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Why leopards commit infanticide

Guy A. Balme^{a,b,*}, Luke T. B. Hunter^{a,c}^a *Panthera*, New York, U.S.A.^b *Department of Biological Sciences, University of Cape Town, South Africa*^c *School of Life Sciences, University of KwaZulu-Natal, South Africa*

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Infanticide is a widespread but seldom observed behaviour that has been shown to convey strong selection forces on some social mammals. However, infanticide in nonsocial species is less clearly understood, particularly the evolutionary function of infanticide. Here we present direct and indirect evidence of infanticide in a large, solitary felid, the African leopard, *Panthera pardus*, and determine its likely causes in light of six explanatory hypotheses. Observed and inferred rates of infanticide for leopards were among the highest recorded for mammalian carnivores, accounting for almost half of juvenile mortality and nearly a third of all offspring. Our results demonstrate that infanticide in leopards is mainly an adaptive behaviour which provides reproductive benefits to perpetrators. Infanticidal males were typically unrelated to their victims, the death of unweaned offspring shortened the interbirth intervals of mothers, and perpetrators increased their chances of mating with and siring the mother's subsequent litter. Female leopards also appear to have developed a profusion of strategies to counter the risk of infanticide, providing further support for the sexual selection hypothesis. Cannibalism may provide some incentive for infanticide (perpetrators usually consumed their victims) but this is probably an added, minor benefit rather than the primary driver for the behaviour. Our findings suggest that infanticide is a key factor shaping the sociospatial ecology of leopards. They also highlight the importance of accounting for functional components of population dynamics when managing large carnivores, particularly for invasive activities that artificially elevate adult male turnover.

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Infanticide, the killing of conspecific young, has been documented in a diverse array of animals (Hausfater & Hrdy 1984; Parmigiani & vom Saal 1994; van Schaik & Janson 2000). Among mammals, infanticide is best described in social species, particularly primates (van Schaik 2000a), rodents (Ebensperger & Blumstein 2007) and carnivores (Packer & Pusey 1984). Despite its apparent ubiquity, the proximate causes of infanticide are still contested (Rees 2009). There are two main diverging interpretations: that infanticide is an adaptive behaviour that provides benefits to perpetrators (Hrdy et al. 1995) or that it is a neutral or even pathological behaviour (Sussman et al. 1995).

Several hypotheses have been proposed to explain the adaptive benefits of infanticide (Hausfater & Hrdy 1984; Ebensperger 1998). Most prominent is the sexual selection hypothesis, which posits that infanticide is a reproductive strategy that improves the fitness of males by accelerating their opportunity to sire offspring (Hrdy 1979). Infanticidal males should gain reproductive advantage

provided that: (1) the death of unweaned offspring shortens the interbirth interval of mothers; (2) there is a low probability that perpetrators are related to their victims; and (3) males increase their chances of mating with and siring the mother's next offspring (Ebensperger 1998). Patterns of infanticide commensurate with the sexual selection hypothesis have been observed in numerous taxa (van Schaik 2000a), although few studies provide strong support for the latter two conditions, as some knowledge of paternity is required (but see Borries et al. 1999; Bellemain et al. 2006).

The predation hypothesis suggests that infanticide is simply a mechanism to procure food (Hrdy 1979). Predictions of the predation hypothesis include that perpetrators should consume the infants that they kill and it should be more prevalent among energy-stressed individuals, regardless of sex (Ebensperger 1998). Among carnivores, the consumption of young has been recorded in canids (Latham & Boutin 2011), felids (Logan & Sweaner 2001), herpestids (Young & Clutton-Brock 2006), hyaenids (White 2005), mustelids (Begg et al. 2005) and ursids (Bellemain et al. 2006).

The resource competition hypothesis postulates that infanticide provides perpetrators or their descendants with increased access to resources (Hrdy 1979). Similar to the predation hypothesis, it predicts that infanticide will increase when resources are limited, such

* Correspondence: G. A. Balme, 13 Orchard Ave, Lakeside, Cape Town 7945, South Africa.

E-mail address: gbalme@panthera.org (G. A. Balme).

as under food scarcity or at high population densities (Ebensperger 1998). Infanticidal individuals may also preferentially target the sex most likely to become future rivals. For example, newly established male hanuman langurs, *Presbytis entellus*, show a significant bias towards killing male offspring (Sommer 1994).

The adoption avoidance hypothesis states that infanticide functions to prevent the misdirected provision of parental care to unrelated offspring (Elwood & Ostermeyer 1984). Accordingly, infanticide should be committed by the sex that bears the primary costs of adoption, namely females (Ebensperger 1998). Although female carnivores of several species commit infanticide (Packer & Pusey 1984), the strongest support for the adoption avoidance hypothesis comes from observations of pinnipeds. Lactating female pinnipeds frequently attack and sometimes kill unrelated young that attempt to suckle (Bruemmer 1994).

Nonadaptive interpretations for infanticide suggest that it might not be the result of any selected behaviour, but rather a consequence of environmental (e.g. habitat reduction) or social (e.g. overcrowding) disturbance caused by humans (social pathology hypothesis; Boggess 1979). Infanticide does appear more common among some primate species in captivity than in natural conditions (Sussman et al. 1995). Alternatively, infanticide may be a by-product of male aggression and offspring are simply accidental victims killed inadvertently during attacks on females (side-effect hypothesis; Bartlett et al. 1993).

Although existing evidence generally supports adaptive explanations for infanticide, and particularly the sexual selection hypothesis, the debate persists (Dagg 1998; Bartlett 2003; Rees 2009). In this study we examined the evolutionary function of infanticide in a large, solitary felid; the African leopard, *Panthera pardus*. With the exception of some ursids (McLellan 2005; Bellemain et al. 2006), infanticide is poorly understood in solitary carnivores. The function and consequences of infanticide may differ in solitary species compared to social ones owing to their contrasting population dynamics.

Leopards are territorial carnivores that exhibit a polygynous mating system (Bailey 2005). Male home ranges typically encompass the ranges of several females, and both sexes defend home

ranges against same-sex conspecifics, although some overlap is typical (Mizutani & Jewell 1998; Marker & Dickman 2005). Female leopards usually give birth for the first time at 3.8 years and breed throughout the year, although in our study area births peaked in the early wet season, presumably to coincide with the birth season of impalas, *Aepyceros melampus*, their primary prey (Balme et al. 2013). Litters are born after a gestation of 90–106 days and comprise one to three altricial young that are cared for exclusively by females (Hunter et al. 2013). Cubs are kept in dens among thick vegetation or rocks for their first 6–8 weeks, after which they accompany their mother on hunting forays and to kills (Le Roux & Skinner 1989). Infant mortality is high; only 37% of leopard cubs survive to independence at our site which is almost entirely insulated from anthropogenic threats (Balme et al. 2013). Upon independence, females attempt to establish territories adjacent to their mother's range, while males generally disperse far from their natal home range (Bailey 2005). The result is a kin-related spatial structure with matrilineal assemblages that can last several generations.

Previous discussions on patterns of infanticide in leopards (Bailey 2005; Balme et al. 2009; Packer et al. 2009) were limited by a lack of direct observations of infanticidal behaviour and the context in which it occurs. In this paper, we present direct and indirect evidence of infanticide in a protected leopard population in the Sabi Sand Game Reserve, South Africa, and determine its likely function. Specifically, we assess the fit between our observations and the six explanatory hypotheses described above (a summary of the predictions associated with each hypothesis is provided in Table 1). Most studies on infanticide have examined its causes in light of only one of these hypotheses (Ebensperger 1998). By considering the different explanations simultaneously, we were able to disentangle many of the previous disputes surrounding this topic.

METHODS

Study Area

The Sabi Sand Game Reserve (hereafter SSGR) is situated in the lowveld region of the Mpumalanga Province, South Africa

Table 1
Predictions for six explanatory hypotheses for infanticide and expected observations associated with each prediction for leopards in the Sabi Sand Game Reserve, South Africa

Interpretation	Hypothesis	Prediction	Expected observation
Adaptive	Sexual selection	Sex bias among infanticidal perpetrators	Most perpetrators are male
		Infanticide hastens the mother's return to sexual receptivity	Entire litter is killed
			Age of victims is less than the mean age of cubs at independence
		Low probability that perpetrators are related to victims	Interbirth intervals are shorter for litters suffering infanticide than other litters
		Increased probability that perpetrators will sire the mother's subsequent offspring	Perpetrators and mothers are not previous mates
Predation		No sex bias among perpetrators	Perpetrators and mothers are not close relatives (e.g. siblings)
		Perpetrators gain nutritional benefits from infanticide	Perpetrators mate with mothers shortly after infanticide
Resource competition		Infanticide peaks during periods of prey shortage	Similar numbers of male and female perpetrators
		No sex bias among perpetrators	Perpetrators consume victims
Adoption avoidance		Infanticide peaks during periods of resource limitation	Infanticide rates are inversely related to prey abundance
		Perpetrators eliminate potential future competitors	Similar numbers of male and female perpetrators
		Sex bias among perpetrators	Infanticide rates are inversely related to prey abundance
Nonadaptive	Social pathology	Inability by mothers to recognize related and unrelated offspring	Infanticide rates are positively related to leopard abundance
			Most victims are male (if perpetrators are primarily male)
	Side-effect	Population suffers from anthropogenic disturbance	Most perpetrators are female
		Infanticide is a result of overcrowding	Adoption of nonfilial offspring is common
	Sex bias among perpetrators	High levels of human-mediated mortality	
	Overt aggression by males towards females	Infanticide rates are positively related to leopard abundance	
	Random selection of victims	Most perpetrators are male	
		Attacks are directed at females (i.e. offspring are accidental victims)	
		Similar numbers of attacks on females with and without offspring	
		Offspring are always killed in the presence of mothers	
		Only part of the litter may be killed	
		Victims may be related to the perpetrator	

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