction 1**: Males will exhibit distinct behavioural styles; some may exhibit approaches characterised by more submissive signals, while others might demonstrate behaviours that are more assertive or dominant.
- **Prediction 2**: Males who adopt a more aggressive or dominant style of approach are more likely to display aggression towards females, as noted in Szykman et al. (2003) who solely focused on immigrant males during baiting, whereas my research encompasses both immigrant and natal males during habitual approaches.

Question 2: Do females adjust their response according to the male's approach style?

- **Prediction 3**: Previous studies suggested that females typically react aggressively to male advances (Szykman et al., 2007), but that the female tolerance depends on the tenure of the approaching male (East and Hofer, 2001). I predict that female hyenas are more likely to exhibit aggressive responses when approached by males expressing aggression or dominance, as opposed to when males employ a more neutral or submissive approach. Aggressive actions or signals expressed by males during their approach may allow females to predict a male's intention and respond accordingly.

Question 3: What are the most important predictors of the outcome of the interaction, whether or not there is a possibility to bond? Does a male's approach style matter more than his life history traits and those of the females?

- **Prediction 4**: When a male invests more time in interacting with a specific female, it increases the likelihood of mating between them (Szykman et al., 2001). Thus, I predicted that the outcome of the interaction is more likely to be positive if the approach is done by a long-tenured male rather than a short-tenured one and by a philopatric male rather than an immigrant male, due to the pre-existing relationships with females within the clan.
- **Prediction 5**: Previous studies show that higher-ranking and older females are courted more (East and Hofer, 2001; Szykman et al., 2007, Davidian et al., 2021). High-ranking females don't have to accept low-quality males for mating, while lower-ranking females do not have that benefit (East et al., 2003). Based on these findings, I predicted that lower-ranking females are more likely to respond positively to any approach, in contrast to higher-ranking and established females.

- **Prediction 6**: Females of many species can be very protective of their offspring or show increased aggressiveness when caring for their young (Gubernick and Klopfer, 1981). Given the prominent maternal care exhibited by spotted hyenas (Gicquel et al., 2022), I therefore predicted that females who are suckling when they are approached by a male should be protective of her cubs and will be more likely to respond aggressively to an approach, compared to females who are resting.

2. Materials and methods

2.1 Study species

Spotted hyena, often called laughing or bone-crushing hyena, whose full classification can be seen in Table 1, is a highly social carnivore (Höner et al., 2005; Vullioud et al., 2019). The spotted hyena belongs to one of the smallest carnivoran families, Hyaenidae, and together with the striped and brown hyenas, it belongs to the subfamily Hyaeninae. Despite their dog-like appearance, spotted hyenas actually belong to the feliform suborder, aligning more closely with cats than dogs (Smith and Holekamp, 2019).

Table 1. Scientific classification of *Crocuta crocuta*

KINGDOM:	Animalia
PHYLUM:	Chordata
CLASS:	Mammalia
ORDER:	Carnivora
SUBORDER:	Feliformia
FAMILY:	Hyaenidae
GENUS:	*Crocuta*
SPECIES:	*Crocuta crocuta* (Erxleben, 1777)

Spotted hyenas are widespread across Africa but primarily found in regions south of the Sahara Desert. They are notably prevalent in East Africa, on the plains of Kenya and Tanzania (Bohm and Höner, 2015).

2.2 The study location and data collection

The Ngorongoro Crater covers an area of almost 260 square kilometres and has a diameter of around 20 kilometres. This impressive crater is located in Northern Tanzania and is adorned with diverse habitats such as rivers, swamps, grasslands and woodlands (see Figure 1). Consequently, it is home to one of the highest concentrations of large carnivores and herbivores in the world such as; African elephant, Grant's and Thomson's gazelle, African buffalo, plains zebra and many more (Ngorongoro Hyena Project, n.d., Ngorongoro Conservation Area Authority, n.d.).

Figure 1. Ngorongoro Crater.

From *View of the south-eastern side of the Ngorongoro Crater* [Photograph], by Oliver Höner, n.d.

And the name of the crater itself has a fascinating story: the combination of the Maasai saying "'orgirra le kkorongorro" which translates as "Big Bowl" and the misspelling of the word "kkorongorro" led to the current name Ngorongoro Crater (Ngorongoro Conservation Area Authority, n.d). Most importantly, currently there are eight resident spotted hyena clans inhabiting the floor of the Crater: Airstrip, Engitati, Forest, Lemala, Munge, Ngoitokitok, Shamba and Triangle (Ngorongoro Hyena Project, n.d.) (see Figure 2).

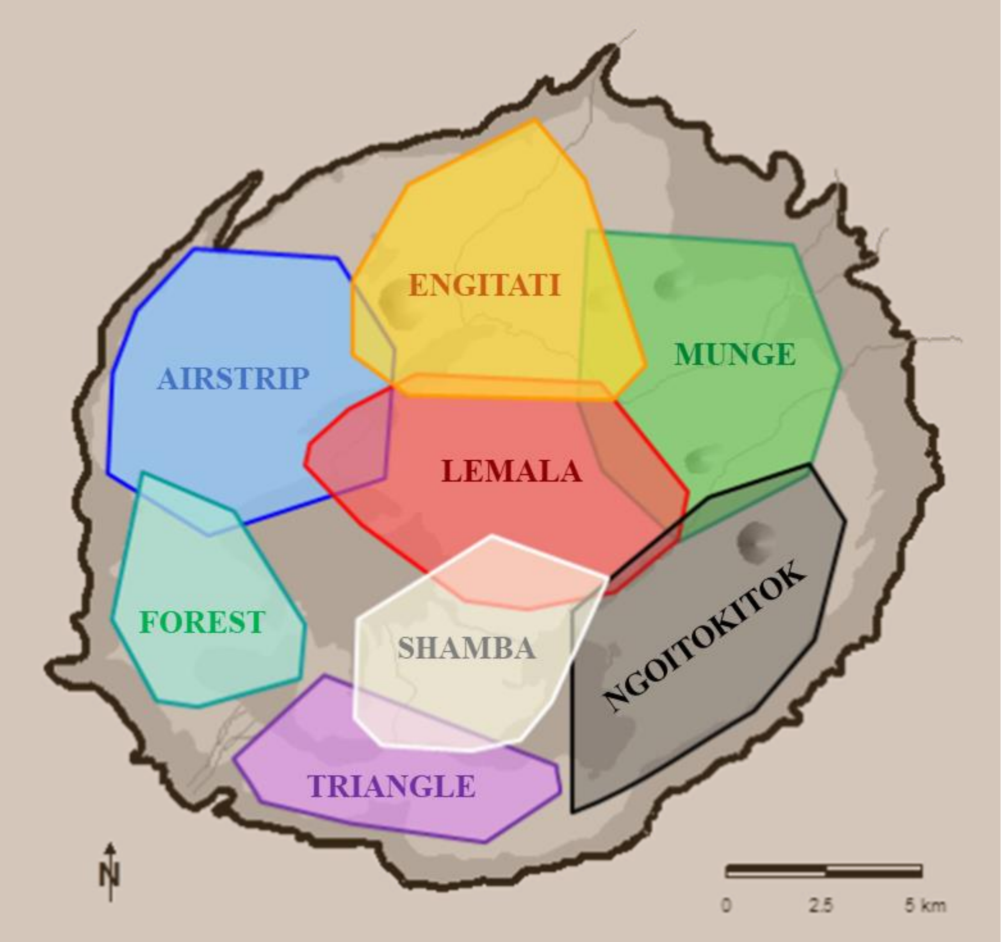

Figure 2. Distribution of the territories of the eight study clans of spotted hyenas living on the floor of Ngorongoro Crater in Tanzania. Adapted from Ngorongoro Hyena Project, n.d.

The Ngorongoro Hyena Project (NHP) has dedicated the past 28 years to monitoring behaviours, gathering demographic records, and collecting individual life-history data about the free-roaming hyenas belonging to all eight resident clans in the Crater. Observations take place from within a vehicle, typically during the hours of 06:00 to 12:00 and 16:00 to 19:00 (Höner et al., 2005).

2.3 Construction of the ethogram

To facilitate the detailed analyses of behaviours and interactions, I participated in the reconstruction and revision of the existing ethogram of the NHP. An ethogram can be defined as a species-specific, detailed catalogue of behaviours and their detailed descriptions (Martin and Bateson, 2007). Ethograms are widely used in behavioural research (Stanton et al., 2015), conservation biology, and as a tool for monitoring species-specific natural behaviours and assessing the welfare state of an animal in zoos (Watters et al., 2009).

During the review of the ethogram, I conducted a thorough review of existing literature on spotted hyenas, to align our observational framework with current ethological standards. After reviewing the current literature, we collaboratively updated the ethogram by introducing new definitions for behaviours and improving any codes that were deemed ambiguous or unclear. I have collaborated on the development of functional definitions for observed acts and signals, standardising the terminology, and enhancing the clarity and consistency of the ethogram.

I also selected videos that provided clear examples of the behaviours mentioned in the digital ethogram, further contributing to the refinement of the ethogram and ensuring that the dataset accurately reflected the diversity of male-female interactions as observed in the field.

2.4 Behavioural analyses

Most behavioural analyses were based on video recordings. The majority of male-female "approach" interactions (N = 1463) were already transcribed and made available for statistical analysis. I transcribed 191 additional videos and integrated them into this dataset, capturing the same interactions. The transcription itself consisted of several steps. First, I identified both the male and the female using the NHP database while recording the date and time of approach and female activity. After the identification, I transcribed the behaviours.

The entire video transcription can be divided into two steps: male approach and remainder of the interaction. When the male approached the female, I recorded signals such as the position of the tail, ears, and penis, as well as the speed at which the male approached and whether he approached directly or indirectly (changing the path and circling around the female). I used all the mentioned information and formed a dataset comprised of six active variables (see Table 2 for details) to characterise male approach styles using Multiple Correspondence Analysis.

Table 2. Behavioural categories and functional definitions for each of the six variables used for the Multiple Correspondence Analysis.

Variable	Category	Definition	Count
Trajectory	Direct	Male approaches in a straight line without pausing.	1263
	Indirect	Male approaches in multiple attempts, with pauses in between, and may circle around the female before coming close to her.	278
Velocity	Normal	Male approaches the female at average speed.	1097
	Slow	Male walks at a slow pace, without tiptoeing.	276
	Tip-toe	Male walks very slowly, with a decomposed rhythm of the walk. The male lifts his front and hind paws off the ground and sets them down softly, as if trying to move silently and "walk on tiptoes".	123
	Fast	Male approaches using a fast walk or runs towards the female.	45
Angle	Back (BK)	Approach towards the rear area and/or from a direction facing the back of the targeted female, i.e., the male who is approaching may not be visible by the female.	833
	Front (FR)	Approach towards the head and/or from a direction facing the belly or face of the targeted female, i.e., the male approaching may be visible by the female.	612
	Side (S)	A lateral approach, in which a male approaches the side of the targeted female or faces her side rather than approaching directly from the front or back.	96
Tail	Tail normal (TN)	Tail relaxed pending along hind legs.	882
	Tail down (TD)	Tail tucked between hind legs. The bum is often held low. Submissive signal.	463
	Tail wagging (TW)	Tail rapidly swings from one side to other, similar to the motion used to swat away flies.	151
	Tail up (TU)	Tail in upward position. Tail may be either tensed with compact hairs, bristled (tail fully extended and bushy), or hooked (fluffy tip that hangs down). Dominant signal.	23
	Tail horizontal (TH)	Tail in horizontal position, tensed. Aggressive signal.	22
Ears	Ears normal (EN)	Ears relaxed and round.	893
	Ears forward (EF)	Ears cocked toward front and in direction of where male is looking. Aggressive/dominant signal.	393
	Ears back (EB)	Ears pulled backwards. Submissive signal.	255
Penis	Penis normal (PN)	Penis in its default, resorbed position. It is hardly visible.	1463
	Penis relaxed (PR)	Penis elongated and pending.	43
	Penis erect (PE)	Penis fully grown and straight, close to the belly.	35

If it was possible to discern the direction of the wind, I noted whether the male approached downwind (where the female potentially cannot smell him) or upwind (where the female potentially can smell him). Because precise determination of the direction of the wind on video recordings can be challenging, most of the coded interactions did not include the direction of the wind, and I did not use the wind direction in further analyses.

The remainder of the interaction between a male and a female was systematically divided into four parts: the first response of the female, the first reaction of the male, the second response of the female, and the second response of the male (if applicable). Recording data in this way allowed me to easily extract information on the initial response or reaction from the female to the male approach. It also allowed me to track the progression of the interaction, specifically in terms of aggressive behaviours, and what the final outcome was. Additionally, a separate category that solely focused on whether there was body contact, helped me as well while categorising the final outcome of each interaction.

2.5 Definition of covariates of interest

2.5.1 Social rank

The social rank of the mother is of extreme importance; offspring acquire social ranks just below that of their mother (Hofer and East, 2003). Hyenas are ranked by using dyadic agonistic interactions. The individual with the greatest number of victories in these interactions receives the top ordinal position of 1, while the one with the fewest victories is assigned an ordinal position that matches the total count of clan members (Davidian et al., 2021).

Ordinal ranks are converted into proportional ranks, to accounts for changes in the clan size and allows comparisons between clans of different sizes, using the formula: Proportional rank_i = ([number of clan members – ordinal rank_i] / ([number of clan members – 1]/2)) – 1. The range of proportional rank extends from -1, representing the lowest, to +1, indicating the highest. Based on their position within this range, both males and females can be categorised into three distinct groups: those in the upper third are deemed high ranking, those in the middle third are considered medium ranking, and those in the lower third are classified as low ranking (Davidian et al., 2021). Spotted hyenas usually maintain their maternal rank as long as they stay in their natal clan (Holekamp and Smale, 1993).

2.5.2 Dispersal status

In spotted hyenas, most males leave their natal clan (Höner et al., 2007). Adult males can therefore be classified into two categories: philopatric males, who remain and reproduce within their natal clan, and immigrant males, who depart from their natal clan and choose to reproduce within a different clan (Davidian et al., 2016). It is considered that a male has chosen his clan if he has shown sexual interest in females and/or has taken steps to integrate into the social hierarchy of sexually active males during a period of at least three months (Davidian et al., 2016).

2.5.3 Tenure

The date of clan choice is defined as the date of first observation of sexual behaviours for philopatric males and of first sighting in the new clan territory for immigrant males. This as well defines the start of a male tenure in his chosen clan (Davidian et al., 2021). When an immigrant male joins a new clan, he occupies the lowest rank of the hierarchy (East and Hofer, 2001), and he can rise in rank over time, due to a queuing convention, when a higher-ranking male leaves the clan or dies (East and Hofer, 2001; Holekamp et al., 2012).

2.5.4 Age

The longevity (the difference between the date of last sighting and the individual's date of birth) of hyenas in the wild is up to 19 years (Ngorongoro Hyena Project, n.d, Gicquel et al., 2022). Individual date of birth is estimated with an accuracy of ± 7 days, based on behaviours, size of the cub and the fur when seen for the first time, as the cubs can be seen shortly after birth (Golla et al., 1999). To ensure a valid comparison of my results with those from earlier studies (East and Hofer, 2001, East et al., 2003), I used the commonly accepted criteria for categorising female age (East and Hofer, 2001; East et al., 2003; Höner et al., 2007). In line with the categorization employed in prior research, females are categorised as either young (less than five years of age) or old (five years of age or older).

2.5.5 Identifying hyenas

As the name suggests, the spotted hyena generally has light or dark brown fur with dark spots all over its body. Each individual has a unique pattern of spots that does not change during life, but the colour of the fur and its length are variable. Cubs are characterised by black fur (see Figure 3), which fades after one month of life, and with the fourth month of life, a characteristic dotted pattern appears. It is precisely because of this dotted pattern that individual identification is possible using "ID cards" that are made by the NHP for each individual hyena. Each "ID card" includes photos showing both sides of the individual's body, as well as their name and date of birth. In addition to the mentioned fur, scars and ear notches are also commonly used for identifying individuals. Identifying individuals usually happens on-site, either immediately or afterwards through examining photos or videos (Ngorongoro Hyena Project, n.d.).

Figure 3. Mother carrying her cub. The image shows an age-related distinction in fur colour: the cub's coat is solid black, while the mother's is distinctly spotted, indicative of her age.
From *Hyena mother carrying her cub* [Photograph], by Oliver Höner, n.d.

2.5.6 Defining aggression

Based on previous studies on aggression in hyenas (Yoshida et al., 2016; McCormick and Holekamp, 2022) I modified and established a framework to identify aggressive behaviour in both male and female hyenas. Although it is possible to distinguish various intensity levels of aggressive behaviours (Yoshida et al., 2016; McCormick and Holekamp, 2022), my research concentrated solely on determining the presence or absence of aggression. My main interest was to determine whether the male had the opportunity to bond with the female, while recognising that the occurrence of aggression prevents such bonding. Therefore, aggressive behaviours that range from threatening gestures (head jerks, jaw snapping, lunges) up to forms of attack (biting, chasing) were all collectively classified under the broad term of aggression. While determining the presence of aggression, I focused solely on acts/postures and excluded signals from the analysis. I focused solely on acts and postures as direct indicators of aggressive intent because they can potentially harm and incur costs to the target. This approach allows for a more direct description of aggression without the ambiguity that could arise from the inclusion of signals in analyses.

3. Statistical analyses

3.1 Dataset overview

The combined dataset encompasses 1654 recorded interactions, involving 175 unique female individuals and 159 unique male individuals. 53 interactions were excluded from the analyses because the identities of the involved female (N=52) and male (N=2) individuals were unknown. Table 3 provides a summary of descriptive statistics for the number of repeated interactions involving the males, females and male-female pairs.

Table 3. Number of interactions involving a given male, female or male-female pair. Provided are the range, mean and standard error of such repeated interactions. Numbers in brackets indicate the number of distinct individual or pair.

	Min	*Max*	*Mean*	*SE*
Male (159)	1	111	10.13	1.41
Female (175)	1	91	9.15	1.26
Male-female pair (695)	1	19	2.30	0.09

While preparing the dataset for the Generalized Linear Mixed-Effect Models (GLMM), I excluded 236 observations due to incomplete or non-applicable data in one or more of the key categories, such as male tenure, male dispersal status, female rank, and female age. Consequently, the dataset for the GLMMs consists of 1,418 interactions.

All analyses were conducted using R Statistical Software (R Core Team, 2023). For inferential statistics, I used $p < 0.05$ as the threshold for defining statistical significance (Andrade, 2019).

3.2 Characterizing approach styles using Multiple Correspondence Analysis

To define approach styles, I performed a Multiple Correspondence Analysis (MCA). MCA is a descriptive method that is applied to tables where individuals are listed in rows and where multiple variables are subdivided into multiple categories and placed in columns (Husson et al., 2017; Ogunsakin et al., 2021). The key objective of an MCA is to describe relationships among distinct categories of two or more nominal variables and to synthetize as much of the existing variance in the original dataset in a reduced dimensional space (Moschidis et al., 2022).

MCA is similar and build upon principal components analysis (PCA), but differs primarily in the type of variables it handles: MCA is designed for categorical variables, whereas PCA is used for continuous variables (Atkinson, 2024). MCA is conducted using an N × K indicator matrix. N represents the number of data samples (number of male individuals, here, N=1541), and K is the number of features that describe these samples (variables, here, N=6 which were further divided into categories, N=20). In this matrix, each cell at position (n, k) contains information about an individual (n) and the specific category (k) associated with the variable. Using this data, MCA allows us to analyse and visualise the links between individuals and categories. MCA produces three clouds of points: the cloud of individuals, the cloud of variables, and the cloud of categories of variables (Le Roux and Rouanet, 2010). Given the substantial number of individuals, variables, and categories present in my dataset, a detailed analysis of each one individually is impractical. Therefore, my attention has been directed towards the categories, as they hold the most significance for my goal of characterizing approach styles by identifying which categories frequently co-occur in the majority of approaches.

The amount of deviation from independence among the categories is quantified using the inertia metric. This metric measures the dispersion of individual profiles around the mean profile. As the differences among individual behaviours increase, the inertia metric increases correspondingly (Husson et al., 2017; Moschidis et al., 2022). Importantly, the inertia of the cloud of variables is calculated on the basis of active variables (Husson et al., 2017).

In the process of deciding how many dimensions to emphasise, alongside inertia, eigenvalues offer essential information. Eigenvalues reveal the extent to which each dimension contributes to capturing categorical data. A higher eigenvalue signifies a greater overall variance in the contributions of variables within that dimension (and it's standardised to 1, signifying the total information of all variables across all dimensions) (Das and Sun, 2016; Rodriguez-Sabate et al., 2017).

Due to the matrix setup needed for MCA, its unique properties are lost if some of the data is missing, and the widely accepted way to address this problem is to remove the rows that have missing data (Josse et al., 2011; Ochoa Muñoz et al., 2019). Among the total interactions (N = 1654), I excluded 113 due to missing values in one or more of the six active variables of interest, which represented approximately 6.83% of the original dataset. As a result, the dataset used to define approach styles was reduced to 1541 interactions. The dataset comprised of six active variables: trajectory, velocity, angle, tail, ears, and penis (see Table 2 for more details).

As seen in Table 3, there are repeated interactions among male, female, and male-female pairs in my dataset. To circumvent the issue of repeated observations for a given male, I implemented data weighting. Data weighting ensures that the analysis takes into account the behaviour of each male in a proportionate manner, thus mitigating the influence and potential distortions arising from repeated observations of specific males on the overall findings. Weights (w) were assigned to each observation using the following formula: $w = 1/ni$, where ni correspond to the number of observations/interactions/approaches done by a given male i.

I employed the '*FactoMineR*' and '*factoextra'* packages, enabling the calculation of MCA results and the creation of classical factorial maps using the '*MCA()*' function with default settings. For 3D visualisation, I employed the '*plotly*' package. Furthermore, to identify the variables most correlated within each dimension, I used the '*dimdesc()*' function.

3.3 Relationship between approach style and aggression

To investigate the relationship between aggressive behaviours across genders and males' styles of approach I implemented two models. Model $_{\text{males}}$ explores whether males who approach with a certain style are more likely to be aggressive. Model $_{\text{females}}$ expands on Model $_{\text{males}}$ by examining if specific approach styles, which are more likely to be linked to male aggression, influence the likelihood of females displaying aggressive behaviours towards males as a form of self-defence.

In Model $_{\text{males}}$ I classified the males' first reactions as aggressive or non-aggressive, coding the response variable as a binary outcome, where 'yes' or '1' indicates aggression, and 'no' or '0' signifies the absence of aggression. I applied the same classification in Model $_{\text{females}}$, where the first female reaction was classified as aggressive or non-aggressive. By classifying the reaction this way and using only the first reaction, I isolated the effect of the initial interaction from any subsequent interactions that might unfold between the male and the female. Specifically, for Model $_{\text{males}}$, this method let me directly observe how the male's first approach influenced the interaction before the female responded in a way that might deter the approach. Similarly, for Model $_{\text{females}}$, using only the first response made it easier to examine the female's reaction before the male proceeded with any additional actions, allowing the interaction to further unfold.

I included male approach styles (casual, cautious, and sneaky) which I identified using the MCA as fixed effects; specifically, I used "casual" as the reference category, and both male and female identity were used as a random effect in their respective models.

To explore the connection between aggression across sexes and male approach styles, I utilised Generalized Linear Mixed-Effect Models (GLMM), with a binominal distribution, using the '*lme4*' package (Bates et al., 2015).

I used the function *'residuals()'* to plot the residuals and to check visually if the assumptions of normal distribution and homogeneity of variance were met. The dispersion of residuals remained fairly consistent across various levels of the fitted values in both Model $_{\text{males}}$ and Model $_{\text{females}}$ No distinct pattern or systematic variation in the spread was apparent, confirming that the two model assumptions were not violated. I also confirmed the absence of multicollinearity by examining the variance inflation factors (VIF), all of which were found to be below the widely accepted threshold of 5 (James et al., 2013).

To calculate parameter estimates, I used Laplace approximation, and the p-values were calculated using parametric bootstrapped likelihood ratio tests. The coefficients estimated by the model were log(odds), and I converted them into odd ratios using the formula: exp[coefficient]. I compared a null GLMM models, which included only random effects, against full models that incorporated the mentioned fixed effects and random effects to evaluate the significance of including male approach styles in the model. I then performed a contrast analysis using the '*emmeans*' package, examining differences between each approach style (casual-cautious, casual-sneaky, and cautious-sneaky) while adjusting for multiple comparisons using the Bonferroni method. I visualised predictions using the '*ggplot2*' package in R, after estimating marginal means with the package '*effects*'.

3.4 Outcome of male-female interactions

To explore the outcome of the approach, I introduced a new classification for both male and female interactions. This classification is unique in that it focuses exclusively on identifying interactions that result in positive outcomes with respect to the development of social bonds. An interaction is deemed to have a positive outcome — if the male manages to approach the female and establish physical contact, engage in investigative sniffing, if they display any affiliative behaviour like rubbing against each other or touching muzzles, and if the male can stay close and lie down next to the female without either party showing signs of aggression.

Additionally, I consider the outcome positive even if the male approaches, sniffs the female, and then walks away, as this allows the male to get olfactory information on the female and provides an opportunity for bonding, provided that the female does not react aggressively.

In the Model$_{\text{outcome}}$, I incorporated both male and female life history traits, including male tenure, male dispersal status, female rank, female age, and female activity.

For the Model$_{\text{outcome}}$, I used tenure as a continuous and as a quadratic variable. Continuous tenure alone, may not accurately capture the relationship between tenure and positive outcome. Therefore, I have also included the quadratic tenure, to account for the potential non-linear relationship between tenure and the positive outcome. Both continuous and quadratic tenure in my analyses were expressed in years. Subadult males and adult males who have not yet selected their breeding clans were excluded from the analysis. I have used only males who have already selected a clan to reproduce; either their natal (philopatric) or a different (immigrant) clan.

Previous studies showed that young females were more aggressive towards long-tenured males than short-tenured males, while old females show the opposite behavioural pattern (East and Hofer, 2001). I therefore included in the model an interaction term between male tenure and female age to explore if the relationship between positive outcome and male tenure varies with the age of the female. In the model, I used female rank as a continuous variable and female age as categorical with two categories ('young' and 'old' for female ≤ 5 years old and > 5 years old, respectively). Lastly, I included female activity ('lying' and 'suckling'). It was included in the Model$_{\text{outcome}}$ to explore whether the presence of cubs, with the assumption that the female will be protective of her cubs, impacts the female's response to a male approach and, consequently, the interactions outcome. I included both male and female IDs as random factors in the model. To address convergence issues arising from this inclusion, I increased the maximum number of function evaluations to 100,000.

To obtain parameter estimates, I utilised the same approach that was applied to previous two models using Laplace approximation method and using parametric bootstrapped likelihood ratio tests to obtain p-values. For every variable I included, I assessed its significance by comparing a full Model$_{\text{outcome}}$ against a version without that specific variable. By doing that, I evaluated the significance of including each variable in the full Model$_{\text{outcome}}$. Then, for every categorical variable I performed a contrast analysis using the '*emmeans*' package, adjusting for multiple comparisons using the Bonferroni method. I estimated marginal means using the package '*effects*', and used 'ggplot2' to create all data visualisations.

To check for normal distribution and homogeneity of variances, I used the ‘*residuals ()*’ function. The dispersion was consistent, and no noticeable pattern was present, which led me to the conclusion that the assumption of content variance is met for the proposed model. The model as well did not show signs of multicollinearity, with values of variance inflation factors (VIF) below the widespread critical threshold of 5 (James et al., 2013).

To explore the proximate outcome of the approach, I utilised Generalized Linear Mixed-Effect Model (GLMM), with a binominal distribution, using the ‘*lme4*’ package (Bates et al., 2015).

After reviewing a study by Siegmann et al. (2021) that utilised multilevel, multinomial behaviour models in naked mole rats, I attempted to adapt a modified version to my own dataset to explore weather male life history traits influence the choice of an approach style. However, due to the intricacies of this statistical analysis, which required familiarity with the programming language Stan for Bayesian statistics (Carpenter et al., 2017), the model I made exhibited poor predictive power and failed to produce satisfactory results. As a result, I chose to omit that model from my thesis.

4. Results

4.1 Characterising approach styles

The contribution of the variable to a dimension, otherwise known as eigenvalues, consistently decreased along the first 10 dimensions (see Table 4). The first three dimensions of the MCA cumulatively contributed to 30.61% of the total variance in the dataset, indicating that the plane formed by these three dimensions elucidates a significant portion of the overall dataset variance. In subsequent steps of the MCA, I therefore focused on these three dimensions, as their eigenvalues exceeded the value of 0.2, as recommended by Hair et al. (2009), indicating that only they should be included in further analysis and interpretation of the results.

Table 4. Eigenvalue, percentage variance and cumulative percentage variance of top ten dimensions.

Eigenvalues	**Dimension**									
	1	2	3	4	5	6	7	8	9	10
Eigenvalue	0.28	0.22	0.21	0.19	0.19	0.18	0.17	0.16	0.15	0.14
Percentage of variance	12.15	9.56	8.89	8.29	8.06	7.59	7.38	6.89	6.66	6.19
Cumulative percentage of variance	12.15	21.70	30.61	38.90	46.9	54.56	61.94	68.83	75.49	81.69

To identify which variable is most correlated with each dimension, I referred to Figure 4. Variables were positioned using their respective squared correlations (R^2) to each dimension as coordinates. Variables that share similarities are located close together; reciprocally, proximity between variables indicates a stronger correlation (Ogunsakin et al., 2021). The variables '*Ear*' and '*Velocity*' were correlated and make the most significant contributions to the first dimension (see Figure 3). On the other hand, the variable '*Angle*' had the most influence on the second dimension. The '*Trajectory*' was positioned closer to the centre of the plot and had a relatively smaller impact on the eigenvalues of these dimensions. To complement the visual findings from Figure 4, I also calculated eta-squared (η^2) values for the first three dimensions, providing a precise quantification of the correlation between each dimension and the variables. These values confirm the patterns observed in the graphical representation and offer a more detailed correlation analysis (see Table 5).

Table 5. Association strength of categorical variables across MCA dimensions

The table presents the eta-squared (η^2) values, quantifying the relationship strength between variables and the principal dimensions derived from the MCA. This measure of association indicates the proportion of variance in the dimensional space that is attributable to each categorical variable. High eta-squared values suggest a strong association, implying that the variable significantly contributes to the variance explained by that particular dimension.

Categorical variables	Eta-squared (η^2) values		
	Dimension 1	Dimension 2	Dimension 3
Trajectory	0.001	0.002	0.098
Velocity	0.676	0.061	0.428
Angle	0.024	0.499	0.114
Tail	0.308	0.408	0.169
Ear	0.605	0.154	0.387
Penis	0.086	0.215	0.048

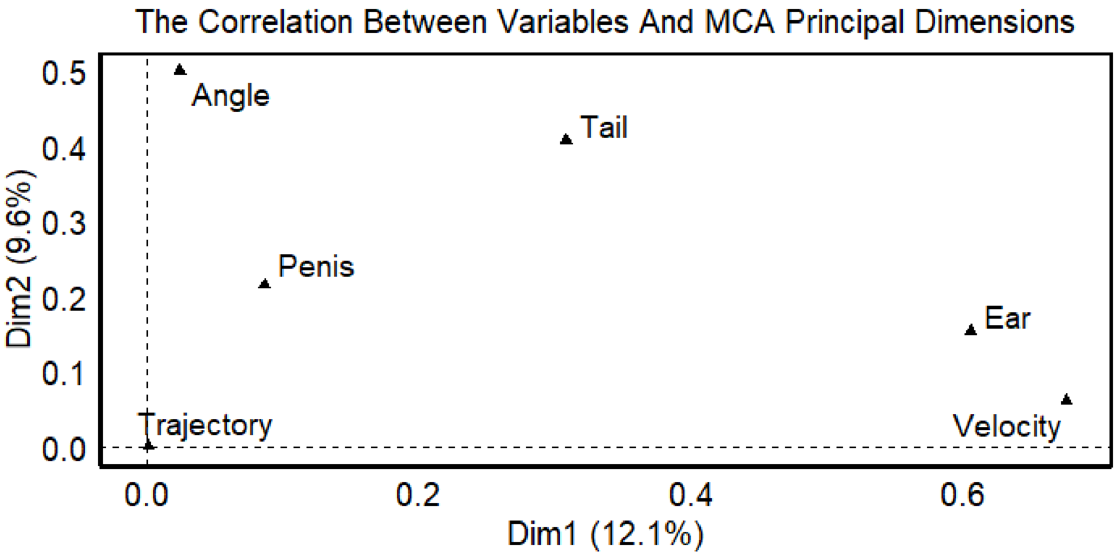

Figure 4. Plot of all active variables and the principal dimensions. This plot illustrates six specific features exhibited by male spotted hyenas when they approach a female.

A more detailed representation of the results can be achieved by plotting the categories of variables. I provide two types of visualisations: a two-dimensional (Figure 5) and a three-dimensional display (Figure 6).

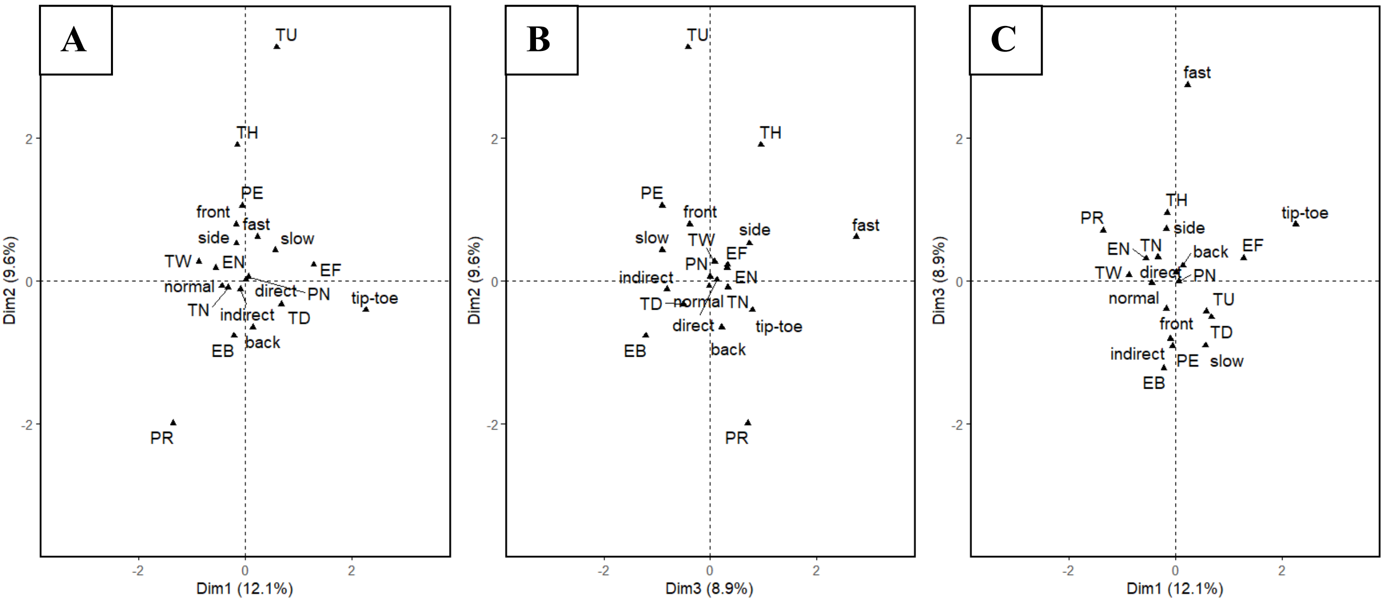

Figure 5. Categories factor map (MCA) for the first three dimensions. (**A)** Categories in the first and second dimension; (**B)** Categories in the second and third dimension; (**C)** Categories in the first and third dimension. Categories: trajectory (direct, indirect), velocity (normal, slow, tip-toe, fast), angle (back (BK), front (FR), side (S)), tail (tail normal (TN), tail down (TD), tail wagging (TW), tail up (TU), tail horizontal (TH)), ears (ears normal (EN), ears forward (EF), ears back (EB)), penis (penis normal (PN), penis relaxed (PR), penis erect (PE)).

To interpret the graphs generated by MCA, the primary criterion is the spatial proximity between categories. Proximity among categories within the same variable indicates their similarity (redundant information) regarding a given dimension. Categories that contribute equally to the observed variance in the dataset (i.e., are highly similar and redundant) can then be merged without losing valuable information. In contrast, when categories from different variables are close, it indicates a meaningful relationship or pattern between those variables, which in my case can be indicative of a behavioural style.

Based on the combined information provided by Figures 4-6 and focusing on variables '*Ear'* and '*Velocity'* as they are the primary contributors to the first three dimensions, I am able to distinguish three different clusters of categories and thus identify three distinct male approach styles. The additional information I provided is derived from my observational data; the patterns identified align with the behavioural observations recorded in the field.

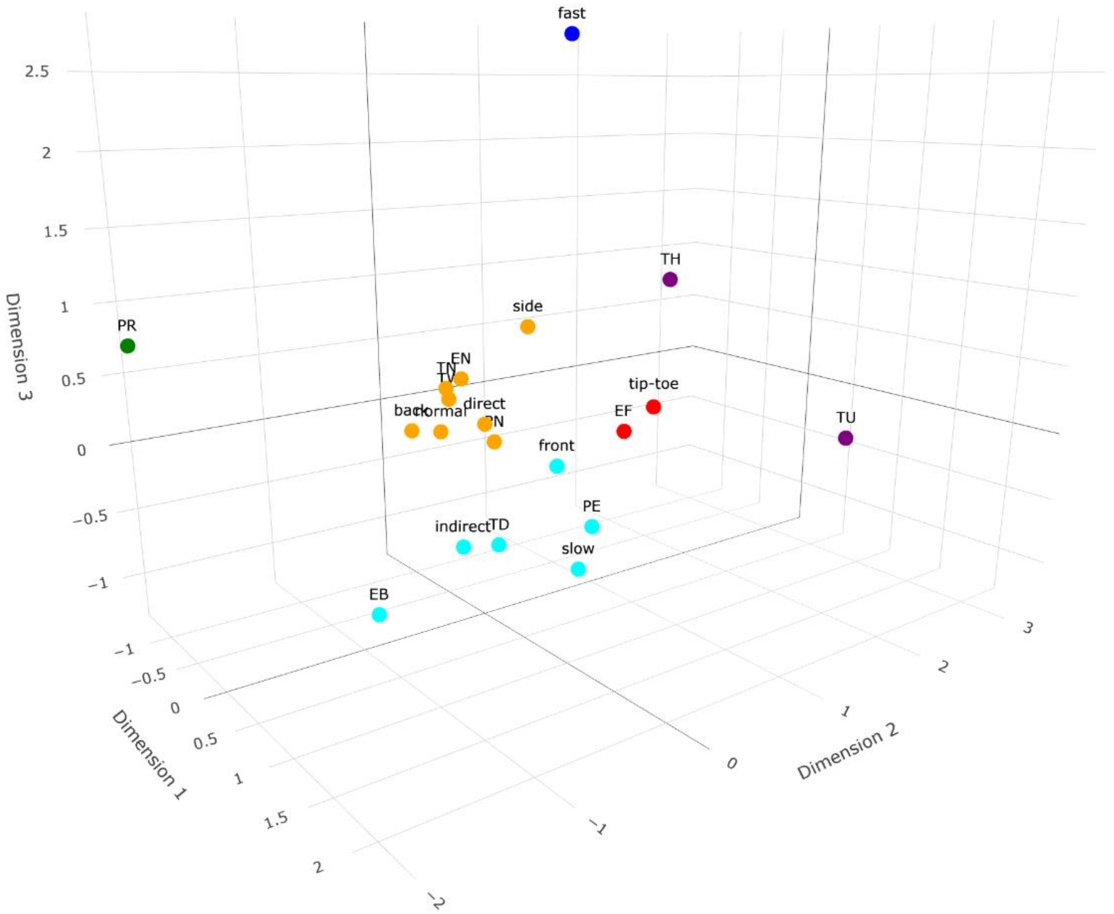

Figure 6. Three-dimensional representation of the clustering of categories. Points represent acts or signals that were expressed during male approaches. Points that have the same colour were consistently grouped together in the MCA. The proximity of similarly coloured points in the three-dimensional space indicates a strong correlation in their contribution to the dataset's inertia on each axis. Categories: trajectory (direct, indirect), velocity (normal, slow, tip-toe, fast), angle (back (BK), front (FR), side (S)), tail (tail normal (TN), tail down (TD), tail wagging (TW), tail up (TU), tail horizontal (TH)), ears (ears normal (EN), ears forward (EF), ears back (EB)), penis (penis normal (PN), penis relaxed (PR), penis erect (PE)).

Figure 7. Approach style 'sneaky'. The male approaches in a deliberate manner, taking more time to approach than the other two approach styles. He tries to stay undetected by the female, easily maintaining the position depicted for an extended period as he stealthily moves closer to the female. Throughout this approach, he maintains a focused and intense gaze towards the female, all while displaying a sign of dominance by keeping his ears pointed forward [Photograph by NHP].

Approach style 'sneaky' is characterised by velocity tip-toe and ears forward (EF), as depicted in Figure 6 with colour red. This style is distinguished by a deliberate, almost silent gait, similar to tiptoeing. Males that adopt this style may minimise noise by purposefully lifting their hind and front paws off the ground and putting them down gently. Additionally, the clearly dominant signal of ears forward is displayed as shown in the Figure 7 indicating a focused and alert state. This approach style reflects a careful, deliberate, and stealthy movement, often associated with situations where a male aims to avoid detection by the female or navigate discreetly within their environment.

Figure 8. Approach style 'cautious'. The approaching male is distinguished by his ears pointing back, his tail between his legs and a careful approach. The male in the picture is reaching towards the female, with his forelegs closer to the female while his hind legs are behind, indicating both insecurity and submission [Photograph by NHP].

Approach style 'cautious', as depicted in Figure 6 with light blue colour, is characterised by a slow pace, ears back (EB), indirect approach, and tail down (TD). This style is described by a set of behaviours that collectively convey a hesitant, timid, and non-threatening disposition. A cautious male approaches indirectly, circling and pausing as he assesses the situation, all the while clearly signalling submission through the positions of his tail and ears (see Figure 8). These signals are unambiguous and often displayed during daily agonistic dominance interactions to clarify a subordinate status within the clan.

Figure 9. Approach style 'casual'. Most aspects of this approach correspond to the normal way hyenas move, regardless of whether they are approaching someone or simply walking around [Photograph by NHP].

Approach style 'casual', depicted in Figure 6 with orange colour, is characterised by a normal pace, ears normal (EN), direct approach, tail normal (TN), and penis normal (PN). This style is characterised by relaxed and unhurried behaviours. These include approaching at a standard, unhurried pace with calm and relaxed ear positioning, indicating both a lack of submission and aggression (see Figure 9). Similarly, his tail hangs down along his hind legs in a relaxed manner, while he approaches the female with a direct and uninterrupted approach.

After defining the approach styles, I used them to explore whether males differed in their propensity to apply one style over the others depending on their tenure (short- and long tenured) and their dispersal status (philopatric and immigrant males) (see Figure 10).

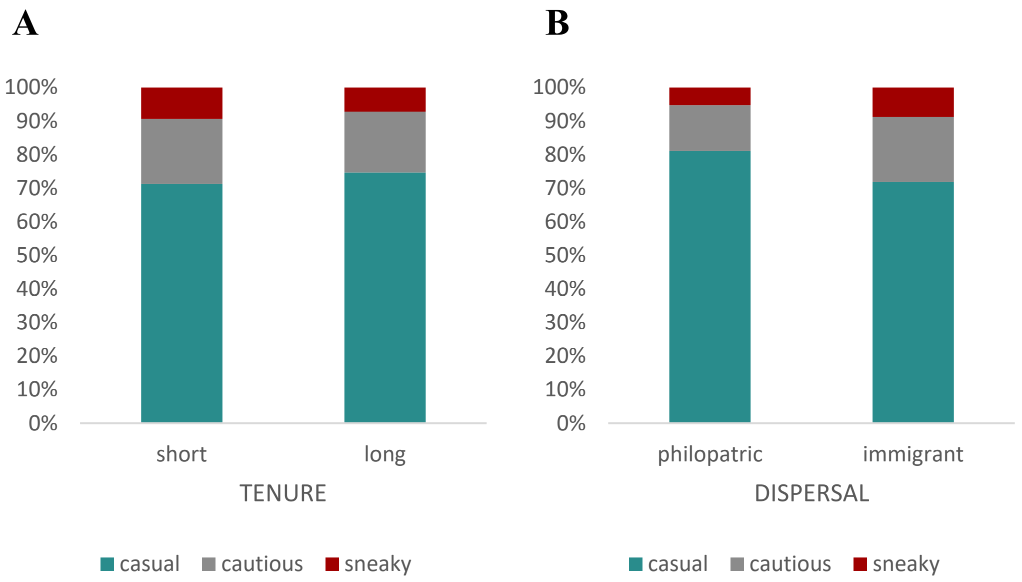

Figure 10. Prevalence of approach styles by tenure and dispersal status. This 100 percent stacked chart illustrates the prevalence of three approach styles (casual, cautious, and sneaky) in relation to both tenure (A) and dispersal status (B).

Within the observed population, approach styles exhibit a different distribution according to tenure length. For the casual approach, 56.5% is attributed to short-tenured males, while the remaining 43.5% is associated with those of long tenure. In the cautious approach, short-tenured males represent a larger proportion, accounting for 59.2%, in contrast to long-tenured males, who constitute 40.8%. Similarly, the sneaky approach is predominantly exhibited by short-tenured individuals, who comprise 64.2% of this behaviour, as opposed to the 35.8% exhibited by long-tenured individuals. Figure 10 depicts the prevalence of these three approach styles across short and long tenures.

Among the philopatric males, 81.1% of approaches are casual, while cautious approaches account for 13.6%, and sneaky approaches make up 5.3% of their approaches. On the other hand, among immigrant males, 71.9% engage in casual approaches, 19.4% take part in cautious approaches, and 8.8% use sneaky approaches. These numbers suggest that the proportions of each approach style are very similar between philopatric and immigrant males (see Figure 10).

4.2 Relationship between approach style and aggression

4.2.1 Male propensity to behave aggressively

Male approach style had a significant effect on the probability of males to express aggression toward the female they approached (GLMM; LR = 100.25, $p < 0.001$, N = 1418 approaches).

Overall, male aggression was rare. Out of 1418 observed approaches, only 36 instances of male aggression were observed. Casual approaches resulted in male aggression in only 0.43% of cases, while for cautious approaches, the rate of aggression was slightly higher at 1.4%. For sneaky approaches, as predicted by the model, the likelihood rises to 22.5% (see Figure 11).

The post-hoc tests revealed that male likelihood to express aggression does not differ between casual and cautious approaches. As shown in the Table 5, the probability of male aggression is pronounced for a sneaky approach (estimate= 4.19, SE = 0.52, $p < 0.001$), but not for casual (estimate= -5.44, SE= 0.48, $p < 0.001$) and cautious (estimate= 1.19, SE= 0.68, $p = 0.08$). The odds of expressing aggression were approximately 65 times higher for the sneaky approach compared to the reference level (see Table 6).

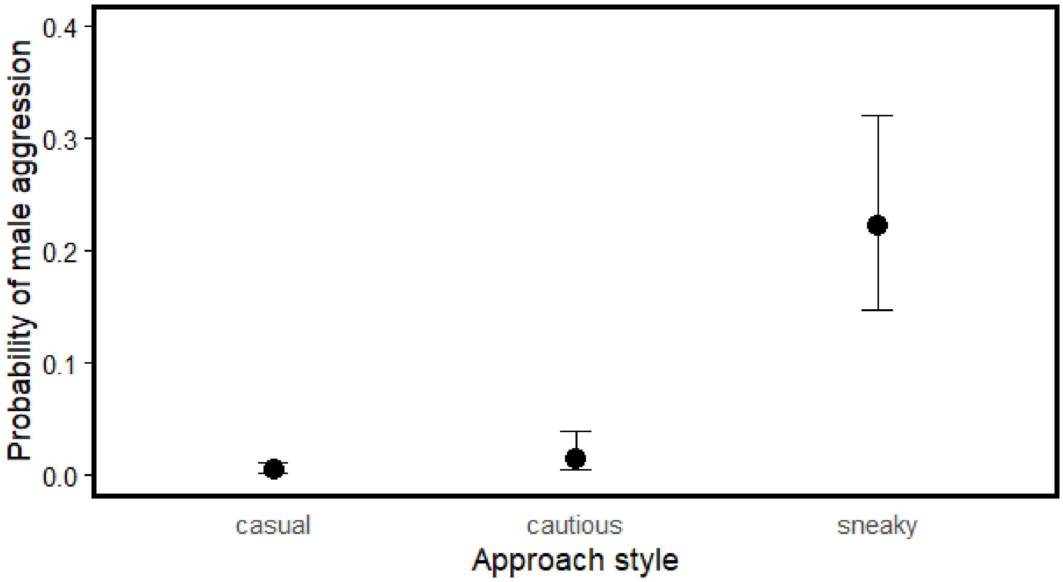

Figure 11. Predicted probability of male aggression in regards to three styles of male approach. Values are means with $CI_{95\%}$ and were predicted by a GLMM that also considered male identity as a random factor.

Table 6. The likelihood of male aggression as a function of male approach style.

Shown are the regression coefficients and standard errors (SE) in natural log units, z ratios, their corresponding P-values for each predictor variable and calculated odds ratio, as estimated by a generalized linear mixed-effect model with a binominal distribution (male ID as random factor; random factor variance = 0.32; N = 1418 approaches of 129 males). The reference category for the approach style (intercept) is set to the casual style.

Variable	Coefficient	SE	Z value	P	Odds ratio
Intercept	-5.44	0.48	-11.14	p < 0.001	0.004
cautious	1.19	0.68	1.75	P = 0.08	3.29
sneaky	4.19	0.52	8.00	p < 0.001	65.73

4.2.2 Female aggression and male approach style

Male approach style had a significant effect on the probability of females to respond aggressively to males (GLMM; LR = 19.43, $p < 0.05$, N = 1418 females).

Overall, females rarely responded aggressively to male approaches. Out of 1418 approaches, only 31 lead to female aggression; 1.08% following a casual approach, 1.75 % following a cautious approach, and 7.98% following a sneaky male approach, as predicted by the model (see Figure 12).

The post-hoc tests reveal that female propensity to respond aggressively did not differ between casual approaches and cautious approaches (estimate = 0.479, SE = 0.50, $p = 1$). However, both casual (estimate = -2.065, SE = 0.44, $p < 0.0001$) and cautious (estimate = -1.586, SE = 0.55, $p = 0.0123$) approaches significantly differed from the sneaky approach, even after applying Bonferroni correction.

The model suggests that when males adopt a sneaky approach, females are significantly more likely (coefficient = 2.06; $p < 0.001$) to respond aggressively compared to when males approach casually. The intercept coefficient is low (odds ratio = 0.011), indicating that females are more likely to respond non-aggressively than aggressively when males approach casually (see Table 6 for details). The results also indicate that the probability of cautious approaches triggering an aggressive response from females does not differ from that of casual approaches. The cautious approach, while having a positive coefficient (0.48), does not reach statistical significance (p = 0.34), which implies that it had a similar effect on female aggression as casual approaches.

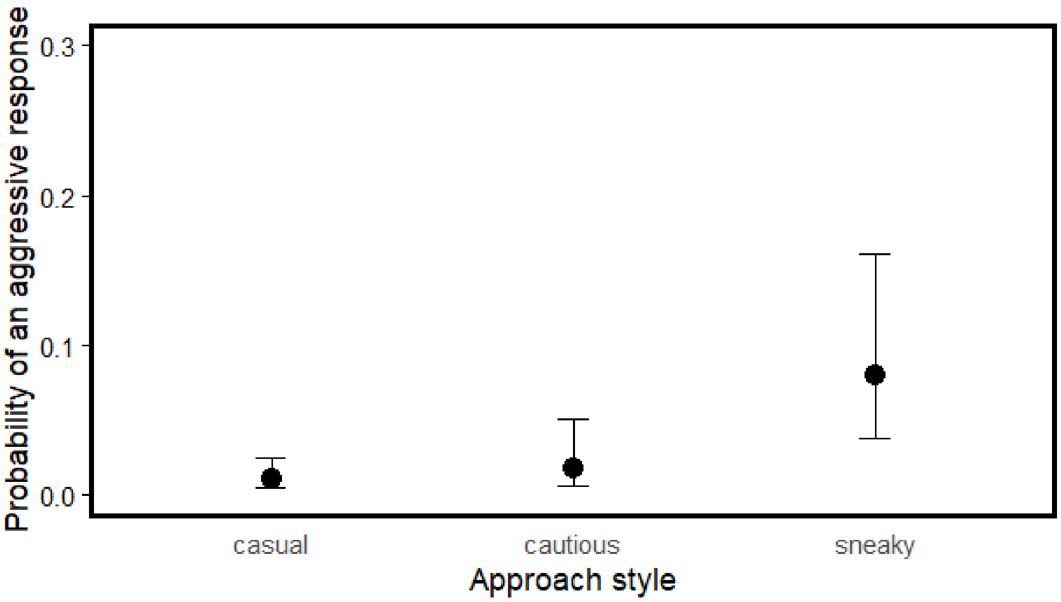

Figure 12. Predicted probability of aggressive responses by females to three styles of male approach. Values are means with $CI_{95\%}$ and were predicted by a GLMM that also considered female identity as a random factor.

The probability of female aggression is higher for the sneaky approach, indicating a strong association between this style and female aggressive behaviour, which is not the case for the casual and cautious approach styles (see Figure 12). The odds ratio of aggressive response by a female were approximately 8 times higher for the sneaky approach compared to the casual style (see values for the intercept; Table 7).

Table 7. The likelihood of female aggressive response as a function of male approach style.

Shown are the regression coefficients and standard errors (SE) in natural log units, z ratios, their corresponding P-values for each predictor variable and calculated odds ratio as estimated by a generalized linear mixed-effect model with a binominal distribution (female ID as random factor; random factor variance = 0.53; N = 1418 approaches, reaction of 152 females). The reference category for the approach style (intercept) is set to the casual style.

Variable	Coefficient	SE	Z value	P	Odds ratio
Intercept	-4.51	0.42	-10.72	$p < 0.001$	0.01
cautious	0.48	0.50	0.95	0.337	1.61
sneaky	2.06	0.44	4.66	$p < 0.001$	7.88

4.3 Proximate outcome of male approaches

Male approach style (LR: 43.38, $p < 0.001$), dispersal status (LR: 9.52, $p = 0.002$), and female rank (LR: 6.64, $p = 0.009$), and activity (LR: 4.45, $p = 0.003$), as well as the interaction term between male tenure and female age (LR: 15.79, $p < 0.001$), all significantly affect the likelihood of a positive outcome (see Figure 13 and Table 8, for more details).

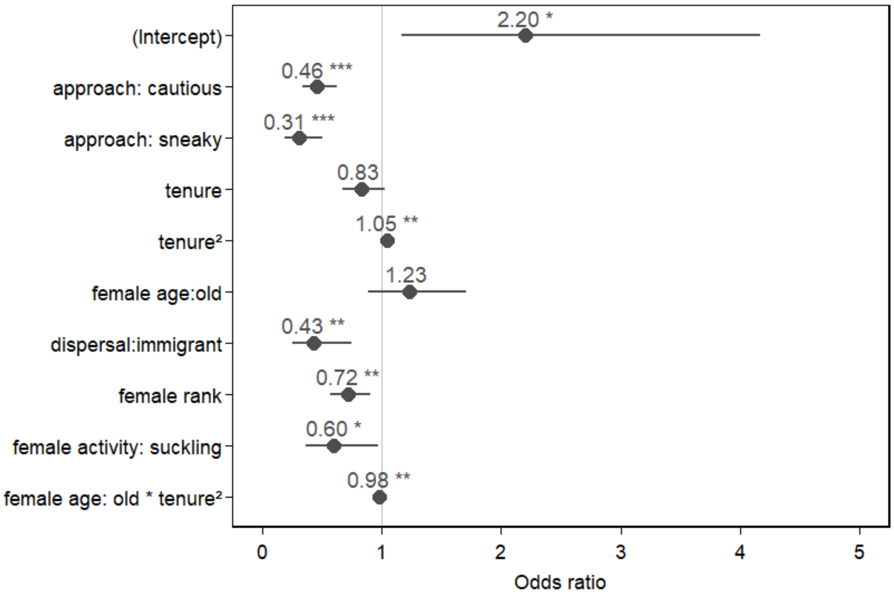

Figure 13. Factors influencing the likelihood of a positive outcome in a male-female interaction. Model estimates are presented as odds ratios ±CI$_{95\%}$ for each covariate as derived from the logistic regression. The solid vertical line signifies the line of null effect. Asterisks signify the degrees of statistical significance: *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.0001$.

The casual approach had a very high likelihood to lead to a positive outcome (estimate = 0.79, SE = 0.33, $p = 0.015$); significantly higher than for both the cautious approach (estimate = -0.78, SE = 0.16, $p < 0.001$) and sneaky approach (estimate = -1.18, SE = 0.25, $p < 0.001$) as seen in Figure 13. The post-hoc test with Bonferroni correction also reveals that sneaky and cautious approaches are not significantly different (estimate = 0.40, SE = 0.28, $p = 0.459$). Following these results, both cautious and sneaky approaches are significantly less likely to lead to a positive outcome compared to a casual approach.

Dispersal status had a significant effect with immigrant males being significantly less likely (35%) to achieve a positive outcome of the interaction compared to the philopatric males (56%). Females who were suckling their cubs were less likely (27%) to respond positively compared to females who were resting (coefficient = -0.52, *p* = 0.037), when controlling for other covariates.

Table 8. The likelihood of a positive outcome of a male-female interaction

Shown are the regression coefficients and standard errors (SE) in natural log units, z ratios, their corresponding P-values for each predictor variable as estimated by a generalized linear mixed-effect model with a binominal distribution (male and female IDs as random factors; male ID random factor variance = 0.23; female ID random factor variance=0.04, N = 1418 approaches, of 129 males and 152 females). Coefficients indicate the likelihood of a positive outcome in regards to the intercept and the reference levels for the categorical variables (approach: casual, year of tenure: 0, female age: young, dispersal: philopatric, female rank: -1, female activity: lying)

Variable	**Coefficient**	**SE**	**Z value**	**P**
Intercept	0.79	0.33	2.43	0.015
approach: cautious	-0.78	0.16	-4.99	$p < 0.001$
approach: sneaky	-1.18	0.25	-4.67	$p < 0.001$
Tenure	-0.19	0.11	-1.73	0.084
tenure^2	0.05	0.01	3.21	0.001
female age: old	0.21	0.17	1.26	0.207
dispersal: immigrant	-0.84	0.28	-3.03	0.002
female rank	-0.33	0.12	-2.80	0.005
female activity: suckling	-0.52	0.25	-2.08	0.037
female age: old * tenure^2	-0.02	0.007	-3.17	0.002

As shown in Figure 14 D, the likelihood of a positive outcome decreased for every one unit increase in the female rank (see Table 8. for details), which corresponds to a switch from a low-ranking female to a medium-ranking female or from a medium-ranking to a high-ranking female.

Tenure modelled with a linear effect did not reach statistical significance (*p* = 0.084). Notably, the tenure's quadratic effect varied with female age, as evidenced by the significant interaction term between quadratic tenure and female age categorised as old (estimate = -0.022, *p* = 0.0015). While overall, the likelihood of a positive outcome increased with male tenure, the increase was higher for young females than it was for old female, as evidenced by the negative – though weak - coefficient of the interaction term (see also Figure 14 E). The difference was most prominent for males with a tenure of 5 years and more.

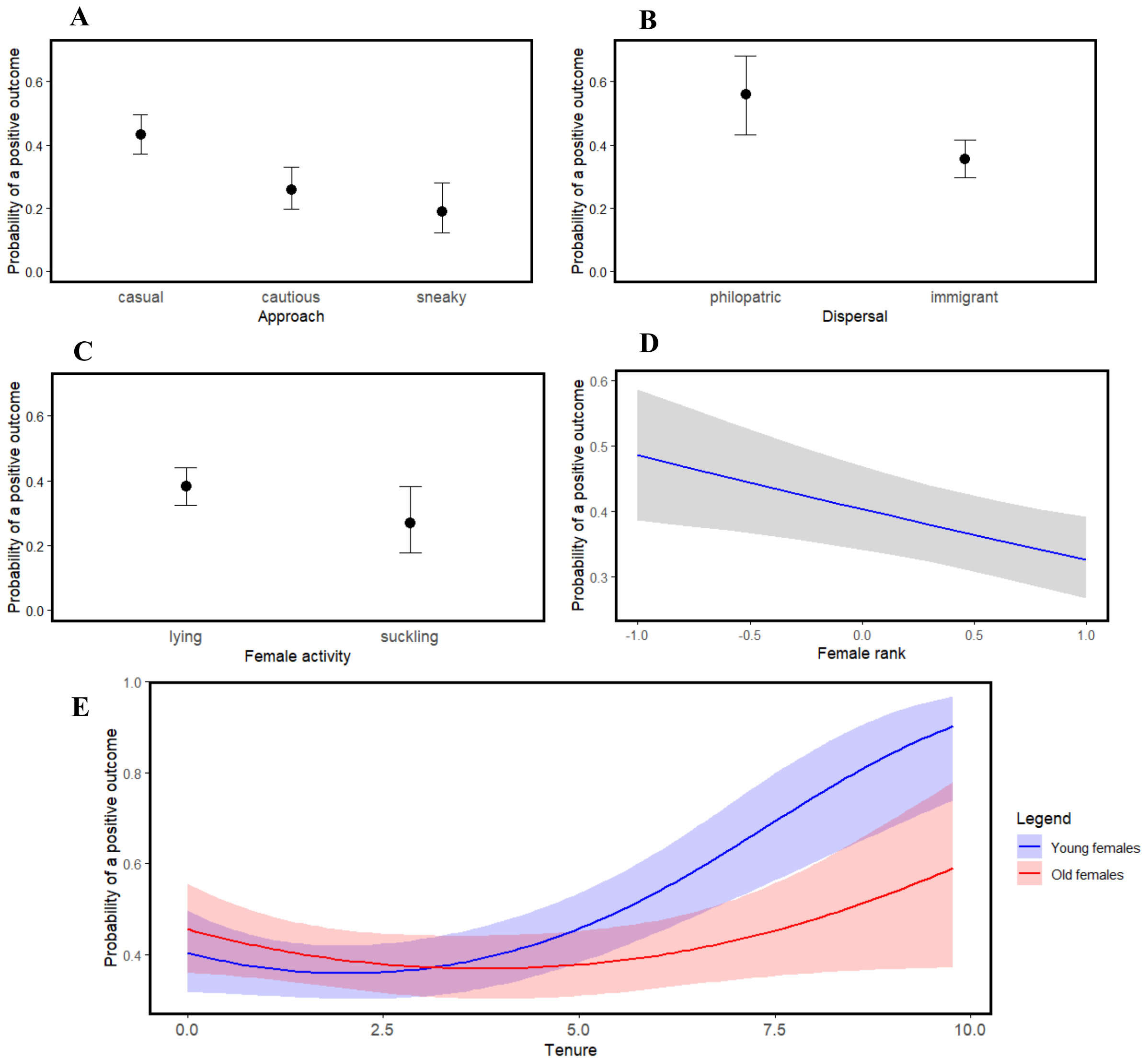

Figure 14. Predicted probability of a positive outcome of the interaction. Values are means with $CI_{95\%}$ and were predicted by a GLMM that also considered both male and female identity as random factors. Plotted are predictions for approach (A), dispersal (B), female activity (C), female rank (D), and interaction term (E) between tenure and female age, while holding all other covariates constant.

5. Discussion

My thesis aimed at addressing two main objectives: to describe the various styles males adapt to approach females, and to explore if these interactions lead to different opportunities to bond with females.

I identified three distinct approach styles: casual, cautious, and sneaky. The results validated my prediction that there are distinct approach styles that are marked by unique signals. For instance, the cautious approach is often shown through submissive signals like keeping the ears back and tail down, whereas the sneaky approach tends to involve more dominant signals, such as holding the ears forward while fixing a gaze on the female.

I investigated the relationship between aggression and male approach styles across the female and male sexes. I expected that males who take on a more aggressive or dominant approach would be more likely to express aggression, and indeed, my results supported this. Males who used a sneaky approach, characterised by dominant signals, tended to show more aggression towards females. This indicates that the style of approach truly mirrors the males' intentions. My results align with those of Szykman et al. (2003), who noted that in the specific context of one or more males expressing unprovoked aggression towards a single female, the male aggressors are identified by their ears pointing forward, elevated heads, and tails and manes bristled. Additionally, my results are in agreement with those of Szykman et al. (2003) concerning the observation that female hyenas tend to show aggressive reactions when approached by males displaying aggression. This supports my prediction that aggressive behaviours or signals from males allow females to react in a corresponding manner, but females equally do have the opportunity to pre-emptively react based on those signals emitted by males.

I obtained the prevalence of three different approach styles based on the tenure and dispersal status of male hyenas. However, it is important to acknowledge a limitation of this data set, as it is made using raw numbers, and the number of approaches involving immigrant males (N = 1286) significantly exceeded the number of approaches made by philopatric males (N = 132). To achieve more precise data, employing a multinomial model would be necessary.

Considering this limitation, the data suggests that immigrant and philopatric males are similar in the proportions of using different approach styles, but there is a slightly stronger preference for casual approaches in philopatric males. This is potentially reflecting a tendency towards lower-risk interactions in the context of bonding within their well-known environments and social circle. Contrary to that, immigrant males show a more diverse choice of approach styles, with a notable proportion using cautious and sneaky approaches compared to philopatric males. This variation implies that immigrant males may employ a wider array of strategies, possibly as a means of adapting to unfamiliar conditions upon integrating into a new clan.

Addressing whether the outcome of the interaction is influenced by the life history traits of both males and females as well as the approach styles of males, the results show that both factors play a role.

An interaction is more likely to result in a positive outcome if males adopt a casual approach devoid of any submissive or aggressive signals. I expected that interactions involving long-tenured and philopatric males would lead to positive outcomes because of their pre-existing relationships with the females. This prediction was formed from a study (Szykman et al., 2001) which indicated that females have a preference for mating with males with whom they have familiarity or social bonds, which often develops through spending more time with the prospective mate. And indeed, my results demonstrated that philopatric males have a higher likelihood of experiencing positive outcomes compared to immigrant males.

To investigate whether the tendency for assortative mating is reflected in the outcome of an approach, I included an interaction term between male tenure and female age in the analysis. Generally, the probability of a positive outcome rose with male tenure, in concordance with findings from earlier research (East et al., 2003). Most male-female bonds in spotted hyena, are almost always initiated and maintained by males (Szykman et al., 2001). As a male spends more time within a specific clan and forms a bond with a chosen female, the likelihood of a positive outcome increases. This suggests that males may change or adjust their approach style as their tenure in the clan increases. If a male has been associated with a female for an extended period, there may be no need to use aggression to test her reciprocation, as such tactics pose risks of injury and are costly for both males and females (Szykman et al., 2003).

Prior studies on male baiting of females demonstrated that females were targeted in all stages of reproduction, with increased frequencies observed between weaning and conception (Szykman et al., 2003). In my analysis, the precise reproductive status of the females was not known. However, as predicted, the presence of cubs influenced the interaction's outcome, based on the assumption that females would exhibit protective behaviour towards their cubs.

Ultimately, the question arises: what is the significance of these relationships, aggression and affiliation? Females possess full control over copulation and can exercise mate choice (Cunha et al., 2014), thus making it improbable for male hyenas to use aggression as a means to manipulate female mate selection. East et al. (2003) concluded that harassing females does not provide reproductive benefits to males, aligning with the findings of Szykman et al. (2001), who associated a strong bond between male and female hyenas with paternity.

But male aggression still does occur, as mentioned in previous research (East and Hofer 2001; East et al., 2003; Szykman et al., 2007) and found in this study. It is plausible that male harassment is used by males to gain attention and forge social bonds with females. This is corroborated by research on great apes (Laumer et al., 2024), which found that teasing could be used for capturing attention, is typically initiated by the teaser, and can encompass various playful as well as aggressive elements.

An idea was put forward suggesting that aggressors should seek appeasement and direct reconciliatory behaviours towards their targets. Such reconciliations have been observed in over thirty primate species (Aureli et al., 2002), as well as in other animals such as ravens (Fraser and Bugnyar, 2011), dogs (Cools et al., 2008), wolves (Baan et al., 2014), and hyenas (Wahaj et al., 2001).

There is a foundation that may support the hypothesis that teasing and exhibiting aggression towards females could be a means to build social bonds. Findings from Wahaj et al. (2001) indicate that greetings and approaches are more common after conflicts, and these affiliative gestures signal the formation of relationships and the repair of damage resulting from aggression, but further research is needed to justify these claims.

6. Conclusions and outlook

In my thesis, I identified three distinct approach styles among males and that these styles could serve as indicators of potential aggression, affecting both the approaching male and the female being approached. The outcome of these interactions is influenced by the life-history traits of both sexes as well as by the approach styles.

Males who use a sneaky approach are exposing themselves to the potential risk of injuries; the overall result of that approach is less successful than casual and cautious approaches, as the male cannot approach the female and form a social bond with her. As male tenure increases, the likelihood of a positive outcome is greater, indicating that long-tenured males do differ from recent immigrant males in the context of forming socio-sexual bonds. But further research is needed to shed light on whether life history traits influence the choice of an approach style, whether it changes as a result of a female's response, and whether males change their approach style as their tenure increases.

Another exciting opportunity for further research is connected to the question of whether the approach style, as a proxy of aggression, correlates with the initiation of male reproduction within the clan. I didn't directly explore this aspect, but it presents a next logical step following the results of my thesis.

Continuing with the exploration of aggression, there is also an intriguing avenue of research into its function, further examining whether it acts as coercion or teasing in this highly interesting social carnivore.

7. References

Andrade C. (2019). The P Value and Statistical Significance: Misunderstandings, Explanations, Challenges, and Alternatives. *Indian journal of psychological medicine, 41*(3), 210–215. https://doi.org/10.4103/IJPSYM.IJPSYM_193_19

Aloise King, E.D., Banks, P.B., Brooks, R.C. (2013), Sexual conflict in mammals. Mammal Review, 43: 47-58. https://doi.org/10.1111/j.1365-2907.2011.00200.x

Atkinson, W. (2024). Charting fields and spaces quantitatively: from multiple correspondence analysis to categorical principal components analysis. Quality and Quantity, 58, 829-848. https://doi.org/10.1007/s11135-023-01669-w

Aureli, F., Cords, M., Schaik, C.P. (2002). Conflict resolution following aggression in gregarious animals: a predictive framework. Animal Behaviour, 64, 325-343.

Baan, C.D., Bergmüller, R., Smith, D.W., Molnar, B. (2014). Conflict management in free-ranging wolves, Canis lupus. *Animal Behaviour, 90*, 327-334.

Baniel, A., Cowlishaw, G., Huchard, E. (2017). Male Violence and Sexual Intimidation in a Wild Primate Society. *Current biology: CB*, *27*(14), 2163–2168 https://doi.org/10.1016/j.cub.2017.06.013

Bateman, A.J. (1948) Intra-sexual selection in Drosophila. *Heredity 2*: 349–368.

Bates, D., Mächler, M., Bolker, B., Walker, S. (2015). "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software*, 67(1), 1–48. doi:10.18637/jss.v067.i01

Bohm, T. and Höner, O.R (2015). *Crocuta crocuta*. The IUCN Red List of Threatened Species 2015: e.T5674A45194782. http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T5674A45194782.en

Cameron, E. Z., Setsaas, T. H., Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of the United States of America, 106*(33), 13850–13853. https://doi.org/10.1073/pnas.0900639106

Cappozzo, H. L., Túnez, J. I., Cassini, M. H. (2008). Sexual harassment and female gregariousness in the South American sea lion, Otaria flavescens. Die Naturwissenschaften, 95(7), 625–630. https://doi.org/10.1007/s00114-008-0363-2

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M. A., Guo, J., Li, P., & Riddell, A. (2017). Stan: A Probabilistic Programming Language. *Journal of statistical software*, *76*, 1. https://doi.org/10.18637/jss.v076.i01

Clutton-Brock, T. H., Parker, G. A. (1995). Sexual coercion in animal societies. *Animal Behaviour, 49*(5), 1345–1365. https://doi.org/10.1006/anbe.1995.0166

Connor R. C. (2007). Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 362(1480), 587–602. https://doi.org/10.1098/rstb.2006.1997

Cools, A., Hout, A.J., Nelissen, M. (2008). Canine Reconciliation and Third-Party-Initiated Postconflict Affiliation: Do Peacemaking Social Mechanisms in Dogs Rival Those of Higher Primates? Ethology, 114, 53-63.

Cunha, G. R., Risbridger, G., Wang, H., Place, N. J., Grumbach, M., Cunha, T. J., Weldele, M., Conley, A. J., Barcellos, D., Agarwal, S., Bhargava, A., Drea, C., Hammond, G. L., Siiteri, P., Coscia, E. M., McPhaul, M. J., Baskin, L. S., & Glickman, S. E. (2014). Development of the external genitalia: perspectives from the spotted hyena (*Crocuta crocuta*). *Differentiation; research in biological diversity, 87*(1-2), 4–22. https://doi.org/10.1016/j.diff.2013.12.003

Das, S., X. Sun. (2016). Association Knowledge for Fatal Run-Off-Road Crashes by Multiple Correspondence Analysis. IATSS Research, Vol. 39, 2016, No 2, pp. 146-155

Davidian, E., Courtiol, A., Wachter, B., Hofer, H., Höner, O.P. (2016), Why do some males choose to breed at home when most other males disperse? *Sci. Adv*. 2, e1501236

Davidian, E., Wachter, B., Heckmann, I., Dehnhard, M., Hofer, H., Höner, O.P. (2021). The interplay between social rank, physiological constraints and investment in courtship in male spotted hyenas. *Funct Ecol*. 2021; 35: 635–649. https://doi.org/10.1111/1365-2435.13733

Davidian, E. and Höner, O.P. (2021). A king among queens. *Frontiers EcoPics. Frontiers in Ecology and the Environment 19*(10): 573. doi: 10.1002/fee.2441

East, M. L., Hofer, H., Wickler, W. (1993). The Erect "Penis" Is a Flag of Submission in a Female-Dominated Society: Greetings in Serengeti Spotted Hyenas. *Behavioral Ecology and Sociobiology, 33*(6), 355–370. http://www.jstor.org/stable/4600895

East, M.L. and Hofer, H. (2001). Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. *Behavioral Ecology*, 12, 558-568

East, M. L., Burke, T., Wilhelm, K., Greig, C., Hofer, H. (2003). Sexual conflicts in spotted hyenas: male and female mating tactics and their reproductive outcome with respect to age, social status and tenure. *Proceedings. Biological sciences*, 270(1521), 1247–1254. https://doi.org/10.1098/rspb.2003.2363

Fox, E.A. (2002). Female tactics to reduce sexual harassment in the Sumatran orangutan (Pongo pygmaeus abelii). *Behavioral Ecology and Sociobiology, 52*, 93-101.

Fraser, O.N., Bugnyar, T. (2011) Ravens Reconcile after Aggressive Conflicts with Valuable Partners. PLoS ONE 6(3): e18118. https://doi.org/10.1371/journal.pone.0018118

Gicquel, M., East, M. L., Hofer, H., Benhaiem, S. (2022). Early-life adversity predicts performance and fitness in a wild social carnivore. *Journal of Animal Ecology*, 91, 2074–2086. https://doi.org/10.1111/1365-2656.13785

Golla, W., Hofer, H., East, M. L. (1999). Within-litter sibling aggression in spotted hyaenas: Effect of maternal nursing, sex and age. *Animal Behaviour, 58*(4), 715–726. https://doi.org/10.1006/anbe.1999.1189

Gowaty, P. (2019). Rape, Forced and Aggressively Coerced Copulation. Editor: Choe, J.C., Encyclopedia of Animal Behavior. Academic Press.

Gubernick, D. J., Klopfer, P. H. (1981). *Parental care in mammals*. Plenum.

Hair, J.F., Black, W.C., Babin, B.J., Anderson, R.E. (2009). Multivariate Data Analysis (7th ed). Prentice Hall.

Harris, H.S., Oates, S.C., Staedler, M., Tinker, M.T., Jessup, D.A., Harvey, J.T., Miller, M.A., Landing, M., & Bay, M. (2010). Lesions and behavior associated with forced copulation of juvenile Pacific harbor seals (Phoca vitulina richardsi) by southern sea otters (Enhydra lutris nereis). *Aquatic Mammals, 36*, 331-341.

Hofer, H., East, M. L. (2003) Behavioral processes and costs of coexistence in female spotted hyenas: a life history perspective. *Evol Ecol 17*: 315–331.

Holekamp, K. E., Smale, L. (1993). Ontogeny of dominance in free-living spotted hyaenas: Juvenile rank relations with other immature individuals. *Animal Behaviour*, 46(3), 451–466. https://doi.org/10.1006/anbe.1993.1214

Holekamp, K.E., Smith, J.E., Strelioff, C.C., Van Horn, R.C., Watts, H.E. (2012), Society, demography and genetic structure in the spotted hyena. *Molecular Ecology*, 21: 613-632. https://doi.org/10.1111/j.1365-294X.2011.05240.x

Höner, O. P., Wachter, B., East, M. L., Runyoro, V. A., & Hofer, H. (2005). The Effect of Prey Abundance and Foraging Tactics on the Population Dynamics of a Social, Territorial Carnivore, the Spotted Hyena. *Oikos, 108*(3), 544–554. http://www.jstor.org/stable/3548799 (Höner et al., 2005)

Höner, O. P., Wachter, B., East, M. L., Streich, W. J., Wilhelm, K., Burke, T., & Hofer, H. (2007). Female mate-choice drives the evolution of male-biased dispersal in a social mammal. *Nature*, 448(7155), 798–801. https://doi.org/10.1038/nature06040

Höner, O.P., (n.d), Hyena mother carrying her cub [Photograph], Retrieved February 23, 2024, from https://hyena-project.com/hyenas/

Höner, O.P., (n.d), View of the western side of the Ngorongoro Crater [Photograph], Retrieved February 23, 2024, from https://hyena-project.com/the-crater/

Husson, F., Le, S., Pagès, J. (2017). Exploratory Multivariate Analysis by Example Using R (2nd ed.). Chapman and Hall/CRC. https://doi.org/10.1201/b21874 (Husson et al., 2017)

James, G., Witten, D., Hastie, T., Tibshirani, R. (2013). An Introduction to Statistical Learning: with Applications in R. Springer.

Josse, J., Chavent, M., Liquet, B., & Husson, F. (2011). Handling Missing Values with Regularized Iterative Multiple Correspondence Analysis. Journal of Classification, 29, 91 - 116.

Kokko, H., Jennions, M.D. (2008). Sexual conflict: the battle of the sexes reversed. *Current Biology 18*: 121–123.

Kruuk, H. 1972. The spotted hyena. A study of predation and social behavior. University of Chicago Press

Langergraber, K. E., Mitani, J. C., Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America, 104*(19), 7786–7790. https://doi.org/10.1073/pnas.0611449104

Laumer, I.B., Winkler, S.L., Rossano, F., Cartmill, E.A. (2024). Spontaneousplayful teasing in four great ape species.Proc. R. Soc. B291: 20232345. https://doi.org/10.1098/rspb.2023.2345

Le Boeuf, B. J., Mesnick, S. (1991). Sexual Behavior of Male Northern Elephant Seals: I. Lethal Injuries to Adult Females. *Behaviour, 116*(1/2), 143–162. http://www.jstor.org/stable/4534913

Le Roux, B. L., Rouanet, H. (2010). Multiple correspondence analysis. SAGE.

Martin, P., Bateson, P. (2007). Measuring behaviour: An introductory guide (3rd ed.). Cambridge University Press, New York, USA.

McCormick, S. K. and Holekamp, K. E. (2022). Aggressiveness and submissiveness in spotted hyaenas: one trait or two?, *Animal Behaviour*, 186, 179–190. https://doi.org/10.1016/j.anbehav.2022.01.012

Moschidis, S., Markos, A., Thanopoulos, A. (2022). "Automatic" interpretation of Multiple Correspondence Analysis (MCA) results for non-expert users, using R programming. Applied Computing and Informatics https://doi.org/10.1108/ACI-07-2022-0191

Moss, C. J., Croze, H., Lee, P. C. (2013). The Amboseli Elephants: A long-term perspective on a long-lived mammal. University of Chicago press.

Ngorongoro Hyena Project, (n.d.). Ngorongoro Hyena Project. Retrieved March 8, 2024, from https://hyena-project.com/

Ngorongoro Crater – Ngorongoro Conservation Area Authority (NCAA). Ngorongoro Conservation Area Authority NCAA. (n.d.). Retrieved March 8, 2024, from https://www.ncaa.go.tz/ngorongoro-crater

Ngorongoro Hyena Project (n.d.). Distribution of spotted hyena clan territories [Photograph] Ngorongoro Hyena Project. Retrieved March 8, 2024, from https://hyena-project.com/the-clans/

Ochoa Muñoz, A.F., Gonzalez Rojas, V.M., & Pardo Turriago, C.E. (2019). Missing data in multiple correspondence analysis under the available data principle of the NIPALS algorithm. DYNA

Ogunsakin, R., Moyo, S., Oludayo, Olugbara, O., Israel, C. (2021). Relating Student Engagement Indicators to Academic Performance Using Multiple Correspondence Analysis. *Cybernetics and Information Technologies,21*(1) 87-102. https://doi.org/10.2478/cait-2021-0007

Owen, E.C.G., Hofmann, S., Wells, R.S. (2002). Ranging and social association patterns of paired and unpaired adult male bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Canadian Journal of Zoology 80*, 2072–2089.

Parker, G.A. (2006) Sexual conflict over mating and fertilization: an overview. Philosophical Transactions of the Royal Society of London. Series B, *Biological Sciences* 361: 235–259.

Rodriguez-Sabate, C., Morales, I., Sanchez, A., & Rodriguez, M. (2017). The Multiple Correspondence Analysis Method and Brain Functional Connectivity: Its Application to the Study of the Non-linear Relationships of Motor Cortex and Basal Ganglia. Frontiers in neuroscience, 11, 345. https://doi.org/10.3389/fnins.2017.00345

Scott, E. M., Mann, J., Watson-Capps, J. J., Sargeant, B. L., & Connor, R. C. (2005). Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour, 142*(1), 21–44. https://doi.org/10.1163/1568539053627712

Seyfarth, R. M., Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual review of psychology, 63*, 153–177. https://doi.org/10.1146/annurev-psych-120710-100337

Siegmann, S., Feitsch, R., Hart, D.W., Bennett, N.C., Penn, D.J., Zöttl, M. (2021). Naked mole-rats (*Heterocephalus glaber*) do not specialise in cooperative tasks. *Ethology*. 2021; 127: 850–864. https://doi.org/10.1111/eth.13160

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral ecology and sociobiology, 64*(11), 1733–1747. https://doi.org/10.1007/s00265-010-0986-0

Smith, J. E., Van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K., Holekamp, K. E. (2010). Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology, 21*(2), 284–303. https://doi.org/10.1093/beheco/arp181

Smith, J.E, Holekamp K. E. (2019). Spotted Hyenas. Editor: Choe, J.C, Encyclopedia of Animal Behavior. Academic Press.

Stanton, L.A., Sullivan, M.S., Fazio, J.M. (2015). A Standardized Ethogram for the Felidae: A Tool for Behavioral Researchers Applied Animal Behaviour Science. 173. 10.1016/j.applanim.2015.04.001.

Szykman, M., Anne L. Engh, Russell C. Van Horn, Funk, S. M., Scribner, K. T., & Holekamp, K. E. (2001). Association Patterns among Male and Female Spotted Hyenas (*Crocuta crocuta*) Reflect Male Mate Choice. *Behavioral Ecology and Sociobiology*, *50*(3), 231–238. http://www.jstor.org/stable/4601958

Szykman, M., Engh, A.L., Van Horn, R.C., Boydston, E.E., Scribner, K.T., Holekamp, K.E. (2003). Rare male aggression directed toward females in a female-dominated society: Baiting behavior in the spotted hyena. *Aggressive Behavior*, 29(5), 457– 474

Szykman, M., Van Horn, R. C., Engh, A. L., Boydston, E. E., Holekamp, K. E. (2007). Courtship and mating in free-living spotted hyenas. Behaviour, 144, 815–846. https://doi.org/10.1163/156853907781476418

Vullioud, C., Davidian, E., Wachter, B., Rousset, F., Courtiol, A., & Höner, O. P. (2019). Social support drives female dominance in the spotted hyaena. *Nature Ecology & Evolution*. doi:10.1038/s41559-018-0718-9

Wahaj, S.A., Guse, K.R., Holekamp, K.E. (2001), Reconciliation in the Spotted Hyena (*Crocuta crocuta*). Ethology, 107: 1057-1074. https://doi.org/10.1046/j.1439-0310.2001.00717.x

Watters, J. V., Margulis, S. W., Atsalis, S. (2009). Behavioral monitoring in zoos and aquariums: a tool for guiding husbandry and directing research. *Zoo biology, 28*(1), 35–48. https://doi.org/10.1002/zoo.20207

Watts, H. E., Tanner, J. B., Lundrigan, B. L., Holekamp, K. E. (2009). Post-weaning maternal effects and the evolution of female dominance in the spotted hyena. *Proceedings. Biological sciences, 276*(1665), 2291–2298. https://doi.org/10.1098/rspb.2009.0268

Watts, D. P. (2022). Male chimpanzee sexual coercion and mating success at ngogo. *Am J Primatol*, 84, e23361. https://doi.org/10.1002/ajp.23361

Weingrill, T., Lycett, J. E., Henzi, S. P. (2000). Consortship and mating success in chacma baboons (*Papio cynocephalus ursinus*). *Ethology, 106*(11), 1033–1044. https://doi.org/10.1046/j.1439-0310.2000.00616.x

Wedell, N., Kvarnemo, C., Lessells, C.K.M., Tregenza, T. (2006) Sexual conflict and life histories. *Animal Behaviour* 71: 999–1011.

Wilson, M., Mesnick, S.L. (1997) An empirical test of the bodyguard hypothesis. Gowaty. Feminism and Evolutionary Biology. Chapman Hall, New York

Yee, J. R., Cavigelli, S. A., Delgado, B., & McClintock, M. K. (2008). Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary tumors and lifespan. *Psychosomatic medicine, 70*(9), 1050–1059

Yoshida, K., Van Meter, P., Holekamp, K.E. (2016). Variation among free-living spotted hyenas in three personality traits. *Behaviour*, *153*, 1665-1722.

8. CV

My name is Dora Berger. I was born on 28th of May 1995 in Varaždin, Croatia. During my high school education at Medical School Varaždin, I gained the title of general care nurse while developing a passion for zoology. In the academic year 2016/2017, I enrolled in the Undergraduate study of Biology at the Josip Juraj Strossmayer University in Osijek, Croatia. During my undergraduate studies, I have developed a further fascination with behavioural biology and spotted hyenas. After I concluded my undergraduate study with the final paper titled "Behavioural approach and anthropological impact on species *Crocuta crocuta*," I enrolled in the in the Graduate Study of Experimental Biology at the Faculty of Science, University of Zagreb.