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Infanticide by females is a leading source of juvenile mortality in a large social carnivore

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Abstract

Infanticide, or the killing of offspring by a conspecific, occurs in many animal species. Although both males and females can kill infants, sexually selected infanticide by males has been the primary focus in studies of infanticide. In contrast, the prevalence and function of infanticide by females is less well understood. Here we use 30 years of data collected from several social groups studied in the Masai Mara National Reserve and Amboseli National Park in Kenya to describe the prevalence of, and explore functional hypotheses explaining, infanticide in the spotted hyena (*Crocuta crocuta*), a carnivore that lives in mixed-sex matrilineal groups structured by rigid dominance hierarchies. Hyenas breed year-round and raise their cubs in communal dens concurrently with other mothers from the same social group. We document cases of infanticide at the communal den and relate the observed patterns to hypothesized functions of infanticide. We find that infanticide is a significant source of mortality experienced by young juveniles. Victims were equally likely to be male or female, but in all observed cases the killers were adult females. Killers tended to be higher-ranking than the mothers of victims, and killers were sometimes aided by kin. Our results are most consistent with the hypothesis that infanticide by females in this species serves as a form of social competition among matrilines.

Key words: infanticide by females, matrilineal society, thanatology, female-female competition

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Introduction

Infanticide is the killing of an individual's offspring by a conspecific, whether a direct relative or an unrelated member of the species (Hausfater & Hrdy, 1984). This phenomenon has been observed in both lab settings and the wild, and may be committed by either males or females (Agrell, Wolff, Ylönen, & Ylonen, 1998; Hrdy, 1979). Occurrences of infanticide are especially prominent in mammals, where it has been observed in over 100 species; however, this behavior has also been documented in birds, fish, and invertebrates (Agrell et al., 1998; Hausfater & Hrdy, 1984; Hrdy, 1979). In species where infanticide represents a common source of infant mortality, infant defense and avoidance of infanticidal individuals may function importantly in the social behavior of adults and juveniles (Balme & Hunter, 2013; Lowe, Hobaiter, & Newton-Fisher, 2018; Packer & Pusey, 1983a). However, because infanticide events occur infrequently and take place rapidly, it can be difficult to identify the circumstances under which they occur and to assess their importance; for example, in the late 1990s there was a debate in the literature over whether or not infanticide by male African lions (*Panthera leo*) occurred regularly during pride takeovers, which are rarely observed (Dagg, 1998; Packer, 2000; Silk & Stanford, 1999).

Hrdy (1979) introduced the first adaptive hypotheses regarding the evolution of infanticide, positing that infanticide functions to provide fitness-related benefits to infanticidal individuals (Agrell et al., 1998). Hypothesized functions of infanticide include the killing of conspecific offspring for food, to reduce intra-group competition for other resources, or as a means of increasing the killer's reproductive opportunities (Hrdy,

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1979). This final hypothesis, known as the sexual selection hypothesis, is best supported in cases where infanticide is committed by males (Lukas & Huchard, 2014). In African lions, males kill cubs sired by other males to bring the mothers of those cubs back into estrus more quickly (Packer & Pusey, 1983b). The sexual selection hypothesis has also been supported in African leopards (*P. pardus*), where infanticide by males accounts for nearly half of all infant deaths (Balme & Hunter, 2013). In baboons (*Papio spp.),* infanticide as a mechanism of sexual selection has been well documented and accounts for anywhere from 2 to 70 percent of infant mortality depending on geographic location and demography (Alberts, 2018; Cheney et al., 2004). The sexual selection hypothesis is frequently invoked because it is easy to identify the fitness advantage accruing to males by killing infants sired by others, and because this type of infanticide can represent a significant mortality source, as seen in African leopards.

In contrast to infanticide by males, infanticide committed by females is less well studied, nor is it well explained by the sexual selection hypothesis; nevertheless, infanticide by females occurs in at least 89 mammalian species and can be a significant source of infant mortality (Lukas & Huchard, 2019). A recent phylogenetic study by Lukas & Huchard (2019) suggests that infanticide by females is often motivated by competition with other females, and that the contexts in which this competition occurs varies with social organization and ecology.

In cooperatively breeding species, infanticide by females is committed primarily by the dominant breeder and serves to increase the number of available helpers by preventing would-be breeders from reproducing. In studies of captive dingoes (*Canis*

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familiaris dingo) and wild African wild dogs (*Lycaon pictus*), dominant females kill many cubs born to subordinate females, making infanticide the leading cause of infant mortality (Corbett, 2010; Creel & Creel, 1998). A study of meerkats (*Suricata suricatta*) found that infanticide by dominant breeding females was a common means of reducing future resource competition between pups (Clutton-Brock et al., 1998). In plural breeders with female philopatry, infanticide by females generally occurs in species where dominance hierarchies are influenced by nepotism (i.e., the ranks of daughters are influenced by the ranks of their mothers), and killers are typically lactating females of high social status (Lukas & Huchard, 2019). These findings offer a starting point for understanding the evolution of infanticide by females, but our knowledge remains limited by the available data on each species included in the Lukas & Huchard study. In some cases, patterns of infanticide in a species were inferred based on only one or a few observations, suggesting that more descriptive studies of infanticide by females are needed to better understand this behavior.

Here we use three decades of behavioral observations of spotted hyenas (*Crocuta crocuta*) to assess the prevalence and context of infanticide by females in a plural breeding species with female philopatry and nepotistic rank inheritance. We describe cases of infanticide as they occur in spotted hyenas, and assess the contribution of infanticide to cub mortality. Finally, we consider our observations in relation to two non-mutually exclusive hypotheses (Table 1) regarding the evolution of infanticide by female spotted hyenas suggested by the results obtained by Lukas and Huchard (2019). The exploitation hypothesis posits that infanticide by females in spotted hyenas functions as a

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form of predation, with juvenile groupmates serving as a source of prey. This hypothesis predicts that infanticide should take place more frequently under conditions of low food availability, that the killer or offspring of the killer should primarily feed on the carcass, and that there should be no sex bias in the perpetrators or victims of infanticide. By contrast, the resource competition hypothesis posits that infanticide serves to reduce numbers of social allies available to other group-members, and is likely to occur primarily in species where kin play an important role in determining social status. As outlined by Lukas and Huchard, this hypothesis predicts that infanticide by high-ranking individuals against low-ranking individuals should be prevalent in spotted hyena societies because of their nepotistic dominance hierarchies. Additionally, this hypothesis predicts that the victims and perpetrators of infanticide should be biased towards the philopatric sex (females, in this instance), as they are the individuals that will be long-term competitors for social rank or resource access.

Methods

Study Animals

Spotted hyenas are large carnivores found widely across sub-Saharan Africa (Holekamp & Dloniak, 2010). Individuals reside in mixed-sex, groups, called “clans,” each of which contains multiple matrilineal kin groups and is structured by a linear dominance hierarchy (Frank, 1986). Spotted hyenas are polygynandrous and breed year-round. Males disperse during the years after reproductive maturity, which occurs at around 24 months of age (Holekamp et al., 2012). Females are philopatric and usually

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mate with immigrant males (Engh et al., 2002). Females give birth to one or two cubs in an isolated natal den, where they are maintained for a few weeks before being moved to the clan's communal den. The communal den may contain up to 31 cubs at any given time (Johnson-Ulrich & Holekamp, 2020), and cubs typically remain in or around the den until they are approximately nine months of age (Holekamp et al., 1997). These cubs, which belong to several different mothers, are often left unattended during much of the day while the mothers are away. Spotted hyena societies are characterized by fission-fusion dynamics where individuals associate in subgroups that change composition throughout the day (Smith et al., 2008). Both mothers and other groupmates visit the communal den regularly, either alone or with others. Starting at 1-2 months of age, cubs emerge from the den to socialize when their mothers are present and, as they get older, when their mothers are absent.

Study Area

Data presented here were collected from two study areas in Kenya near the Tanzanian border. Most observations come from eight clans in the Masai Mara National Reserve (MMNR, 1510 km^2), a savanna ecosystem in southwestern Kenya that is contiguous with the Serengeti National Park in Tanzania and grazed year-round by multiple herbivore species (Holekamp et al., 1997). The greater Serengeti ecosystem (including the MMNR) contains millions of migratory ungulates that seasonally visit the MMNR, with their numbers peaking there between June and September (Smith, Kolowski, Graham, Dawes, & Holekamp, 2008). Data were collected in MMNR from 1988 to 2018; we observed one clan for the entire study period, and seven other clans

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during subsets of that period. Our second study area was in Amboseli National Park (ANP, 392 km^2), which is located in southeastern Kenya; data were collected from two clans in ANP from 2003 to 2005 (Watts, Scribner, Garcia, & Holekamp, 2011).

For describing cases of infanticide and their frequency, we use data from all ten clans of spotted hyenas located in both study areas to capture the full breadth of circumstances under which infanticide occurs. For tests of hypotheses regarding the function of infanticide in spotted hyenas, we limited the dataset to only our six most well-studied clans of hyenas in the MMNR. We elected to use this restricted dataset for exploring the function of infanticide because these clans live under similar ecological conditions, because all covariate data was available for these clans, and because these clans account for the majority of our data (86.7% of juvenile mortality from the larger dataset).

Data Collection and Analysis

Data were collected during twice-daily observation periods that took place around dawn and dusk. Observers used vehicles as mobile blinds to find and observe hyenas. Scan sampling (Altmann, 1974) was used to collect demographic data. Maternity was determined based on nursing associations and genotyping. Data documenting specific types of social interactions, including observed infanticide events, were collected using all-occurrence sampling (Altmann, 1974). Individual hyenas were identified by their unique spot patterns, and the sexes of juveniles were determined based on the dimorphic morphology of the erect phallus. Juvenile age was determined (to ± 1 week) based on appearance when first seen. Social ranks of adult females were determined based on the

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outcomes of aggressive interactions as described elsewhere (Strauss, 2019; Strauss & Holekamp, 2019a). In three recent cases of infanticide, ranks from the prior year were used to determine ranks of mother or infant-killer. All statistical analysis and visualization was done using the statistical software environment, R (R Development Core Team, 2018).

Juvenile mortality

We assessed various causes of mortality among juveniles less than 1 year of age. In our 30 years of data, the most common sources of mortality for young juveniles were starvation, humans, lions, flooded dens, illness, siblicide, and infanticide (n = 99 cases with known mortality sources). Starvation was identified in cases where juveniles were observed to be becoming progressively more gaunt before they vanished, or in cases where dead juveniles were found in an emaciated state. Death by humans was assigned when there was a clear anthropogenic cause of the mortality; for example, hit by a car, speared, poisoned, etc. Death by lions was either observed or could be inferred based on the deep, widely spaced puncture wounds typically inflicted during lion attacks. Death due to flooded dens was determined when we arrived at a den to find it flooded and we knew that juveniles had been residing in the den at the time that were never seen again. Death by illness was assessed based on whether cubs exhibited disease symptoms before they disappeared (e.g., canine distemper).

We identified 21 cases of infanticide, divided into three categories based on the certainty with which we could determine infanticide as the cause of death. In 12 cases of ‘observed’ infanticide, a cub was observed being killed by another hyena or dying as a

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result of having its skull recently crushed by another hyena (Figure 1). Additionally, we identified five 'presumed' cases of infanticide where observers arrived at the den to find a cub that had been killed recently with its skull crushed. We used skull crushing as diagnostic of infanticide because 1) it was directly seen in all of the 'observed' cases of infanticide, 2) it does not occur during death by siblicide, and 3) it is a common predation strategy used by hyenas on small prey (Holekamp et al. unpublished data). Finally, we identified four 'likely' cases of infanticide, where no information on the state of the skull was available (either due to observer omission or because the victim had already been largely consumed), but other common aspects of 'observed' cases of infanticide were noted (e.g., mother guarding or grooming the victim, victim consumed by mother or others, victim found at communal den).

To assess support for the exploitation hypothesis, we examined the frequency of different mortality sources as a function of seasonal prey availability. In the Masai Mara National Reserve, prey availability peaks when seasonal migrations of millions of ungulates are present in our study area June – September (Smith et al., 2008). We used a Chi-squared test to evaluate whether infanticide was more or less likely to occur than other sources of mortality during these periods of high prey availability.

Results

Our results suggest that infanticide appears to be a leading source of mortality for cubs under 1 year old. Of the 99 cases of death of den-dependent juveniles with a known mortality source (of 543 total juvenile mortality cases), infanticide accounted for 21.2 %

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of mortality (Figure 2). This figure places infanticide as the second largest mortality source for den-dependent juveniles, ranking below starvation (36.4%) but above lions (17.2%) and humans (9.1%) (Figure 2, dark bars).

Next, we used these proportions of known causes of mortality in young juveniles to infer the potential cause of death in 444 cases of mortality in young cubs where the cause of death was unknown. Cub deaths of both known and unknown causes of mortality were first separated into two categories: 1) cases where the mother disappeared prior to the cub's death, and 2) cases where the mother was alive upon the cub's death. In cases where the mother disappeared prior to the cub's death, known cause of death was frequently starvation (n = 29/35 cases), and in most cases of known starvation (29/36), the mother preceded the cub in death. To use this extra information about starvation in inferring unknown mortality sources, any cub death of unknown cause where the mother disappeared prior to the cub's death was attributed to starvation (n = 37). Next we inferred the cause of death in unknown cases where the mother was alive upon the cub's death, and the number of deaths attributable to each cause were inferred using the proportions of observed mortality in each category, limited to cases where the mother was alive upon the cub's death. Uncertainty around these inferred cases was estimated using bootstrapping with 1000 replicates. We found that, of the 444 cases of mortality where the cause was unknown, a significant number of deaths could be potentially attributed to infanticide (Figure 2, light bars). Including both inferred and observed sources of mortality, infanticide became the leading cause of death for juveniles under 1

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year of age, although the 95% confidence interval for infanticide overlapped the intervals for starvation and lions.

The distribution of ages of death associated with each of these mortality sources supports the hypothesis that infanticide is a leading cause of mortality in young spotted hyenas; whereas the other three leading sources of mortality generally occurred among older juveniles (> 5 months old), the peak age distribution of deaths by infanticide aligned with the peak age at death in cases of juvenile mortality where the cause of death was unknown (Figure 3).

Every observed case of infanticide in our dataset was perpetrated by an adult female. All cases of infanticide occurred at a communal den, although in one case the victim was killed by other groupmates as its mother was transferring it from the natal den to the communal den. Attackers sometimes acted alone, and other times were aided by groupmates. In three cases where infanticide took place while the victim's mother was present, multiple hyenas displayed aggression against the mother while her offspring was being attacked. In one of these events, the highest-ranking female killed a low-ranking juvenile while her offspring chased away the victim's mother. In two other cases where the victim's mother was present, multiple hyenas attacked the mother while the perpetrator killed the cub. In cases where females committed infanticide unaided, they often did so during what appeared to be normal social behavior, and in a few cases prosocial 'groan' vocalizations were emitted by the attacker immediately before attacking. Close kinship did not prevent females from committing infanticide: in one case, a female coaxed each of her full sister's two offspring out of the den by groaning,

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then killed both cubs (previously reported in (White, 2005)). However, although we did not have full pedigree data available for most killed infants, infanticidal females most often killed juveniles other than those born to their closest relatives.

Infanticidal females typically targeted young juveniles (<5 months old), although we did observe two cases of infanticide in older juveniles (Figure 2). Victims with known sexes were evenly split between males (n = 4) and females (n = 5), suggesting that juveniles of both sexes were equally likely to be attacked by conspecifics. Finally, comparison of attacker and victim ranks revealed that infanticidal females were on average higher ranking than the mothers of victims (Welch's two-sample t-test: t = -3.44, df = 20.98, p = 0.003; Figure 3).

Victims of infanticide were sometimes consumed, but we did not find any evidence that infanticide in this species was sensitive to prey abundance. A Chi-squared test revealed that death by infanticide was no more strongly associated with seasonal prey availability than any other juvenile mortality source (X^2=0.787, df = 1, p = 0.531). Victims' bodies were consumed by one or more hyenas in 11 out of 21 cases; they were sometimes consumed by the killer (n = 3) or the killer's offspring (n = 3), sometimes by the mother of the dead infant (n = 4), and sometimes by other group-members (n=3; note that these numbers don't add to 11 because multiple hyenas were often observed consuming infanticide victims). When given the opportunity, mothers sometimes (n = 7) groomed or otherwise cared for their deceased offspring after its death. In 3 cases, observers noted unusual, unprovoked, and distressed-sounding vocalizations emitted by the mother. In 5 cases, the body was either carried away from the den or completely

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consumed in less than 50 minutes, with one cub being completely consumed in 13 minutes. These records may underestimate the frequency with which victims are consumed because observers collected the victim's body for biological samples in 6 cases, and halted observations before the fate of the body was determined in 4 cases. However, it is clear from our observations that the remains of victims of infanticide do not persist for long.

Discussion

We found that infanticide is a significant source of mortality among young juvenile spotted hyenas. Extrapolating information from cases where the mortality source was known suggested that infanticide was a leading cause of death for den-dependent juveniles (Figure 2). We found no evidence for sex-bias in the victims of infanticide, and most victims were under five months of age at the time of death. The killer was always female, and the mean rank of the perpetrators was significantly higher than the mean rank of the mothers of victims (Figure 3). Killers acted alone or with assistance from others; in the latter cases, other group members (often members of the killer's matriline) displayed aggression towards the cub's mother during the infanticide event. All cases of infanticide occurred at the communal den. Bodies of killed cubs were often consumed by the killer or her offspring, the mother of the dead infant, or other clan-mates. Mothers of victims sometimes displayed grooming or other maternal behaviors towards the deceased cub, which may be of interest to those interested in comparative thanatology (Anderson & Anderson, 2016; Carter, Baniel, Cowlishaw, & Huchard, 2020).

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Our results provide mixed support (Table 1) for both the exploitation and resource competition hypotheses, although we suggest that the latter is more strongly supported by our data. The resource competition hypothesis predicts that infanticide by females should be prevalent in this species, typically should be directed by high-status individuals toward low-status individuals, and should preferentially target females over males. We find support for the first two of these predictions. Although we do not find support for the third prediction, the low sample size for victims of known sex (n = 9) provides minimal power for detecting a possible difference. In support of the exploitation hypothesis, killers and their offspring did sometimes consume the victims. However, the killer did often left the victims body for others to consume, and in some cases, a killer quickly crushed the skull of a cub then walked away from it. Furthermore, there was no evidence that infanticide was more likely to occur during times of prey scarcity. Finally, females were the killers in all observed cases, whereas males were never observed to engage in infanticide, even though immigrant males should theoretically be leaner and hungrier than females because of female dominance in this species. Our results are therefore more consistent with victim consumption as a secondary, opportunistic use of the product of infanticide rather than the primary driver of the decision to commit infanticide, as found in chimpanzees (Lowe, Hobaiter, Asiimwe, Zuberbühler, & Newton-Fisher, 2020).

Support for the resource competition hypothesis suggests that infanticide by females in spotted hyenas may serve as a mechanism of matrilineal competition. Social support has been found to be a significant force for establishing and maintaining dominance in spotted hyenas (Engh, Esch, Smale, & Holekamp, 2000; Strauss &

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Holekamp, 2019b; Vullioud et al., 2019), and kin provide a significant portion of that support (Smith et al., 2010). Thus, reducing another female's matriline size via infanticide may serve to prevent potential coalitions of lower-ranked matrilines aspiring to improve their status. Interestingly, we did observe one case of infanticide directly related to escalated aggression between matrilines. Observers arrived at the den to find a recently killed offspring from a high-ranked matriline. Many hyenas were acting highly agitated, and roughly one hour later we observed a coalition of related low-ranking adult females viciously attacking members of the high-ranking matriline. However, in a contrasting example, we observed one hyena kill two cubs born to her full sister. A larger sample size than ours will be needed to further assess the relationship between kinship, infanticide and matrilineal competition, and to learn more about the function of infanticide in spotted hyenas.

In addition to competition over social status *per se*, it may be that infanticide by females in this species reflects social competition more generally. For example, rather than serving to reduce the number of social allies available in another matriline and therefore lowering their potential standing in the dominance hierarchy, infanticide by females might instead serve to reduce the number of individuals with which the killer or the killer's offspring would need to compete for resources in the future. Furthermore, although the observed difference in rank between killers and victims may arise as a result of strategic social competition by high-ranking females against low-ranking females, it is possible that this pattern instead reflects differential vulnerability to infanticide among juveniles of different rank. Rank-related variation in the number of kin present and time

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spent at the communal den has already been demonstrated in this system (White, 2007). Our observations of relatives assisting killers during infanticide events demonstrate how social context can influence the occurrence of infanticide. Further observations are needed to identify situations presenting opportunities for infanticide to evaluate the contexts in which females elect to commit infanticide, and when they elect not to.

Regardless of the cause of rank-related patterns in infanticide, our results demonstrate that infanticide is another in a long list of ways in which rank influences fitness among spotted hyenas. In addition to having greater reproductive success (Holekamp, Smale, & Szykman, 1996; Höner et al., 2010), higher priority of access to resources (Smith et al., 2008), better immune defenses (Flies, Mansfield, Flies, Grant, & Holekamp, 2016), and greater longevity (Holekamp et al., 2012), we find that high-ranking females are less likely to suffer offspring loss via infanticide than their lower-ranking group-mates.

Our findings also indicate the dual use of the communal den as protection against both outside predation sources such as lions, and intraspecific killing via infanticide. The diameter of den holes limits the size of individuals able to enter the den, such that cubs can escape inside when threatened by adults or large predators, which cannot follow cubs into the den hole. This function has been born out in our observations: we have seen larger cubs killed by lions while they attempted escape into the communal den, as well as cubs escaping into the den while lions attempt (and fail) to extract them with their paws (unpublished data). In our observations of infanticide, we occasionally observed perpetrators coaxing cubs out of the den before attacking them, and in one case a targeted

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juvenile attempted to escape into the den but was caught and killed before reaching safety (Supplemental Videos).

Our results highlight the conflicting forces that characterize the lives of gregarious animals. The prevalence of infanticide highlights risks faced by females choosing to rear their cubs in a social environment. More solitary individuals could choose to keep their cubs at a natal den for several months, and thereby avoid the potential risks of infanticide, but female hyenas rarely choose to do so. This suggests that the benefits of social integration for cubs raised at communal dens outweigh the costs to females imposed by conspecific infanticide.

Finally, our results indicate the power of using long-term data to study rare or difficult-to-observe phenomena. Rarity of phenomena can obscure their importance, and rapidly occurring, high-impact events like infanticide are the sorts of phenomena that require extensive data collection to permit analysis. Our results highlight both the importance of long-term studies and the value of recording rare, but potentially important, events that may not be the focus of ongoing study.

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Figure 1. Adult female spotted hyena carrying a cub recently killed by infanticide. Infanticide was typically achieved by crushing the skull, as seen here. Photo by Kate Yoshida.

Figure 2. Age distribution of observed causes of juvenile (<1-year-old) mortality in spotted hyenas (left), and frequencies of the 7 leading causes of juvenile mortality (right). Dark bars indicate cases where the mortality source was known (n = 99). Lighter bars indicate inferred mortality sources for cases where the cause of mortality was unknown (n = 444). Inferred mortality source was calculated based on frequencies of observed mortality, and 95% confidence intervals were obtained by bootstrapping the known cases of mortality to obtain new observed frequencies. For inferred mortality sources, cases where the mother disappeared prior to offspring death were attributed to starvation, and frequencies used to infer remaining unknown mortality causes excluded cases where the mother preceded her cub in death. Inferred sources of mortality point to infanticide as a leading cause of death among juvenile hyenas, and this is supported by the overlap in age distributions of juveniles killed by infanticide and juveniles with unknown mortality sources.

Figure 3. Rank distributions of killers and mothers of cubs killed by infanticide. Ranks of infant-killers were on average higher than the ranks of mothers of infants killed by infanticide (Welch's two-sample t-test: $t = -3.44$, $df = 20.98$, $p = 0.003$).

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Table 1. Two non-mutually exclusive hypotheses suggesting functions of infanticide in spotted hyenas, along with associated predictions, and observations in support (+) or not in support (-) of those predictions.

Hypothesis	Prediction	Observation
Exploitation	Infanticide is more likely during prey scarcity	(-) Infanticide no more sensitive to seasonal changes in prey availability than other sources of juvenile mortality
	Perpetrators and their kin benefit nutritionally from infanticide	(+/-) Perpetrator or their kin consume the victim in a subset of cases. Victim consumed by mother or other group-mates in other cases.
	No sex bias of perpetrators	(-) Only females commit infanticide
	No sex bias of victims	(+) Female and male cubs killed with equal frequency
Resource Competition	Perpetrators commit infanticide against potential future competitors (philopatric sex)	(-) Female and male cubs killed with equal frequency
	Perpetrators are long-term residents of social group	(+) Only females (philopatric sex) commit infanticide
	Infanticide reflects competition among matrilines	(+) Killers are of higher rank and mothers of victims more likely to be of lower rank
		(+) Infanticide observed during inter-matriline competition
		(+) Kin aid each other while committing infanticide
		(-) Infanticide observed against kin

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Figure 1.

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Figure 2.

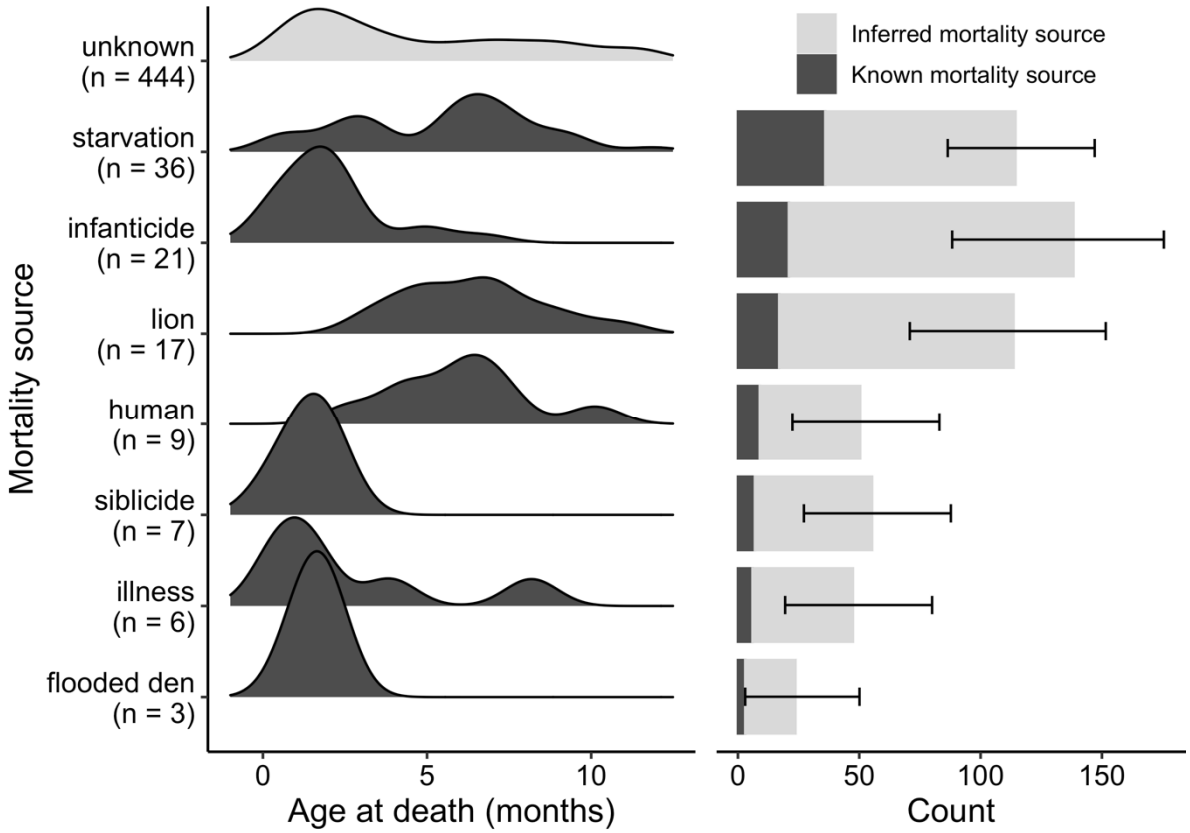

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Figure 3.