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Abstract: Infanticide, in which males kill unrelated juveniles presumably to advance their genetic contribution, has been documented in many felids, a notable exception being the cheetah *Acinonyx jubatus*. Males apparently always tolerate cubs during encounters between females with litters but indefinite paternity has confused the issue in previous reports. We observed cheetah females with cubs interact with known sire and non-sire males, and infanticide never occurred. Sires and non-sires also did not differ in the frequency of different aggressive behaviours directed towards females and cubs during encounters. We suggest that cheetahs are unusual among wild felids in that males do not kill unrelated cubs and discuss possible reasons why infanticide does not occur in the species.

Do male cheetahs *Acinonyx jubatus* commit infanticide?

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Key words: Cheetah, *Acinonyx jubatus*, infanticide, Phinda, reintroduction.

Infanticide, in which males kill unrelated juveniles presumably to advance their genetic contribution has been documented in many felids, a notable exception being the cheetah *Acinonyx jubatus*. Males apparently always tolerate cubs during encounters between females with litters but indefinite paternity has confused the issue in previous reports. We observed cheetah females with cubs interact with known sire and non-sire males, and infanticide never occurred. Sires and non-sires also did not differ in the frequency of different aggressive behaviours directed towards females and cubs during encounters. We suggest that cheetahs are unusual among wild felids in that males do not kill unrelated cubs and discuss possible reasons why infanticide does not occur in the species.

INTRODUCTION

The occurrence of infanticide has been documented for numerous cat species, most dramatically in the lion *Panthera leo* (Bertram, 1975; Packer & Pusey 1983, 1984; Pusey & Packer 1994). It is generally accepted that the infanticidal male gains reproductive advantages by eliminating unrelated offspring so that females come into oestrus sooner, thus accelerating his own genetic contribution (Agrell *et al*., 1998). The most detailed support for this hypothesis in felids comes from lions in the Serengeti ecosystem where pride take-overs result in the deaths of almost all cubs younger than 9mo as well as the eviction of older cubs and sub-adults (Pusey & Packer, 1987). While data from other species are less detailed, infanticide has been documented in most felids subjected to intensive behavioural observations (tigers *P. tigris*, Schaller, 1967; Smith & McDougal, 1990; leopards *P. pardus*, Ilany, 1990; cougars *Puma concolor*, Hornocker, 1970; Logan & Sweanor, 2001; Canada lynxes *Lynx canadensis*, Quinn & Parker, 1987; ocelots *Leopardus pardalis*, Emmons, 1988 and feral domestic cats *Felis catus*, MacDonald *et al*., 1986). As for lions, infanticidal males of these species frequently had exclusive access to bereaved females and subsequently sired cubs by them.

Among felids, a possible exception to this pattern is the cheetah *Acinonyx jubatus*. Cheetahs are often conspicuous and easily observed, and many thousands of hours of observation has been devoted to their study (e.g. Caro, 1994). Despite this, while encounters between males and females with cubs have been observed (McVittie, 1979; Caro, 1994; Marker-Kraus *et al.*, 1996), infanticide has never been recorded. Circumstantial evidence suggests a possible case in the Masai Mara (J. Scott cited in Burney, 1980) and one case of a male apparently attempting to separate a cub from its mother so the male could mate with her was reported (Graham & Parker, 1965). Although Laurenson (1995) considered it a possibility in her comprehensive study of cub mortality, she never observed it.

A feature of all reported interactions between male(s) and females is the degree of apparent aggression in which the males rush or slap at the female (Burney, 1980; Caro, 1994). If cubs are present, males may also direct some of this aggression towards them. However this behaviour appears more an aspect of the animals' general state of excitement than directed aggression such as has been observed in infanticidal male lions. This tolerance towards the cubs would suggest the males were the sires and as such, would have no interest in killing their own offspring. However, in studies to date, paternity could not be ascertained so this idea has yet to be tested. Here we present observations of associations between males and females with cubs and compare incidents where the males were the sires and where they were not.

MATERIALS AND METHODS

The study took place in the Phinda Resource Reserve (27°50'S, 32°00'E, hereafter Phinda) a fenced reserve of 170 km^2 in the Maputaland region of northern KwaZulu-Natal, South Africa. Phinda is a privately owned reserve operated primarily as a wildlife tourism destination. Aside from previously cultivated areas which have given rise to fire-maintained grasslands and wooded grasslands, the dominant vegetation type is mixed bushveld dominated by *Acacia* species (Moll, 1980). Between March 1992–April 1994, Phinda released 13 lions and 15 cheetahs in an effort to re-establish these two species in the region (Hunter, 1998). In addition to re-introduced carnivores, leopards *Panthera pardus* and spotted hyaenas *Crocuta crocuta* occur as well as caracal *Caracal caracal*, serval, *Leptailurus serval*, two species of jackals, three mustelids and five viverrids. Except for black rhinoceros *Diceros bicornis*, the full complement of ungulates indigenous to the region occur in the reserve, the three most important prey species for cheetahs being nyala *Tragelaphus angasii*, impala *Aepyceros melampus* and southern reedbuck *Redunca arundinum* (Hunter, 1998).

Observations on cheetah interactions took place between May 1992 and October 1996 during the course of a long-term project monitoring the behaviour and ecology of re-introduced felids (Hunter, 1998; Hunter & Skinner, 1995). Female cheetahs and at least one male of each coalition were radio-collared (Telonics^{TM}, Arizona) prior to release and all were located at

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least once every day. We recorded daily locations, date of observed consortings between males and females, and the birth date of litters. During the first 12 months of the study, an electrified game fence divided Phinda into two halves (Hunter & Skinner, 1998); there was only a single coalition of males present on each half at any one time. The interactions we describe took place after the removal of the fence when the acting females already had cubs sired by the males of 'their' half so we were certain of paternity to the coalition level. We also recorded incidences of three aggressive behaviours (rush, slap and bite) to females and cubs during encounters and used a Wilcoxon 2-sample test to assess whether non-sire males were more aggressive to cubs than sires. Rates of aggressive acts were calculated from hourly observation periods during encounters lasting three days or less, and from the first three days of longer encounters. Individual rates were averaged for coalitions.

RESULTS

Females with cubs were approached on 100% of occasions males saw them (*n*=19). Associations lasted for between 21 minutes and 18 days, and the age of cubs involved in the encounters varied between three and 14 months (Table 1). In all encounters, coalitions of two or three males attempted to surround the female. There was a high degree of apparent aggression in which the males regularly rushed or slapped at a female, and males bit females on 10 occasions. Females never showed visible injuries from these attacks. The female repeatedly tried to break away from the males who invariably pursued her and pinned her down. There was always a great deal of vocalisation from all protagonists. The female growled and hissed at the males constantly and if they moved close, she made yipping and churring sounds (Caro, 1994). The males made constant excited yips and stutters throughout the encounter and occasionally growled in response to a female's aggression.

Cubs usually sat away from the adults up to distances of 50 m. Older cubs (>12mo) sometimes fled at the appearance of males and returned to the mother when the males had left: males did not attempt to pursue cubs in these occasions. Young cubs attempted to stay near the mother but often scattered in fright when males rushed the female. Generally, cubs were mostly ignored and it was evident that the primary focus of the males' interest was the female. However, cubs were sometimes attacked in which the male(s) slapped them to the ground (*n*=17) and bit at limbs (*n*=5). These attacks were more severe than the non-injurious attacks on females: bleeding injuries on cubs were inflicted on six occasions, two involving unrelated males. However, the injuries were relatively minor and all cubs survived the encounters. The frequency of aggressive behaviour by males to the cubs did not differ between sires and non-sires (Table 2). During these attacks on cubs, we never observed mothers attempting to defend cubs as lionesses and female pumas are sometimes known to do against attacks from immigrating males (Pusey & Packer, 1994; Logan & Sweanor, 2001). Only one encounter resulted in mating (Encounter #5, Table 1) despite males remaining with females for up to 18 days during which they showed constant sexual interest in her. All encounters were terminated by the males leaving.

DISCUSSION

The fact that infanticide has never been observed and that non-sires do not appear to behave more aggressively to cubs than sires suggests that the behaviour does not occur in cheetahs. Caro (1994) suggested the migratory movements of females in the Serengeti may preclude the benefits of infanticide as females would not predictably remain in male territories following the loss of cubs. In contrast to most felids, the female cheetah does not establish a territory: average home range size was 833 km^2 in the Serengeti (Caro, 1994) and may be larger than 1500 km^2 in Namibia (Marker-Kraus *et al.,* 1996). In such a situation, males would stand to gain little by killing unrelated cubs as there is no guarantee that they will have subsequent reproductive access to the female. However, if she resumed oestrus very quickly, there could be positive selection for infanticide and in a study on the same Serengeti population, females conceived an average of only 21 days after losing cubs (Laurenson *et al*., 1992). Furthermore, in our study, the size of the reserve is only 170 km^2 and overlap of male territories and female ranges was extensive (Hunter, 1998). Although female cheetahs used the

Table 1. Observed associations between cheetah males and females with cubs. [a] Coalition A: two adult males unrelated to all females; Coalition B: two males born to female 2; Coalition C: three males born to female 3. All males were sexually mature territory holders during observations. [b] Female conceived. [c] Grown half-siblings of the cubs.

Encounter number	Male coalition[a]	Female	Duration of encounter	Cubs' age (months)	Sires of litter
1	A	1	23 hours	8	yes
2	A	1	18 hours	12	yes
3	A	1	2 days	14	yes
4	A	2	27 hours	12	no
5	A	2[b]	24 hours	13	no
6	A	3	15 hours	3	yes
7	A	3	4 days	4	yes
8	A	3	2 days	6	yes
9	A	3	30 hours	6	yes
10	A	3	2 days	6.5	yes
11	A	3	5 days	6.5	yes
12	A	3	2 days	7	yes
13	B	3	18 days	12	no
14	B	3	10 days	14	no
15	B	2	4 days	8	no[c]
16	B	2	2 days	9	no[c]
17	B	2	2 days	9.5	no[c]
18	B	2	5 days	13	no[c]
19	C	2	21 minutes	5	no

entire reserve, they spent periods of up to six months exclusively within a single coalition's territory (Hunter, 1998) and males at Phinda were seen to investigate females with cubs more frequently (100% of 19 occasions) than males in the Serengeti (27.5% of 40 occasions; Caro, 1994: 316). The rapid resumption of oestrus and relatively localised movements by females would suggest that male cheetahs at Phinda would stand to gain considerable reproductive benefits by killing cubs they have not sired.

Female reproductive flexibility may be a factor. Female cheetahs can conceive while still with dependent cubs. We observed this on one occasion and six females in a study group of 20 in the Serengeti were reported to have conceived before their previous litter had left (Laurenson, *et al.*, 1992). Importantly, in all of these cases, the accompanying young were over 12 months old and close to independence: the mother left them to give birth to the second litter. When non-sire males encounter a family group in which the cubs are at this stage of development, there may be no need for them to kill the cubs since the mother is likely to be sexually receptive already. The males would therefore gain little from killing the cubs and by tolerating them, also avoid the possibility of injury incurred from attacking large cubs which could probably fight back in self-defence. Even so, the behaviour of males observed here may indicate greater tolerance towards cubs by cheetah males than by males of other felids. Male lions evict all unrelated sub-adult males and any sub-adult females too young to breed during take-overs, even though their presence does not challenge reproductive access to the females (Pusey & Packer, 1994).

We do not have sufficient observations of mothers with very young cubs approached by unrelated males to test if male tolerance is restricted to cubs approaching independence. Presumably in this situation, unrelated males could substantially accelerate the female's return to oestrus by killing cubs. The youngest cubs we saw interact with non-sire males were five months old which would pose little threat to infanticidal males; the cubs were ignored in this case. In three additional encounters with non-sires, the cubs were younger than a year (Table 1). However the males, while not the sires, were the grown half-siblings of the cubs. While they did not noticeably differ from unrelated males in their behaviour towards the female (their mother, in which they displayed overt sexual interest) and cubs, the possibility that they were more tolerant of the cubs because of their relatedness cannot be excluded. Pusey & Packer (1994) reported two male take-overs in lions in which cubs survived because the males returned to breed in their natal pride and were close relatives of the mothers. However, Ilany (1990) documented a case in which a male leopard killed its younger half-siblings and mated with its mother, and male pumas are known to kill related cubs they have not sired, e.g. a male killed his daughter's cubs sired by a different male (Logan & Sweanor, 2001: 120). More observations of interactions between female cheetahs with young cubs and completely unrelated males are required to test if the age of the cubs is related to male tolerance.

Our data are inadequate in other respects. Our observations involved a small number of the same known individuals (three male coalitions totalling seven animals and three females with numerous litters, see Table 1). Individuality in aggressive behaviour by male pumas towards conspecifics has been suggested (Logan & Sweanor, 2001) so perhaps the male cheetahs of our study were simply exceptionally tolerant individuals. This seems unlikely given the highly aggressive behaviour displayed by the same males in fatal territorial clashes with unrelated adult males (Hunter & Skinner, 1995) but a larger sample size involving more animals would be more compelling. While the lack of any observations of infanticide and the data presented here on non-sire males' tolerance of cubs suggest the behaviour does not occur in cheetahs, further observations are required. Recent studies on female cheetahs in woodland habitats where range sizes may be smaller (e.g. Broomhall *et al.*, 2003) might shed further light on this question and the inclusion of relatedness data from genetic studies of a known population would add further confidence.

Table 2. Mean rate of aggressive acts per hour towards cheetah females and cubs by sire and non-sire males during encounters. *Z*-values on Wilcoxon 2-sample tests (d.f.=1) and significance levels are shown.

Behaviour	Sires	Non-sires	*Z*-value	P-value
rush female	0.87	0.90	0	1.0
slap female	0.43	0.31	–0.67	0.51
bite female	0.08	0.10	0.78	0.43
rush cub	0.38	0.36	0.37	0.71
slap cub	0.16	0.14	–0.05	0.96
bite cub	0.02	0.03	1.21	0.22

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