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NATURAL HISTORY NOTE

Infanticide by Females Is a Leading Source of Juvenile Mortality in a Large Social Carnivore

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ABSTRACT: Social animals benefit from their groupmates, so why do they sometimes kill each other's offspring? Using 30 years of data from multiple groups of wild spotted hyenas, we address three critical aims for understanding infanticide in any species: (1) quantify the contribution of infanticide to overall mortality, (2) describe the circumstances under which infanticide occurs, and (3) evaluate hypotheses about the evolution of infanticide. We find that infanticide, although observed only rarely, is in fact a leading source of juvenile mortality. Infanticide accounted for 24% of juvenile mortality, and one in 10 hyenas born in our population perished as a result of infanticide. In all observed cases of infanticide, killers were adult females, but victims could be of both sexes. Of four hypotheses regarding the evolution of infanticide, we found the most support for the hypothesis that infanticide in spotted hyenas reflects competition over social status among matrilines.

Keywords: hyena, matrilineal society, thanatology, female-female competition, nepotism, cannibalism.

Introduction

Why do animals kill the offspring of their group members? Infanticide is a taxonomically widespread behavior, found in mammals, birds, reptiles, fish, and invertebrates (Hrdy 1979; Hausfater and Hrdy 1984; Agrell et al. 1998; O'Connor and Shine 2004). In species where infanticide represents a common source of infant mortality, infant defense and avoidance of infanticidal individuals may function importantly in the developmental biology and social behavior of both adults and juveniles (Packer and Pusey 1983; Muller and Wrangham 2002; Balme and Hunter 2013; Lowe et al. 2018). Thus, infanticide can play an important role in the biology of many species, provided that it occurs frequently enough to be an agent of selection. However, because mortality events occur infrequently and take place rapidly, the significance of infanticide is difficult to evaluate and remains unknown in many species. For instance, the existence of infanticide by male lions, now a canonical example of infanticide, was hotly debated as recently as the late 1990s (Dagg 1998; Silk and Stanford 1999; Packer 2000).

Comparative studies have emphasized that a lack of observational data is a major barrier to the understanding of infanticide in ecology and evolution (Lukas and Huchard 2019). For species in which infanticide has not been specifically studied in detail, there is thus a critical need to (1) quantify the contribution of infanticide to overall mortality, (2) describe the contexts under which infanticide occurs, and (3) evaluate hypotheses about the evolution of infanticide. In this study, we address these needs in spotted hyenas (*Crocuta crocuta*), a large African group-living carnivore.

Quantifying the Contribution of Infanticide to Overall Mortality

The first step to understanding the evolution of infanticide is to identify its contribution to mortality. In some species, infanticide contributes dramatically to overall mortality. For example, in one study, nearly a third of all African leopard offspring were killed by infanticide, suggesting strong selection pressure on juveniles and mothers to avoid infanticide (Balme and Hunter 2013). No studies have yet investigated the frequency of infanticide in spotted hyenas

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or how mortality due to infanticide compares with mortality from other sources. However, in a prior study, 48% of spotted hyenas perished in their first year of life, suggesting that juvenile mortality sources are strong agents of selection in this species (Watts and Holekamp 2009). Furthermore, hyenas invest heavily in each offspring, typically bearing only litters of one or two juveniles, nursing them for over a year, and achieving an average lifetime reproductive success of only approximately two juveniles successfully reared to adulthood (Hofer and East 2003; Strauss and Holekamp 2019*b*). Taken together, this evidence suggests that infanticide might be an important behavior in this species if it represents a significant source of juvenile mortality.

Describing the Contexts in Which Infanticide Occurs

Observational data describing infanticide are necessary to understand the impact of infanticide and its evolution (Lukas and Huchard 2019), but such data for spotted hyenas are rare. Kruuk (1972) reported a case of attempted infanticide against a 6-month-old hyena and suggested that protection against infanticide by males was a potential driver of female dominance over males. In support of this view, a study of hyenas in the Serengeti documented two cases of males attempting infanticide against juveniles (East et al. 2003). Mills (1990) provided an alternative perspective on infanticide in spotted hyenas, suggesting that infanticide may be a form of intergroup competition, noting cases of cubs sustaining injuries or disappearing after hyenas from a neighboring clan visited the communal den. In a study of the uniquely masculinized genitals of female hyenas, Muller and Wrangham (2002) suggest that this unusual morphology may have evolved to protect female cubs against infanticide. In our study population, White (2005) reported a case of one female hyena killing two cubs (also reported here) and suggested that cubs may be at greatest risk of suffering infanticide right after being moved from the natal den to the communal den. This lack of consensus on infanticide in hyenas, paired with the paucity of observational data, reflects the need for more observational study of infanticide in this species.

Evaluating Hypotheses about the Evolution of Infanticide

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 motivations to commit infanticide include the killing of conspecific offspring to increase the killer's reproductive opportunities (the sexual selection hypothesis), as a source of food (the exploitation hypothesis), and to reduce intragroup competition for resources (the resource competition hypothesis; Hrdy 1979).

Lukas and Huchard (2019) divide the resource competition hypothesis into four types, which vary by the societies in which they are expected to occur and the types of resources over which individuals compete. The breeding space hypothesis suggests that infanticidal individuals eliminate infants occupying spaces critical to reproduction, such as nest sites or dens. The milk competition hypothesis suggests that infanticidal mothers kill unrelated offspring that attempt to nurse from them. The allocare hypothesis posits that in cooperatively breeding species, dominant individuals maximize the number of helpers caring for their offspring by killing the offspring of subordinates within their group. Finally, the social status hypothesis suggests that in stable societies, more dominant individuals kill the offspring of subordinate individuals to eliminate future rivals and protect the dominance status of themselves and their kin (Clutton-Brock and Huchard 2013; Lukas and Huchard 2019; Vullioud et al. 2019).

These hypotheses about the evolution of infanticide make different predictions about the circumstances under which infanticide is likely to occur. In our study of the evolution of infanticide in spotted hyenas, we ignore the allocare and milk competition hypotheses because hyenas are not cooperative breeders and because they have no trouble preventing unrelated offspring from nursing (Kruuk 1972). We focus instead on the sexual selection, exploitation, social status, and breeding space hypotheses and their predictions (table 1). The sexual selection hypothesis predicts that infanticide will be perpetrated by males and that mating opportunities should increase for males after they have committed infanticide. The exploitation hypothesis predicts that infanticide should occur when prey are scarce, and infanticidal individuals should consume the victim. Although hyenas do not compete with individuals from other groups over breeding space, they do share limited space in communal dens with their clanmates. Thus, the breeding space hypothesis predicts that infanticide should occur more frequently when there are many juveniles residing at the communal den. The social status hypothesis predicts that infanticide should be perpetrated by high-ranking adults against the offspring of low-ranking individuals and that the sex of the victims and perpetrators of infanticide should be biased toward the philopatric sex. Finally, it is worth noting that these hypotheses are not mutually exclusive, and it is possible that infanticidal individuals accrue multiple benefits from committing infanticide (Hrdy 1979; Lukas and Huchard 2019).

Here we use three decades of behavioral observations from multiple social groups to provide the first quantitative assessment of the prevalence and context of infanticide in spotted hyenas, a plural-breeding species with female

Table 1: Hypotheses and predictions about the evolution of infanticide

Hypothesis	Prediction	Observation
Sexual selection hypothesis	Infanticide committed by males	−
	Infanticidal males increase reproductive opportunities	−
Exploitation hypothesis	Infanticide more likely during low prey availability	−
	Infanticidal individuals consume infant	+/−
Resource competition: breeding space	Infanticide more likely when many cubs at communal den	−
Resource competition: social status	Infanticide committed by high-ranking individuals	+
	Infanticide perpetrators and victims more likely philopatric sex (female)	+/−

Note: Shown are four hypotheses about the evolution of infanticide in hyenas, the predictions made by these hypotheses, and whether our observations support (+) or fail to support (−) each prediction.

philopatry and nepotistic rank inheritance. We first examine the biological significance of infanticide in this species by quantifying its contribution to overall mortality. We then describe the contexts in which infanticide occurs. Finally, we evaluate the predictions of these four hypotheses regarding the evolution of infanticide in spotted hyenas.

Methods

Study Animals

Spotted hyenas are large carnivores found widely across sub-Saharan Africa (Holekamp and Dloniak 2010). Individuals reside in mixed-sex clans, each of which contains multiple matrilineal kin groups and is structured by a linear dominance hierarchy (Frank 1986). The dominance hierarchy is maintained by social support from groupmates, especially kin (Smith et al. 2010; Strauss and Holekamp 2019*b*; Vullioud et al. 2019), and rank is inherited through a learning process akin to what is found in many cercopithecine primates (Holekamp and Smale 1991). Spotted hyena societies are characterized by fission-fusion dynamics where individuals associate in subgroups that change composition throughout the day (Smith et al. 2008). Males disperse during the years after reproductive maturity, which occurs at around 24 months of age (Holekamp et al. 2012). Spotted hyenas are polygynandrous and breed year-round. Females give birth to one or two (and rarely, three) 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 and Holekamp 2020), and cubs typically remain in or around the den until they are 9–12 months of age (Holekamp and Dloniak 2010). These cubs, which belong to several different mothers, are often left unattended during much of the day while the mothers are away. Both mothers and other groupmates visit the communal den regularly, either alone or with clanmates. Starting at 1–2 months of age, cubs emerge from the den to socialize when their mothers are present and, increasingly as they get older, when their mothers are absent.

Study Area

Data presented here were collected from two study areas in southern Kenya. Most observations come from eight clans in the Masai Mara National Reserve (MMNR; 1,510 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). Data were collected in MMNR from 1988 to 2018 during 149,377 observation sessions; we observed one clan for the entire study period and seven other clans 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 during 4,651 observation sessions (Watts et al. 2011).

For describing cases of infanticide and their contribution to mortality, we use data from all 10 clans of spotted hyenas located in both study areas to capture the full breadth of circumstances under which infanticide occurs. For tests of hypotheses about the evolution of infanticide, we limited the data set to only our four most well-studied clans of hyenas in the MMNR. We elected to use this restricted data set because these clans live under similar ecological conditions, because all covariate data were available for these clans, and because these clans account for the majority of our data (73% of juvenile mortality from the larger data set).

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 from which to find and observe hyenas. Scan sampling (Altmann 1974) was used to collect demographic data. Maternity was determined on the basis of 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 on the basis of the dimorphic morphology of the erect phallus (possible after cubs are 2–3 months old). Juvenile age was determined (to ±1 week) on the basis of appearance when first seen. All statistical analysis and visualization was done using the statistical software environment R (R Core Team 2020).

Juvenile Mortality

We assessed various causes of mortality among juveniles less than 1 year of age. To do this, we monitored all births in our study groups ($n = 1{,}643$) and identified mortality events when a juvenile disappeared or when we directly observed mortality. In our 30 years of data, we documented 705 cases of juvenile mortality (43% of total births), and in 102 cases (15% of mortality) we were able to determine a cause of mortality. We observed five typical mortality sources for young juvenile hyenas: starvation, humans, lions, siblicide, and infanticide. Starvation was identified in cases where juveniles were observed to be becoming progressively gaunter 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 mortality; for example, hit by a car, speared, poisoned, and so on. Death by lions was either observed or could be inferred on the basis of the deep, widely spaced puncture wounds typically inflicted during lion attacks. Death by siblicide occurred when a cub prevented its littermate from nursing (Golla et al. 1999; Smale et al. 1999).

We identified 21 cases of infanticide in our data set, divided into two categories based on our confidence in the cause of death. We identified 17 "confident" cases of infanticide, where we observed a cub being killed by another hyena by having its skull crushed or found a cub dead as a result of having its skull recently crushed (fig. 1). Additionally, we identified four "likely" cases of infanticide, where a dead cub was found but no information on the

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.

state of the skull was available (usually because the victim had already been largely consumed), but other common aspects of confident cases of infanticide were noted (e.g., mother guarding or grooming the victim, victim consumed by mother or others, victim found at communal den). Finally, cubs dying as a result of causes other than those listed here were combined into an "other" mortality source.

Determining the Contribution of Infanticide to Overall Mortality

We next examined the extent to which infanticide contributes to juvenile mortality compared with other mortality causes. The first step in this process was to account for the occurrence of orphaning. We separated mortality into cases where the cub was orphaned before death and cases where the cub perished with a living mother. We did this because cubs under 12 months old whose mothers die also perish in almost all cases. These juveniles are still dependent on their mother's milk, and therefore 81% of juvenile deaths in this category are a result of starvation. In the remaining 19%, although cause of death was not directly starvation (causes of death were humans [$n = 3$], infanticide [$n = 1$], and lions [$n = 3$]), prolonged absence of the mother combined with nutritional stress likely motivated the cubs to engage in abnormal behavior (video S1; videos S1, S2 are available online). To account for these cases, we reclassified these known mortality sources to be "death of mother." For orphaned cubs with an unknown cause of death ($n = 38$), we inferred their mortality source to be death of mother. Together, this known and inferred mortality due to orphaning made up 11% of juvenile mortality.

We next explored the contributions of different mortality sources to the remaining 89% of mortality cases, where juveniles perished with living mothers. Because most juvenile mortality in the data set had unknown causes and because mortality of different types was nonrandom with respect to age (see "Results"), determining the contributions of different sources of mortality was not as simple as adding up all observed cases. Instead, we used differences in age distributions of known mortality sources to partition mortality of unknown cause into likely sources. We did this using a two-step modeling process to estimate the overall contribution of different mortality sources to this subset of juvenile mortality: we (1) modeled known mortality source as a function of age at death and (2) used this model to partition mortality with unknown cause into likely causes. To do this, we built a Bayesian multinomial model of mortality source for the remaining juveniles with living mothers ($n = 66$) as a function of their age at death. We assessed the efficacy of this model by using leave-one-out cross validation to compare it to a null model without age at death as a predictor (Vehtari et al. 2017). We then used 200 posterior samples from this model to generate 200 predictions for the cause of death for each juvenile with an unknown mortality source ($n = 565$). In other words, for each juvenile with unknown mortality, we used the model to generate 200 predicted mortality sources based on the age of death of the juvenile, and these predictions were used to estimate the mean contributions (with 95% prediction intervals [PIs]) of each mortality source to unknown mortality. The overall contribution of each mortality source was thus estimated as the sum of these posterior means from the multinomial model and the number of observed cases with known mortality due to each cause.

Evaluating Hypotheses about the Evolution of Infanticide

To test whether infanticide was more likely to occur when prey were scarce, we compared the average prey density in the study group of each individual using prey transect surveys. Twice each month we drove a designated prey transect and counted all prey animals within 100 m of the vehicle, then divided the number by the total area covered by the transect to calculate the density of prey animals in the clan's territory. For each cub with a known mortality source, we calculated the average prey density in all transects conducted in the cub's clan's territory in the month prior to death. We then used a Bayesian multinomial model to model mortality source as a function of prey density (supplemental PDF, available online). We evaluate the model by comparing it to a null model without prey density using leave-one-out cross validation (Vehtari et al. 2017).

To test whether infanticide was more likely to occur when there were many cubs using the communal den, we measured the density of den-dwelling cubs in the month prior to death. For each cub with a known mortality source, we calculated the average number of cubs with which they were observed over all observation sessions in the month prior to death. We again used a multinomial model to model mortality source as a function of cub density (supplemental PDF). We evaluated the model by comparing it to a null model without cub density using leave-one-out cross validation (Vehtari et al. 2017).

All three multinomial models were implemented in Stan using the rstan and brms R packages (Bürkner 2017; Stan Development Team 2018). We assessed model convergence using the potential scale-reduction factor ($\hat{R}$), which was required to be below 1.1 (Gelman and Rubin 1992). See the supplemental PDF for model details and diagnostics.

To test whether killers and mothers of victims differed in rank, we first determined ranks of adult females based on the outcomes of aggressive interactions, as described elsewhere (Strauss 2019; Strauss and Holekamp 2019*a*). Rank was standardized to account for group size so that it ranged from 1 (highest rank) to −1 (lowest rank). We then compared the ranks of killers with the ranks of victims' mothers using an unpaired Welch's two-sample *t*-test.

Results

Quantifying the Contribution of Infanticide to Overall Mortality

Infanticide was a leading source of mortality for cubs under 1 year old. Of the 102 cub deaths with a known mortality source (of 705 total juvenile mortality cases), infanticide accounted for 20% of mortality (fig. 2, dark bars). This number places infanticide as the second largest mortality source for den-dependent juveniles, ranking below death of mother (35%) but above lions (15%) (fig. 2, dark bars). Mortality sources were age structured, with the model including age at death as a predictor outperforming the null model without the predictor in leave-one-out cross validation (elpd = 16.2, SE = 6.2). The multinomial model revealed that cubs that died young were most likely victims of infanticide, whereas cubs that died at ages over 4.2 months were most likely victims of lions (fig. 3). After using this model to predict cause of death for cubs dying as a result of an unknown cause (fig. 2, light bars), infanticide and lions were the leading causes of death for juveniles, respectively accounting for a mean of 24% (95% PI = 18%–30%) and 24% (95% PI = 18%–31%) of juvenile mortality. Death of mother, starvation, siblicide, humans, and other mortality sources together accounted for 52% of total juvenile mortality (fig. 2). This analysis estimates that 10% (95% PI = 8%–13%) of all hyenas born in our population are killed by infanticide.

Describing the Contexts in Which Infanticide Occurs

In every case of infanticide with a known killer, the act was perpetrated by an adult female ($n = 10$). Infanticidal females typically targeted young juveniles (<5 months old), although we did observe two cases of infanticide among older juveniles (fig. 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.

All of the cases of infanticide occurred at a communal den, although in one case the victim was killed by other

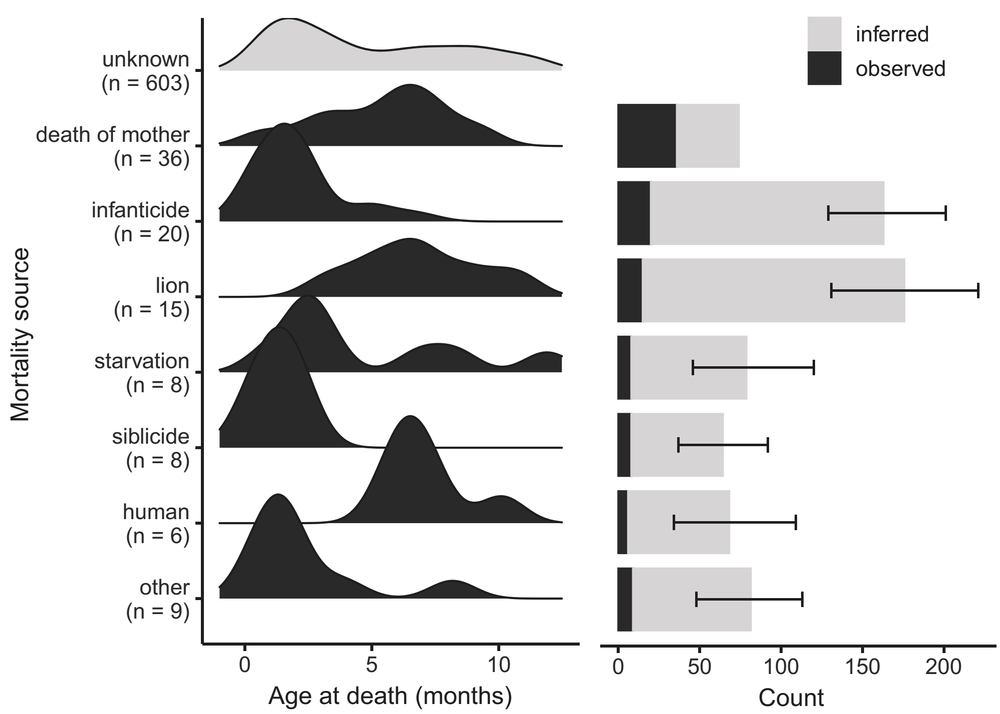

Figure 2: Age distribution of observed causes of juvenile (<1-year-old) mortality in spotted hyenas (*left*) and frequencies of the six leading causes of juvenile mortality (*right*). Dark bars indicate cases where the mortality source was known ($n = 102$). Light bars indicate inferred mortality sources for cases where the cause of mortality was unknown ($n = 603$). Error bars indicate the 95% prediction intervals for inferred mortality cases based on a Bayesian multinomial model of mortality source as a function of age. Mortality by death of mother was inferred analytically rather than statistically.

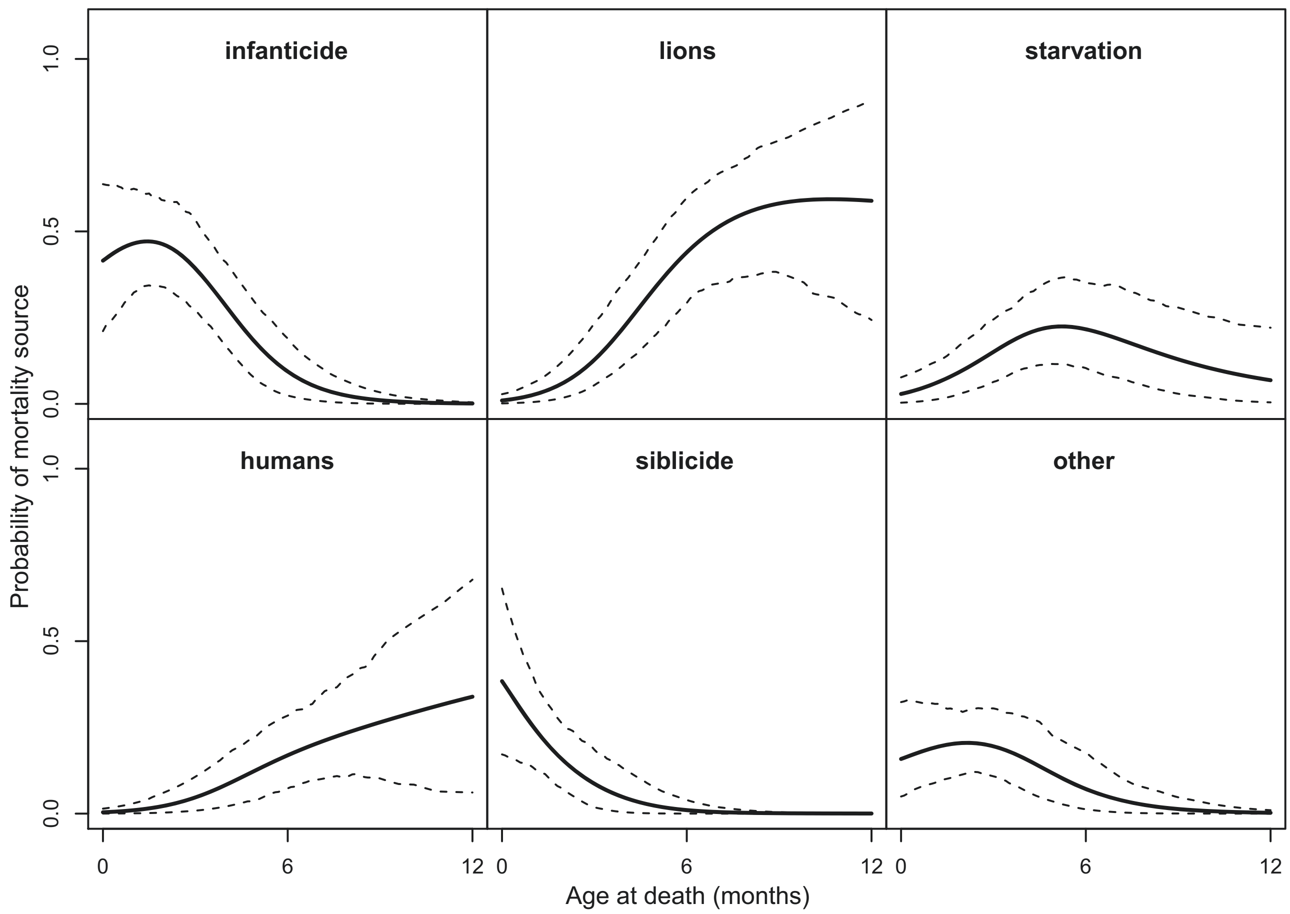

Figure 3: Probability of different mortality sources as a function of age at death, as estimated by a Bayesian multinomial model. Juveniles under 4.2 months old are most at risk of death by infanticide, whereas older juveniles are most at risk of death by lions.

groupmates as its mother was transferring it from the natal den to the communal den. Attackers sometimes acted alone ($n = 7$) and other times were aided by groupmates ($n = 3$). 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, a low-ranking juvenile was killed by the highest-ranking female while her adult offspring chased away the victim's mother (video S2). 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, 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. Thus, this prior report of infanticide against kin was not representative of typical patterns of infanticide in this species.

Victims' bodies were consumed by one or more hyenas in 11 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 do not add to 11 because multiple hyenas were often observed consuming infanticide victims). Consumption of deceased conspecifics was not restricted to infanticide—the remains of juveniles dying of other causes were also sometimes consumed, and hyenas are known to consume deceased adult conspecifics as well (Kruuk 1972). When given the opportunity, mothers sometimes ($n = 7$) groomed, guarded, or otherwise cared for their infanticide victim for up to 2 h after its death (supplemental PDF). Posthumous care and consumption by the mother were not mutually exclusive events, as we observed the mother eat her cub after grooming the dead body in two cases. In three cases, observers noted unusual, unprovoked, and distressed-sounding vocalizations emitted by the mother. In five cases, the body was either carried away from the den or completely consumed in less than 50 min, with one cub being completely consumed in 13 min. These records may underestimate the frequency with which victims are consumed because observers collected the victim's body for biological samples in six cases and halted observations before the fate of the body was determined in four cases.

Evaluating Hypotheses about the Evolution of Infanticide

We found differential support for the four hypotheses regarding the evolution of infanticide in spotted hyenas. These results come from a combination of observations of infanticide events and targeted tests of the predictions made by these hypotheses (table 1). Neither prey density ($n = 85$) nor the number of cubs at the den ($n = 80$) were good predictors of mortality source (fig. 4)—in both cases, leave-one-out cross validation suggested that null models were as good as or better than the models including prey density (elpd = 5.5, SE = 3) or cub density (elpd = 2.1, SE = 3.2) as a predictor. Furthermore, the parameter estimate for infanticide overlapped the 95% credible intervals surrounding parameter estimates for all but one of the other mortality sources in both the prey density model and the number of cubs model (supplemental PDF). We found significant differences between the average rank of killers and the average rank of the mothers of victims—adult females were on average higher ranking than the mothers of victims (Welch's two-sample t-test: $t = -3.54$, df $= 21.89$, $P = .002$; fig. 5). Whereas victims of infanticide were of diverse ranks, perpetrators of infanticide were almost exclusively high-ranking females.

Discussion

Our results indicate that infanticide is a significant source of mortality among young juvenile spotted hyenas (fig. 2). Overall, there was significant age structuring in mortality sources for juveniles over their first year of life, where juveniles dying young were most likely victims of infanticide and juveniles dying at older ages were most likely killed by lions. Our observations most strongly support

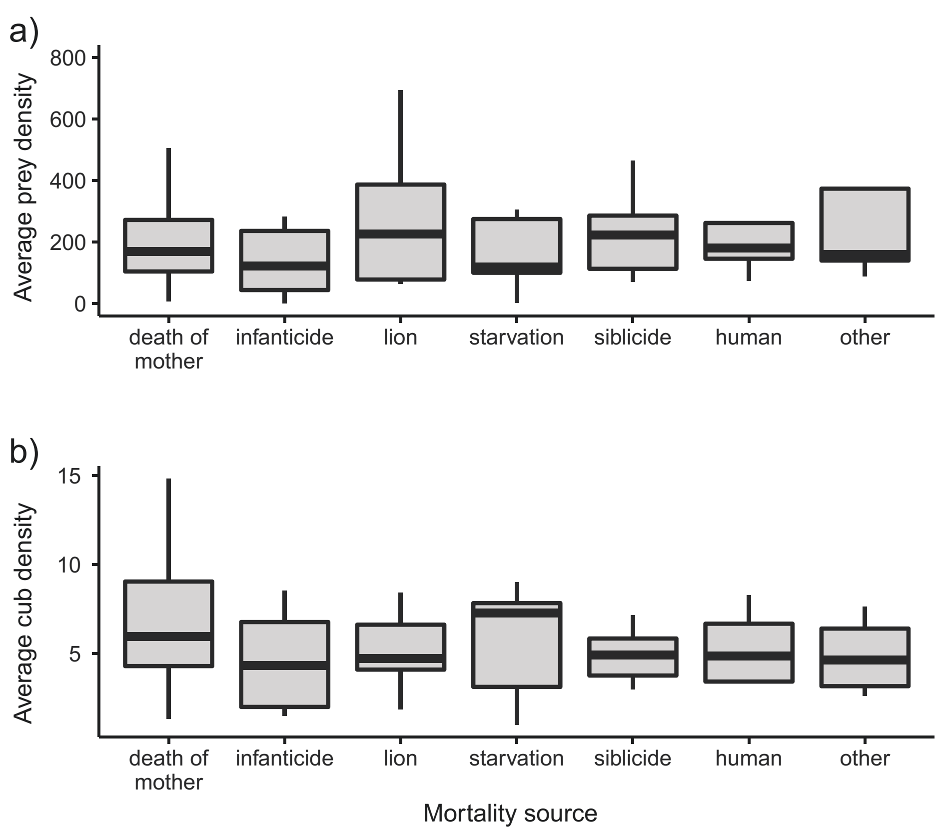

Figure 4: Differences in average prey density (*a*) and cub density (*b*) in the month prior to death by the leading causes of mortality. Neither prey density nor the number of cubs alive in the social group were good predictors of mortality source.

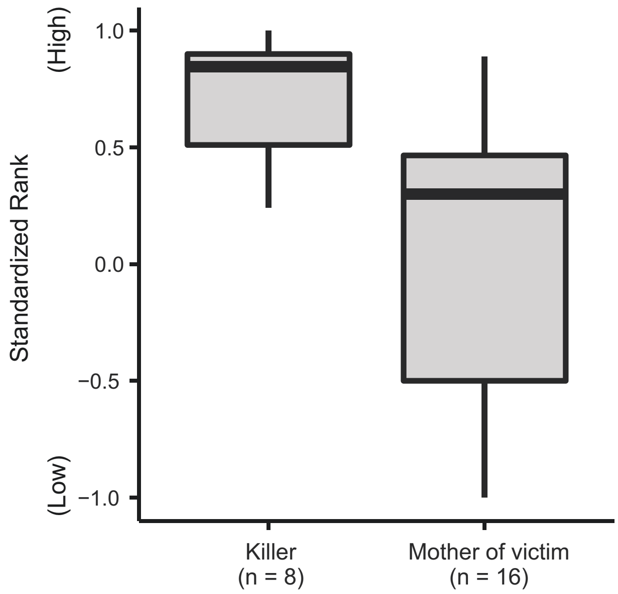

Figure 5: Rank distributions of killers and mothers of cubs killed by infanticide. Ranks of infant killers were on average higher than the ranks of mothers of infants killed by infanticide (Welch's two-sample t-test: $t = -3.54$, df $= 21.89$, $P = .002$).

the competition over social status hypothesis for the evolution of infanticide in spotted hyenas. In support of predictions about infanticide in nepotistic societies (Clutton-Brock and Huchard 2013; Lukas and Huchard 2019; Vullioud et al. 2019), we found that infanticide was typically perpetrated by high-ranking females against the offspring of lower-ranked groupmates. The prediction of the social status hypothesis about the sex of perpetrators and victims was only partially supported—females were the only sex to commit infanticide but were not a more frequent target of infanticide. Contrary to the predictions of the sexual selection hypothesis, no males were documented committing infanticide in this study. The exploitation hypothesis received only middling support. Killers did sometimes consume the victims of infanticide, but they often chose instead to leave the body to be consumed by other clan members, and infanticide was not more associated with low prey density than other mortality sources. The prediction made by the breeding space hypothesis—that infanticide will be more associated with high densities of cubs—was also not confirmed.

Social support has been found to be a significant force for establishing, maintaining, and changing dominance relationships in spotted hyenas (Engh et al. 2000; Strauss and Holekamp 2019*b*; 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 1 hour later we observed a coalition of related low-ranking adult females viciously attacking members of the high-ranking matriline. Our observations of infanticide events where the perpetrator's kin assisted by chasing away the victim's kin reflects how infanticide might both arise as a function of disparities in social support within groups and serve to reinforce those disparities.

Interestingly, our findings suggest that many of the infanticide anecdotes that have previously been published are not representative of infanticide in this species. Contrary to what was suggested by Kruuk (1972) and East et al. (2003), infanticide in our study was never perpetrated by males. We also found no support for the suggestion that infanticide is committed by members of other social groups, as suggested by Mills (1990). We were not able to test Muller and Wrangham's (2002) hypothesis about a potential infanticide-avoidance function to the peniform clitoris of spotted hyenas. We found that males and females were equally likely to be targeted by infanticide, which could indicate either that females faced the same risk of infanticide as males (contrary to Muller and Wrangham's hypothesis) or that the peniform clitoris was successful at reducing this risk (in support of Muller and Wrangham's hypothesis).

Our findings also indicate a dual function 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 predators too large to fit into the den hole. This function has been borne 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 attacking cubs in or around the den hole opening, and in one case a targeted juvenile attempted to escape into the den but was caught and killed before reaching safety (videos S1, S2). Mothers of victims sometimes displayed grooming or other maternal behaviors toward the deceased cub, which may be of interest to those interested in comparative thanatology (supplemental PDF; Anderson and Anderson 2016; Carter et al. 2020).

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 (White 2007). This suggests that the benefits of social integration for cubs raised at communal dens outweigh the costs to females imposed by the risk of conspecific infanticide. However, these conflicting forces may also lead to a trade-off between the quality of social development and survival if the behavior required for social integration in early life is associated with infanticide risk.

Overall, our results suggest strong selection in this species for behaviors that mitigate infanticide risk and thus alleviate the trade-offs of social reproduction. For instance, females may mitigate infanticide risk by timing den visits to avoid infanticidal groupmates or to coincide with the presence of kin who may help protect against infanticide. Future work should aim to identify potential behaviors that reduce the risk of infanticide and their links to survival.

Finally, our results demonstrate the power of using long-term data to study rare or difficult-to-observe phenomena. Rarity of phenomena can obscure their importance, and ephemeral, high-impact events like infanticide are the types of phenomena that require extensive data collection to permit analysis. The frequency of infanticide relative to other sources of infant mortality suggest that it is a significant feature of spotted hyena biology, which was unclear prior to this study. Continued direct study of this phenomenon has the potential to answer outstanding questions about the function of infanticide and conflicts of interest within complex societies.

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Statement of Authorship

The data were collected and validated by M.O.P., K.E.H., and E.D.S. Data processing, analysis, and visualization were done by A.K.B. and E.D.S. A.K.B., K.E.H., and E.D.S. wrote the original draft of the manuscript. A.K.B., M.O.P., K.E.H., and E.D.S. edited the manuscript.

Data and Code Availability

Data and code used for this study are available on GitHub (https://github.com/straussed/infanticide) and in the Dryad Digital Repository (https://doi.org/10.5061/dryad.4qrfj6q9r; Brown et al. 2021).

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